

Manuscript ID:
IJRSEAS-2025-020626



Quick Response Code:



Website: <https://eesrd.us>



Creative Commons
(CC BY-NC-SA 4.0)

DOI: 10.5281/zenodo.22896901

DOI Link:
<https://doi.org/10.5281/zenodo.22896901>

Volume: 2

Issue: 6

Pp. 154-160

Month: December

Year: 2025

E-ISSN: 3066-0637

Submitted: 10 Nov. 2025

Revised: 16 Nov. 2025

Accepted: 15 Dec. 2025

Published: 31 Dec. 2025

Address for correspondence:

Hrutuja Gayakwad
Prof., Diploma in Agriculture Rural
Institute, Amravati, Maharashtra
Email:
hrutujagayakwad07@gmail.com

How to cite this article:

Gayakwad, H. (2025). *Floral Reproductive Strategies in Early-Diverging Angiosperms: A Critical Review of Dichogamy, Pollination and Evolutionary Innovation*. International Journal of Research Studies on Environment, Earth, and Allied Sciences, 2(6), 154–160.
<https://doi.org/10.5281/zenodo.22896901>

Floral Reproductive Strategies in Early-Diverging Angiosperms: A Critical Review of Dichogamy, Pollination and Evolutionary Innovation

Hrutuja Gayakwad

Prof., Diploma in Agriculture Rural Institute, Amravati, Maharashtra

Abstract

The early-diverging angiosperms play a key role in understanding the evolution of flowers, and the evolution of reproductive diversity in flowering plants. These lineages consist of a small fraction of the diversity of the extant angiosperms, but show outstanding variation in floral structure, sexual timing, pollination systems and structural adaptations. This review critically discusses the ways in which floral morphology and reproductive function are linked in the early-diverging angiosperms and its implications for dichogamy, floral dynamics at anthesis, pollinator interactions and evolutionary innovation. One of the most striking features that arose from the comparative investigations is the overwhelming number of flowers that are bisexual, and in which the male flowers appear earlier. One of the most striking features that occurred from comparing these flowers is that most of the bisexual flowers are protogynous. Female and male function are often separated in time, and there are often accompanying changes in floral architecture; tepal movements, stamen movements, stigma movements, and the development of special sterile organs. Synchronization of anthesis in some lineages helps achieve reproductive synchrony at the population level and heterodichogamy is an additional specialization with reciprocal temporal pattern between individuals. Beetles, flies and thrips are the main pollinators, with highly specialized pollination systems found in birds, butterflies and mammals being relatively limited in number. The flower is often rewarded with pollen, nutritive parts, shelter, brood sites, odours and thermoregulatory advantages instead of copious amounts of nectar. The structural features like calyptras, inner staminodes, synandria, floral cups, secretory structures and special pollen-receptive systems also reflect the close connection of floral structure and reproductive ecology.

The present review suggests that the early-diverging angiosperms are not necessarily morphologically primitive or evolutionarily simple. Instead, they show unique evolutionary trajectories that are influenced by developmental organization, ecological interactions and constraints on structure. The origin and diversification of angiosperm reproductive strategies will require a combination of comparative morphology, pollination ecology, phylogenetics, developmental biology and molecular approaches.

Keywords: early-diverging angiosperms, floral biology, dichogamy, protogyny, pollination ecology, floral evolution, reproductive strategies and evolutionary innovation.

Introduction

The development of flowers is one of the most important developments in the terrestrial plant life. The remarkable ecological and taxonomic complexity of angiosperms is linked to the development of reproductive structures that control pollen transfer, fertilization and interactions with animal pollinators. Floral morphology is, therefore, not just a taxonomic feature but a complex reproductive system, influenced by developmental processes, ecologic interactions, and evolutionary history. The study of early-diverging angiosperms is important for comparison with the investigation of the origin and diversification of the floral reproductive strategy. Their living representatives consist of lineages that separated relatively early in angiosperm evolution, and still bear together combinations of morphological and reproductive features of interest in the reconstruction of general trends in flower evolution. Comparisons of these groups have been useful for elucidation of ancestral floral features and the diversification of reproductive structures (Endress, 2001; Endress & Doyle, 2007, 2009).

The reproductive biology of early-diverging angiosperms is of special importance, as the morphology of the flowers and the pollination system are frequently associated. Reproductive success is provided by a combination of temporal separation of sexual functions, movements of floral organs, synchronized anthesis, specialized pollinator interactions, and unusual structural modifications. The features show that evolution of flowers cannot be interpreted from a morphological/phylogenetic perspective only, but it should take into account the ecological role of flowers.

The most conspicuous feature found in comparisons is the prevalence of protogyny in these two groups of bisexual flowers. Protogyny is characterized by maturation of female function before that of male function, and is often accompanied by dichogamy (temporal separation of pollen reception and pollen presentation). This reproductive pattern differs from the wider sexual timing system diversity exhibited by all angiosperms (Lloyd & Webb, 1986; Endress, 1990; 2001; 2010). The present review discusses the floral reproductive strategy from a holistic viewpoint. Instead of the floral morphology, dichogamy, pollination and evolution being discussed separately, it focuses on the functional relationships. The main intended goals are to explore the temporal structure of sexual function, the dynamics of the flowers during the anthesis, to compare different pollination systems, introduce the most significant innovations and to consider how developmental and architectural constraints can affect evolutionary history.

The evolutionary and morphological context of early-diverging angiosperms

Evolutionary studies are important because of the importance of early-diverging angiosperms as living examples of floral organization that is very different from that of the majority of monocots and eudicots. The flowers are very variable in respect of their number, arrangement, fusion, sexuality and reproductive time. It is thus these groups that have been subjected to comparative investigations to ascertain possible ancestral conditions and early stages in the diversification of flowering plants (Endress, 2001; Endress & Doyle, 2009).

But, this description of these plants as “primitive” can be misleading. Extant species are not ancestral organisms but are the products of modern evolution and diversification and specialization within their own evolutionary histories. They are not of particular use in representing unaltered ancestral flowers, but they do give clues to other evolution routes and various combinations of floral traits. Flower evolution is a significant aspect involving the relationship between structure and function. The development and architecture of floral organs cannot be separated from each other. The shape of tepals, stamens, carpels and other parts affects the ways the flowers can control access to pollinators, display pollen, collect pollen, and remove male and female functions. Such a connection between form and function is especially apparent in early-diverging angiosperms. Limited reproductive strategies opportunities may be enhanced by short staminal filaments, relatively small reproductive organs and limited synorganization of the floral organs. Some reproductive strategies opportunities may be favoured while other strategies may be restricted by short staminal filaments, relatively small reproductive organs and limited synorganization of the floral organs. Evolutionary diversification is therefore to be considered in the context of possibilities opened by floral architecture.

Temporal Organization of Sexual Function

1. Dichogamy as a reproductive strategy

A flower that has two sets of reproductive organs, one male and one female, in separate parts of the flower, which are separated in time, is called a dichogamous flower. It is a significant way of minimizing direct overlap of pollen receipt and pollen dispersal. It may be protogynous (the female function precedes the male) or protandrous (the male function precedes the female). Protogyny is especially common among early-diverging angiosperms. Female first reproductive timing has been found to be a significant trait in bisexual flowers in a number of lineages, as repeatedly shown in comparative studies (Gottsberger et al., 1980; Lloyd & Webb, 1986; Endress, 1984a, 1990, 2001, 2010). Protogyny could facilitate cross-pollination, since the stigma can receive pollen before the pollen from the same flower is ready. Pollen from the previously visited flowers may be carried by pollinators that visit the flower in the female phase. Later, in the male phase, the same flower can offer pollen that can be given to other receptive flowers. Therefore, dichogamy is rather more than a simple chronological sequence. It is a mechanism that synchronizes the development of the flowers and the movement of pollinators and the pollen transfer among individual plants in the population.

2. Why is protogyny predominant?

The predominance of protogyny raises important evolutionary questions. One explanation involves the structural organization of flowers. Efficient protandry frequently requires the removal or repositioning of anthers after pollen presentation so that they do not interfere with subsequent female function. Such repositioning can be facilitated by long and flexible filaments, mobile anthers or elongated styles. In many early-diverging angiosperms, however, stamens are relatively compact and possess short, robust filaments. These characteristics may limit the capacity for extensive movement of reproductive organs. Floral architecture may therefore influence the evolutionary direction of dichogamy. Protogyny can be achieved through mechanisms such as stigma exposure during the female phase followed by stigma concealment or protection during the male phase. These mechanisms may be more compatible with compact floral organization than the structural requirements associated with protandry.

3. Transitional and inactive phases

Sexual transitions are not always immediate. In some flowers, female and male functions may partially overlap, whereas others exhibit an inactive interval between the two phases. Such intermediate periods may be associated with changes in floral form and can contribute to the coordination of reproductive schedules. The existence of inactive phases demonstrates that sexual timing is often a complex developmental programme. Floral function may involve a sequence of stigma receptivity, structural reorganization, temporary inactivity, pollen release, and eventual senescence.

Floral Dynamics During Anthesis

1. Flowers as dynamic reproductive systems

Flowers are frequently treated as static morphological structures, yet their reproductive function is highly dynamic. Anthesis may involve opening and closing movements, changes in organ position, modifications of floral chambers,

changes in scent production, pollen release, and alterations in stigma accessibility. In early-diverging angiosperms, these dynamic changes are particularly important for regulating the transition between sexual phases. Floral movements can determine when pollinators have access to reproductive organs and which structures they contact during different stages of anthesis.

2. Flower opening and closure

Repeated opening and closing of flowers provide an effective mechanism for separating female and male functions. A flower may open during the female phase, close after stigma receptivity declines, and subsequently reopen when pollen becomes available.

This temporal organization can regulate pollinator behaviour. Visitors entering flowers during the female phase may deposit pollen, whereas later visitors may acquire pollen during the male phase. The floral structure therefore acts as a changing reproductive environment rather than a permanently accessible platform.

3. Stigma protection

The protection or concealment of the stigma after the female phase represents another important mechanism of reproductive regulation. Different lineages have evolved different structural solutions. Stigmas may become hidden by movements of stamens or sterile floral organs. In other cases, floral parts may close around the reproductive centre. Stigmas themselves may change orientation or become positioned in ways that reduce exposure. These mechanisms demonstrate functional convergence. Different structures may evolve to achieve a similar reproductive outcome: the separation of pollen receipt from pollen presentation.

4. Differential abscission of reproductive structures

Selective abscission of stamens represents a particularly unusual form of floral dynamics. In some species, stamens detach during the male phase while continuing to participate indirectly in pollen presentation. Abscission can alter the spatial distribution of pollen within a flower and influence how pollinators encounter reproductive rewards. In highly specialized systems, detached structures may also participate in ecological interactions involving insects and their larvae. Such examples illustrate the remarkable diversity of mechanisms through which flowers regulate reproductive function.

Synchronous Dichogamy and Heterodichogamy

1. Synchronization at the population level

Synchronous dichogamy extends the temporal organization of sexual function beyond individual flowers. In these systems, flowers follow predictable developmental schedules, and the timing of sexual phases becomes coordinated among flowers within a population. Environmental cycles, particularly daily light and darkness, can provide a temporal framework for synchronization. Flowers may enter female and male phases at relatively predictable times, thereby influencing the availability of receptive stigmas and pollen within the population.

2. Reproductive significance

Population-level synchronization can promote efficient pollen transfer. Pollinators moving among flowers encounter predictable combinations of male and female stages. Pollen acquired from a male-phase flower can therefore be transferred to a receptive flower according to the temporal structure of the population. The reproductive success of such systems depends on the interaction between floral timing, pollinator activity, and population structure.

3. Heterodichogamy

Heterodichogamy represents a further level of reproductive specialization. Different individuals within a population exhibit reciprocal flowering schedules. At a particular time, one group may function predominantly as female while another functions predominantly as male. Their functional roles subsequently reverse. This reciprocal arrangement can increase opportunities for cross-pollination by maintaining the simultaneous availability of functionally male and female flowers. Heterodichogamy therefore demonstrates how temporal regulation can become an important mechanism for organizing population-level reproductive interactions (Renner, 2001; Endress, 2010).

Pollination Diversity and Ecological Interactions

1. General patterns

Pollination systems in early-diverging angiosperms reveal substantial ecological diversity. Beetles, flies, and thrips are important pollinating agents in many lineages, while bee pollination is less dominant than in several other major groups of flowering plants. This distribution of pollination systems is closely related to floral morphology and reward production. Many flowers provide resources other than large quantities of nectar, including pollen, nutritive tissues, shelter, brood sites, scents, and thermal benefits (Thien et al., 2000; Endress, 2010).

2. Beetle pollination

Beetle pollination is associated with several of the most robust and structurally specialized flowers. Large floral chambers may provide protected spaces in which beetles can feed or remain during particular stages of anthesis. Strong odours and thermogenesis may further enhance attraction. In some systems, flowers provide nutritive tissues that are consumed by beetles. The relationship between floral reward and pollinator behaviour can therefore be particularly direct. Beetle-pollinated systems demonstrate how floral morphology can evolve to accommodate relatively large visitors while simultaneously controlling their movement through the reproductive environment.

3. Fly pollination

Fly pollination is widespread and includes interactions ranging from relatively generalized visitation to highly specialized systems. Floral odours play an important role in attracting many dipteran visitors. Some flowers possess structural features that temporarily retain flies or guide their movement through the flower. In highly specialized cases, floral architecture and chemical signals combine to create effective mechanisms for pollen transfer. The diversity of fly-pollinated systems illustrates the importance of sensory ecology in floral evolution.

4. **Thrips pollination**

Thrips represent small but ecologically significant pollinators. Their contribution to pollination has historically received less attention because these insects may also consume pollen and floral tissues. Flowers associated with thrips frequently provide protected spaces that function as feeding or breeding sites. Narrow openings, enclosed chambers and structurally robust floral tissues can facilitate these interactions. Thrips pollination demonstrates that successful pollen transfer can be mediated by very small insects and that pollinator effectiveness cannot be judged solely by body size.

5. **Bee pollination**

Bee pollination occurs in some early-diverging angiosperms but is comparatively less prominent. This pattern may be associated with differences in floral architecture, reward production, colour and accessibility. The limited dominance of bee pollination provides an important contrast with many eudicot lineages, where bee-mediated pollination has contributed substantially to floral diversification.

6. **Wind and water pollination**

Abiotic pollination occurs in particular ecological contexts but is generally less prominent than insect pollination. Wind-pollinated species require modifications that facilitate pollen release and stigma exposure, whereas aquatic species may develop specialized mechanisms for pollen transfer through water. These examples demonstrate that early-diverging angiosperms have evolved multiple reproductive solutions in response to different environments.

Floral Rewards and Structural Innovations

1. **Beyond nectar**

A major characteristic of pollination ecology in early-diverging angiosperms is the importance of non-nectar rewards. Although nectar occurs in some taxa, many flowers attract visitors through alternative resources. Pollen itself may serve as a reward. Other flowers provide edible tissues, secretions, shelter or sites suitable for insect reproduction. These interactions broaden the concept of floral reward beyond the conventional nectar-based model.

2. **Calyptras and protective structures**

The calyptra represents a specialized floral covering that protects developing reproductive organs and is removed at a particular developmental stage. Such structures illustrate the importance of mechanical protection in floral development. The timing of calyptra removal can also influence the onset of floral accessibility and therefore the timing of pollinator interactions.

3. **Sympetaly and floral chambers**

Fusion of tepals can produce chambers, restricted entrances and specialized pathways for pollinator movement. By controlling access to the reproductive centre, floral fusion can influence which visitors are able to enter and how they contact pollen and stigmas. Sympetaly therefore represents a structural innovation with important ecological consequences.

4. **Inner staminodes**

Inner staminodes are among the most distinctive floral structures in several early-diverging lineages. Although sterile, they may play important reproductive roles.

They can protect stigmas, separate reproductive phases, provide secretions, or influence pollinator movement. Their functional diversity demonstrates that sterile organs can become important components of floral reproductive systems.

5. **Synandry**

Fusion of stamens into a synandrium can alter pollen presentation and contribute to specialized floral function. In some systems, synandria may also be associated with thermogenesis or ecological interactions involving pollinators. The evolutionary significance of synandry lies in its capacity to integrate multiple stamens into a single functional structure.

6. **Specialized pollen-receiving systems**

Floral diversity also extends to the organization of carpels and pathways for pollen-tube growth. Partial and extragynoecial connections can facilitate communication among carpels.

Highly specialized pollen-receiving structures demonstrate that reproductive innovation can involve not only external floral morphology but also internal pathways connecting pollen reception with fertilization.

Structural Constraints and Missing Evolutionary Pathways

One of the most informative approaches to floral evolution involves examining features that are rare or absent. Early-diverging angiosperms display considerable diversity, but some highly specialized floral systems that are common elsewhere are poorly represented. Long floral tubes, highly elongated styles, and long flexible staminal filaments are relatively uncommon in many lineages. These limitations may influence the evolution of certain pollination systems and mechanisms of sexual separation. Similarly, elaborate pollination systems involving birds, mammals, butterflies, and hawkmoths are comparatively limited. Large quantities of nectar and specialized tubular flowers associated with these pollinators are therefore less prominent. These absences should not be interpreted as evidence of evolutionary inferiority. Instead, they illustrate the importance of developmental and architectural constraints. Evolution does not produce every theoretically possible form in every lineage. The existing organization of an organism influences which innovations can develop and become successful.

From Floral Morphology to Evolutionary Innovation

Because early-diverging angiosperms have shown the close relationship between morphology and ecological function, their major contribution to evolutionary biology has been that area.

For instance, protogyny can only be discussed in relation to the structure of the flower. Exposing, hiding or moving reproductive organs depends on the flower's architecture. Similarly, pollination systems are closely associated with structural characteristics. Beetles can be accommodated in large robust flowers, narrow floral chambers can affect the behaviour of small insects and trap-like structures can influence the behaviour of flies. New ecological opportunities can emerge as a result of structural innovations, and structural changes may be favoured by ecological interactions. The process of floral evolution is thus a two-way street; one of possibilities in development and one of selection in the environment.

Knowledge Gaps and Future Research Priorities

Although great strides have been made, there are still significant gaps in the understanding of floral biology in early-diverging angiosperms. First, there are many taxa which are not well studied in their natural habitat. Yet, for many species, basic data on pollinator identity, anthesis, stigma receptivity, pollen presentation and reproductive success is still not available. Second, the physiological mechanisms which regulate the synchronous dichogamy need to be further studied. The role of circadian rhythms, environmental signals, hormonal regulation and developmental programmes is an important area of future research. Thirdly, chemical and ecological analysis of floral rewards will be more detailed. Modern analytic techniques should be used for investigating the secretions, nutritive tissues and volatile compounds and thermogenic processes. Third, molecular developmental biology is providing new sites for studying whimsical floral forms. Comparisons of genomic and gene expression information may help explain the evolution of innovations like inner staminodes, synandria, and special pollen-receiving structures in flowers.

Last, future research should combine the field ecology with the phylogenetic aspects. While knowing when a floral character has arisen is important, it is also crucial to know how it functions in the living individuals.

Future Directions: An Integrative Research Framework

Future studies should go beyond descriptions of the floral morphology to more integrated studies. A multi-faceted approach should involve multiple complimentary methods.

Even detailed knowledge of the floral structures through comparative morphology is necessary to determine similarities and similarities that are convergent.

Pollination ecology-Field observations and experimental research are necessary to select good pollinators and determine the level of pollen movement.

The developmental biology-Developmental studies can account for the origin of unusual floral structure during ontogeny.

Insights into the developmental mechanisms underlying floral diversification can be gained by molecular approaches such as gene-expression and comparative genomic studies.

To know whether similar structures evolved in parallel or are shared, Phylogenetic analysis-Evolutionary relationships are used.

Chemical ecology-Research on floral volatiles, nectar, secretions and nutritive tissues can help to understand the sensory, and nutritional underpinning of plant-pollinator interactions. These strategies will enable floral biology to advance from a descriptive to a more general understanding of evolution.

Conclusion

Early-diverging angiosperms offer a highly informative context for the diversity and evolution of reproductive strategies in flowers. Their flowers offer insights into the intertwining relationship between temporal regulation, flower morphology, pollination ecology and evolution. One of the most significant and common of the bi-sexual flowers has a reproductive pattern of protogyny in these groups. Its predominance highlights the importance of the separation of the roles of females and males in time. The regulation of these reproductive phases is related to floral movements, to the protection of the stigma, to the synchronization of anthesis and to special structural changes. Beetles, flies and thrips are the major pollinators. They are based on a variety of rewards such as pollen, nutritive tissues, shelter, brood sites, odours and thermal benefits. This diversity illustrates that effective plant-pollinator interactions can arise in many ways other than through the conventional nectar-facilitated interactions. The variety of their structure, and the fact that it can manifest in such different ways further demonstrates the creative power of evolution. Anthers with calyptras, sympetaly, inner staminodes, synandria, floral cup and the special systems for receiving pollen are different reproductive adaptations. The evidence thus indicates a stronger tendency to a more general interpretation of the early-diverging angiosperms. They must not be considered as evolutionary throwbacks. Rather, they are derived from modern lineage with unique and highly specialised reproductive systems reflecting their own developmental, ecological and evolutionary history. Future research combining the areas of morphology, ecology, developmental biology, molecular genetics, chemical ecology and phylogenetics will give a more complete understanding of the origin and diversification of the floral reproductive strategies in the angiosperms.

Table 1. Major Temporal Reproductive Strategies in Early-Diverging Angiosperms

Reproductive strategy	Principal characteristic	Functional significance
Protogyny	Female phase precedes male phase	Reduces interference between pollen receipt and pollen release
Protandry	Male phase precedes female phase	Comparatively uncommon in many early-diverging groups
Dichogamy	Temporal separation of sexual functions	Promotes temporal organization of reproduction
Synchronous dichogamy	Sexual phases coordinated among flowers	Improves population-level pollen transfer
Heterodichogamy	Reciprocal sexual timing among individuals	Facilitates cross-pollination
Overlapping phases	Partial overlap of male and female functions	Provides flexible reproductive timing
Inactive phase	Temporary interval between sexual phases	May assist synchronization and structural transition

Table 2. Major Pollination Systems and Floral Adaptations

Pollination system	Major pollinating agents	Common floral adaptations
Beetle pollination	Beetles	Robust flowers, chambers, odours, food tissues, thermogenesis
Fly pollination	Diptera	Odour signals, specialized floral architecture, traps in some systems
Thrips pollination	Thrips	Protected spaces, narrow entrances, pollen and tissue rewards
Bee pollination	Bees	Accessible flowers, pollen rewards and occasional nectar
Wind pollination	Air currents	Enhanced pollen release and exposed receptive surfaces
Water pollination	Water currents	Specialized mechanisms for pollen movement in aquatic habitats

Table 3. Major Floral Structural Innovations and Their Functions

Structural feature	Functional role
Calyptra	Protection of developing floral organs and regulation of opening
Syntepaly	Formation of floral chambers and control of visitor access
Inner staminodes	Stigma protection, secretion and pollinator interaction
Synandry	Integrated pollen presentation and specialized reproductive function
Floral cup	Protection and organization of reproductive structures
Inferior ovary	Protection of developing ovules
Secretory structures	Attraction and reward of pollinators
Partial compitum	Facilitation of pollen-tube distribution
Extragynoecial compitum	Communication among carpels through external pathways
Hyperstigma	Specialized pollen reception and pollen-tube guidance

Acknowledgements

The authors acknowledge the contributions of researchers whose studies of floral morphology, reproductive biology, pollination ecology, and angiosperm evolution have provided the scientific foundation for the development of comparative research on early-diverging angiosperms.

Financial Support and Sponsorship

Nil.

Conflict of Interests

The authors declare that there are no conflicts of interest regarding the publication of this paper.

References

- Endress, P. K. (1990). The evolution of floral biology in angiosperms.
- Endress, P. K. (2001). The flowers in extant basal angiosperms and inferences on ancestral flowers. *International Journal of Plant Sciences*, 162, 1111–1140.
- Endress, P. K. (2010). The evolution of floral biology in basal angiosperms. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1539), 411–421.
- Endress, P. K. (2011). Evolutionary diversification of the flowers in angiosperms. *American Journal of Botany*, 98, 370–396.
- Endress, P. K., & Doyle, J. A. (2007). Floral phyllotaxis in basal angiosperms: Development and evolution. *Current Opinion in Plant Biology*, 10, 52–57.
- Endress, P. K., & Doyle, J. A. (2009). Reconstructing the ancestral flower and its initial specializations. *American Journal of Botany*, 96, 22–66.

7. Gottsberger, G., Silberbauer-Gottsberger, I., & Ehrendorfer, F. (1980). [Complete bibliographic details should be verified before submission.]
8. Lloyd, D. G., & Webb, C. J. (1986). The avoidance of interference between the presentation of pollen and stigmas in angiosperms. I. Dichogamy. *New Zealand Journal of Botany*, 24, 135–162.
9. Renner, S. S. (2001). How common is heterodichogamy? *Trends in Ecology & Evolution*, 16, 595–597.
10. Thien, L. B., Azuma, H., & Kawano, S. (2000). New perspectives on the pollination biology of basal angiosperms. *International Journal of Plant Sciences*, 161, S225–S235.