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HIERARCHICAL DEVELOPMENTAL MORPHOLOGY: THE CASE OF THE INFLORESCENCE OF *PHILODENDRON ORNATUM* (ARACEAE)

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This study deals specifically with floral organogenesis and the development of the inflorescence of *Philodendron ornatum*. The development of the inflorescence of *P. ornatum* can be divided into two morphogenetic phases: (i) before and (ii) after the initiation of the floral organs. Before the initiation of the floral organs, the ratio between the width and the length of the inflorescence is greater than after their initiation. The first phase corresponds to the establishment of the phyllotactic pattern, and the second phase corresponds to the differentiation of floral organs. Pistillate flowers are initiated on the lower portion of the inflorescence, and the staminate flowers are initiated on the distal portion. An intermediate zone consisting of sterile male flowers and atypical bisexual flowers (ABFs) with carpels and staminodes inserted on the same whorl is also present. The portion of the ABFs facing the male zone forms staminodes, and the portion facing the female zone develops an incomplete gynoecium with a few carpels. This phenomenon raises the issue of relationships between hierarchical levels and their mutual influence on the developmental morphology of ABFs. In this article, this question is addressed in the context of the basic triadic system developed by Salthe.

Keywords: positional information, gradient, flower, homeosis, developmental constraint.

Introduction

The structure of the inflorescence of *Philodendron* constitutes an interesting morphological model to analyze the relationship between local and global processes acting during the morphogenesis of floral organs. The unique morphology of the inflorescence allows us to study a poorly known phenomenon in angiospermous flowers: the homeotic transformations involving carpels and staminodes on the same floral whorl. The phenomenon of homeosis, defined in plants as the complete or partial replacement of one organ by a different organ (Lehman and Sattler 1992), is believed to play an important role in the ontogeny and phylogeny of reproductive organs (Sattler 1994; Frohlich and Meyerowitz 1997; Mouradov et al. 1998; Purugganan 1998; Winter et al. 1999; Ambrose et al. 2000; Becker et al. 2000; Kramer and Irish 2000; Theißen 2001; Lee et al. 2003; Nagasawa et al. 2003; Ronse De Craene 2003; Yamaguchi et al. 2004). Although the concept of homeosis is widely used in molecular biology, it was first defined from a morphological perspective at the end of the nineteenth century without specific reference to homeotic genes (for a review of this concept in developmental plant morphology, see Sattler 1988; Vergara-Silva 2003).

In *Philodendron*, as in other members of the Aroideae sensu Mayo et al. (1997), the female flowers are located in the lower portion of the inflorescence and the male flowers in the upper portion. These two zones are separated by a zone of sterile male flowers. Between the sterile male zone and the female zone, there is a row of atypical bisexual flowers (ABFs; Engler and Krause 1912, p. 16; Mayo 1986, fig. 393). These ABFs consist of carpels and staminodes that are initiated on the same whorl (Barabé et al. 2004). It is important to note that the ABFs are not true functional bisexual flowers. The pistillate portion is fertile, whereas the staminate portion consists of staminodes. Even though from a functional reproductive point of view these flowers remain unisexual, they can be considered as bisexual from a developmental point of view because pistillate and staminate primordia are initiated on the same flower (Barabé et al. 2004).

Our previous studies allowed us to analyze the range of homeotic transformations in the genus *Philodendron* and to deduce common patterns of development in ABFs belonging to different species (Boubes and Barabé 1996; Barabé et al. 2000, 2002, 2004). The ABFs arise through the homeotic replacement of carpels with staminodes. However, is this pattern of development common to all species of *Philodendron*? The great number of species belonging to the genus *Philodendron* (700) does not allow us to claim that the developmental morphology is similar for all species. For example, Mayo (1986, 1989) showed that there is a great amount of variability in anatomical characters among inflorescences in *Philodendron*. Therefore, although the overall developmental morphology of the inflorescence of *Philodendron* is consistent, one may expect to find some variability and alternate modes of floral development in a genus consisting of several hundred species.

In species of *Philodendron* previously studied, it was shown that the number of appendages present in sterile and female flowers acts as a constraint on the number of appendages in ABFs (Barabé et al. 2004). How do those border conditions

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established by the stable morphological zones of the female and sterile male flowers influence the morphology of ABFs found in the transition zone?

This question raises the issue of relationships between hierarchical levels and their mutual influence on the developmental morphology of ABFs. It can be addressed in the context of the basic triadic system developed by Salthe (1985), which represents the minimal cluster of levels required to describe fundamental interactive relationships: "the dynamics of upper and lower levels produce output that can influence the dynamic of the focal level" (Salthe 1985, p. 75). The lower-level constraints are defined as initiating conditions that autonomously give rise to focal-level dynamics. Higher-level constraints refer to boundary conditions, and they regulate the results of focal-level dynamics (Salthe 1985, p. 69). We will adapt the concept of the basic triadic system developed for levels of organization in biology to the more narrowly defined field of developmental biology by using the organogenesis of the inflorescence of *Philodendron ornatum* as a case study. In the domain of developmental morphology, one needs to identify levels that interact with the focal level. Therefore, in the case of atypical flowers, what are the initiating conditions and boundary conditions?

The development of the inflorescence of *Philodendron* also highlights the problem of recognition of morphogenetic phases during the ontogenesis of aroid inflorescences. Two different morphogenetic phases were identified in the inflorescence of *Symplocarpus*, a genus with bisexual flowers (Barabé 1995). Does the same phenomenon occur in genera with unisexual flowers, in particular *Philodendron*? This point, which has not been discussed in our previous studies of *Philodendron*, is addressed in the context of the developmental morphology of *P. ornatum*.

In the general context of the development of the inflorescence and flowers of the Araceae, the specific goals of this study using *P. ornatum* are (1) to show that the nature of flowers surrounding ABFs canalize the morphological potentialities of ABFs, (2) to characterize the morphogenetic periods in the development of the inflorescence, and (3) to integrate the developmental morphology of the inflorescence of *Philodendron* within the general framework of Salthe's (1985) basic triadic system.

Material and Methods

Samples. *Phildendron ornatum* Schott belongs to the subgenus *Philodendron* (Croat 1997). Specimens used for this study were collected in French Guiana (voucher specimen deposited at MT: Barabé 33). Inflorescences at various stages of development were dissected under a stereo microscope to expose the spadix, fixed in formalin–acetic acid–alcohol (1 : 1 : 9 by volume), and later transferred to 70% ethanol for storage.

Microscopy. Thirty-six inflorescences of *P. ornatum* were dehydrated in a graded ethanol series to absolute ethanol. They were then dried in a LADD model 28000 critical-point dryer using CO_2 as a transitional fluid, mounted on metal stubs, and grounded with conductive silver paint. Specimens were sputter-coated with gold/palladium to ~30 nm using a Denton Vacuum Desk II sputter-coater and viewed with a Cambridge S604 SEM with digital imaging capabilities (SEMICAPS).

Results

Morphology of the mature flowers. The length of the mature spadices of *Philodendron ornatum* ranges from 12 to 15 cm (fig. 1.1). Neither staminate nor pistillate flowers have a perianth. The staminate flowers occupy the upper portion of the inflorescence and make up ~50% of the total length of the inflorescence (figs. 1.1, 1.2), whereas the female flowers are located on the lower portion and occupy ~40% of the total length (figs. 1.1, 1.4). Modified stomata in the sense of Vogel (1977) are found on the surface of the apical portion of the stamens (fig. 1.2) and staminodes on male and sterile male flowers, respectively. The epidermis of stamens and staminodes consists of pegged and ridged cells, giving the surface a rough appearance (fig. 1.2). Mature female flowers have a prominent stigmatic surface (fig. 1.4).

Between the male and the female portions of the inflorescence, there is an intermediate zone (~10% of the total length of the spadix) consisting of sterile male flowers and ABFs (figs. 1.1, 1.3). ABFs are inserted at the boundary between the sterile male zone and the female zone. They generally consist of carpels and staminodes inserted on the same whorl. On mature flowers, it is difficult to determine whether the staminode and carpels are inserted on the same whorl (fig. 1.3). However, during early stages of development, this phenomenon is visible (fig. 5.22). The portion of the bisexual flower facing the male zone consists of staminodes, and the portion facing the female zone consists of an incomplete gynoecium (fig. 5.22).

Inflorescence and floral development. The inflorescence of *P. ornatum* is conical to subcylindrical in shape during early stages of development (figs. 2.5, 2.6). The different flower types are initiated acropetally along the axis of the inflorescence (fig. 2.6). Pistillate flowers develop near the basal portion of the inflorescence, and staminate flowers develop on the terminal portion. At this stage of development, the primordia of the intermediate zone are not as clearly outlined as those of the other two zones (fig. 2.6). The floral primordia of the female zone cover approximately one-third of the inflorescence at this very early stage (fig. 2.6). Once all the floral primordia have been initiated, the different types of flower are all approximately the same size and form a regular lattice on the surface of the inflorescence (fig. 2.7). At this point, there is no discontinuity in the phyllotactic pattern of the flowers across the different zones of the inflorescence. Pistillate flowers, sterile male flowers, ABFs, and staminate flowers are inserted on the same parastichies (fig. 2.7, long arrows). However, when the floral organs expand, the flowers of the male and sterile zone lose their regular arrangement, and the recognition of symmetrical patterns becomes less evident. The flowers of the sterile zone also appear to be more interspersed (fig. 2.8).

Stamen primordia are initiated simultaneously on the periphery of more or less circular floral primordia (fig. 3.9). There is an average of 4.5 (±0.5 SD) stamens (range 4–5) per flower (figs. 3.10, 3.11). During later stages of development, the floral primordia come in contact with each other, and the size of the stamens increases to the point that they will eventually occupy all the available space between flowers (fig. 3.11).

On the apical portion of the inflorescence, the male flowers lose their typical symmetrical organization, and the boundary between flowers becomes fuzzy (figs. 3.12, 3.13). In this par-

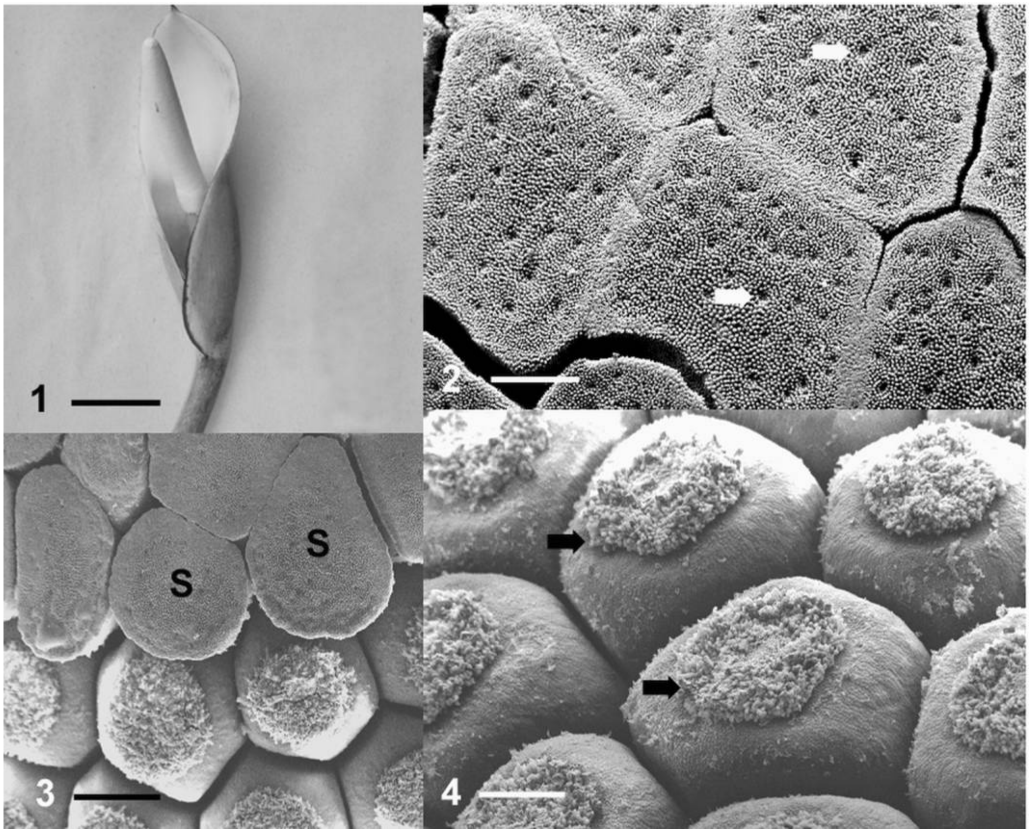

Fig. 1 Mature inflorescence and flowers of *Philodendron ornatum*. Fig. 1.1, General view of mature inflorescence partially enclosed by a spathe. Scale bar = 3 cm. Fig. 1.2, Top view of mature stamens. Arrows indicate stomatal pores. Scale bar = 300 μm. Fig. 1.3, Top view of intermediate zone on mature inflorescence. *S* = staminodes. Scale bar = 750 μm. Fig. 1.4, Top view of mature female flowers. Arrows indicate stigmatic surface. Scale bar = 300 μm.

ticular zone, individual flowers are unrecognizable. Some flowers belonging to the same parastichies or different parastichies amalgamate to form irregular sets of stamens that appear to develop more or less normally.

During early stages of development, female floral primordia have a hemispherical shape (fig. 4.14). The carpel primordia are initiated on the periphery of the floral primordia. During later stages of development, the entire ovary wall of typical flowers is formed by the concrescence of the walls of adjacent carpels (fig. 4.15). There is an average number of 4.6 (±0.8 SD) carpels (range 3–6) per flower. The small holes that are visible on the periphery of floral primordia during later stages of development represent the upper portion of the stylar canals (figs. 4.16, 4.17). Even though the carpels are concrescent, individual stylar canals are found in the mature ovary up to a level directly below the stigma (fig. 4.16, centrally located holes). A stigmatic surface with papillae develops when the ovary is nearly mature (fig. 4.17).

The sterile male flowers and ABFs form a transition zone between typical male and female flowers. During early stages of development, the primordia of sterile male flowers and ABFs have approximately the same shape as the primordia of staminate flowers (fig. 4.18). However, during later stages of development, they appear more globular due to the absence of distinctive thecae (fig. 4.19).

The staminodes of sterile male flowers are initiated on the periphery of the floral primordium (fig. 4.18). Although the floral organs of the sterile male flowers and ABFs are initiated later than those of the pistillate flowers, their relative rate of growth is faster than that of the other types of flowers. Consequently, sterile male flowers and ABFs are larger than female flowers at maturity mainly due to the expansion of the staminodes (figs. 4.20, 4.21).

ABFs form a more or less continuous single row on the inflorescence and are located directly below the sterile male flowers (figs. 4.19, 4.20). The floral organs are initiated on the periphery of a discoid floral primordium, and their nature, number, and form vary considerably. There is an average of 4.2 (±0.6 SD) floral appendixes (range 3–5) per flower. The types of floral organs produced on bisexual flowers depend on their proximity to the other floral zones. The female organs of ABFs tend to be initiated on the side of the flower adjacent to the female zone, and the male organs are initiated on the side of the flower closer to the sterile male floral zone (fig. 4.19; figs. 5.22, 5.23). In our samples, the number of carpels in ABFs ranged from one (fig. 5.25, flower *B*) to four (fig. 5.22) and the number of staminodes from one to three (fig. 5.25, flower *A*). Even though floral appendages are easily identifiable with specific flowers during early stages of development, it becomes difficult to determine which staminodes belong to

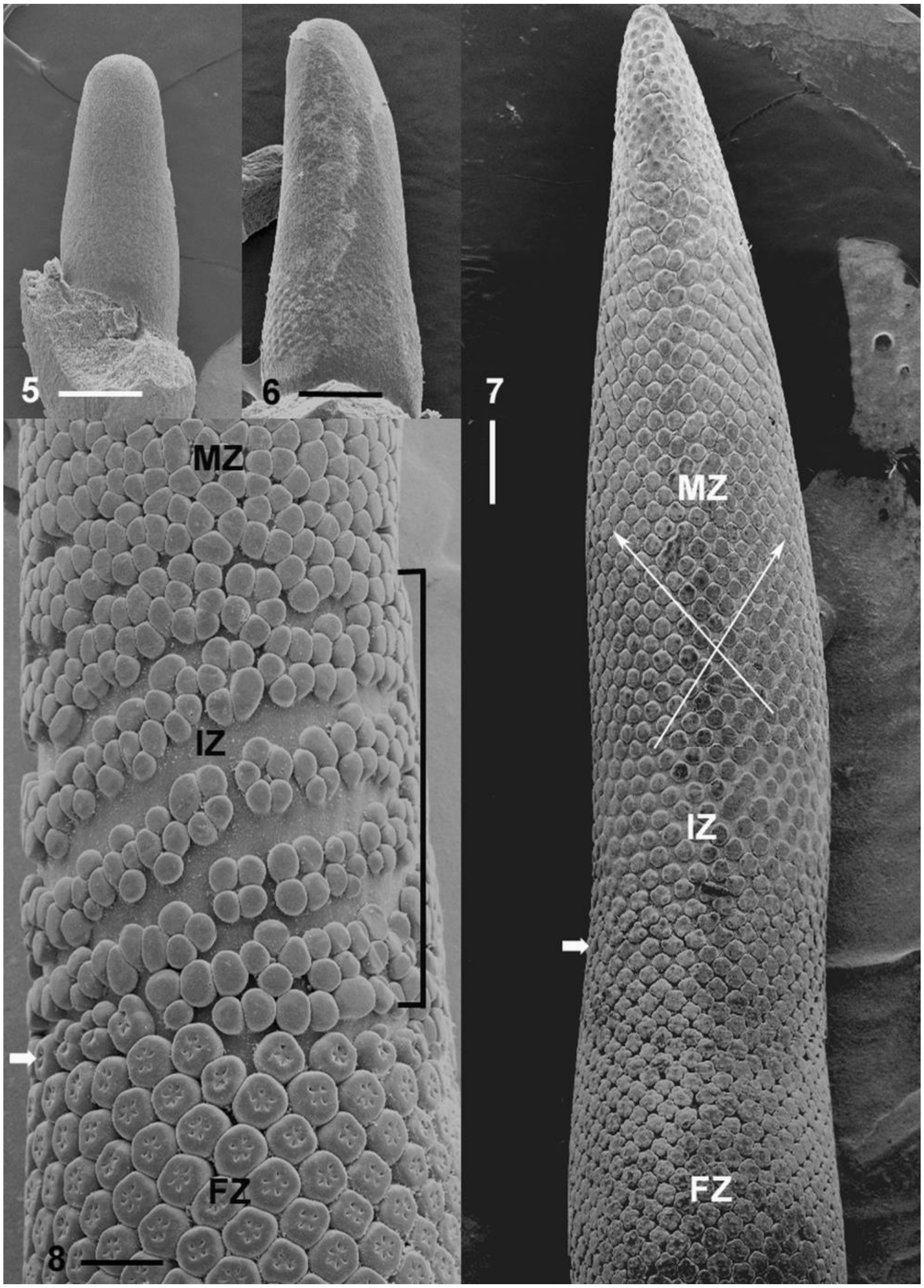

Fig. 2 Early stages of development of inflorescences of *Philodendron ornatum*. Scale bars = 300 μm. Fig. 2.5, Side view of young inflorescence before the initiation of flowers. Fig. 2.6, Side view of young inflorescence showing the initiation of floral primordia in a latticelike pattern. Fig. 2.7, Composite view of inflorescence after all floral primordia have been initiated. Short arrow indicates the location of bisexual flowers; long arrows indicate parastichies. Fig. 2.8, Side view of central portion of a young inflorescence showing a visible transition from female flowers to male flowers. Arrow indicates the location of bisexual flowers. *MZ* = male zone; *FZ* = female zone; *IZ* = intermediate zone.

which flowers during later stages of development (figs. 4.20, 4.21).

The staminodes and carpels on ABFs are inserted on a single whorl in a ring formation (figs. 5.22–5.24). In many ABFs, there is an incomplete separation between staminodes and carpels. Figure 5.24 shows ABFs where staminodes are united to the gynoecium by a portion of the ovary wall (flowers *B*, *C*). However, it is difficult to determine whether the aberrant structures correspond to an open carpel or a staminode. For example, flower *C* in figure 5.24 consists of two closed carpels on the lower portion of the flower and two aberrant structures corresponding to open carpels on the upper portion. From a

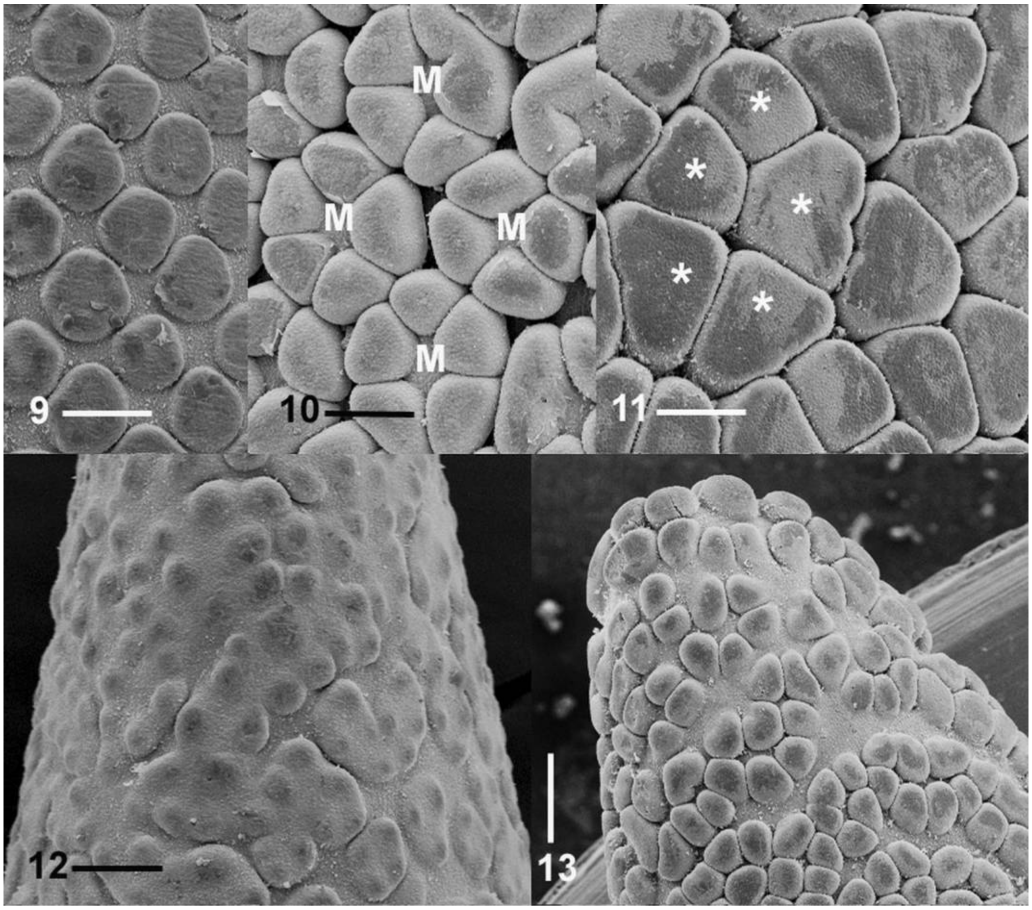

Fig. 3 Development of male flowers of *Philodendron ornatum*. Fig. 3.9, Early stage of initiation of male flowers. Scale bar = 75 μm. Fig. 3.10, Male flowers (*M*) with four or five stamen primordia. Scale bar = 75 μm. Fig. 3.11, Male flower with five nearly mature stamens (asterisks). Scale bar = 150 μm. Fig. 3.12, Tip of inflorescence showing irregular aggregations of male flowers. Scale bar = 75 μm. Fig. 3.13, Tip of inflorescence showing disorganized pattern of flowers in comparison with latticelike pattern at lower level. Scale bar = 75 μm.

morphological point of view, however, these aberrant structures could also be interpreted as staminodial primordia that are incompletely separated from adjacent carpels or as intermediate structures between carpels and staminodes. These morphological observations provide strong evidence that staminodes and carpels are inserted on the same whorl in ABFs.

Discussion

Morphogenetic Phases

The development of the inflorescence of *Philodendron ornatum* can be divided into two morphogenetic phases: (i) before (figs. 2.5, 2.6) and (ii) after (figs. 2.7, 2.8) the initiation of the floral organs. Before the initiation of floral organs, the ratio between the width and the length of the inflorescence is higher than after their initiation. This is in accordance with what has been observed in other species of *Philodendron* (Barabé et al. 2000) and in genera with bisexual flowers, such as *Symplocarpus* (Barabé 1995) and *Anthurium* (Barabé and Lacroix 2008).

The first phase corresponds to the establishment of the phyllotactic pattern and the second phase to the differentiation of floral organs (fig. 6). In *Philodendron*, the mechanisms responsible for the emergence of floral primordia at a given position on the inflorescence are believed to be different from those that regulate the nature of the floral organs that will be formed (Barabé et al. 2000). Given the specific developmental morphology characterizing each phase, we can further hypothesize that the biochemical and molecular processes involved in these two distinct phases are not the same.

In *P. ornatum*, the initiation and development of the floral primordia occur when the inflorescence has grown to ~3%–4% of its full length. At this stage, the phyllotactic pattern is already in place, and the initial phyllotactic organization has been neither obscured nor transformed by local morphogenetic processes. The more or less simultaneous appearance of floral primordia and their organization on the surface of the spadix is similar to the biophysical model involving the formation of bumps on a constrained sheet (Green et al. 1998). The upper portion of the inflorescence contains a zone where primordia appear in clusters instead of as clearly identifiable flowers (figs. 3.12, 3.13). This pattern is comparable to the phyllotactic organization obtained in simulations of physical buckling on a heating plate (figs. 3, 5 in Green et al. 1998). The size

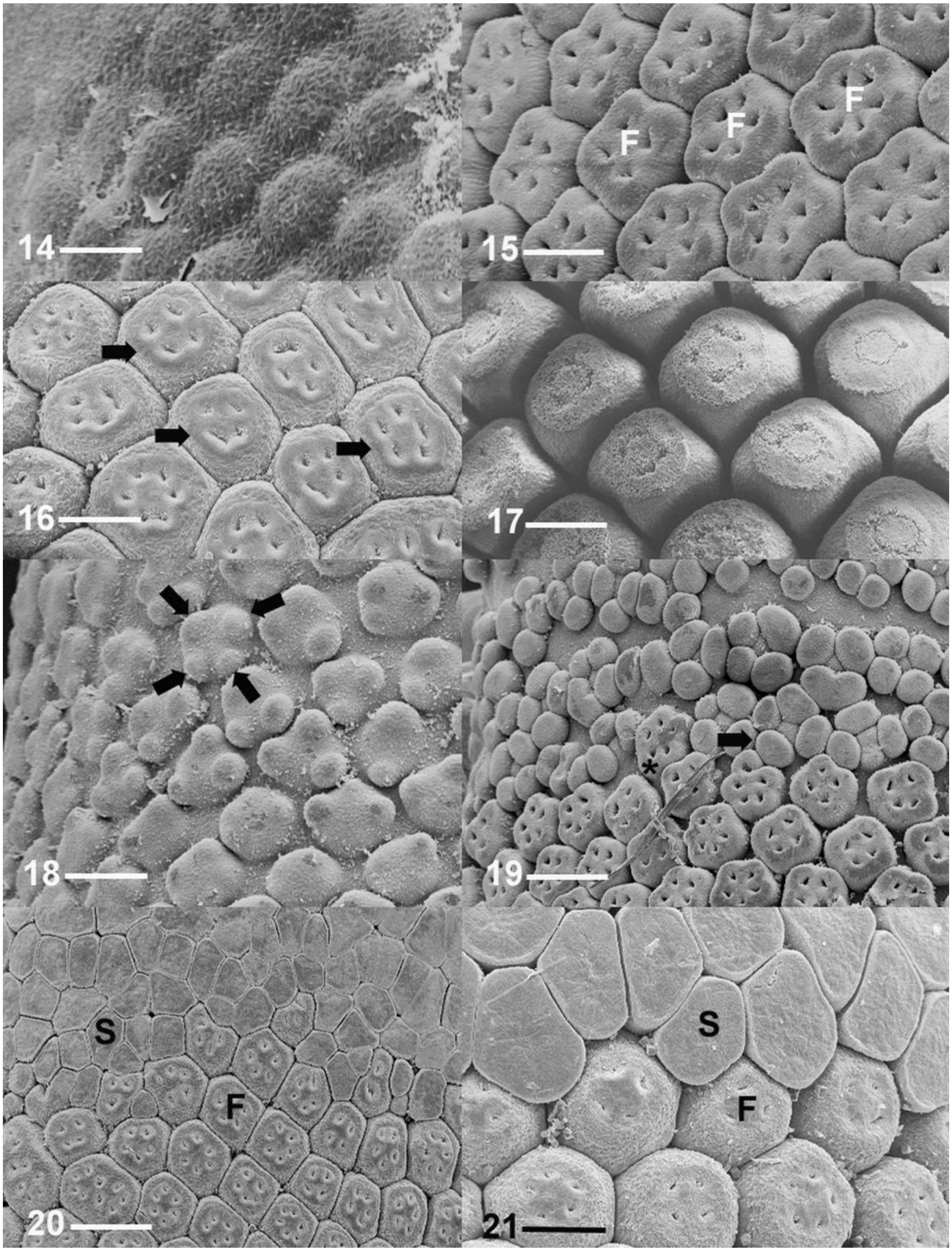

Fig. 4 Development of female flowers of *Philodendron ornatum*. Fig. 4.14, Early stage of initiation of female flowers. Scale bar = 300 μm. Fig. 4.15, Young female flowers (*F*) with four, five, or six carpels. Scale bar = 75 μm. Fig. 4.16, Early stage of development of the stigmatic surface (arrows). Scale bar = 150 μm. Fig. 4.17, Nearly mature female flowers with visible stigmatic surfaces. Scale bar = 300 μm. Fig. 4.18, Early stage of initiation of floral primordia in the intermediate zone of the inflorescence. Arrows indicate staminodes. Scale bar = 75 μm. Fig. 4.19, Intermediate zone of flowers with distinguishable staminodes (arrow) and carpels (asterisk). Scale bar = 150 μm. Fig. 4.20, Intermediate zone at a later stage of development than fig. 4.19, showing the tight packing of staminodes (*S*) and female flowers (*F*). Scale bar = 150 μm. Fig. 4.21, Nearly mature flowers in the intermediate zone where staminodes (*S*) can no longer be associated with a specific flower (*F*). Scale bar = 150 μm.

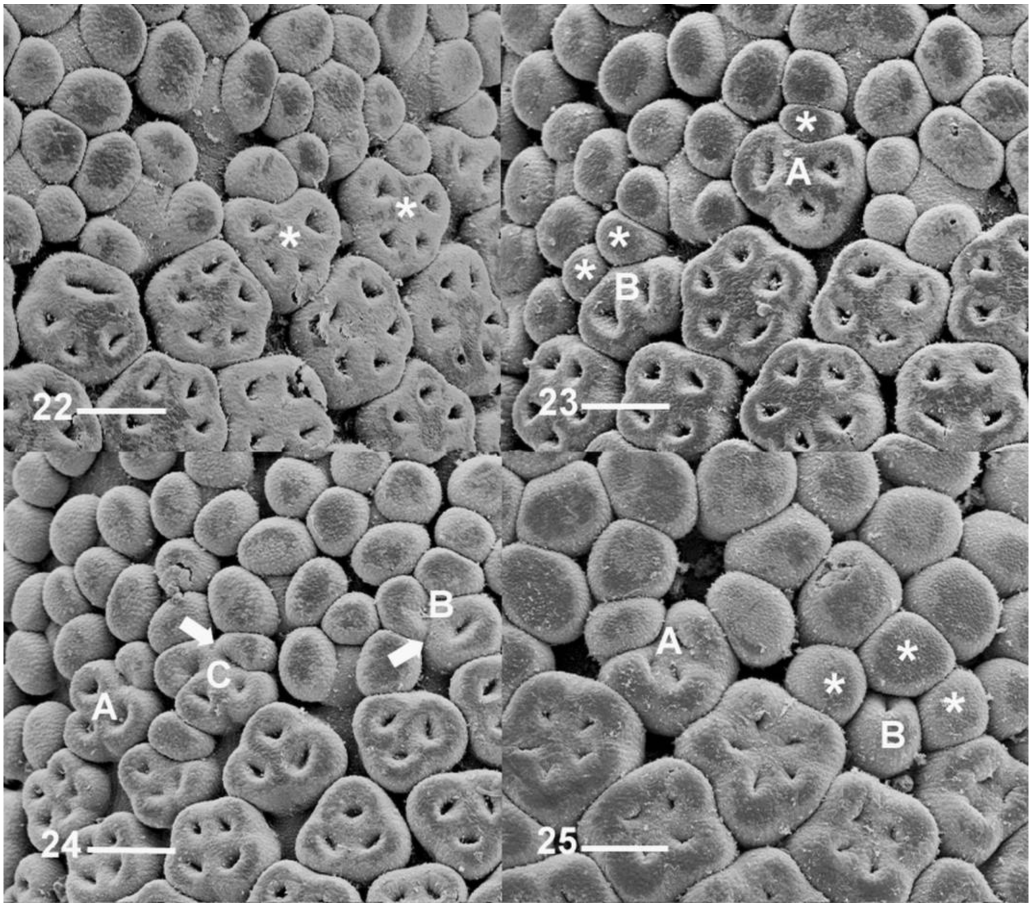

Fig. 5 Morphological diversity of bisexual flowers in the intermediate zone of the inflorescence of *Philodendron ornatum*. Scale bars = 75 μm. Fig. 5.22, Examples of bisexual flowers (asterisks) with four carpels and one staminode. Fig. 5.23, Bisexual flowers. *A*, Three carpels and one staminode (asterisk). *B*, Two carpels and two staminodes (asterisks). Fig. 5.24, Examples of bisexual flowers. *A*, Three carpels and one staminode. *B*, One carpel and two staminodes. *C*, Two open carpels and two closed carpels. Arrows point to bridge of tissue between staminode and gynoecium. Fig. 5.25, Bisexual flowers. *A*, Three carpels and one staminode. *B*, One carpel surrounded by three staminodes (asterisks).

and shape of floral primordia, which are genetically determined, may constitute the initial conditions of the system, whereas the propagation of the phyllotactic pattern on the surface of the inflorescence depends on the physical variables involved in the dynamics of the system.

The second phase of the development of the inflorescence is characterized by the formation and maturation of different types of flowers (fig. 6). The pattern of floral development on the inflorescence of *P. ornatum* is comparable to that of previously described species of *Philodendron* (Barabé et al. 2004), particularly *Philodendron fragrantissimum* (Barabé et al. 2000) and *Philodendron melinonii* (Barabé and Lacroix 2000).

The development of ABFs in *P. ornatum* also follows what has been observed in other species: there is a homeotic transformation of carpels into staminodes on the same whorl (Barabé et al. 2004). The existence of sterile stamens (staminodes) and carpels on the same whorl on single flowers of *Philodendron* indicates that the identity of organs that will be formed is independent of the floral whorl on which they arise. This is in accordance with the idea (Coen and Meyerowitz 1991) that floral organ identity is whorl independent and does not depend of the sex of its neighbors. These observations concur with the boundary analysis used by Bossinger and Smyth (1996) to study the mode of initiation of floral organs in *Arabidopsis*. In the case of *P. ornatum*, as in other species of *Philodendron*, the nature of the floral organs that will be formed depends on their position along the axis of the inflorescence (fig. 6).

The average total number of appendages on ABFs may in some cases exceed that of appendages on sterile male flowers, but it is never greater than the number of carpels on female flowers. Additionally, the number of staminodes on ABFs is always lower than the number of staminodes on sterile male flowers. In ABFs, it appears that the potential to form carpels is greater than that to form staminodes. This seems to indicate that the number of appendages on ABFs is influenced to a greater extent by female flowers than by male sterile flowers. The number of appendages in female flowers may consequently impose a constraint on the maximum total number of appendages (carpels or staminodes) that can develop on ABFs. In previous studies, it was concluded that ABFs represent modified female flowers (Barabé and Lacroix 2001; Barabé et al. 2004). This could explain why the number of appendages on ABFs never exceeds that of female flowers. The number of appendages on ABFs would therefore depend on the "female

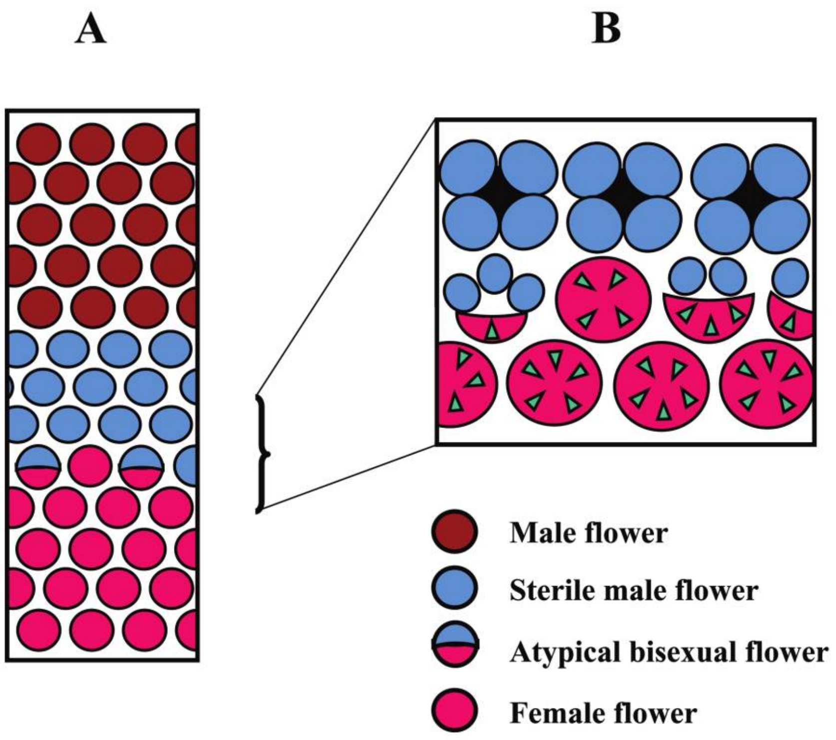

Fig. 6 Schematic representation of the two morphogenetic phases in the development of the inflorescence of *Philodendron ornatum*. *A*, Before the initiation of floral organs. *B*, After initiation of floral organs.

nature" of the abnormal flowers while the type of appendages (carpels or staminodes) that form on the floral primordia would depend on their position on the inflorescence.

In the general context of the basic triadic system (Salthe 1985), the relationships between hierarchical levels in the developmental morphology of ABFs of *P. ornatum* can be interpreted in terms of lower- and upper-level constraints. The central question is how do the border conditions imposed by the stable morphological female and sterile male zones influence the morphology of ABFs in this transition zone?

The lower hierarchical level representing the initiation conditions would involve the biochemical (diffusing substances) or genetical processes governing the nature of floral organ parts that will be formed. Since the ABFs are modified female flowers (Barabé and Lacroix 2001), this could indicate that the signal governing the differentiation of flowers moves from the base to the top of the inflorescence. The upper hierarchical level, which refers to the boundary conditions that canalize the maximum number of floral organs in ABF, would determine the maximum number of carpels developing in female flowers. The characteristics of female flowers therefore set the boundary conditions for the types of flowers that can develop in the zone of ABFs.

Morphogenetic Gradient

In *P. ornatum*, the pathway of floral differentiation (male or female) could depend on the concentration of hormones acting more or less simultaneously at a particular point along the inflorescence (Barabé et al. 2000). In dioecious plants, we know that it is possible to induce the formation of female flowers by using hormonal treatment on plants that normally produce male flowers (Dellaporta and Calderon-Urrea 1993; Greyson 1994; Juarez and Banks 1998). For example, the concentration of gibberellic acid (GA) has an effect on the regulation of the development of staminate flowers of maize (Bortiri and Hake 2007). Verglat and Sawhney (1997) expressed the idea that there could be a cytokinin gradient suppressing the expression of certain genes in the peduncle of the inflorescence of *Arabidopsis* (FMI genes). It is plausible to think that cytokinin and GA, two hormones that are differentially expressed in stamen and ovary development in maize (Bommineni and Greyson 1990*a*, 1990*b*; Greyson et al. 1994), could also be involved in the determination of the sex of flowers along the inflorescence of *Philodendron*.

The main challenge is to make a link between the hypothesis of a morphogenetic gradient and the morphological diversity observed in ABFs. Because the flowers that develop in the zone of ABFs may be experiencing the influence of both female flowers and sterile male flowers, we can hypothesize that the row of ABFs is located at the threshold of transition between two or more substances that cause a fluctuation in the number and nature of appendages.

The presence of ABFs may be due to a misinterpretation of the message (chemical or genetic) that induces the development of a particular type of organ on a floral primordium (fig. 6). However, the presence of staminodes and carpels on the same whorl indicates that the nature of the organ that will be formed depends on its position in the zone of transition instead of its position on individual flowers.

Although the mode of transmission of the positional information remains unknown, the cells involved in the formation of floral organs could interpret the message received differently depending on their interactions with neighboring cells. The model of Furusawa and Kaneko (2003) has characteristics that could potentially be useful to interpret the developmental morphology of *P. ornatum* in terms of positional information. These authors have developed a theoretical model to explain how positional information based on chemical concentrations can lead to the differentiation of cells. The differentiation of cells is spatially regulated by the concentration of chemicals in the medium, while the concentrations are locally influenced by intracellular interactions. This model (see fig. 6*a* in Furasawa and Kaneko 2003), based on the diffusion of chemical substances, shows that the boundary between two types of cells is not sharp. This is due to the fact that cells interpret positional information differently depending on their status and their interactions with surrounding cells. In this type of model, the concentration of a chemical substance can be viewed as corresponding to the intensity of activity of a particular set of genes. Therefore, the development of each type of flower in *P. ornatum* is probably dependent on patterns of gene expression that are linked to the concentration of particular hormones. Ultimately, there is no incompatibility between this model and developmental genetics.

Conclusion

In *Philodendron ornatum*, the development of floral primordia on the surface of the inflorescence represents a global phenomenon, and sex determination represents a local phenomenon. Given that the presence of a morphogenetic gradient is now well documented in the inflorescence of *Philodendron*, we still need to determine whether it is associated with a physiological or a molecular gradient and how positional information is communicated to cells involved in the formation of floral primordia.

Acknowledgments

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Literature Cited

Ambrose BA, DR Lerner, P Ciceri, CM Padilla, MF Yanofsky, RJ Schmidt 2000 Molecular and genetic analyses of the *Silky1* gene reveal conservation in floral organ specification between eudicots and monocots. Mol Cell 5:569–579.

Barabé D 1995 Open and closed systems in phyllotaxis. J Biol Syst 3: 917–927.

Barabé D, C Lacroix 2000 Homeosis in the flower of the Araceae: the case of *Philodendron melinonii* (Araceae). Ann Bot 86:479–491.

——— 2001 Aspects of floral development in *Philodendron grandifolium* and *P. megalophyllum* (Araceae). Int J Plant Sci 162: 47–57.

——— 2008 Developmental morphology of the flower of *Anthurium jenmanii*: a new element in our understanding of basal Araceae. Botany 86:45–52.

Barabé D, C Lacroix, B Jeune 2000 Development of the inflorescence and flower of *Philodendron fragrantissimum* (Araceae): a qualitative and quantitative study. Can J Bot 78:557–576.

——— 2002 Developmental morphology of normal and atypical flowers of *Philodendron insigne* (Araceae): a new case of homeosis. Can J Bot 80:1160–1172.

——— 2004 The game of numbers in homeotic flowers of *Philodendron* (Araceae). Can J Bot 82:1459–1467.

Becker A, K-U Winter, B Meyer, H Saedler, G Theißen 2000 MADS-box gene diversity in seed plants 300 million years ago. Mol Biol Evol 17:1425–1434.

Bommineni VR, RI Greyson 1990*a* Effects of gibberellic acid and indole-3-acetic acid on growth and differentiation of cultured ear inflorescences of maize (*Zea mays* L.). Plant Sci 68:239–247.

——— 1990*b* Regulation of flower development in cultured ears of maize (*Zea mays* L.). Sex Plant Reprod 3:109–115.

Bortiri E, S Hake 2007 Flowering and determinacy in maize. J Exp Bot 58:909–916.

Bossinger G, DR Smyth 1996 Initiation patterns of flower and floral organ development in *Arabidopsis thaliana*. Development 122:1093–1102.

Boubes C, D Barabé 1996 Développement des inflorescences et des fleurs du *Philodendron acutatum* (Araceae). Can J Bot 74:909–918.

Coen ES, EM Meyerowitz 1991 The war of the whorls: genetic interactions controlling flower development. Nature 353:31–37.

Croat TB 1997 A revision of *Philodendron* subgenus *Philodendron* (Araceae) for Mexico and Central America. Ann Mo Bot Gard 84: 311–704.

Dellaporta SL, A Calderon-Urrea 1993 Sex determination in flowering plants. Plant Cell 5:1241–1251.

Engler A, K Krause 1912 *Araceae-Philodendroideae-Philodendreae*. Pages 1–134 *in* A Engler, ed. Das Pflanzenreich. Regni vegetabilis conspectus. IV. 23Da. Heft 55. Engelmann, Leipzig.

Frohlich MW, EM Meyerowitz 1997 The search for flower homeotic gene homologs in basal angiosperms and Gnetales: a potential new source of data on the evolutionary origin of flowers. Int J Plant Sci 158(suppl):S131–S142.

Furusawa C, K Kaneko 2003 Robust development as a consequence of generated positional information. J Theor Biol 224:413–435.

Green P, CR Steele, SC Rennich 1998 How plants produce patterns: a review and a proposal that undulating field behavior is the mechanism. Pages 359–392 *in* RV Jean, D Barabé, eds. Symmetry in plants. World Scientific, Singapore.

Greyson RI 1994 The development of flowers. Oxford University Press, Oxford.

Greyson RI, DR Pareddy, PL Polowick, VR Bommineni 1994 In vitro culture of maize inflorescences. Pages 125–140 *in* YPS Bajaj, ed. Biotechnology in agriculture and forestry. Vol. 25. Springer, Berlin.

Juarez C, JA Banks 1998 Sex determination in plants. Curr Opin Plant Biol 1:68–72.

Kramer EM, VF Irish 2000 Evolution of the petal and stamen developmental programs: evidence from comparative studies of the lower eudicots and basal angiosperms. Int J Plant Sci 161(suppl): S29–S40.

Lee S, J-S Jeon, K An, Y-H Moon, S Lee, Y-Y Chung, G An 2003 Alteration of floral identity in rice through ectopic expression of *OsMADS16*. Planta 217:904–911.

Lehmann N, R Sattler 1992 Irregular floral development in *Calla palustris* (Araceae) and the concept of homeosis. Am J Bot 79:1145–1157.

Mayo SJ 1986 Systematics of *Philodendron* Schott (Araceae) with special reference to inflorescence characters. PhD thesis. University of Reading.

——— 1989 Observations of gynoecial structure in *Philodendron* (Araceae). Bot J Linn Soc 100:139–172.

Mayo SJ, J Bogner, PC Boyce 1997 The genera of Araceae. Royal Botanic Gardens, Kew.

Mouradov A, TV Glassick, BA Hamdorf, LC Murphy, SS Marla, Y Yang, RD Teasdale 1998 Family of MADS-box genes expressed early in male and female reproductive structures of Monterey Pine. Plant Physiol 117:55–61.

Nagasawa N, M Miyoshi, Y Sano, H Satoh, H Hirano, H Sakai, Y Nagato 2003 *SUPERWOMAN1* and *DROOPING LEAF* genes control floral organ identity in rice. Development 130:705–718.

Purugganan MD 1998 The molecular evolution of development. Bioessays 20:700–711.

Ronse De Craene PL 2003 The evolutionary significance of homeosis in flowers: a morphological perspective. Int J Plant Sci 164(suppl): S225–S235.

Salthe SN 1985 Evolving hierarchical systems: their structure and representation. Columbia University Press, New York.

Sattler R 1988 Homeosis in plants. Am J Bot 75:1606–1617.

——— 1994 Homology, homeosis and process morphology in plants. Pages 423–475 *in* BK Hall, ed. Homology: the hierarchical basis of comparative biology. Academic Press, London.

Theißen G 2001 Development of floral organ identity: stories from the MADS house. Curr Opin Plant Biol 4:75–85.

Vergara-Silva F 2003 Plants and the conceptual articulation of evolutionary developmental biology. Biol Philos 18:249–284.

Verglat SP, VK Sawhney 1997 Cytokinin regulation of floral meristem identity in *Arabidopsis*. Flower Newsl 23:33–38.

Vogel S 1977 Nektarien und ihre ökologische Bedeutung. Apidologie 8:321–335.

Winter K-U, A Becker, T Münster, JT Kim, H Saedlerand, G Theißen 1999 MADS-box genes reveal that gnetophytes are more closely related to conifers than to flowering plants. Proc Natl Acad Sci USA 96:7342–7347.

Yamaguchi T, N Nagasawa, S Kawasaki, M Matsuoka, Y Nagato, H-Y Hirano 2004 The *YABBY* gene *DROOPING LEAF* regulates carpel specification and midrib development in *Oryza sativa*. Plant Cell 16:500–509.