

HOFMEISTER'S RULE AND PRIMORDIUM SHAPE : INFLUENCES ON ORGAN POSITION IN *HEDYCHUM CORONARIUM* (ZINGIBERACEAE)

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Abstract

Hofmeister's Rule states that leaf primordia form as far as possible from each other on the shoot apex. Here, I evaluate the use of Hofmeister's Rule as a tool to explain bract and sepal initiation in *Hedychium coronarium* (Zingiberaceae). The flowers of *Hedychium* occur in cincinni. A cincinnus apex arises in the axil of a primary bract, produces a lateral prophyll and a terminal flower. Development continues with the production of a new cincinnus apex in the axil of the prophyll. Up to six flowers may be produced in this way. In *Hedychium*, the sepals are initiated in sequential order following a modification of Hofmeister's Rule. Each sepal forms in the region of the flower that satisfies two conditions: it is as far as possible from other primordia, and it is part of the larger portion of the floral apex. The second criterion suggests that primordium shape is an important influence on the position of newly formed organs. An evaluation of published data on flower development in three genera of Fabaceae suggests that these influences are not restricted to the Zingiberaceae. The influences operating to place the bracts and sepals in these three genera are similar to those operating in *Hedychium*. The influences are similar even when the identity of the organs is different. This supports the hypothesis that the specification of organ position is independent of the specification of identity.

Key words: Hofmeister's rule, flower development, inflorescence development, phyllotaxy, developmental constraints, organ position, Zingiberales, monocots

INTRODUCTION

One of the most frequently made observations in the study of leaf arrangement is that new leaf primordia appear as far as possible from the primordia already present on the apex (Hofmeister 1868). This phenomenon, known as Hofmeister's Rule (Weisse 1932; Smith 1941; Jean 1984), is one of the limiting criteria for the establishment of Fibonacci and related phyllotactic patterns (Richards 1951), and is the basis of many theories of phyllotaxy (first available space theory, morphogen theory, etc.) (Rutishauser 1981; Rutishauser and Sattler 1985; Lacroix and Sattler 1988). Yet, despite widespread interest in the factors that influence leaf arrangement, there have been few attempts to relate patterns of floral organ initiation to Hofmeister's Rule (Lyndon 1978a, b). This oversight may be related to the common

assumption that flower development can be meaningfully separated from inflorescence development. By separating flower and inflorescence development investigators limit the factors that can influence organ position in flowers. The positions of bracts, bracteoles and flower buds are specifically excluded from influencing development. Flower development is frequently presented in a phylogenetic context, but not in a developmental context in which Hofmeister's Rule can be applied.

An additional complicating factor is that most developmental studies tacitly assume that flower development at all positions of an inflorescence is identical. The flower that forms in the axil of the first bract is assumed to follow the same developmental pattern as that in the axil of the second bract, etc. When flowers occur in axillary clusters, most studies do not distinguish between the first and later formed flowers. If data from more than one position are included, they are often used as part of the general developmental sequence presented as typical for the spe-

cies. The photographs used to illustrate this typical developmental sequence may come from flowers that occur in several positions on the inflorescence.

In defense of these assumptions, one can argue that if flowers in different positions do follow different developmental pathways, these variants will stand out because they cannot be integrated into the consensus sequence constructed from the study of many positions. Support for this view is found in the occasional descriptions of positional variation in development that appear in the literature. For instance, Ramírez-Domenech and Tucker (1989) briefly describe the development of the lowermost flowers of the inflorescence of *Mimosa strigillosa* (Fabaceae). These flowers develop more slowly than do those in the distal portions of the inflorescence, and so differ in at least one character from these flowers.

The fact that major variants can be discovered using current methods only partially answers my criticism. Subtle developmental differences that are closely tied to position are likely to be overlooked by combining data from different flowers to produce a consensus sequence. The question of whether or not these 'subtle' differences have important developmental or functional consequences must wait until we know the nature of these differences. Assuming that they are insignificant is premature.

This paper explores the relationship between flower position and developmental sequence in the context of Hofmeister's Rule. If floral organs are initiated following this rule, we would expect them to appear on the regions of the apex that are farthest from older primordia. These older primordia may be bracts, prophylls, floral organs or the sympodial apices that continue the growth of a partial florescence. In all cases, these primordia have the potential to influence the position of the subsequently formed organs.

MATERIAL AND METHODS

Young inflorescence buds of *Hedychium coronarium* Koenig were collected from Fairchild Tropical Garden, Miami, FL (accession no. 78-333), and Harold H. Lyon Arboretum, Oahu, HI (accession no. 67.1051). A voucher is deposited at Fairchild Tropical Garden (Kirchoff 84-12).

Development was studied using the epi-illumination, light microscopy technique of Sattler (1968), Posluszny *et al.* (1980) and Charlton *et al.* (1989). Living material was fixed in formalin-acetic acid-alcohol (FAA) (Berlyn and Miksche 1976), dehydrated to 100% ethanol and stained for several days in Fast Green (Johansen 1940; Charlton *et al.* 1989). Destaining was carried out in 100% ethanol for two days to several weeks. Photographs were taken with Kodak Technical Pan Film on a Leitz Ortholux 2 photomicroscope equipped with an Ultropak illuminator. Exposure time was regulated by varying the film speed set at the camera. Kodak Dektol was used to develop the film for three minutes at 68 °C (Kodak 1983). The negatives were scanned to disk with a Nikon Super Cool Scan LS1000 slide scanner, or onto Kodak Photo CD's by one of several commercial photographic laboratories. The images were edited and assembled into plates using Adobe Photoshop 4.0.

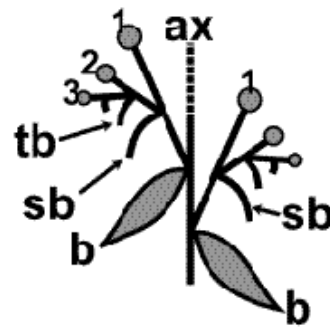


Fig. 1. Diagram of thyrse with two cincinni. ax, main axis of inflorescence; 1, 2, 3, flowers numbered in the order of their formation; b, main or primary bract; sb, secondary bract; tb, tertiary bract.

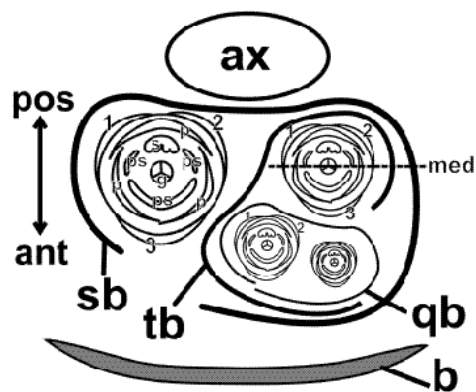


Fig. 2. Diagram of cincinnus and flowers of *Hedychium coronarium*. Each prophyll (secondary bract, tertiary bract, etc.) surrounds the remainder of the cincinnus. The flowers are all oriented with the fertile stamen backing on the inflorescence axis (Kirchoff 1997). 1, 2, 3, sequentially formed sepals; ant, anterior side of the cincinnus; ax, main axis of inflorescence; b, main or primary bract; g, gynoecium; med, median plane of second flower; p, petal; pos, posterior side of the cincinnus; ps, petaloid staminode; qb, quaternary bract; s, stamen; sb, secondary bract; tb, tertiary bract.

Terminology

The branches of an inflorescence are numbered according to their position within the ramification. The primary (or first order) axis bears the foliage leaves and terminates in an inflorescence. The bracts borne directly on this axis are the primary (or main) bracts. In a thyrse, cincinni arise in the axils of the primary bracts and terminate in primary (or first order) flowers (Fig. 1). Secondary bracts are borne on the axes that terminate in primary flowers. Secondary bracts subtend secondary flowers, the second flowers of the cincinni (Figs 1, 2). This branching pattern continues to tertiary and higher order bracts and flowers. Cymose inflorescence units, such as cincinni, are termed partial florescences (Troll 1964; Weberling 1989).

Since the secondary, tertiary, etc., bracts are the first phyllomes on each branch, they are also prophylls. I will use this term to refer to a bract when its position within the ramification is not essential. I will call the apex that arises in the axil of a prophyll a continuation apex because it continues the growth of the cincinnus by producing a prophyll and terminal flower.

The terms median and transverse refer to the orientation of a flower relative to the axis that bears it (Weberling 1989). The

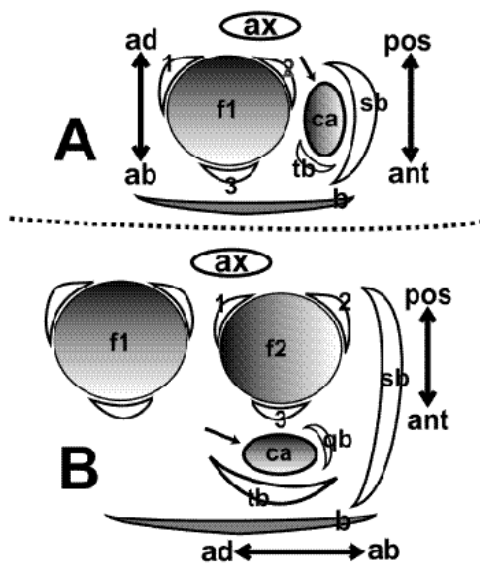


Fig. 3. Diagrammatic summary of terminology relating to flower orientation, and of factors influencing prophyll and sepal position in *Hedychium coronarium*. The terms adaxial (ad) and abaxial (ab) always relate the flower to the axis that bears it. The terms posterior (pos) and anterior (ant) relate the flower to the inflorescence axis (ax). Deepness of shading indicates the raised side of the flower primordium at the time of sepal initiation or, in other words, shortly after the initiation of the continuation apex (ca). **A.** Cincinnus at time of sequential sepal initiation (1, 2, 3) of the first flower (f1). The arrow shows the region of the continuation apex that will form the first sepal of the second flower. b, primary bract; qb, quaternary bract; sb, secondary bract, tb, tertiary bract. **B.** Cincinnus at the time of sequential sepal initiation (1, 2, 3) of the second flower (f2). The arrow indicates the region of the continuation apex (ca) that forms the first sepal of the third flower. b, primary bract; qb, quaternary bract; sb, secondary bract, tb, tertiary bract; f1, first flower.

median plane bisects the flower and the axis that bears it. The transverse plane bisects the flower at right angles to the median plane. The adaxial side of a flower is the side toward the lower order axis, and the abaxial side lies away from this axis (Fig. 3). For the purposes of this paper I treat the posterior side of the flower as the side that backs on the main inflorescence axis and the anterior side as the side away from this axis (Figs 2, 3). The use of these terms in this unconventional sense is necessary because of the unusual orientation of the flowers in the cincinnus (Fig. 2) (Kirchoff 1997). Unless otherwise noted, the anterior side of the flower is always at the bottom of the photographs in polar views of flower buds.

RESULTS

The inflorescence of *Hedychium coronarium* is a simple thyrse, which bears cincinni in the axils of spirally arranged primary bracts (Figs 1, 2). Each cincinnus contains up to six prophylls and flowers arranged in a monochasium. Cincinni with one or more abnormal 'flowers' occasionally occur in the axils of the first bracts of the inflorescence (Fig. 4).

Cincinni arise when a lateral bud forms in the axil of a primary bract, bears a prophyll, and terminates in the first flower (Figs 1, 5, 6). A sympodial, continuation apex arises in the axil of the prophyll (Figs 6, 7), produces a prophyll, and terminates in the second flower of the cincinnus (Figs 1, 8). Repetitions of this

pattern produce the third and higher order flowers of the cincinnus (Figs 1, 9, 10).

Flowers of *H. coronarium* have a three-lobed synsepalous calyx, three petals, one stamen that bears pollen, and three petaloid staminodes (Fig. 2). The gynoecium is trilocular and inferior. All of the floral members except the sepals and gynoecium are united into a long floral tube, above the ovary. The petals and androecial members become free at the top of this tube.

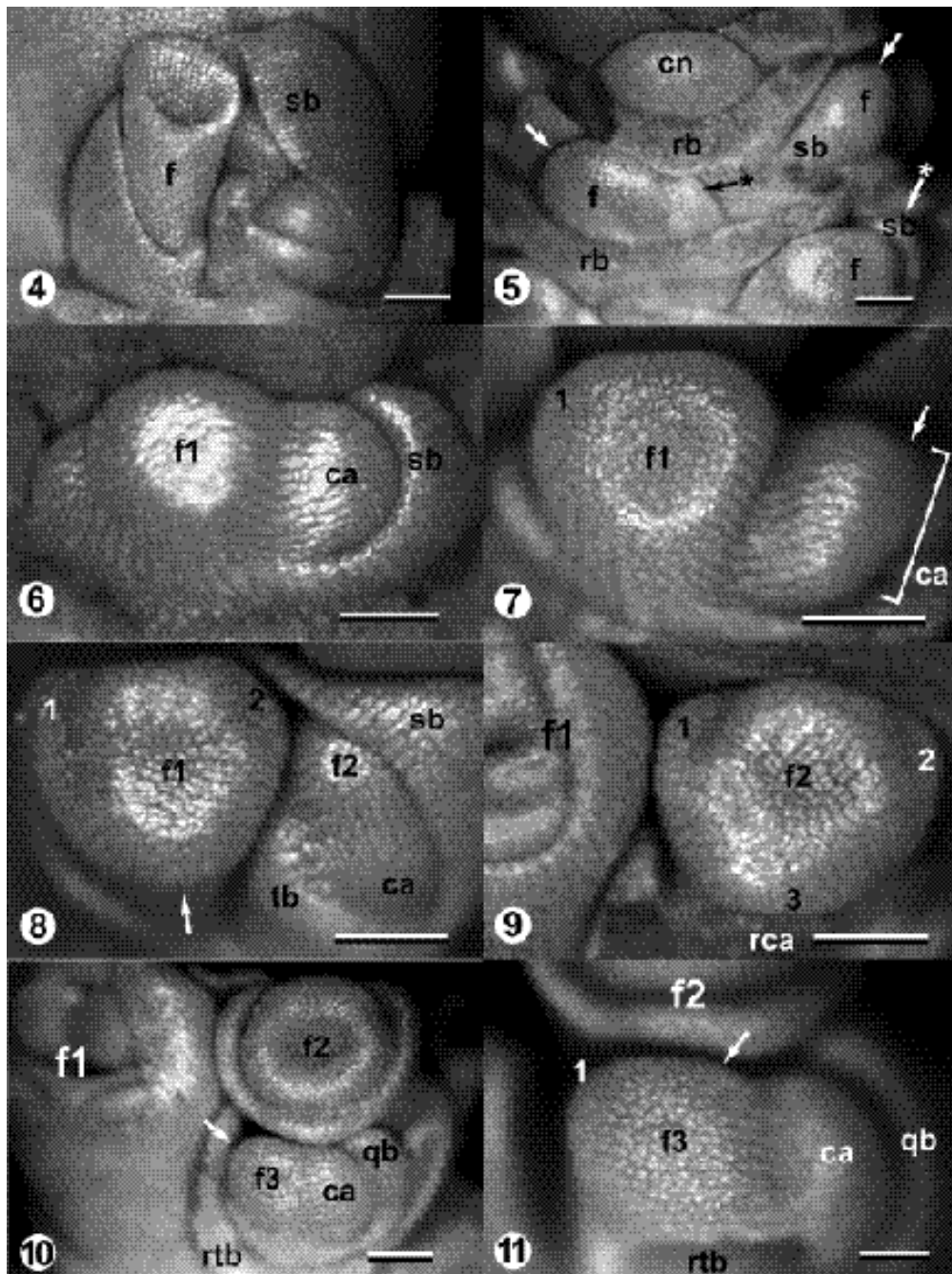
Cincinnus development begins with the formation of a bud (the primary cincinnus apex) in the axil of a primary bract (Fig. 5). This bud expands and initiates a prophyll (the secondary bract) on one of its lateral flanks. The position of the prophyll determines the symmetry of the cincinnus. Both left- and right-handed cincinni occur in the same inflorescence.

A continuation apex forms in the axil of the secondary bract, while the apical region of the cincinnus forms the first flower (Figs 6, 7). Following its initiation, the continuation apex forms a prophyll (the tertiary bract) and terminates in the second flower of the cincinnus (Fig. 8). Unlike the secondary bract, the tertiary bract is always initiated on the same side of the cincinnus, anterior and slightly adaxially of medial (Figs 3A, 8). A new continuation apex appears in the axil of the tertiary bract (Figs 3B, 8), forms a prophyll (the quaternary bract) and terminates in the third flower of the cincinnus (Figs 10, 11). The quaternary bract is always initiated on the same side of the cincinnus as the secondary bract (compare Figs 6, 10). A new continuation apex arises in the axil of the quaternary bract and the pattern continues (Fig. 10).

Enlargement of the primary and continuation apices is not uniform. By the time of secondary bract initiation the adaxial portion of the primary apex is larger and better developed than the abaxial (Fig. 5). One indication of this difference is the fact that the adaxial side of the secondary bract is slightly larger than the abaxial at, or soon after, initiation (Fig. 5, asterisks). This asymmetry persists throughout the early stages of floral development and influences the sequence of sepal initiation. The adaxial side of the primordium forms the first and second sepals while the abaxial side forms the third (Figs 3A, 7). In a similar way, the continuation apices in the axils of the secondary and tertiary bracts are formed so that their adaxial sides are larger and better developed than their abaxial (Figs 3, 7, 10). These shape differences persist and influence the sequence of sepal formation in these flowers (Fig. 3B).

The first sepal of the first flower forms in the position that is both larger and farthest from other primordia of the cincinnus. These two conditions place it in an adaxial and transverse position, approximately 150° – 160° from the insertion of the secondary bract (Figs 3A, 7, 8). The formation of the second sepal is influenced by the same two factors: shape of the apex and presence of other primordia. It forms in an adaxial and transverse position, approximately 100° – 110° from the first sepal (Fig. 8). The third sepal forms abaxially (Fig. 8, arrow).

The description of sepal initiation in the second flower has been limited by lack of material. The following description is based on only three flowers similar to the one illustrated here (Fig. 9). In



Figs 4–11. Inflorescence and flower development in *Hedychium coronarium*. Fig. 4. Abnormal ‘flower’ (f) in the first position of a cincinnus from the axil of the lowest bract of an inflorescence. The ‘flower’ resembles the primordial style and stigma of a normal flower. sb, secondary bract. Scale = 100µm. Fig. 5. Four cincinni from the upper regions of an inflorescence. The lower three cincinni have distinct secondary bracts (sb) and show the results of the uneven development that makes their adaxial and abaxial sides different sizes. The flattened area of each flower (f) is the region where organ formation will occur. Arrows, larger (adaxial) region of flower primordia; arrows with asterisks, larger sides of secondary bracts; cn, primary cincinnus apex; rb, removed primary bract. Scale = 100µm. Fig. 6. Cincinnus from the lower portion of an inflorescence. ca, continuation apex; f1, first flower; sb, secondary bract. Scale = 100µm. Fig. 7. First flower (f1) and continuation apex (ca) of a cincinnus, at the stage of first sepal formation (1). The continuation apex is larger adaxially. The flattened portion of the apex (area below arrow) is the site of floral organ formation. Scale = 100µm. Fig. 8. Cincinnus with first (f1) and second flowers (f2), and continuation apex (ca). Note that the tertiary bract (tb) is inserted slightly adaxially (toward the first flower) and that the continuation apex does not occur precisely in the axil of the bract. arrow, site of third sepal formation; 1, 2, sequentially formed sepals; sb, secondary bract. Scale = 100µm. Fig. 9. Second flower (f2) of cincinnus showing sequential sepal initiation (1, 2, 3). The continuation apex and its subtending tertiary bract occur on the anterior side of the flower, but have been removed in this preparation (rca). f1, first flower of cincinnus. Scale = 100µm. Fig. 10. Cincinnus with three flowers (f1–3) and continuation apex (ca). The adaxial portion of the third flower is larger than the abaxial. arrow, site of first sepal initiation on the third flower; qb, quaternary bract; rtb, removed tertiary bract. Scale = 100µm. Fig. 11. Third flower of cincinnus (f3) with continuation apex (ca) in axil of quaternary bract (qb). 1, site of first sepal formation; arrow, site of second sepal formation; f2, second flower of cincinnus; rtb, removed tertiary bract. Scale = 50µm.

Table 1: Developmental influences on sepal position in *Hedychium coronarium*

	flower 1	flower 2	flower 3
sepal 1	shape of apex; position of continuation apex	shape of apex; position of tertiary bract and continuation apex	shape of apex; position of continuation apex
sepal 2	shape of apex; position of first sepal	positions of first sepal tertiary bract and continuation apex	conjecture: shape of apex; position of the first sepal
sepal 3	position of other sepals; shape of apex	positions of other sepals	conjecture: position of the other sepals; shape of apex

the second flower, sepal initiation begins with the formation of the first sepal in the position that is both larger and farthest away from all existing primordia. Since a gradation in size is established at the time that the continuation apex is produced (Fig. 7), the adaxial side of the second flower is slightly larger than the abaxial side. The position of the first sepal is thus restricted to the adaxial side of the flower. It forms in an adaxial, posterior position, almost adjacent to the first flower of the cincinnus (Figs 3B, 9). The position of the second sepal is constrained to the abaxial, posterior side of the flower by the position of the first sepal, and the tertiary bract–continuation apex pair, which occupies the space anterior to the flower (Fig. 9, *rca*). The second sepal forms 140°–150° from the first sepal, abaxially and slightly posterior of the median plane of the flower (Figs 3B, 9). The third sepal forms anteriorly, adjacent to the tertiary bract and continuation apex (Figs 2, 3B, 9).

Scarcity of material only permitted study of the initiation of the first sepal of the third flower. The position of the first sepal is influenced by the shape of the apex and the position of the continuation apex that arises in the axil of the quaternary bract (Figs 3B, 10). These two factors place the first sepal in an adaxial, transverse position (Figs 10, 11). Although I have not seen the initiation of the second sepal, the shape of the floral apex suggests that it will form approximately 100° from the first in an adaxial, transverse position (Fig. 11, arrow). This region of the flower is larger than the abaxial side, and is one of two positions that are as far as possible from the first sepal. The second of these positions is adjacent to the tertiary bract.

The developmental pattern described here produces flowers that all have the same symmetry (handedness) (Fig. 2). This symmetry arises naturally out of the developmental influences that constrain the placement of the prophylls, continuation apices and sepals. These influences are the shape of the floral apex and the positions of the other floral organs (Hofmeister's Rule).

DISCUSSION

The influences on organ position in *Hedychium* are the shape of the apex and the positions of the surrounding organs (Table 1). The one exception to this rule is the position of the secondary bract, which forms randomly on either side of the cincinnus apex. Once this bract is initiated, the symmetry (handedness) of the cincinnus and flowers is determined. The tertiary and quaternary bracts are situated in relation to the shape of the apex and the positions of the primordia that surround them.

In the first flower, the position of the first sepal is influenced by the shape of the apex and the position of the continuation apex (Table 1; Fig. 3A). The position of the second sepal is influenced

by the shape of the apex and the position of the first sepal. The third sepal is placed based on the position of the first two sepals, though the shape of the adaxial part of the floral apex is also involved (Table 1).

In the second flower, the position of the first sepal is influenced by the shape of the floral apex and the position of the tertiary bract and continuation apex (Table 1; Fig. 3). These factors place the first sepal in a posterior and transverse position, adjacent to the first flower. The second sepal is positioned by the attachment of the first sepal and the positions of the tertiary bract and continuation apex (Figs 3B, 8). Based only on the shape of the floral apex and the position of the first sepal, we would expect the second sepal to form adaxially and anteriorly, approximately over the site of tertiary bract initiation (i.e. in the position occupied by the third sepal in Fig. 9). This is because the adaxial side of the second flower is larger than the abaxial, early in development (Fig. 7). The fact that the second sepal forms in the abaxial, posterior part of the flower is most likely due to the influence of the continuation apex and its subtending bract, which are present on the anterior side of the flower at the time of second sepal initiation (Figs 3, 9). The position of the third sepal is influenced by the positions of the other sepals and may be affected by the elongation of the pedicel below the second flower. As the pedicel elongates it may separate the flower from the inhibitory influence of the continuation apex and its subtending bract (Schwabe 1998). A comparable elongation of the pedicel occurs in the first flower (compare Figs 6, 7). A similar effect could also be achieved by the decay of the inhibitory field of the tertiary bract and continuation apex (Thornley and Cockshull 1980).

In the third flower, the first sepal forms in an adaxial, transverse position. This placement is influenced by the shape of the floral apex and the position of the continuation apex (Table 1; Fig. 3). From the time of its initiation the floral apex is larger adaxially (Figs 3, 10). This places the sepal on the adaxial side of the flower. Its lateral position is influenced by the position of the continuation apex, which forces the first sepal to the opposite side of the flower (Fig. 10). Although I have no direct evidence on the initiation of the second or third sepals, it is possible to infer their position based on the shape of the apex at the time of first sepal initiation (Fig. 11). The second sepal is likely to form in an adaxial, transverse position. The factors that influence this placement are most likely the shape of the floral apex and the position of the first sepal (Table 1). If the place of initiation of the third sepal is determined by the positions of the other sepals and the shape of the floral apex, then it will appear abaxially, approximately midway between the insertions of the other two sepals.

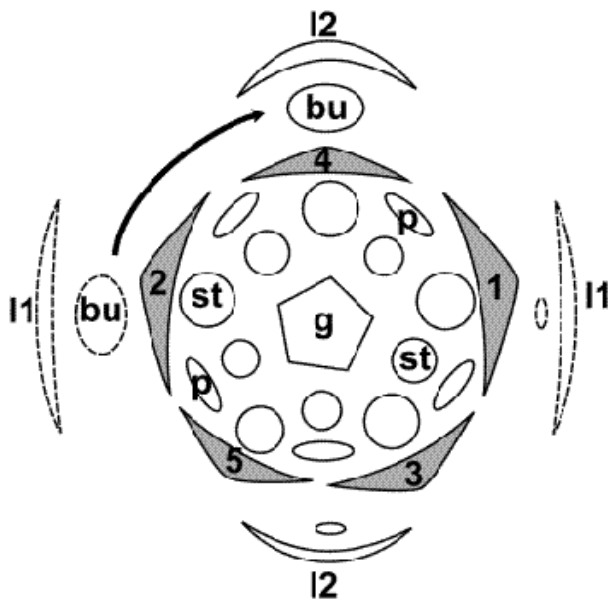


Fig. 12. Diagram of flower structure in *Silene coeli-rosa* showing the positions of sepal initiation (after Lyndon 1978a). Note that the first two sepals (1, 2) are displaced toward the larger of the two buds (bu) at the node below the flower. The position of the first sepal (1) continues the phyllotactic sequence established by the larger of the buds at the lower nodes (Lyndon 1998a,b). 1–5, sepals labeled in order of initiation; g, gynoecium; I1, lower (dashed lines) pair of opposite leaves; I2, upper pair of opposite leaves; p, petal; st, stamen.

Comparison with other families

Comparing developmental sequences between families can be difficult both because of differences in inflorescence and flower structure, and because of the varying levels of detail with which the data are presented. Some authors focus on the organogenic stages of development, while others present data from a greater developmental range. The former are detailed presentations of a single aspect of development, while the latter give a broader developmental perspective, but often lack the detail of the former. Because of these differences it is difficult to compare descriptions of the development based on literature reports. However, some progress can be made by using the published photographs instead of the written descriptions as a primary source of data. The descriptions can then be used to supplement the data available from the photographs. Using this method, a brief review of the flower development literature shows that young floral apices are frequently to some degree asymmetric, a factor that could influence the position or sequence of organ formation.

As a further step toward determining if primordium shape and position influence organ position in plants other than *Hedychium*, I compare bract and sepal development in *Hedychium* with the development of these same organs in *Silene coeli-rosa* (Caryophyllaceae) (Lyndon 1978a, b, 1998a, b) and three genera of the Fabaceae (Tucker 1998).

Silene coeli-rosa (Caryophyllaceae)

Silene coeli-rosa has opposite, decussate leaves and an inflorescence with cymose branching (Lyndon 1978a). Each leaf subtends an axillary bud. At each node, one bud develops earlier and is much larger than the other (Fig. 12). These large buds occur

along a parastichy, spiraling up the stem from node to node (Fig. 12, arrow). The vegetative axis of the plant terminates in a flower, with additional flowers produced from the axillary bud(s) at the node immediately below. The floral apex is symmetrical and dome-shaped during sepal formation (Lyndon 1978a, Fig. 1B). The most distal pair of leaves do not contact the apical dome during this time, and so are unlikely to influence the position of the sepals by exerting pressure on the apex (Lyndon 1978a, Figs 1B, C). Sepals one and two are initiated on the same orthostichies as a pair of leaves, but are displaced slightly toward the larger bud at the node below the flower (Fig. 12). The divergence angle between these sepals is 156.1° (Lyndon 1978b). The first sepal occurs along the same parastichy as the larger buds. The remaining sepals are initiated in a helical sequence, but in a direction opposite to that established by the parastichy of the larger buds (Lyndon 1998a, b) (Fig. 12). Lyndon (1978b) presents evidence that the positions of the later formed sepals (sepals three through five) are influenced by the positions of the two previous primordia. That is, the position of sepal three is influenced by the positions of one and two, four by two and three, etc. Younger primordia do not affect the positions of sepals three through five.

Based solely on Hofmeister's Rule we would expect the first two sepals to appear on the same orthostichy as a pair of leaves. The displacement of these sepals toward the larger bud is difficult to explain. Since the floral apex is symmetric, we cannot invoke shape or maturity differences to explain the displacement. Lyndon (1978a) suggests two possible explanations. First, the sepals could be displaced at the time of their initiation. This explanation implies that there is an interaction between the leaves, or axillary buds, and the apical dome, an interaction that shifts the position of sepal initiation. Such an influence could be a stronger inhibitory field associated with the leaf with the smaller axillary bud. Second, the displacement could arise after sepal initiation by the differential growth of the apical dome. This would push the sepals toward the larger bud. In this case, the larger axillary bud would inhibit the growth of the apex on the side closest to the bud. Lyndon (1978a) estimates that a 15% difference in the growth rates of the two sides of the apex would lead to the observed displacement.

Lyndon's (1978a, b) results are significant for the present study because they show a case where apical shape plays little role in determining the position of the sepals. In cases like these we must seek other explanations to account for the phyllotactic changes correlated with flower formation. Such explanations might include a diffusion-reaction system of primordia inhibition (Lyndon 1998b).

Petalostylis, *Labichea*, *Dialium* (Fabaceae)

Petalostylis, *Labichea*, and *Dialium* are three genera of the Fabaceae (subfamily Caesalpinioideae, tribe Cassieae) studied by Tucker (1998). The development of their partial florescences and flowers shows interesting similarities with flower development in *Hedychium*. These similarities suggest that comparable developmental influences can be found in widely divergent taxa. They also suggest that there are influences on organ position that

Table 2: Partial florescence structure, bract and sepal position.

	<i>Hedychium</i>	<i>Petalostylis</i> ¹	<i>Labichea</i> ¹	<i>Dialium</i> ¹	<i>Silene</i> ²
partial florescence structure	cincinnus	reduced cyme	reduced cyme	cyme	cyme
number of phyllomes below flowers	one bract	two bracts	two bracts	two bracts	two leaves
bud(s) in axil(s) of phyllomes	yes	no	no	yes	yes, one bud larger
partial florescence apex larger adaxially	yes	slightly (Figs 8–10)	yes (Fig 52)	slightly (Figs 95, 97)	not applicable ³

¹ Figure citations refer to Tucker (1998).

² Figure citations refer to Lyndon (1978a).

³ Lyndon (1978a, b, 1998a, b) only deals with development of the terminal flower.

operate independently of the genetic specification of organ identity (Bowman 1997).

For my purposes, the structure and development of the lateral partial florescences are most important. A partial florescence is a cymosely branched unit of a florescence (Weberling 1989). The partial florescences in these genera consist of two sterile (*Petalostylis*, *Labichea*) or fertile (*Dialium*) bracts and a terminal flower (Table 2). In *Dialium*, the axillary buds form additional flowers in a cymose pattern.

To compare developmental patterns among *Hedychium*, *Petalostylis*, *Labichea*, and *Dialium* we need to deal with the fact that *Hedychium* has fewer organs than do the other genera. Where in *Hedychium* there is a single secondary bract, in the other genera there are two bracts (Table 2). *Hedychium* has three sepals. The other genera have five. Given these differences, the choice of which organs to compare will be arbitrary. Since my intention is to demonstrate similar developmental influences in unrelated genera, I have chosen to compare organs that will serve this purpose. I will compare aspects of bract initiation among the genera, but I will also compare sepal initiation in the first flower of *Hedychium* with bract initiation in the three genera of the Fabaceae (Table 3). In making these comparisons I do not intend to imply anything about the homology of these organs. Since one of my points is that the circumferential position of organ initiation is determined independently of organ identity, the fact that I am comparing bracts with sepals only strengthens my point. I deal with the difference in the number of sepals between the families by only following sepal development through the initiation of the second sepal in the Fabaceae.

Prior to bract initiation, the partial florescence apex is larger adaxially, similar to the situation in *Hedychium* (Table 2). This asymmetry is reflected in bract initiation. In all four genera the bracts are larger adaxially at initiation (Table 3). The fact that we find a similar constraint affecting organ initiation in phylogenetically distant taxa shows that the basis of this constraint can occur in a wide range of taxa. Similar apical shapes appear to affect the position(s) of organ initiation in similar ways, regardless of the taxa in which these shapes occur.

When we compare bract formation in *Petalostylis*, *Labichea*, and *Dialium* with sepal formation in *Hedychium*, we also find similarities. The position of the first bract in the former genera is influenced by the shape of the partial florescence apex, just as the position of the first sepal is influenced by the shape of the apex in *Hedychium* (Table 3). Similarly, the position of the first bract and the shape of the apex influence the position of the second bract in the Fabaceae genera, just as the position of the first sepal

and the shape of the apex influence the position of the second sepal in *Hedychium* (Table 3).

Following the initiation of the two bracts in *Petalostylis*, *Labichea*, and *Dialium*, the adaxial and abaxial sides of the paracladium apex have not yet formed organs (Tucker 1998, Figs 11, 53, 99). In theory, the first sepal could form on either side of the apex to begin flower formation. However, the initiation of the first sepal is restricted to the abaxial side of the apex by the slightly more adaxial insertion of the bracts and the presence of the inflorescence axis on the adaxial side of the partial florescence (Table 3). In *Hedychium*, the formation of the third sepal is constrained to the abaxial side of the flower by the positions of the first two sepals, and secondarily by the shape of the floral apex (Table 3).

In the three genera of Fabaceae, the first sepal is initiated 'non-medianly' (Tucker 1998). Its largest point forms slightly toward one or the other of the two bracts. This 'displacement' does not appear to be correlated with the size of the subtending bracts. Based on the photographs in Tucker (1998, Figs 9, 11, 51, 98, 99), the bracts are initiated sequentially, though the time between their formation is very slight in some cases. In some flowers, the largest point of the first sepal is displaced toward the older of the two bracts (Tucker 1998, Figs 11, 51, 54; Tucker pers. comm.). In others, it is displaced toward the younger (Tucker 1998, Fig. 13; Tucker pers. comm.). Because there is no consistent correlation between the side favored by the off-median sepal and the size of the bracteole, it is difficult to suggest a developmental explanation for the placement of this sepal. In this context, it is worth noting that the displacement of the first sepal is not maintained in *Labichea* and *Dialium*. In these genera there is differential growth to return the tip of the sepal to a median position (Tucker 1998).

Hofmeister's rule predicts that the second sepal should form as far away as possible from the other primordia already present on the apex. In *Petalostylis*, *Labichea*, and *Dialium* the second sepal forms in an adaxial and transverse position, almost above the initiation point of one of the two bracts. If normal phyllotactic constraints operate to place this sepal, it should be possible to find it on either side of the flower, to produce either right- or left-handed flowers. All three genera have flowers of both symmetries (Tucker 1998, Figs 12, 13, 56–59, 101, 103; Tucker, pers. comm.).

If the positions of the preceding organs are the only factors affecting the position of the second sepal, then it should appear approximately 137° from the insertion of the first sepal. In the two apices of *Petalostylis* that are at the proper stage the second sepal occurs 131° and 132° from the first sepal, respectively (Tucker 1998, Figs 12, 13). In *Labichea* the angles are 140° and

Table 3: Influences on organ position in *Hedychium* and Fabaceae (Caesalpinioideae: Cassieae)

	<i>Hedychium</i>	<i>Petalostylis</i> ¹	<i>Labichea</i> ¹	<i>Dialium</i> ¹
bract initiation	bracts larger adaxially	bracts larger adaxially (Figs 10, 11)	bracts larger adaxially (Figs 51–53)	bracts larger adaxially (Figs 97–99)
first sepal (<i>Hedychium</i>); first bract (Fabaceae)	shape of apex; position of continuation apex	shape of apex ² (Figs 9–11)	shape of apex ² (Figs 50–53)	shape of apex ² (Figs 97–99)
second sepal (<i>Hedychium</i>); second bract (Fabaceae)	shape of apex; position of first sepal	shape of apex; position of first bract (Figs 9–11)	shape of apex; position of first bract (Figs 50–53)	shape of apex; position of first bract (Figs 97–99)
third sepal (<i>Hedychium</i>); first sepal (Fabaceae)	position of other sepals; shape of apex	adaxial positions of bracts (Figs 11, 12)	adaxial positions of bracts (Figs 51, 53)	adaxial positions of bracts (Fig 100)
second sepal (Fabaceae)	not applicable	positions of bract(s) and first sepal (Figs 12, 13)	positions of bract(s) and first sepal (Figs 56, 57)	positions of bract(s) and first sepal (Figs 101, 102)

¹ Figure citations refer to Tucker (1998).

² Tucker (1998; personal communication) shows that the first bract forms with equal probability on the right or left side of the apex.

138° (Tucker 1998, Figs 56, 57), and in *Dialium* they are 130° and 137° (Tucker 1998, Figs 101, 102). These measurements suggest that there is an influence from the bracts and the first sepal (Table 3). The same placement of the sepal is predicted no matter if all three organs (two bracts and one sepal) or only the last two of them (one bract and sepal) affect the position of the second sepal (see Lyndon 1978b for discussion of this point).

Beginning with the initiation of the third sepal, it becomes difficult to determine the influences on organ position in the Fabaceae genera. For instance, it is difficult to explain why the third sepal in *Petalostylis* initiated in an adaxial, transverse position, while the third sepal in *Labichea* is initiated laterally, completely filling the space between the first and second sepals (Tucker 1998, Figs 12, 57). I suspect that these differences are related to differences in shape of the floral apices, but lacking additional data I am unable to confirm this hypothesis.

CONCLUSIONS

The evidence presented here suggests that there are two factors that influence the position of floral organs: the positions of the other floral organs present on the apex, and the shape of the apex itself. In some cases, these factors are sufficient to explain the positions of the organs. In other cases, such as the positions of the first two sepals in *Silene coeli-rosa*, other factors must be involved. These factors may be related to the production of unequal inhibitory fields by the older organs.

All of the genera where the influences discussed here have been found to apply (*Hedychium*, *Petalostylis*, *Labichea*, *Dialium*) have cymose partial florescences. This suggests that at least some of the influences found in this study are correlated with this type of inflorescence. One common feature of these genera is that their partial florescences are subtended and enclosed by bracts or leaves. Perhaps these phyllomes restrict the development of the partial florescence apices, flattening them and causing the first bract(s) to be initiated slightly adaxially. This hypothesis finds support in the fact that the inflorescence of *Hedychium* is tightly enfolded in leaf sheaths at the time of cincinnus formation (personal observation). The presence of these sheaths may restrict symmetrical formation of the cincinnus apices. The fact that the floral apex of *Silene coeli-rosa* is symmetrical and does not appear

to be tightly enclosed by leaves supports the hypothesis that, in some cases, enclosing leaves may exert an influence on the shape of the partial florescence apex.

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REFERENCES

- Berlyn, G. P., and J. P. Miksche. (1976). 'Botanical Microtechnique and Cytochemistry.' (Iowa State University Press: Ames.)
- Bowman, J. L. (1997). Evolutionary conservation of angiosperm flower development at the molecular and genetic levels. *Journal of Bio-sciences* **22**, 515–527.
- Charlton, W. A., Macdonald, A. D., Posluszny, U., and Wilkins, C. P. (1989). Additions to the technique of epi-illumination light microscopy for the study of floral and vegetative apices. *Canadian Journal of Botany* **67**, 1739–1743.
- Hofmeister, W. (1868). 'Allgemeine Morphologie der Gewächse.' (Engelmann: Leipzig.)
- Jean, R. V. (1984). 'Mathematical Approach to Pattern and Form in Plant Growth.' (John Wiley and Sons: New York.)
- Johansen, D. A. (1940). 'Plant Microtechnique.' (McGraw-Hill: New York.)
- Kirchoff, B. K. (1997). Inflorescence and flower development in the Hedychieae (Zingiberaceae). *Hedychium. Canadian Journal of Botany* **75**, 581–594.
- Kodak (1983). 'Kodak Technical Pan Film 2415. Eastman Kodak Pamphlet No. P-255.' (Eastman Kodak: Rochester.)
- Lacroix, C., and Sattler, R. (1988). Phyllotaxis theories and tepal–stamen superposition in *Basella rubra*. *American Journal of Botany* **75**, 906–917.
- Lyndon, R. F. (1978a). Flower development in *Silene*: morphology and sequence of initiation of primordia. *Annals of Botany* **42**, 1343–1348.
- Lyndon, R. F. (1978b). Phyllotaxis and the initiation of primordia during flower development in *Silene*. *Annals of Botany* **42**, 1349–1360.

- Lyndon, R. F. (1998a). 'The Shoot Apical Meristem.' (Cambridge University Press: Cambridge.)
- Lyndon, R. F. (1998b). Phyllotaxis in flowers and in flower reversion. In 'Symmetry in Plants': (Eds R. V. Jean and D. Barabé.) pp. 109–124. (World Scientific: Singapore.)
- Posluszny, U., Scott, M. G., and Sattler, R. (1980). Revisions in the technique of epi-illumination light microscopy for the study of floral and vegetative apices. *Canadian Journal of Botany* **58**, 2491–2494.
- Ramírez-Domenech, J. I., and Tucker, S. C. (1989). Phylogenetic implications of inflorescence and floral ontogeny of *Mimosa strigillosa*. *American Journal of Botany* **76**, 1583–1593.
- Richards, F. J. (1951). Phyllotaxis: Its quantitative expression and relation to growth in the apex. *Philosophical Transactions of the Royal Society of London, Series B* **235**, 509–564.
- Rutishauser, R. (1981). Blattstellung und Sprossentwicklung bei Blütenpflanzen unter besonderer Berücksichtigung der Nelkengewächse (Caryophyllaceen s.l.). *Dissertationes Botanicae* **62**, 1–166.
- Rutishauser, R., and Sattler, R. (1985). Complementarity and heuristic value of contrasting models in structural botany. I. General considerations. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **107**, 415–455.
- Sattler, R. (1968). A technique for the study of floral development. *Canadian Journal of Botany* **46**, 720–722.
- Schwabe, W. W. (1998). The role and importance of vertical spacing at the plant apex in determining the phyllotactic pattern. In 'Symmetry in Plants': (Eds R. V. Jean and D. Barabé.) pp.109–124. (World Scientific: Singapore.)
- Smith, B. W. (1941). The phyllotaxis of *Costus* from the standpoint of development. *Proceedings of the Leeds Philosophical and Literary Society (Scientific Section)* **4**, 42–63.
- Thornley, J. H. M. and Cockshull, K. E. (1980). A catastrophe model for the switch from vegetative to reproductive growth in the shoot apex. *Annals of Botany* **46**, 333–341.
- Troll, W. (1964). 'Die Infloreszenzen: Typologie und Stellung im Aufbau des Vegetationskörpers, Vol. I.' (Gustav Fischer: Stuttgart.)
- Tucker, S. C. (1998). Floral ontogeny in legume genera *Petalostylis*, *Labichea*, and *Dialium* (Caesalpinioideae: Cassieae), a series in floral reduction. *American Journal of Botany* **85**, 184–208.
- Weberling, F. (1989). 'Morphology of Flowers and Inflorescences.' (Cambridge University Press: Cambridge.)
- Weisse, A. (1932). Zur Kenntnis der Blattstellungsverhältnisse bei den Zingiberaceen. *Berichten der Deutschen Botanischen Gesellschaft* **50**, 327–366.