

Inflorescence and Flower Development in *Musa velutina* H. Wendl. & Drude (Musaceae), with a Consideration of Developmental Variability, Restricted Phyllotactic Direction, and Hand Initiation

By: [Bruce K. Kirchoff](#)

Kirchoff, B. K. 2017. Inflorescence and flower development in *Musavelutina* H. Wendl. & Drude (Musaceae), with a consideration of developmental variability, restricted phyllotactic direction, and hand initiation. *International Journal of the Plant Sciences* 178: 259–272. DOI: 10.1086/691143. Dryad Digital Repository DOI:10.5061/dryad.5j8p8

Made available courtesy of The University of Chicago: <http://dx.doi.org/10.1086/691143>

©2017 by The University of Chicago. All rights reserved

Abstract:

Premise of research. Inflorescence and flower structure in the Musaceae is unique in the Zingiberales. The inflorescence lacks the obvious cincinnus structure that characterizes the order, and the flowers are unisexual. Previous studies were conducted using cultivated varieties and were carried out with sectioned material, which does not permit accurate developmental descriptions. Developmental study of a wild species with modern methods addresses these shortcomings and provides more accurate descriptions.

Methodology. Young inflorescences and flowers were collected from botanical gardens in Hawaii and Australia and critical-point dried for observation with a scanning electron microscope.

Pivotal results. All shoots and inflorescences have sinistrorse (left-handed) phyllotaxy, and the sequence of flower initiation is usually correlated with this pattern. Initiation begins on the cathodic side of the hand (opposite the direction of phyllotactic rise) and progresses anodically (in the direction of phyllotactic rise). Within this general pattern, the sequence of flower initiation is variable, even within the same inflorescence. Five patterns of initiation are reported, with additional variation within each pattern. Both male and female flowers have similar early developmental patterns but diverge at the time of petal/inner androecial formation. In male flowers the anterior side of the flower develops slightly ahead of the posterior, while in female flowers the posterior side develops slightly ahead of the anterior. While consistently present in the material analyzed here, these differences are not apparent at the time of gynoecial initiation or in the mature flowers.

Conclusions. The banana inflorescence is another example of how higher-level phyllotactic patterns can influence the sequence of organ initiation at lower levels. Despite variability in the sequence of flower initiation in a hand, the best interpretation of the hand remains a cincinnus. Variability in inflorescence and floral development is rarely reported and may be more common than currently supposed.

Keywords: floral development | morphology | banana | Zingiberales

Article:

*****Note: Full text of article below**

INFLORESCENCE AND FLOWER DEVELOPMENT IN *MUSA VELUTINA* H. WENDL. & DRUDE (MUSACEAE), WITH A CONSIDERATION OF DEVELOPMENTAL VARIABILITY, RESTRICTED PHYLLOTACTIC DIRECTION, AND HAND INITIATION

Bruce K. Kirchoff^{1,*}

*Department of Biology, PO Box 26174, University of North Carolina at Greensboro, North Carolina 27402-6174, USA

Editor: Gerhard Prenner

Premise of research. Inflorescence and flower structure in the Musaceae is unique in the Zingiberales. The inflorescence lacks the obvious cincinnus structure that characterizes the order, and the flowers are unisexual. Previous studies were conducted using cultivated varieties and were carried out with sectioned material, which does not permit accurate developmental descriptions. Developmental study of a wild species with modern methods addresses these shortcomings and provides more accurate descriptions.

Methodology. Young inflorescences and flowers were collected from botanical gardens in Hawaii and Australia and critical-point dried for observation with a scanning electron microscope.

Pivotal results. All shoots and inflorescences have sinistrorse (left-handed) phyllotaxy, and the sequence of flower initiation is usually correlated with this pattern. Initiation begins on the cathodic side of the hand (opposite the direction of phyllotactic rise) and progresses anodically (in the direction of phyllotactic rise). Within this general pattern, the sequence of flower initiation is variable, even within the same inflorescence. Five patterns of initiation are reported, with additional variation within each pattern. Both male and female flowers have similar early developmental patterns but diverge at the time of petal/inner androecial formation. In male flowers the anterior side of the flower develops slightly ahead of the posterior, while in female flowers the posterior side develops slightly ahead of the anterior. While consistently present in the material analyzed here, these differences are not apparent at the time of gynoecial initiation or in the mature flowers.

Conclusions. The banana inflorescence is another example of how higher-level phyllotactic patterns can influence the sequence of organ initiation at lower levels. Despite variability in the sequence of flower initiation in a hand, the best interpretation of the hand remains a cincinnus. Variability in inflorescence and floral development is rarely reported and may be more common than currently supposed.

Keywords: floral development, morphology, banana, Zingiberales.

Introduction

Bananas (*Musa* sp., Musaceae) are one of the most important economic crops whose cultivation and taxonomy has been widely studied (Quisumbing 1919; Loesecke 1950; Jacob 1952; Hotta 1964; Simmonds 1966; Argent 1976). Given their importance, it is surprising that there have been no comprehensive studies of inflorescence and flower development in the genus. What is known about flower development comes either from studies based on sectioned material (White 1928; Ram et al. 1962) or from studies conducted before the development of modern epi-illumination methods and scanning electron microscopy (SEM; Payer 1857; White 1928; Fahn 1953; Simmonds 1966). None of these studies provide the type of detail normally expected in contemporary studies. They present only the barest outlines of hand and flower development, concentrating on the

sequence of floral organ initiation and, in the case of studies based on sections, often contain misinterpretations.

The structure of the banana inflorescence is important because, on the surface, it does not appear to fit into the structure that is common to the rest of the order (Kunze 1986). All other members of the Zingiberales possess lateral cincinni or floral structures clearly derived from cincinni (Kunze 1986; Kirchoff and Kunze 1995). On the surface, the hand of the banana does not fit this pattern. Fahn (1953) addresses this problem in his developmental study of the hands of *Musa balbisiana* and *Musa acuminata* cv. Dwarf Cavendish.² In these cultivars, the sequence of flower initiation begins at one end of each hand and proceeds laterally in a zigzag pattern, alternating between the adaxial and abaxial rows of flowers. This sequence of initia-

¹ E-mail: kirchoff@uncg.edu.

Manuscript received October 2016; revised manuscript received December 2016; electronically published March 21, 2017.

² Names of the cultivated bananas are given as originally published by the author or authors. Due to changes in nomenclature, it was not always possible to determine which cultivar was studied according to the system of Simmonds and Shephard (1955). For an overview of banana nomenclature, see <http://www.promusa.org/Nomenclature+of+cultivated+bananas>.

tion is consistent with an interpretation of the hand as a cincinnus. This interpretation was originally proposed by Thompson (1933)—the single reasonable suggestion among the many improbable interpretations proposed by this author. Fahn (1953) produced the first evidence that clearly supports this interpretation, but the fact that he worked on cultivated species raises the question of whether the same results would be found in a wild species. This study was undertaken, in part, to answer this question and to determine if a wild species might show additional features that would support the interpretation of the hand as a cincinnus. For instance, if subtending bracts were present below the flowers, as is common in many cinnini, their presence would strengthen this interpretation. The associated data on flower development also increases our developmental knowledge of this important genus and contributes to a long-term study of flower development in the Zingiberales (Kirchoff 1983a, 1983b, 1988a, 1988b, 1997, 1998, 2003; Kirchoff and Kunze 1995; Box and Rudall 2006; Kirchoff et al. 2009).

Material and Methods

Techniques

Young inflorescence apices of *Musa velutina* H. Wendl. & Drude (section Rhodochlamys, Assam, and NE India) were collected at Lyon Arboretum, Honolulu, Hawaii (accession no. L67.0284), with a voucher specimen deposited at BISH (Kirchoff 88-144). Additional developmental material was collected from the Royal Botanic Gardens Sydney, Sydney, Australia (accession no. 17321), and a voucher specimen deposited at NSW (Kirchoff 01-319). The specimens were dissected and fixed in formalin-acetic acid-alcohol (Berlyn and Miksche 1976) in the field.

Prior to observation, specimens were washed overnight in 50% ethyl alcohol (EtOH), dehydrated with 2,2-dimethoxypropane (Postek and Tucker 1976), stained in fast green (Johansen 1940; Berlyn and Miksche 1976), and transferred to 100% EtOH for dissection. Dissection was carried out by supporting the apices in Permatex black silicone (Loctite, Rock Hill, CT) that had been immersed in 100% EtOH before it had completely hardened. Immersion in 100% EtOH keeps the silicon pliable while retaining sufficient resiliency to support the apices. Following dissection, the apices were stored in 100% EtOH for one to many weeks. At the end of this period, they were transferred to biopsy bags and critical-point dried in a Pelco critical-point dryer (Ted Pella, Redding, CA).

In preparation for viewing in the SEM, 13 specimens were mounted on SEM stubs using carbon- or silver-based adhesive. Further dissection was occasionally done under a binocular dissecting microscope to remove older flower parts and to reveal gynoecial primordia. The specimens were coated with gold/palladium using a Pelco 91000 sputter coater (Ted Pella) and observed using a Leica Stereoscan 430 SEM. Digital images were captured and saved as TIFF files to a Iomega zip disk (LenovoEMC, San Diego, CA) and were arranged into plates using Adobe Photoshop (vers. 6.0.1–CS5; Adobe Systems, San Jose, CA).

Inflorescence Terminology

The inflorescence terminology introduced by Troll (1964) and Weberling (1989) is used in this article to describe inflorescence



Fig. 1 Inflorescence of *Musa velutina* growing at Lyon Arboretum, Honolulu, Hawaii. Note the four hands of female flowers, now in fruit, followed by distal male hands. The bracts subtending the female hands have fallen. Photo by Raymond Baker, used with permission.

structure and development. I use Troll's terms in a descriptive sense, not as part of his larger typological system, which has been criticized on other grounds (Kunze 1989; Claßen-Bockhoff 2000; Endress 2010; Stützel and Trovó 2013).

An inflorescence is a shoot system that is modified to serve the formation of flowers (Troll 1964; Weberling 1982, 1989). Inflorescences are composed of components, which may be repeated at varying levels of complexity (Kunze 1989; Stützel and Trovó 2013). A florescence is a terminal indeterminate

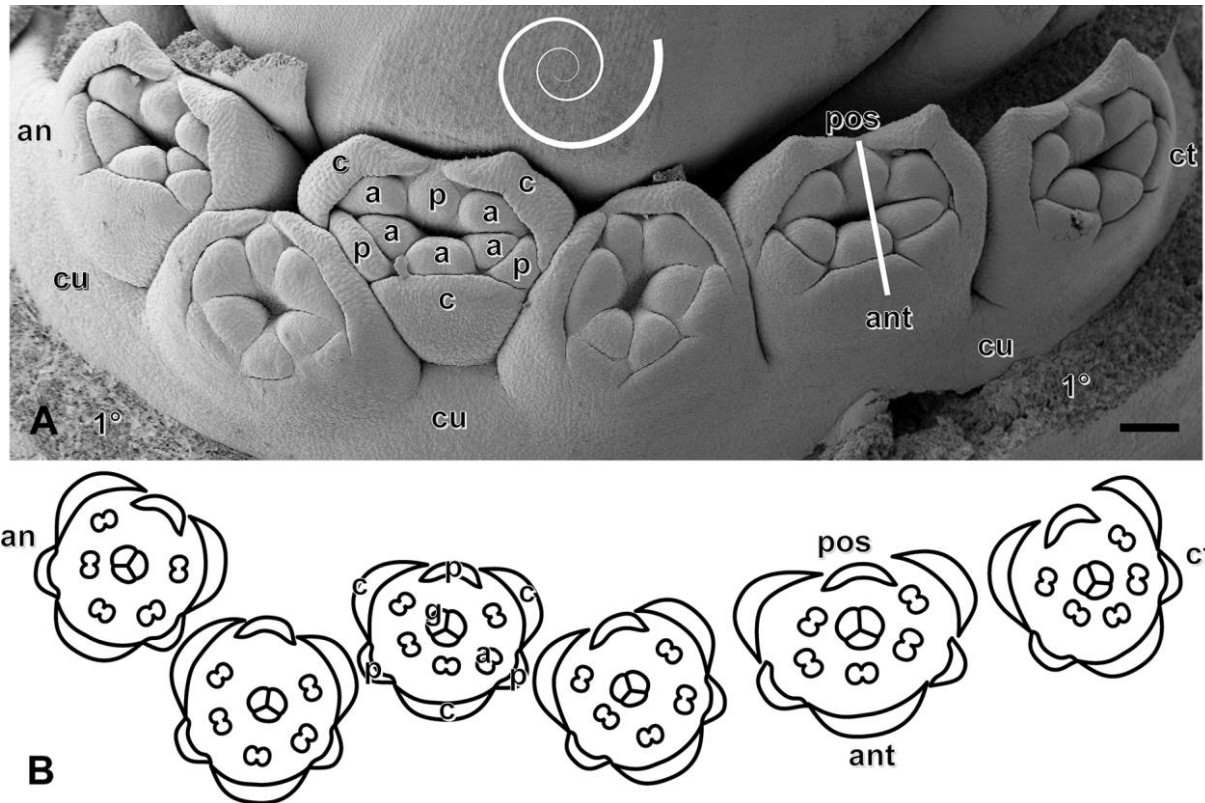


Fig. 2 Hand of female flowers. *A*, Scanning electron microscopy (SEM) image prior to gynoecial initiation but after formation of all other organs. *B*, Drawing showing position of floral organs, including the gynoecium, relative to SEM. 1° = primary or main bract of the inflorescence; a = androecium/stamen; an = anodic side of the hand/flower; ant = anterior side of flower; c = sepal; ct = cathodic side of the hand/flower; cu = cushion on which the flowers are initiated; g = gynoecium (drawing only); p = petal; pos = posterior side of flower; spiral = sinistorse direction of the phyllotactic helix (left-handed/clockwise when viewed from above). Scale bar = 100 μ m.

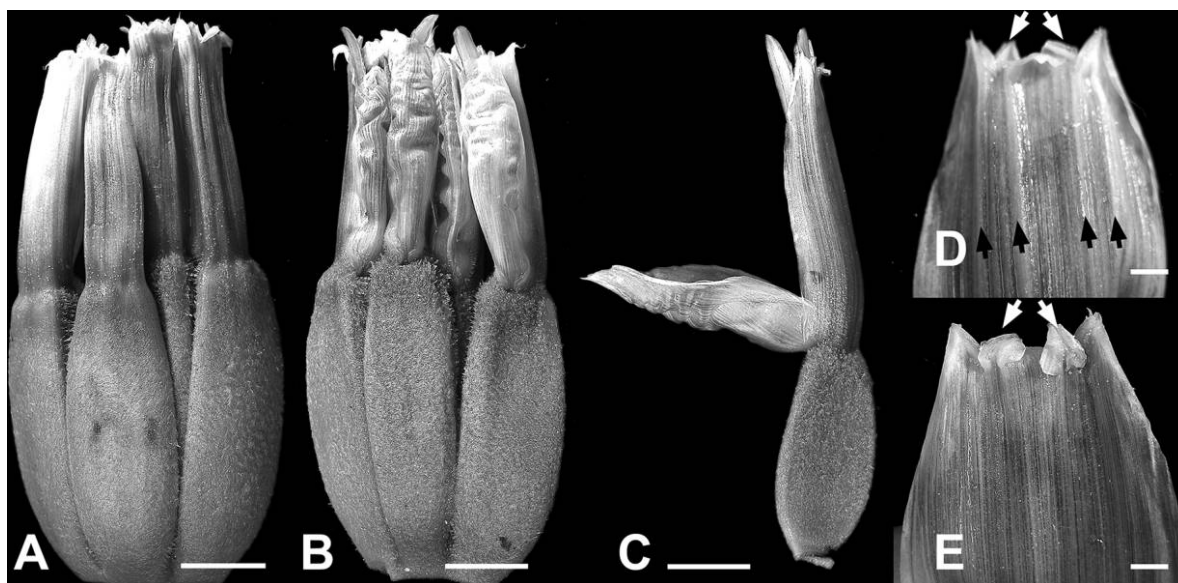
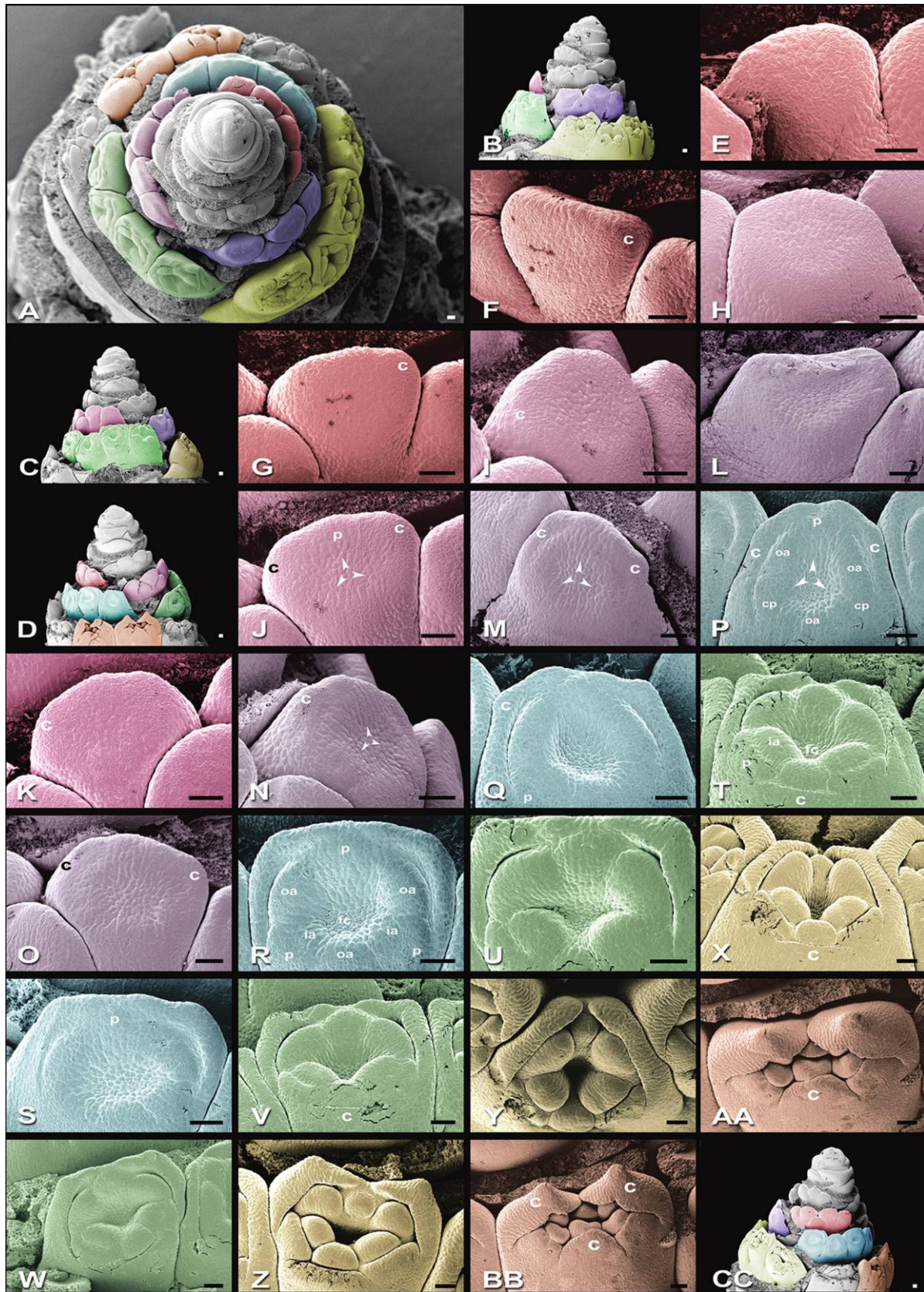


Fig. 3 Hand of female flowers at anthesis. *A*, Anterior view. *B*, Posterior view. *C*, Lateral view with free posterior petal pulled out to show lack of fusion with other perianth members. *D*, Exterior view of fused perianth showing three sepals and two petals (white arrows). Black arrows indicate sutures between the fused perianth members. *E*, Interior view of fused perianth. The sutures between the fused members are not visible from this aspect. White arrows indicate free apices. Scale bars = 10 mm (*A*–*C*), 2 mm (*D*, *E*).



flower-bearing unit of an inflorescence. A florescence terminating the main axis of the plant is the main florescence. In contrast, a florescence terminating a lateral axis is a coflorescence. A synflorescence is a system of florescences collected together into an inflorescence.

Inflorescences may be either monotelic or polytelic (Troll 1964; Weberling 1989). In a monotelic synflorescence, the inflorescence axis ends in a flower, as do all of the lateral floral branches. Polytelic synflorescences have floral axes that end in multiflowered florescences and lack terminal flowers. In both types of synflorescences, the branches below the main florescence repeat the structure of the inflorescence as a whole and are known as paracladia. In polytelic synflorescences, the florescences may be composed of cymose subunits called partial florescences.

In *Musa*, the inflorescence has been interpreted as a form of polytelic synflorescence in which there are no coflorescences (Kunze 1985, 1986; fig. 1). Thus, the banana inflorescence can be thought of as a polytelic synflorescence reduced to a single main (terminal) florescence (Kunze 1985, 1986). In his study of the inflorescence of *Musa acuminata* and *Musa balbisiana* cv. Gros Michele, Fahn (1953) describes the partial florescences as cincinni, a form of monochasium. Since the current results for *M. velutina* are at least partially at variance with this interpretation, I will initially adopt a neutral term from the horticulture literature and refer to the lateral clusters of flowers as “hands” (de Wildeman 1908; Simmonds 1966). I take the term “cushion” from the same sources. The cushion is the primordial tissue that produces and later bears the hand. In *Musa* spp., the cushions occur in the axils of the main (primary) bracts, are tangentially elongated, and produce the hands of flowers (fig. 2).

Phyllotactic helices can be either sinistrorse (left-handed/clockwise when viewed from above) or dextrorse (right-handed/

counterclockwise when viewed from above). The anodic side of a flower is the transverse (or lateral) side of the flower that lies in the direction of the rise of the phyllotactic helix. The cathodic side is the opposite side of the flower, the side that lies opposite the rise of the phyllotactic helix. Seen from above, in a sinistrorse phyllotactic system the cathodic side lies to the right and the anodic side to the left (fig. 2). All of the figures are oriented so that the cathodic side is to the right in this article (fig. 2).

Floral Terminology

The posterior side of the flower is the side that backs on the main florescence axis. The anterior side is away from this axis. In all polar views in this article, the anterior side of the flower is the side at the bottom of the photograph (fig. 2).

The abaxial side of the flower is the side away from the lower-order axis from which the flower arises, in the axil of a bract. The adaxial side of the flower is adjacent to this lower-order axis. Because the position and nature of the lower-order axis is somewhat ambiguous in *Musa*, I will limit my use of these terms.

The perianth of *Musa* consists of six tepals, arranged into two whorls. Although these perianth members are virtually indistinguishable in the mature flower, I will refer to them as sepals and petals because they are initiated as distinct organs in well-defined whorls. I also want to preserve terminology between this account and previously published work on flower structure in *Musa* (Kirchoff 1992).

A Note on Figure 4

Figure 4 has been arranged to show the stages of flower development in the context of a single inflorescence. Panel A shows the inflorescence in polar view, while panels B–D and CC show the lateral views of different sides of the apex.

Fig. 4 Flower development as it occurs on a single inflorescence, arranged to show the developmental stages in the context of inflorescence and hand structure. Color coding links the hands (A–D, CC) to the flowers (E–BB). Flower developmental sequences can be read within a hand diagonally from top right to lower left, horizontally from left to right across hands, and diagonally from upper left to lower right across hands. Note the posture of the flowers: the primordia are oriented at a steep angle due, in part, to being covered by the (removed) primary bracts. A, Inflorescence in polar view. B–D, CC, Lateral views of the inflorescence showing the positions of the hands relative to each other. E–O, Male flowers. P–S, Sex uncertain, likely female or transitional. T–BB, Female flowers. E, Early sepal formation. F, Initiation of the first (c) and second sepals gives the apex a triangular appearance. G, Polar view of same apex shown in F. H, Late sepal formation and formation of the marginal primordia, creating an indistinct ring primordium. I, Early formation of indistinct ring primordium. J, Indistinct ring primordium consisting of three larger petal primordia (white arrowheads) and three less well-developed regions that will form the outer androecium (regions between arrowheads). The posterior petal (p) is more distinct than the other petal primordia. c = sepal. K, Late sepal (c) and early ring primordium formation. L, Abnormal/damaged apex showing marginal primordia formation. M, Later marginal primordia development. A more or less distinct ring primordium is present, composed of three slightly larger petal primordia (white arrowheads) and three smaller outer androecial primordia (between arrowheads). The two sepals (c) are distinct from the ring. N, Oblique view showing two sepals (one labeled c) and three petal primordia (white arrowheads) united below into the floral cup. O, Two sepals (c) and marginal primordia united into an indistinct ring primordium. The posterior petal, between the two sepals, is the largest marginal primordium. P, Distinct sepals (c) partially surrounding the marginal primordia and floral cup (white arrowheads), composed of the posterior petal primordium (p), three outer androecial primordia (oa), and two common petal/inner androecial primordia (cp). Note that the third, anterior sepal has not yet formed. Q, Distinct sepals (c) surround a well-developed ring primordium that is not clearly divided into separate primordia. The posterior petal (unlabeled) is clearly visible, and the initiation of a second petal has taken place on the proximal side of the ring primordium (p). R, Separate petal (p) and androecial primordia (ia, oa) united below into a floral cup (fc). The posterior petal primordia and the inner androecial primordia (ia) have separated from their common primordia. S, Young flower with two posterior sepals and a ring primordium composed of semidistinct marginal primordia. Note that the posterior petal (p) and the three outer androecial primordia are slightly larger than the other marginal primordia. T, Female flower with floral cup (fc) surmounted by petal and androecial primordia. The common petal/androecial primordia have separated into distinct petal (p) and inner androecial (ia) primordia. This is the first stage at which the anterior sepal (c) is clearly visible. U–W, Female flowers at developmental stages similar to those shown in T. X–Z, Female flowers showing deepening of the floral cup prior to gynoecium initiation and enlargement of the anterior sepal (c) following the formation of all other floral organs. AA–BB, Female flowers showing enlargement of the floral organs and closure of the calyx (c) over the flower. Gynoecial formation is well under way by this stage of development. Scale bars = 50 μ m.

The hands are color coded and are thereby linked to the images of flower development. In the main plate, each diagonal is color coded to show one hand of flowers, with the youngest flower in the upper right position and the oldest in the lower left. This arrangement of images allows the figure to be read in multiple ways. Flower development can be read top right to lower left within a hand, horizontally right to left across hands, and diagonally from upper left to lower right across hands. These multiple readings present 23 different developmental sequences, capturing much more variability than can usually be represented.

Results

Organography

The inflorescence of *Musa* terminates an aerial stem that arises from the center of overlapping, spirally arranged leaf sheaths (a pseudostem). The inflorescence consists of a single main florescence that bears spirally arranged main (primary) bracts that subtend hands of flowers and later bananas (fig. 1). *Musa* is monoecious, with flowers arranged in hands. Each hand develops in the axil of a primary bract and usually consists of two rows of flowers. The lower hands are female; these are followed by a number of transitional hands and then an indefinite number of male hands.

The phyllotaxis of all inflorescences of *Musa velutina* is sinistrose (left-handed; figs. 1, 4A), as were the 16 shoots of *Musa basjoo* Siebold & Zucc. ex Linum that were investigated as part of this study. The oldest hands occur at the base, and the youngest occur near the apex of the inflorescence (figs. 1, 4B–4D). Each hand forms in the axil of a primary bract and bears one or two rows (most commonly two) of unisexual flowers (figs. 2, 3, 5A). In *M. velutina*, there are two to four hands of female flowers (Cheesman 1949; Nur 1976; figs. 2, 5A) formed at the base of the inflorescence, followed by an indefinite, but not unlimited, number of hands of male flowers (figs. 1, 4B–4D, 4CC). Transitional hands, containing both male and female flowers, may occur between the unisexual hands. The flowers of a hand are usually arranged in two parallel lines, one posterior and one anterior (figs. fig. 2, 6). An occasional flower may lie between rows (fig. 6, pattern 5).

Both male and female flowers have similar perianth morphologies. The three sepals and the two anterior petals are connate in the mature flower (fig. 3D, 3E) but retain some semblance of their separate structure and can sometimes be torn apart along their sutures (fig. 3D, black arrows). The sixth perianth member, the posterior petal, is free (figs. 2, 3C). The female flowers possess a well-developed trilocular ovary capped with a gynopleural nectary in the tissue that closes the locules (Fahn and Benouaiche 1979; Smets and Cresens 1988). In the male flowers the ovary is reduced to this gynopleural region, with rudimentary locules at the base of the ovary.

Inflorescence Development

The inflorescence apex is a broad dome from which arise the primary bracts and hand primordia (fig. 5). The apex is broadest, and the bracts are initiated farthest from the apex when the

apex is younger. This occurs at or shortly after the time of female flower formation in the first hands (fig. 5A, 5E–5G).

Bract initiation begins with a raised arch of tissue on the flanks of the apex (fig. 5, white arrows) that grows into a ledge-like primordium prior to hand initiation (fig. 5C–5E, 5G, b). As the inflorescence ages and produces more hands, the apex becomes narrower, and bract initiation takes place closer to the tip.

Cushions, which will form the hands, are initiated as tangentially elongated ridges of tissue in the axils of the primary bracts (fig. 5A, 5E–5G, cu). The first sign of the cushion appears at approximately the third plastochron (fig. 5E, cu). From early in its development it is commonly larger cathodically (fig. 7A–7D).

Flower Formation on the Cushion

The sequence of flower formation on the cushion is variable (fig. 6). In general, the cathodic end of the cushion is larger (fig. 7A–7D), and flower formation begins at this end (fig. 6). However, the cathodic-most flower (rightmost in the figures) is seldom the first to form. It is much more common (21 of 29 hands) for the second flower from the right to form first, with development proceeding outward from that point in both directions (fig. 6, patterns 1, 4, 5; fig. 7E, 7F). The second flower to be initiated is usually the one to the immediate left of the first. Less commonly (6 of 29 hands), the rightmost flower forms first, and development proceeds anodically (to the left), first in the posterior and then in the anterior row (fig. 6, pattern 2A–2E; fig. 7G). When a cushion is large enough to support two rows of flowers, those in the posterior row generally form first (figs. 5A, 6, 7E, 7F).

Very occasionally (2 of 29 hands), it is the anodic-most flower that forms first, and development then proceeds opposite the direction of the phyllotactic helix (cathodically; fig. 6, pattern 3A, 3B; fig. 7H). In some of these cases, the difference between the first few flowers is slight, and initiation of these flowers could be considered to be almost simultaneous. All of the major patterns of flower formation are found in both female and male hands (fig. 6).

No bracteoles subtending the flowers were seen in any hands, at any stage of development.

Floral Organogenesis

The following description applies to hands where the first flower is formed on the cathodic side of the cushion (figs. 4, 5, 7A–7G). Hands where the first flower is formed on the anodic side of the cushion are indicated by an asterisk after the figure number (ex. figs. 7H*, 8A*–8I*). In these hands, the sequence of floral organ initiation is the mirror image of that in the cathodic hands (8A*–8I*). Except where noted, the following description applies to both male (fig. 4E–4S) and female (figs. 4T–4BB, 8A*–8I*) flowers.

Flower organogenesis begins with the flattening of the flower primordium and the production of two sepal primordia in posterior-lateral positions (figs. 4E–4G, 7E, 7F, 8A*–8C*). The appearance of the first-formed sepals give the floral apex a distinctly triangular appearance (figs. 4G, 7F). The cathodic sepal forms before the anodic (figs. 4E–4K, 8C*–8E*), although postinitiation changes may cause the anodic sepal to appear

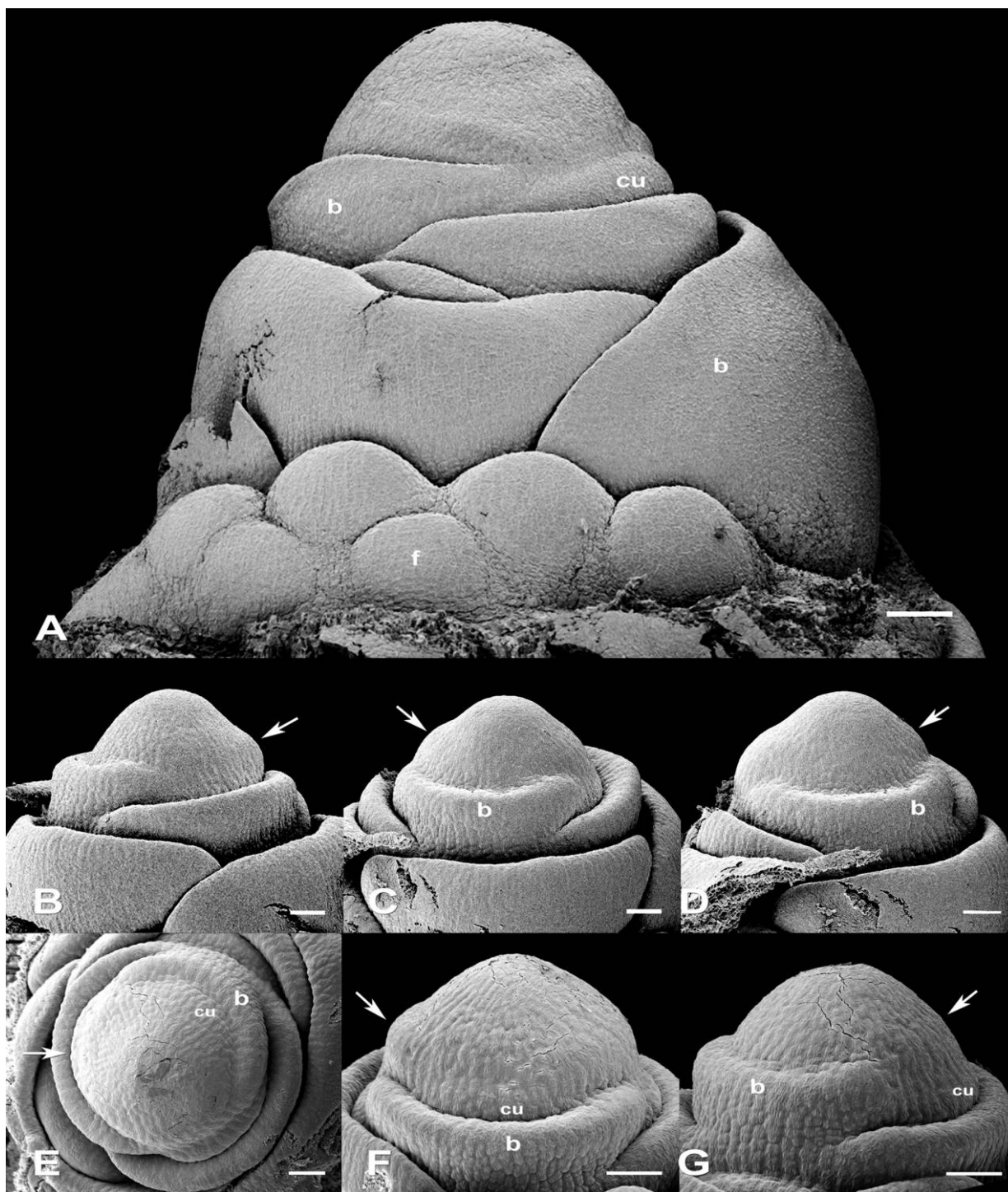


Fig. 5 Inflorescence apices showing sinistrose (clockwise from above) phyllotaxy, primary bract (b) initiation (white arrows) and enlargement, and initiation of the cushion (cu), the axillary primordium that will produce the hand of flowers. *A*, Young inflorescence apex at the time of male cushion (cu) initiation. The flower primordia (f) are of female flowers. Primary bracts (b) are at various stages of enlargement. *B–D*, Three views of the same inflorescence apex showing stages of primary bract (b) initiation (white arrows). *E–G*, Three views of a different apex showing primary bract (white arrows) and cushion (cu) initiation. The position of the primary bracts relative to the cushions is also shown. Scale bars = 50 μm .

No. ♀ No. ♂		Pattern Hands		Sequence of Flower Initiation	
1A		5		3 1 2	
				4	
1B	1			3 2 1 2	
				4 3 1 2	
1C		2		5	
				4 3 1 2	
1D	2	2		5	
				4 3 1 2	
1E		2		4 3 1 2	
				6 5	
1F	1			6 3 1 2	
				5 4	
1G		1		3 2 1 2	
				5 4	
1H	1			4 3 1 2	
				5 4	
1I	2			6/7 4 3 1 2	
				6 5	
2A		1		2 1	
				2 1	
2B		1		3	
				3 2 1	
2C		1		4	
				4 3 2 1	
2D	1 transitional			3	
				4 3 2 1	
2E		2		5	
				4 3 2 1	
3A		1		1 2	
				1 2 3 4 5?	
3B	1			5 6 7	
				6 3 1 2 2	
4		1		7 5 4	
				5 3 4 1 2	
5		1		6	

Fig. 6 Patterns of flower initiation in a hand.

larger on some apices (figs. 4Q, 8G*). At the same time or immediately after initiation of the first two sepals, the periphery of the floral apex interior to the sepals begins to rise and produces a low set of semidistinct marginal primordia (i.e., a ring primordium) surrounding a shallow floral cup (figs. 4H, 4I, 8D*, 8E*). As the ring enlarges, the separate primordia become more distinct (figs. 4M, 4N, 7H*, 8E*–8G*). The constituent primordia are the posterior petal primordium, two common petal/inner androecial primordia, and three outer androecial primordia (fig. 4P). The posterior stamen is lacking in *Musa* and is not initiated. As the petal and androecial primordia are somewhat distinct from early development, a true ring primordium consisting of uniform, symmetric meristematic tissue surrounding a central cavity is not truly present (figs. 4J–4N, 8G*). However, in some apices and at some stages, the marginal tissue is much more uniform, and so the term “ring primordium” will sometimes be used in the remainder of the article (fig. 4Q).

The floral cup, the cavity below the ring primordium and the meristematic region from which the ovary will develop, forms with the ring primordium (fig. 4H–4J). It deepens throughout early floral development until it becomes a significant cavity just prior to gynoecial initiation (figs. 4Z, 8N, 8O).

The posterior petal is the first primordium to appear after the posterior sepals (fig. 4I, 4J). In male flowers the anterior petal/inner androecial common primordia appear next (fig. 4J–4N, anterior white arrowheads), followed by the outer androecial primordia (fig. 4P, 4R, oa). In female flowers the posterior outer androecial primordia form after the posterior petal, followed by the anterior outer stamen (fig. 8E*–8I*, white arrowheads) and then the anterior petal/inner androecial primordia (fig. 8J*, black arrowheads).

Throughout these stages, and throughout much of early organogenesis, the floral apex is oriented at an angle to the vertical, with the posterior side of the flower higher than the anterior (figs. 4A, 4F, 4N, 7G, 7H*). This positional asymmetry is correlated with the unidirectional development of the calyx and corolla, with the posterior sepals and petal forming considerably earlier than the anterior organs (cf. fig. 4G, 4M, 4P–4T). The anterior sepal forms so much later than the other organs that it first appears below the other primordia, on the anterior side of the flower (figs. 4T, 8J, 8K).

In male flowers the anterior petals separate from the petal/inner androecial common primordia at about the same stage as the outer androecial primordia appear (fig. 4P–4R). At this stage, the anterior petal primordia may appear distinctly smaller (fig. 4Q), somewhat smaller (fig. 4T), or larger (fig. 4R) than the inner androecial primordia. In female flowers the anterior petals separate from the petal/inner androecial common primordia after the outer androecial primordia become distinct (fig. 8J–8L).

Once these floral organs have been initiated (figs. 4R, 8L), they enlarge and become more distinct (figs. 4T–4Z, 8M–8O). During this period, the floral cup continues to deepen until it becomes a substantial cavity prior to gynoecial initiation (figs. 4Y, 4Z, 8N, 8O). As the organs enlarge, the androecium closes over the cup. Shortly thereafter, the posterior sepals close over and cover the androecium (fig. 4AA, 4BB). Enlargement of the anterior sepal and anterior petals is slightly delayed relative to the other organs. They do not cover the androecium and floral cup until the posterior sepals and petal have mostly covered the flower (fig. 4AA).

The following description of gynoecial initiation is based on female flowers. Gynoecial initiation in male flowers was not studied in detail, although the first stages of initiation were observed in two flowers. Gynoecial initiation in female flowers begins as the posterior sepals close over the posterior stamens (fig. 8O). The three gynoecial primordia are formed opposite the sepals, but it was not possible to determine the sequence of initiation in female flowers. In the single female apex where very young gynoecial primordia were observed, one of the primordia was conduplicate, and the other two were flat (fig. 8P). Continued upward growth of the primordia closes the locules and eventually produces the style and stigma (fig. 8Q–8V). Throughout this period, the anterior gynoecial primordium remains larger than the others, suggesting that it formed first (fig. 8Q, 8R, 8T). The three primordia undergo postgenital fusion to form the style (fig. 8V). In female flowers the stamen develops slowly and remains smaller than the style and stigma (fig. 8U).

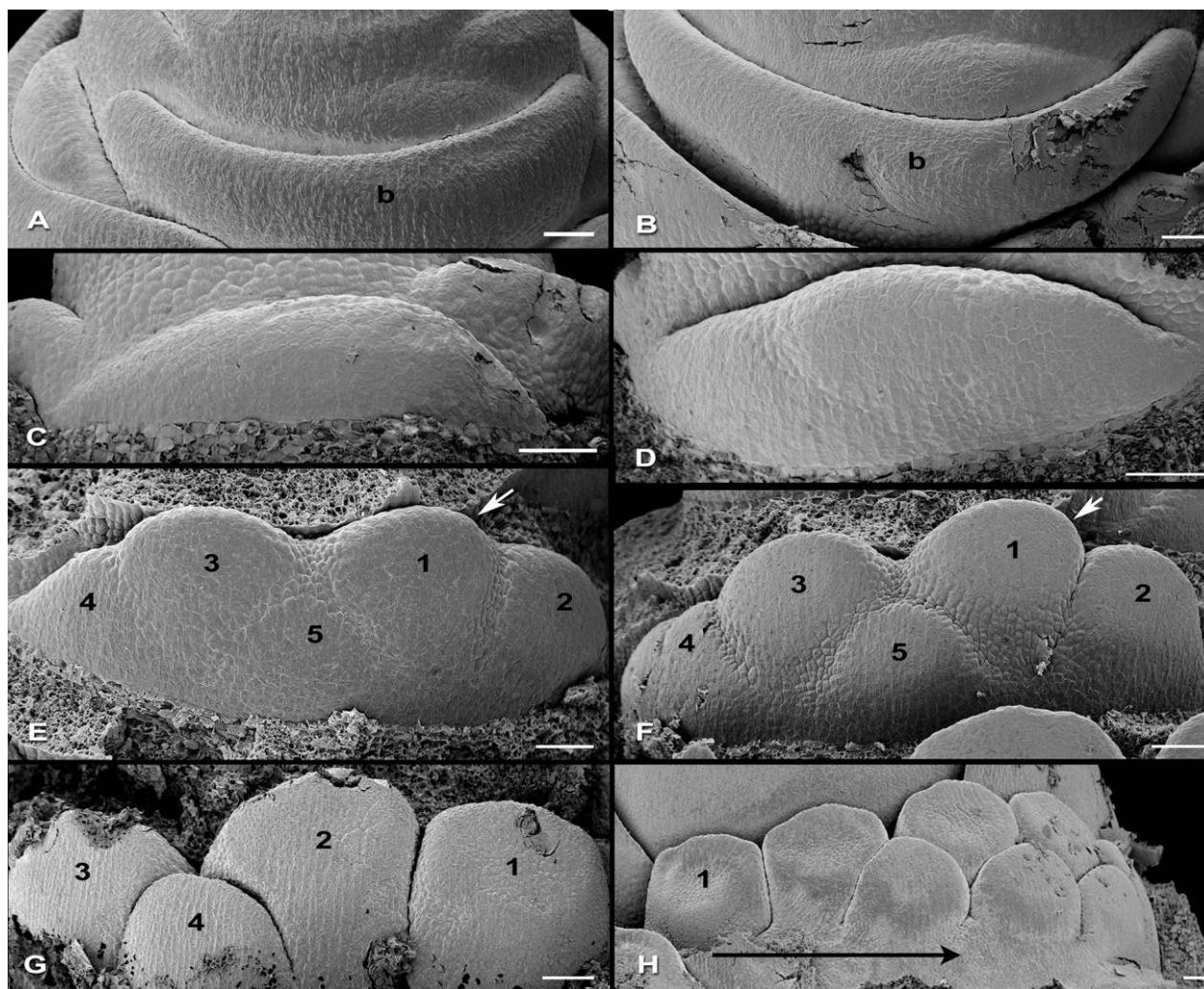


Fig. 7 Cushion and hand development up through the stage of flower formation. *A*, Male cushion showing asymmetric cushion initiation in the axil of a primary bract (*b*). The cathodic side of the cushion is larger than the anodic. *B*, Male cushion showing asymmetric enlargement of the cushion in the axil of a bract (*b*). *C*, *D*, Asymmetric enlargement of the cushion. *E*, *F*, Male hands, with sequence of flower initiation (1–5) on a cushion. The white arrows indicate the position where the first sepal will form. *G*, Male hand, with alternative sequence of flower initiation (1–4) with the cathodic-most flower (1) initiated first. *H*, Female hand, with alternative sequence of flower initiation (black arrow) with the anodic-most flower (1) formed first and development proceeding cathodically. See figure 6 for more information on the order of flower initiation. Scale bars = 50 μm .

In male flowers the first gynoecial primordium was observed forming in the anterior position, opposite the third formed sepal (fig. 8W, 8X).

Discussion

Phyllotaxy of the Shoot and Inflorescence

The phyllotactic helixes of all of the shoots and inflorescences investigated in this study were sinistrose (left-handed/clockwise when viewed from above). Skutch (1927) also found strictly sinistrose phyllotaxy in *Musa sapientum* cv. Gros Michel. This phyllotactic pattern is correlated with leaf veneration, with the right-hand side of the leaf (anodic side) wrapped in four or five turns of the left-hand side (cathodic side).

This pattern means that the phyllotactic helix does not reverse direction on each renewal shoot, as would be predicted by Hofmeister's rule (Kirchoff 2000, 2003; Singer 2006). For instance, Tennakone et al. (1982) found that in *Hibiscus furcatus* shoots with dextrose phyllotaxy always bear sinistrose flowers, while those with sinistrose phyllotaxy bear only dextrose flowers. Similarly, the phyllotactic helix reverses direction with each renewal shoot in *Costus scaber* (Costaceae; Kirchoff and Rutishauser 1990). The same pattern of reversal is seen in the partial florescences of *Phenakospermum* (Strelitziaceae) and *Heliconia* (Heliconiaceae) (Kirchoff 2003). However, there are cases where the phyllotaxy of the lateral organs—the flowers of *Silene* (Caryophyllaceae), for instance—cannot be explained solely on the basis of the phyllotaxy of the subtending shoot (Kirchoff 2000). In *Musa*, the universal sinistrose helix is

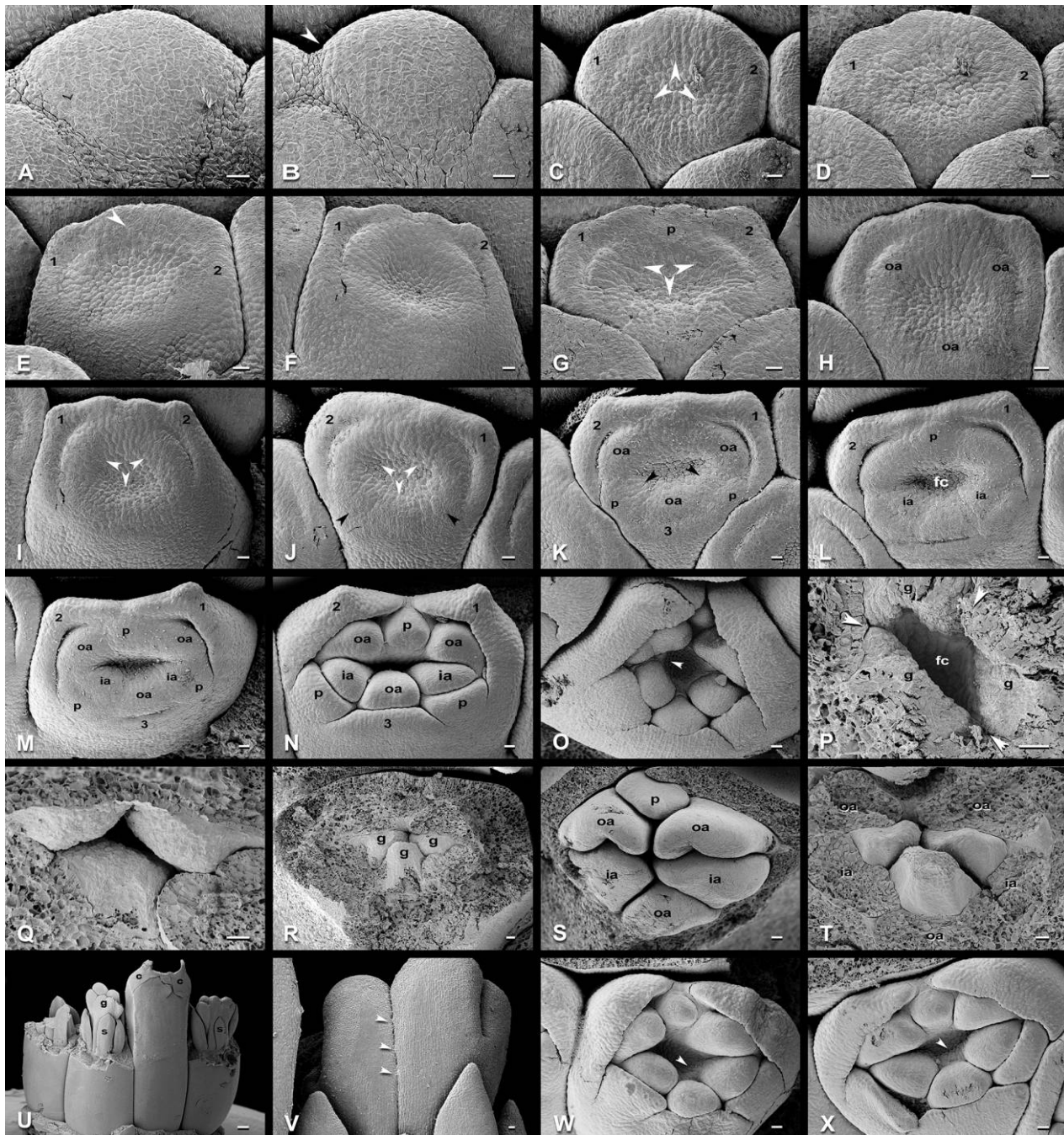


Fig. 8 Female flower and gynoecial development (A–V) and male gynoecial development (W, X). The flowers in A–N occur in a hand where flower formation proceeds anodically to cathodically. In these flowers, sepal (1–3) formation begins not with the cathodic but with the anodic (left side in this view) sepal. A, Flower primordium prior to organ initiation. B, Enlargement and flattening of flower primordium prior to organ initiation. The anodic side of the primordium (white arrowhead), the region from which the first sepal will form, is slightly larger than the cathodic region. C, D, Sepal formation (1, 2) and formation of marginal primordia (i.e., an indistinct ring primordium [white arrowheads] composed of semidistinct primordia). E, Semidistinct marginal primordia surrounding a shallow floral cup. The largest of these primordia occur opposite the sepals (1, 2) and will form the outer androecium before the petals, although the region that will form the posterior petal (white arrowhead) is slightly larger than the other petal/inner androecial regions at this stage. F, Enlargement of the outer androecial and posterior petal primordia. G, Continued development of semidistinct marginal primordia. The outer androecial (posterior white arrowheads) and posterior petal (p) primordia are the largest of these primordia. H, Distinct outer androecial primordia (oa) surmounting the floral cup. I, J, Enlargement of the marginal organ primordia. The primordia of the outer androecial members (white arrowheads) remain the largest, but the common petal/inner androecial common primordia are also now larger (black arrowheads). Note that the sepals are initiated in a sinistrose (left-handed) spiral in I and a dextrose (right-handed) spiral in J. The identity of the first sepal can be determined by its more pointed shape. K, Separation of the petal/inner androecial common primordia to form the anterior petals (p) and inner

correlated with, and perhaps caused by, the fact that the renewal shoots are not axillary but leaf opposed (Fisher 1978). They develop opposite the site of leaf insertion and thus may be free from any mechanical constraints of the subtending leaf.

Although I did not observe any shoots with dextrose (right-handed) phyllotaxy, Ram et al. (1962, their fig. 32) illustrate an inflorescence with this phyllotactic pattern. In this inflorescence, the young cushion is larger cathodically, just as in *Musa velutina*, suggesting that this feature is strongly correlated with the direction of phyllotaxy. That the correlation is not perfect is demonstrated by the two hands that had the first flower on the cathodic side of the cushion in this study (fig. 6, pattern 3).

Interpretation of the Inflorescence and the Hand

Various interpretations of the banana inflorescence have been formulated. These views include the interpretation of the inflorescence as a terminal spike (Payer 1857; Eichler 1875; White 1928), a long terminal raceme (Bentham and Hooker 1880), a terminal panicle (Baker 1893), and a serial flower assemblage (Schumann 1900). The morphological interpretation of the inflorescence hangs on the interpretation of the hand. Thompson (1933) proposed a complicated hypothesis based on his interpretation of the ontogenetic succession of the flower primordia of the banana inflorescence. In this interpretation the ancestor of *Musa* possessed an aerial stem that bore cones (spikes) of spirally arranged flowers in the axils of its leaves (Thompson 1933). During the course of evolution, these spikes eventually became reduced to the familiar hands of flowers seen in the present-day species.

Fahn (1953) favors a different interpretation, also originally proposed by Thompson (1933). In his view, the hands are cincinni (monochasia). This conclusion is based on his work on *Musa balbisiana* and *Musa acuminata* cv. Dwarf Cavendish. As in *M. velutina*, each hand in these species contains two tangential rows of flowers, but the number of flowers per row is much greater than in *M. velutina* (fig. 9). Fahn (1953) found that the sequence of flower initiation in these species begins with the primordia farthest to the right (most cathodic) and continues sequentially to the left (anodically) in a zigzag pattern, alternating between rows. This sequence of initiation is consistent with the interpretation of the hand as a cincinnus.

I never found the alternating abaxial-adaxial development that Fahn (1953) reported. In only 6 of 29 hands was the rightmost (cathodic-most) flower formed first (fig. 6, pattern 2). Five

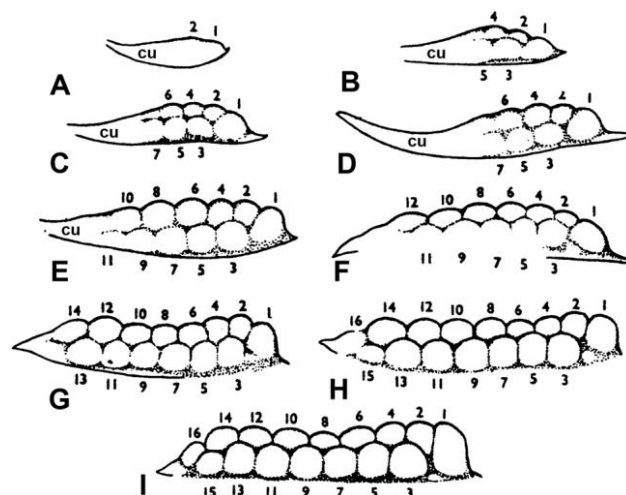


Fig. 9 Series of hands demonstrating different stages of flower development in one Dwarf Cavendish banana inflorescence. A, Nineteenth hand (i.e., the hand nearest the apex) in the inflorescence. cu = cushion. B–H, Intervening hands showing the lateral growth of the cushion (cu) and the sequential formation of the flowers. I, Eleventh hand of the inflorescence, after the initiation of all of the flowers. 1–16 = sequentially formed flower primordia. Modified after Fahn (1953), with permission.

of these hands were male, and one was transitional. All of the hands studied by Fahn were female. In all but one of the female hands of *M. velutina*, it was the penultimate flower that formed first. In the one exception, the sequence of flower initiation was reversed, proceeding from the left to the right (anodically to cathodically; fig. 6, pattern 3B). In most of the hands I studied, the flowers in the adaxial row formed before the flower(s) in the abaxial row.

Fahn (1953) also studied the vasculature of the hand in the Dwarf Cavendish banana. The first vascular bundle to appear in each hand is not the one that supplies the rightmost (cathodic-most) flower but the one that supplies the second flower. Vascularization to the rightmost flower does not develop until later, after about half of the flowers have received their bundles. After formation of the bundle to the penultimate flower, the vasculature continues to develop from right to left in each hand, with that to the extreme leftmost flower developing last. These observations are less consistent with

androecial members (black arrowheads). Note that all of the sepals (1–3) have been initiated. oa = outer androecial member. L, Deepening of the floral cup (fc) after the formation of all other floral organs. 1, 2 = sepals; ia = inner androecial member; p = posterior petal. M, Enlargement of the sepals (1–3), petals (p), and outer (oa) and inner (ia) androecial members and deepening of the floral cup prior to gynoecial initiation. N, Prior to gynoecial initiation, all of the organs are present and distinct. O, Early stage of gynoecial initiation (white arrowhead). The gynoecial primordia form opposite the sepals. Congenital growth of the calyx begins at or near this stage of development. P, One conduplicate and two nonconduplicate gynoecial primordia (g) initiated on the upper margin of the floral cup (fc). White arrowheads = sutures between the carpel primordia. Q, Enlargement of the three gynoecial primordia to close the floral cup. R, Further enlargement of the gynoecial primordia (g) and the beginning of the formation of the stigma and style. S, Posterior petal (p) and androecial members (ia, oa) covering enlarging gynoecial primordia. T, Same apex as in S, dissected to show gynoecial primordia. Outer (oa) and inner (ia) androecial members are removed. U, Hand of female flowers showing the developing style and stigma produced from gynoecial primordia (g). The perianth is composed of a long fused and a short free portion. The stamens are underdeveloped and shorter than the style. V, Enlargement of U showing postgenital fusion (white arrowheads) of the gynoecial primordia to form the style. W, X, Female flower after initiation of the first gynoecial primordium (white arrowheads) opposite an anterior sepal. Scale bars = 20 μ m (A–T, V–X), 200 μ m (U).

the interpretation of the hand as a cincinnus. In a cincinnus, the vasculature to the rightmost (cathodic) flower should develop first.

Maheshwari (1963) describes a variety of *Musa paradisiaca* with a branched inflorescence. From his drawing, the inflorescence appears to be a polytelic synflorescence with cofillorescences born in the axils of scalelike (or rapidly deciduous) bracts below the main florescence. This interpretation is consistent with Kunze's and Kirchoff's interpretations of the inflorescence in other families of the Zingiberales (Kunze 1985; Kirchoff 1986, 1988b, 1997, 1998; Kirchoff and Kunze 1995). If this interpretation is accepted, the hand is best interpreted as a highly modified cincinnus, and the inflorescence as a whole is a polytelic synflorescence that has been reduced to the main florescence (Kunze 1985, 1986).

This interpretation of the hands as cincinni would be easier to accept if the flowers possessed subtending bracts (secondary bracts), as are present in most other species of the Zingiberales (Kunze 1985; Kirchoff 1988b, 2000, 2003; Kirchoff and Kunze 1995). The presence of these bracts might provide additional positional information that could be used to establish the homology of hands. Inflorescence structure can often be determined by examining bract placement, even in the absence of developmental information. It is possible, if unlikely, that genes responsible for bract suppression might be identified in *Musa*, as they have been in the Poaceae (Whipple et al. 2010), and that the expression of these genes might shed light on the structure of the hand.

Although not consistent with the current results, the preponderance of the evidence still suggests that the hand is best interpreted as a cincinnus and the inflorescence as a polytelic synflorescence that has been reduced to the main florescence. This type of inflorescence is sometimes called a thyse (Weberling 1989). If this interpretation is accepted, the unusual patterns of floral initiation that are seen in *M. velutina* must be accounted for. These irregular patterns may be due to the small size of the hands compared with those of the cultivated bananas. The hands observed by Fahn (1953) had 12–16 flowers, whereas the largest hand observed here contained only seven flowers, and it was much more common for the hands of *M. velutina* to have five or fewer flowers. It may also be significant that cushions of *M. balbisiana* and *M. acuminata* continue to enlarge throughout flower initiation (fig. 9), while the flowers of *M. velutina* are initiated approximately simultaneously, and the hands do not enlarge during this time. This fixed cushion size limits the space available for flower formation and may influence the sequence of initiation.

Flower Development

Payer (1857) provides the first description of flower development in *Musa*, based on his study of *Musa coccinea* Andrews. The current findings, while more detailed, are in general agreement with his. Payer (1857) did not study the sequence of flower initiation, nor does he mention any type of ring primordium or similar structure. The gynoecium is formed from three carpel primordia that appear opposite the outer perianth members. These primordia grow into the center of the floral cup to produce the three locules (Payer 1857). The same sequence of development is also reported by Hannah (1916) in her plates showing sectioned material of *M. sapientum* L.

White (1928) based his observations on three species and two cultivars, *M. paradisiaca* L. subsp. *sapientum* (L.) O. Ktze. cv. Gros Michel, *M. paradisiaca* L. subsp. *sapientum* (L.) O. Ktze. var. Apple, *M. cavendishii* Lamb, and *M. bakeri* Hook. His descriptions do not distinguish between these species. The major difference between his observations and those of Payer (1857), whom he does not cite, concerns the marginal primordia (ring primordia) that form early in flower development. He describes them as “distinctly abaxial,” likely due to the oblique posture of the primordia early in development (see fig. 4N), especially when viewed in sectioned material. My observations are in general agreement with these conclusions, although, as discussed below, I do not consider the ring primordium to be as distinct a structure as in other Zingiberales.

Kirchoff (1988a) discusses the structure and evolution of the floral cup and surrounding ring primordium in the ginger group of the Zingiberales. He concludes that the ancestor of this group most likely consisted of three common petal/inner androecial primordia that are united below into a floral cup. This type of semidistinct ring primordium occurs in the Zingiberaceae, as has been confirmed by a number of detailed developmental studies (Kirchoff 1997, 1998, 2000; Box and Rudall 2006; Kong et al. 2010). In the single species of Costaceae that has been studied, the ring primordium is large, symmetric, and not initially divided into common primordia (Kirchoff 1988b). In the Cannaceae and Marantaceae, the floral apex is asymmetric, and the ring is asymmetric to irregular (Kirchoff 1983b, 1988a). In the species of Strelitziaceae, Lowiaceae, and Musaceae that have been studied, both the common primordia and the ring primordium are less well developed (Kirchoff and Kunze 1995; Kirchoff 2003). However, it is difficult to draw any definitive conclusions about the overall evolution of this structure in the order as a whole because of the relatively few taxa that have been sampled and the fact that other taxa have similar developmental patterns with a central depression that enlarges to form the gynoecium (Erbar and Leins 1988, 1997; Soltis et al. 2003; Dadpour et al. 2012; Oraei et al. 2013).

Somewhat surprisingly, I found developmental differences between the male and female flowers. Although relatively minor, the differences were consistently present in my material. The differences concern the order of appearance and the order of separation of the petal/inner androecial common primordia. In male flowers the anterior side of the flower develops slightly ahead of the posterior, while in female flowers the posterior side develops slightly ahead of the anterior. After the appearance of the posterior petal, the anterior petal/inner androecial common primordia appear in male flowers, while in female flowers the posterior outer stamen form next, followed by the anterior outer stamen and the anterior petal/inner androecial common primordia. This difference in timing continues through androecial formation.

Ram et al. (1962) investigated the development of both male and female flowers in *M. sapientum* cv. Gros Michel on the basis of paraffin sections and reported no differences during early development. However, their use of sectioned material precludes the discovery of the types of subtle changes observed here. Even the sequence of initiation is sometimes reported incorrectly in their study. For instance, they describe the floral cup as originating only after stamen formation, not at approximately the same time. Similar misinterpretations occur in *Musa*

errans (Blanco) Teodoro var. *Botoan* Teodoro (probably *Musa acuminata* L. A. Colla subsp. *errans* [F. M. Blanco] R. V. Valmayor [Valmayor 2001]). In this species, Juliano and Alcalá (1933) describe the origin of flowers from the bifurcation of mamillate axillary cushions. This type of bifurcation has not been reported in any other study and is almost certainly an artifact.

Erbar and Leins (1997) point out that the uniform position and number of floral organs in the Apiaceae arise through various developmental patterns. In this case, the variation is interspecific. Although the variation is intraspecific in *M. velutina*, it also does not appear to be correlated with differences in mature floral structure. The differences between the mature female and male flowers concern the size and fertility of the gynoecium and androecium and do not appear to be influenced by subtle differences in the patterns of organ formation.

Conclusions

All shoots and inflorescences of *Musa velutina* have sinistorse phyllotaxy. This means that all renewal shoots have the same phyllotaxy as their parent, an unusual condition that may be associated with leaf-opposed buds in *Musa*. In all but two hands I found a clear relationship between the sequence of flower initiation and the phyllotactic pattern. The axillary cushion is larger cathodically, and the first flowers are initiated on its cathodic side. In two hands this pattern is reversed, with the first flowers formed on the anodic side of the cushion. One of these hands is male, and the other is female. The two hands

occur in different inflorescences and are interspersed with hands that show the normal, cathodic-first pattern of initiation.

The exact sequence of flower formation within a hand varies both within and between inflorescences, with no clear relation to any aspect of inflorescence structure. The sequence of flower initiation is not correlated with the size of the cushion, as both cathodic and anodic initiation of the first flowers were observed on both very small and large cushions. Although this irregular pattern of flower initiation is not consistent with the interpretation of the hand as a highly modified cincinnus, the preponderance of the evidence still suggests that a cincinnus is the most parsimonious interpretation of the hand. Under this interpretation, the inflorescence as a whole is a polytelic synflorescence (Troll 1964; Weberling 1982, 1989) that consists of a single main florescence.

Differences in the sequence of organ initiation in male and female flowers are present beginning shortly after the formation of the first two sepals, but they are no longer apparent by the time of gynoecial initiation and are not apparent in the mature flowers.

Acknowledgments

I thank Max Dulin, Tam Le, Allyson Prevette, Sonja Cauble, Elizabeth Shelton, and Kimberly Hamlet, who collected developmental images and helped determine the sequence of flower formation in partial fulfillment of undergraduate research courses. The layout of figure 4 was prepared by Ross Cangelosi in partial fulfillment of an independent study in the Department of Art. I thank Amy Lixl-Purcell for sponsoring his work.

Literature Cited

- Argent GCG 1976 The wild bananas of Papua New Guinea. Notes R Bot Gard Edinb 35:77–114.
- Baker JG 1893 A synopsis of the genera and species of Museae. Ann Bot 7:189–222.
- Bentham G, JD Hooker 1880 Genera plantarum. Vol 3. Williams & Norgate, London.
- Berlyn GP, J Miksche 1976 Botanical microtechnique and cytochemistry. Iowa State University Press, Ames.
- Box MS, PJ Rudall 2006 Floral structure and ontogeny in *Globba* (Zingiberaceae). Plant Syst Evol 258:107–122.
- Cheesman EE 1949 Classification of the bananas. III. Critical notes on species. j. *Musa velutina* Wendl. & Drude. Kew Bull 4:135–137.
- Claßen-Bockhoff R 2000 Inflorescences in Bruniaceae. Opera Bot Belg 12:1–310.
- Dadpour MR, S Naghiloo, G Gohari, M Aliakbari 2012 Inflorescence and floral ontogeny in *Crocus sativus* L. (Iridaceae). Flora 207:257–263.
- de Wildeman É 1908 Les plantes tropicales de grande culture, tome I. Castaigne, Brussels.
- Eichler AW 1875 Scitamineae. Pages 172–178 in *Blüthendiagramme Constructert und Erläutert. Erster Teil*. W Engelmann, Leipzig.
- Endress PK 2010 Disentangling confusions in inflorescence morphology: patterns and diversity of reproductive shoot ramification in angiosperms. J Syst Evol 48:225–239.
- Erbar C, P Leins 1988 Blütenentwicklungsgeschichtliche Studien an *Aralia* und *Hedera* (Araliaceae). Flora 180:391–406.
- 1997 Different patterns of floral development in whorled flowers, exemplified by Apiaceae and Brassicaceae. Int J Plant Sci 158: S49–S64.
- Fahn A 1953 The origin of the banana inflorescence. Kew Bull 8:299–306.
- Fahn A, P Benouaiche 1979 Ultrastructure, development and secretion in the nectary of banana flowers. Ann Bot 44:85–93.
- Fisher JB 1978 Leaf-opposed buds in *Musa*—their development and a comparison with allied monocotyledons. Am J Bot 65:784–791.
- Hannah M 1916 A comparative study of epigyny in certain monocotyledons and dicotyledons. Trans Am Microsc Soc 35:207–230.
- Hotta M 1964 The edible bananas in Tonga. Acta Phytotax Geobot 21:1–7.
- Jacob KC 1952 Madras bananas: a monograph. Superintendent of Government Press, Madras.
- Johansen DA 1940 Plant microtechnique. McGraw-Hill, New York.
- Juliano JB, PE Alcalá 1933 Floral morphology of *Musa errans* (Blanco) Teodoro var. *Botoan* Teodoro. Philipp Agric 22:91–116.
- Kirchoff BK 1983a Allometric growth of the flowers in five genera of the Marantaceae and in *Canna* (Cannaceae). Bot Gaz 144:110–118.
- 1983b Floral organogenesis in five genera of the Marantaceae and in *Canna* (Cannaceae). Am J Bot 70:508–523.
- 1986 Inflorescence structure and development in the Zingiberales—Thalia-Geniculata (Marantaceae). Can J Bot 64:859–864.
- 1988a Floral ontogeny and evolution in the ginger group of the Zingiberales. Page 56 in P Leins, SC Tucker, P Endress, eds. Aspects of floral development. J Cramer, Berlin.
- 1988b Inflorescence and flower development in *Costus scaber* (Costaceae). Can J Bot 66:339–345.
- 1992 Ovary structure and anatomy in the Heliconiaceae and Musaceae (Zingiberales). Can J Bot 70:2490–2508.

- 1997 Inflorescence and flower development in the Hedychieae (Zingiberaceae): *Hedychium*. Can J Bot 75:581–594.
- 1998 Inflorescence and flower development in the Hedychieae (Zingiberaceae): *Scaphochlamys kunstleri* (Baker) Holttum. Int J Plant Sci 159:261–274.
- 2000 Hofmeister's rule and primordium shape: constraints on organ position in *Hedychium coronarium* (Zingiberaceae). Pages 75–83 in KL Wilson, DA Morrison, eds. Monocots: systematics and evolution. CSIRO, Collingwood.
- 2003 Shape matters: Hofmeister's rule, primordium shape, and flower orientation. Int J Plant Sci 164:505–517.
- Kirchoff BK, H Kunze 1995 Inflorescence and floral development in *Orchidantha maxillarioides* (Lowiaceae). Int J Plant Sci 156:159–171.
- Kirchoff BK, LP Lagomarsino, WH Newman, ME Bartlett, CD Specht 2009 Early floral development of *Heliconia latispatha* (Heliconiaceae), a key taxon for understanding the evolution of flower development in the Zingiberales. Am J Bot 96:580–593.
- Kirchoff BK, R Rutishauser 1990 The phyllotaxy of *Costus* (Costaceae). Bot Gaz 151:88–105.
- Kong JJ, YM Xia, QJ Li 2010 Inflorescence and flower development in the Hedychieae (Zingiberaceae): *Hedychium coccineum* Smith. Protoplasma 247:83–90.
- Kunze H 1985 Die Infloreszenzen der Marantaceen und ihr Zusammenhang mit dem Typus der Zingiberales-Synfloreszenz. Beitr Biol Pflanz 60:93–140.
- 1986 Infloreszenz- und Blütenmorphologie von *Orchidantha maxillarioides* (Ridl.) K. Schum. (Lowiaceae). Beitr Biol Pflanz 61:221–234.
- 1989 Probleme der Infloreszenztypologie von W. Troll. Plant Syst Evol 163:187–199.
- Loesbecke HW von 1950 Bananas. Interscience, New York.
- Maheshwari JK 1963 Abnormalities in the inflorescence of *Musa paradisiaca* Linn. Sci Cult 29:144–145.
- Nur N 1976 Studies on pollination in Musaceae. Ann Bot 40:167–177.
- Oraei M, G Gohari, Z Esmailou, S Naghiloo 2013 Comparative ontogeny of perfect and pistillate florets in *Senecio vernalis* (Asteraceae). Flora 208:285–292.
- Payer JB 1857 Ordre des Musacees. Pages 670–673, planche 143 in Traite d'organogenie comparee de la fleur. V Masson, Paris.
- Postek MT, SC Tucker 1976 A new short chemical dehydration method for light microscopy preparations of plant material. Can J Bot 54:872–875.
- Quisumbing EA 1919 Studies of Philippine bananas. Philipp Agric Rev 12:9–73.
- Ram HYM, M Ram, FC Steward 1962 Growth and development of the banana plant: 3. A. The origin of the inflorescence and the development of the flowers. B. The structure and development of the fruit. Ann Bot 26:657–673.
- Schumann K 1900 Musaceae. Pages 1–45 in A Engler, ed. Das Pflanzenreich. Vol IV, pt 45. W Engelmann, Leipzig.
- Simmonds NW 1966 Bananas. Longmans, London.
- Simmonds NW, K Shephard 1955 The taxonomy and origins of cultivated bananas. J Linn Soc Lond Bot 55:302–312.
- Singer SR 2006 Inflorescence architecture—moving beyond description to development, genes and evolution. Pages 99–113 in C Ainsworth, ed. Flowering and its manipulation. Blackwell, Oxford.
- Skutch AF 1927 Anatomy of leaf of banana, *Musa sapientum* L. var. Hort. Gros Michel. Bot Gaz 84:337–391.
- Smets EF, EM Cresens 1988 Types of floral nectaries and the concepts “character” and “character-state”—a reconsideration. Acta Bot Neerl 37:121–128.
- Soltis DE, M Fishbein, RK Kuzoff 2003 Reevaluating the evolution of epigyny: data from phylogenetics and floral ontogeny. Int J Plant Sci 164:S251–S264.
- Stützel T, M Trovó 2013 Inflorescences in Eriocaulaceae: taxonomic relevance and practical implications. Ann Bot 112:1505–1522.
- Tennakone K, RKD Dayatilaka, S Ariyaratne 1982 Right-left symmetry in phyllotaxy and imbrication of flowers of *Hibiscus furcatus* L. Ann Bot 50:397–400.
- Thompson JM 1933 Studies in advancing sterility. Pt VI. The theory of Scitaminean flowering. Publ Hartley Bot Lab 11:1–111.
- Troll W 1964 Die Infloreszenzen: Typologie und Stellung im Aufbau des Vegetationskörpers. G Fischer, Jena.
- Valmayor RV 2001 Classification and characterization of *Musa exotica*, *M. alinsanaya* and *M. acuminata* ssp. *errans*. Philipp Agric Sci 84:325–331.
- Weberling F 1982 Current problems of modern inflorescence morphology. Aust Syst Bot Soc Newsl 30:5–21.
- 1989 Morphology of flowers and inflorescences. Cambridge University Press, Cambridge.
- Whipple CJ, DH Hall, S DeBlasio, F Taguchi-Shiobara, RJ Schmidt, DP Jackson 2010 A conserved mechanism of bract suppression in the grass family. Plant Cell 22:565–578.
- White PR 1928 Studies on the banana: an investigation of the floral morphology and cytology of certain types of the genus *Musa* L. Z Zellforsch Mikrosk Anat 7:673–733.