Flower Evolution: The Origin and Subsequent Diversification of the Angiosperm Flower

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Abstract

Developmental genetic pathways involved in flower formation in model plants such as *Arabidopsis* and maize enable us to identify genes, gene families, and gene networks that are involved in the regulation of flower initiation, growth and differentiation. These genes can then function as "candidate genes" and their expression, function, and biochemical interactions can be explored in other lineages to determine if they provide a necessary and sufficient toolkit for the development of the flower. Likewise, a view to the fossil record can provide documentation of reproductive innovations occurring within gymnosperms or along the stem lineage leading to angiosperms, elucidating the transitions required for the evolution of the angiosperm flower from an ancestral reproductive strobilus. Here we discuss the origin and subsequent evolution in form of the flower, highlighting recent studies in paleobotany, morphology, evolution, and developmental genetics with the goal of outlining advances in our understanding of flower evolution.

INTRODUCTION

Floral evolution is often thought about from an adaptive perspective with the evolution of floral form viewed as a function of reproductive ecology or pollination biology (Regal 1977). However, developmental constraints and morphological potential can also be viewed as a function of floral organogenesis, morphology, and development rather than as an adaptive response (see Endress 2006). To understand the evolution of flower morphology and development, we first need to understand the phylogenetic context in which the flower originated and evolved.

Two major issues impeding our understanding of the origin of the flower are the difficulty in resolving the phylogenetic relationships among extant and extinct seed plants and not knowing the definitive precursor to flowering plants. These issues make it challenging to reconstruct the ancestral characters and character states of flowering plants (in effect, providing an image of the ancestral flower), and even more difficult to reconstruct the lineage leading up to flowering plants (in effect, providing an image of the precursor involved in the transition between nonflowering and flowering seed plants). Recent advances in molecular phylogenetics have provided more refined ideas about the relationships between gymnosperms and angiosperms (Graham & Iles 2009, Graham & Olmsted 2000), the placement of the earliest angiosperms (Jansen et al. 2007, Moore et al. 2007, Qiu et al. 2006, Zanis et al. 2002), and the relationships within angiosperm lineages (APG 2003, Saarela et al. 2007). All of these levels of understanding of plant evolution are necessary to evaluate the origin and the evolution of the flower.

***Erratum**

At least for molecular phylogenetic analyses, there seems to be a stable angiosperm rooting with *Amborella* as sister to all other angiosperms, regardless of which extant gymnosperm outgroup is used (Graham & Iles 2009) (**Figure 1**). Note that this does not imply that *Amborella* itself is a "primitive angiosperm," retaining the characteristics of the ancestral angiosperm flower. Evolution along the lineage leading to the extant *Amborella trichopoda* taxon undoubtedly involves multiple diversification and extinction events, with the result that the modern *Amborella* flower is as derived, temporally, as any other flower in today's extant floral community. However, the placement of *Amborella* as sister to all other angiosperms confers an important role on the *Amborella* flower in the inference of ancestral floral characters. Characteristics shared between *Amborella* and other modern representatives of early diverging angiosperm lineages, the Nymphaeales and Austrobaileyales, are considered most likely to reflect the plesiomorphic condition of the angiosperm flower (see Endress & Doyle 2009).

FROM CONE TO FLOWER: THE ORIGINS OF THE FLORAL ORGANS

Neo- and paleobotanists alike have attempted to reconstruct the ancestral angiosperm flower using information from the fossil record combined with our understanding of extant angiosperm and gymnosperm morphology. Bateman et al. (2006) and more recently Doyle (2008) differentiate between top-down and bottom-up approaches to understanding the evolution of the flower. In a top-down approach, floral characters are optimized on the angiosperm phylogeny to infer ancestral states, thus reconstructing the common ancestor to all angiosperms based on characters coded for extant taxa. Such reconstructions of ancestral flower characteristics (Endress & Doyle 2007, 2009; Ronse de Craene et al. 2003) can ideally be made more rigorous by the availability and inclusion of fossil taxa that have been unambiguously assigned to early diverging angiosperm lineages. Recent descriptions of Cretaceous floras (Friis et al. 2006, 2007) and enhanced ability to place fossils into a phylogenetic context with extant taxa will no doubt increase our ability to reconstruct the ancestral angiosperm flower using a top-down approach (Crepet 2008). Later fossil deposits such as those of the Turonian (reviewed in Crepet 2008) are useful in detailing the process of diversification of

*This PDF amended on (30 Nov. 2009): See explanation at http://arjournals.annualreviews.org/errata/ecolsys

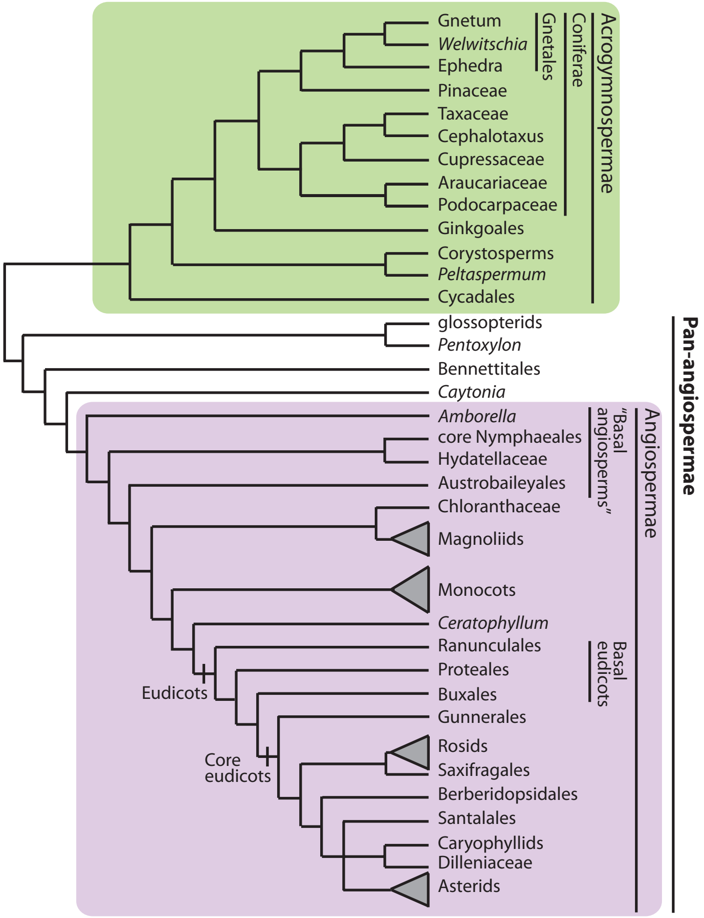

Figure 1

Summary topology of current views and recent advances in deep-level angiosperm and gymnosperm relationships. Acrogymnospermae and stem lineage angiosperm relationships are shown as modified from Doyle's (2008) analysis including fossil taxa with a molecular backbone. Ambiguous nodes and some fossil taxa are excluded if not discussed in text. Angiosperm relationships are from Soltis et al. (2008) summarizing Jansen et al. (2007) and Moore et al. (2007). Terminology used to define larger clades corresponds to that used throughout the text.

some of the early angiosperm lineages such as Nymphaeaceae and Magnoliales, and can provide information about the directionality of morphological evolution within these groups while helping to discern ancestral from derived characteristics.

In addition, new insights from molecular phylogenetic studies continue to augment our understanding of the diversity encompassed by early angiosperm lineages. The inclusion of Hydatellaceae (Saarela et al. 2007), a small family of aquatic plants once placed in Poales, as a well-supported member of the Nymphaeales provides additional information about the diversity in extant "basal" angiosperm lineages (Rudall et al. 2007, 2008, 2009). As a member of the Poales, the diminutive flowers of *Trithuria* were thought to be secondarily simple due to reduction; however, as a member of an early diverging angiosperm lineage it may be more parsimonious to infer that certain floral characters were never obtained rather than gained and subsequently lost (but see Endress & Doyle

Carpel: the derived feature unique to angiosperm flowers in which ovules are borne on and at least partially enclosed by laminar structures

Synorganization: the intimate structural connection of two or several neighboring floral organs to form a functioning system or apparatus ("hyperorgan"). May occur by congenital or postgenital fusion or by coordination of organs without fusion

2009). The accurate positioning of fossils such as *Archaefructus* (see below) can also be assisted by a more thorough understanding of extant lineage diversity, helping us to more accurately place and date morphological innovations that occurred during angiosperm evolution.

In contrast to the top-down approach, the bottom-up approach detailed by Bateman et al. (2006) and applied by Doyle (2008) focuses on reconstructing the precursor to the flower by investigating the reproductive organs in seed plants related to angiosperms. This approach can ultimately answer questions concerning homology of floral organs to vegetative and/or reproductive structures in gymnosperm or angiosperm stem lineages, and help us to understand how the flower is assembled from nonflower reproductive axes. A bottom-up approach requires a reliable seed plant phylogeny that identifies the sister lineage to flowering plants, either as a fossil or extant lineage (Doyle 2008). The common ancestor of the closest known sister lineage and the angiosperms would have borne, hypothetically, the closest knowable reproductive precursor to the flower.

A bottom-up approach also requires careful definition of characters thought to be plesiomorphic in flowering plants so that comparisons of homologous structures among nonflowering seed plants and early angiosperms can be made. Flowers, like the reproductive strobili from which they are likely derived, are determinate short shoots bearing fertile appendages with or without associated sterile appendages (Doyle 2008). Structures in the fossil Bennettitales and even in the extant Gnetales include a condensed reproductive axis with little internodal elongation, approximating the organization of the angiosperm flower. The origin of the flower from a nonflower reproductive strobilus could be conceived of as a gradual transition involving the condensation of a bisexual axis, and it is possible that such an evolutionary trend could occur multiple times without necessarily leading to the ancestral angiosperm. Living Acrogymnospermae [the crown clade that includes all living gymnosperms (Cantino et al. 2007)] are sufficiently divergent from angiosperms to prevent reliable reconstruction of flower origins. Meanwhile, extinction among early crown clade angiosperms (Angiospermae) and especially among their stem relatives (stem Pan-Angiospermae) weakens the value of outgroup comparison and phylogeny reconstruction and makes difficult the interpretation of morphological variation, phylogenetic optimization of character states, and assessment of homology (Bateman et al. 2006). The assessment of homology across such long evolutionary distances remains difficult.

A Rose by Any Other Name: The Definition of a Flower

The basic flower is defined as a bisexual reproductive axis with carpels and stamens. The carpel differentiates the angiosperm (angio-ovulate; enclosed ovules) from the gymnosperm (gymno-ovulate; naked ovules) reproductive axis. The debate concerning the physical appearance of the earliest angiosperm flower has been resolved at least partially by the repeated resolution of *Amborella*, Nymphaeales, and Austrobaileyales (comprising Trimeniaceae, Schisandraceae, Illiciaceae, and Austrobaileyaceae) as a grade of extant taxa sister to all other angiosperm lineages (see **Figure 1**). This proposed resolution provides some idea of what characteristics may have been shared by these early angiosperm lineages and the "ancestral flower," or the reproductive structure borne by the most recent common ancestor of all extant angiosperms (Angiospermae; Cantino et al. 2007). All species within this group have bisexual flowers or are derived from bisexual ancestors, and have multiple organs usually with spiral phyllotaxis (but see discussion below) (Endress & Doyle 2007). Although evidence of the first flowering plant appears as pollen in the fossil record around 125–130 Mya (early Cretaceous; Friis et al. 2006), the first evidence of the canonical eudicot flower with whorled arrangements of floral parts and a distinct corolla is not found until the middle Cretaceous. The whorled floral design may be a baseline for facilitating the origin of more advanced morphologies via synorganization (Endress 1990), whereas the first flowers were likely more similar in structure to those currently found in *Amborella* and other members of the basal grade (**Figure 1**).

Still, the definition of the flower remains contentious (reviewed in Bateman et al. 2006). In many definitions, a list of whorled organs with a linear sequence—sepals, petals, stamens, and carpels—predominates. However, many of these features are not present in early lineages of angiosperms and may not have defined the earliest angiosperm flower. Most evolutionary biologists seem to agree that the origin of the carpel provides a distinctive feature that separates angiosperms from their gymnosperm relatives, although fully closed (that is, fused) carpels are neither found in *Amborella* nor in several other early diverging angiosperm lineages (for example *Trimenia*, *Austrobaileya*, Chloranthaceae) (Endress 2001a; Endress & Igersheim 2000a, 2000b). Bisexuality, another characteristic alluded to in many flower definitions, has been lost multiple times throughout angiosperm evolution if it is indeed ancestral, producing both monoecious and dioecious plants. Many early plant lineages are functionally dioecious, bearing male flowers with sterile carpels and/or female flowers with sterile stamens. *Amborella* has functional female flowers with staminodes that seem to be a morphological transition between stamens and carpels (Buzgo et al. 2004). The perianth (sepals, petals), another feature of many definitions, is possibly missing in *Trithuria* (Hydatellaceae) (Rudall et al. 2007, 2009) and in the Piperaceae-Saururaceae clade.

Using what we would now view as a bottom-up approach, Arber & Parkin (1907) defined what might be considered a flower in the strict sense—that containing derived microsporophylls (stamen) and closed carpels—as being found in only a subset of angiosperms. This flower, which they termed the "euanthostobilus" (Arber & Parkin 1907; see also Bateman et al. 2006 for a review), is that for which we have the most developmental genetic information due to long-standing model organisms such as *Arabidopsis thaliana* and *Antirrhinum majus*. The "anthostrobilus" is defined by the presence of a differentiated perianth, and the "proanthrostrobilus" as containing a series of sterile leaf-like organs that could be interpreted as an undifferentiated primitive perianth (Arber & Parkin 1907). In this way, the flower is simply recognized as a specialized reproductive strobilus in which the common ancestor (anthrostrobilus) is bisexual with microsporophylls exterior to megasporophylls, both surrounded by a differentiated perianth (Arber & Parkin 1907).

Homologies and flower origins. Extant gymnosperm diversity is limited to five groups: cycads, *Ginkgo*, Gnetales, Pinaceae, and the other conifers. Early cladistic studies focusing on relationships among gymnosperms and between gymnosperms and angiosperms placed the Gnetales as sister to Angiosperms (Crane 1985, Doyle & Donoghue 1986) along with two fossil groups, the Bennettitales and the Pentoxylales (= anthophytes; **Figure 2**). Angiosperms, some Gnetales, and some Bennettitales have sterile, laminar stuctures surrounding axes containing both male and female organs, although in Gnetales the ovules are not functional in the staminate shoots and stamens are reduced and nonfunctional when they appear in a compound strobilus terminating in a functional ovule. Later molecular evidence suggesting that extant gymnosperms are monophyletic forces a second look at the presumed homologies between gnetalean and angiosperm reproductive axes, with the conclusion that both whorled arrangement and bisexuality are homoplasious, evolving separately in the two disparate lineages (see sidebar, Consideration of Homology, for a broader discussion of homology).

Accepting molecular relationships among extant taxa, Doyle (2008) concluded that morphological character analyses associate glossopterids, *Pentoxylon*, Bennettitales, and *Caytonia* with angiosperms (**Figure 1**). Below we discuss the origins of floral features in the context of this phylogenetic information.

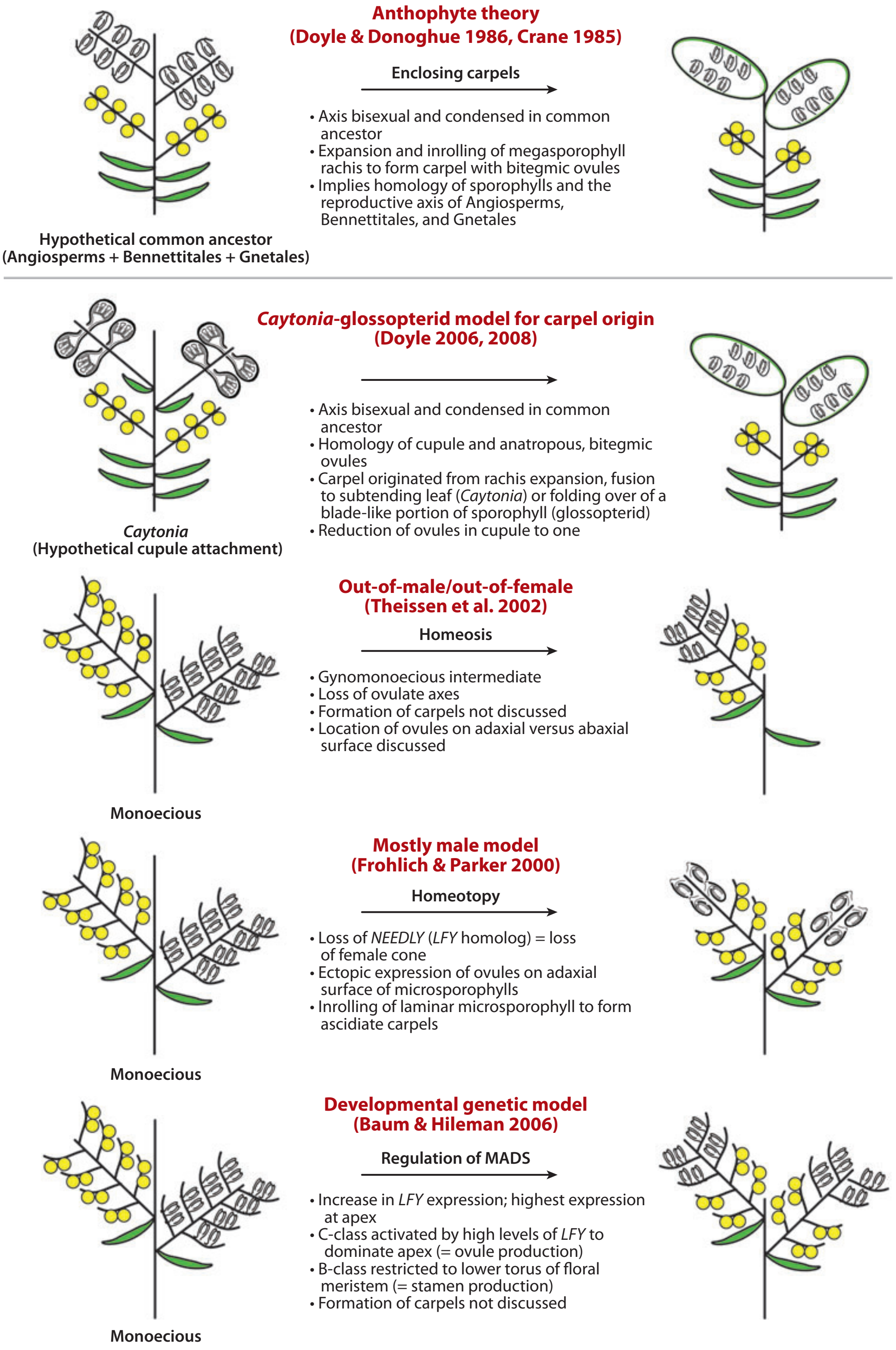

Figure 2

Review and comparison of different theories of the transition to bisexuality and carpel formation leading to the angiosperm flower. The ancestral form is represented on the left, the derived form on the right, and the major transitional process is described with details unique to each model. Ovulate structures remain exposed on sporophyll unless the model specifically indicates the means of carpel evolution.

Anthophyte theory (Doyle & Donoghue 1986, Crane 1985)

- Axis bisexual and condensed in common ancestor
- Expansion and inrolling of megasporophyll rachis to form carpel with bitegmic ovules
- Implies homology of sporophylls and the reproductive axis of Angiosperms, Bennettitales, and Gnetales

***Caytonia*-glossopterid model for carpel origin (Doyle 2006, 2008)**

- Axis bisexual and condensed in common ancestor
- Homology of cupule and anatropous, bitegmic ovules
- Carpel originated from rachis expansion, fusion to subtending leaf (*Caytonia*) or folding over of a blade-like portion of sporophyll (glossopterid)
- Reduction of ovules in cupule to one

Out-of-male/out-of-female (Theissen et al. 2002)

- Gynomonoecious intermediate
- Loss of ovulate axes
- Formation of carpels not discussed
- Location of ovules on adaxial versus abaxial surface discussed

Mostly male model (Frohlich & Parker 2000)

- Loss of *NEEDLY* (*LFY* homolog) = loss of female cone
- Ectopic expression of ovules on adaxial surface of microsporophylls
- Inrolling of laminar microsporophyll to form ascidiate carpels

Developmental genetic model (Baum & Hileman 2006)

- Increase in *LFY* expression; highest expression at apex
- C-class activated by high levels of *LFY* to dominate apex (= ovule production)
- B-class restricted to lower torus of floral meristem (= stamen production)
- Formation of carpels not discussed

CONSIDERATION OF HOMOLOGY

Once the flower originates, homology assessment can continue to be problematic across angiosperms. Processes thought to be homologous often occur multiple times independently, potentially indicating canalization of floral developmental pathways or utilization of different genetic mechanisms to achieve similar but not identical morphologies. An example is unisexual flowers in the grasses, where development was found to be different in four separate subfamilies (Kinney et al. 2008). Even within developmental programs, different levels of homology and homoplasy may be observed: Kinney et al. (2008) found that the development of staminate flowers in the Chloridoideae was distinct from that reported for subfamilies Erhartoideae, Panicoideae, and Pharoideae, whereas pistillate Chloridoideae flowers showed development similar to that described in other pistillate grasses. Therefore, even if unisexual flowers evolved independently in grasses, similar or even identical developmental mechanisms may be used that result in similar developmental conditions. Although expression patterns of genes involved in development may help define homologous structures across taxa (Jaramillo & Kramer 2007), this definition can only be accomplished with an understanding of underlying developmental morphology. Understanding the evolutionary context in which an organ evolved is imperative to identifying homologous structures regardless of gene expression patterns, particularly considering the role of gene duplications in the diversification of floral morphology (Irish & Litt 2005, Jaramillo & Kramer 2007).

Carpel and the bitegmic ovule. Because ovules, microsporangia, and sterile structures interpreted either as bracts or a primitive perianth are present in certain combinations across all known extinct and extant seed plants, the carpel and the bitegmic ovule remain the unique structures defining the angiosperm flower. Unlike the perianth, it is thought that the carpel originated only once along the stem leading to angiosperms, derived either from a megasporophyll that enrolled and fused to surround the ovule(s) (that is, a leaf homolog), or from an ovule-bearing axis surrounded by a bract-like structure (that is, a leaf plus branch homolog). Consistent with either of these theories, the earliest carpels were likely unfused but may have been functionally closed by secretions (Endress 2001a, 2001b).

Of all extant and extinct gymnosperm lineages, the cupules of *Caytonia* are most similar in structure to the bitegmic ovules of angiosperms. The cupules of *Caytonia* are laminar structures containing several ovules in two rows. The transition from a *Caytonia* cupule to the angiosperm ovule would require a reduction in ovule number to one such that the cupule wall would form the outer integument of a bitegmic ovule (**Figure 2**). The ovules appear to be placed adaxially within the cupule lamina, and thus are in the correct position for the cupule wall to become the outer integument (**Figure 2**). If this bitegmic structure is interpreted as a branch borne in the axil of a leaf or bract, it could eventually be surrounded by the subtending leaf or bract during development to resemble, at least superficially, an ascidiate angiosperm carpel (see figure 12 in Doyle 2008) (**Figure 2**).

Data from glossopterids plus *Caytonia* imply that a reduction in ovule number took place along the stem angiosperm lineage, prior to the radiation leading to the extant basal angiosperm lineages. It seems likely that ovule number may have been relatively plastic during early flower evolution and that ovule position on laminar or axillary structures may have been quite labile leading up to and during the initial angiosperm radiation (see Doyle 2008). Such lability would obviate the need for drastic ectopic transformation of organ position required by Frohlich's "mostly male" hypothesis of flower origins (Frohlich 2006).

Based on recent developmental genetics results for YABBY and KANADI gene families, both involved in laminar growth and differentiation of adaxial versus abaxial surface polarity in lateral organs (Floyd & Bowman 2007), the inner and outer integuments of angiosperm ovules were likely to have been derived independently and have different developmental and structural origins (McAbee et al. 2006). Likewise, various laminar or axillary structures holding the ovules and ultimately forming the angiosperm carpel may have undergone transitions in orientations and laminar growth as the YABBY and KANADI gene families diversified in early angiosperms.

Perianth. To achieve a flower, aggregation of both fertile and sterile organs (perianth) must occur. This aggregation does not necessarily need to occur simultaneously and could have a particular ordering in the evolution of the flower. In addition, the accumulation of sterile organs could occur in multiple lineages independently, as seen in Gnetales and angiosperms.

From a top-down approach, the ancestral flower likely had a perianth that would have been derived along the stem lineage (Doyle 2008, Endress 2008, Ronse de Craene et al. 2003) and subsequently lost in several early diverging angiosperm groups including all members of the Hydatellaceae and most Chloranthaceae. Although *Caytonia* was identified as the most likely fossil sister taxon to the crown angiosperms (**Figure 1**), *Caytonia* is not known to have had strobili or associated sterile appendages (Doyle 2008). Strobili with a sterile "perianth" are found in *Pentoxylon* and at least in some if not many Bennettitales, indicating that the sterile structures in these pan-angiosperms may be homologous to the perianth of angiosperms, with a loss in *Caytonia* after the *Caytonia* lineage diverged from its angiosperm sister lineage. However, other most parsimonious reconstructions are possible, including the independent origin of strobili in *Pentoxylon*, Bennettitales, and angiosperms, with a perianth in *Pentoxylon* and angiosperms but either with or without a perianth in Bennettitales (see Doyle 2008). Although this does indicate that the perianth may have evolved prior to the crown group of angiosperms, there are still questions to be answered involving the homology of sterile structures among pan-angiosperm lineages and across the pan-angiosperms and the acrogymnosperms.

Compression. In addition to bisexuality, at some point during flower evolution the condensation of the reproductive axis took place, enabling the female and male structures to develop in close proximity to one another and to the sterile perianth. Although the order of events remains uncertain, a reduction in internodal elongation along an axis such as that found in *Archaefructus* may have led to the condensation of the reproductive and vegetative structures in the form we now refer to as a flower. The reproductive axis of *Archaefructus* has been interpreted as either naked, unisexual structures not yet organized into flowers (Sun et al. 2002) or, more recently, as reproductive organs that are simplified due to secondary reduction, similar to that seen in the Hydatellaceae (Friis et al. 2003). However, when analyzed with a reinterpreted character matrix in a phylogenetic context, Nixon (2006) found no support for *Archaefructus* being nested within the Nymphaeales. It was recently reported that some of the reproductive branches of potentially closely related taxa bear both carpels and stamens, indicating that the reproductive branches of *Archaefructus* may be an inflorescence rather than a precondensed flower (Ji et al. 2004), although these illustrations of the fertile axes may represent several layers of compressed plant organs rather than a bisexual flower. Although it may be too early to comment on a definitive placement of *Archaefructus*, recent inclusion of Hydatellaceae in Nymphaeales makes it easier to hypothesize the existence of an *Archaefructus*-like ancestor within this lineage (Doyle 2008, Endress & Doyle 2009).

Bisexuality. Although there are no extant gymnosperms with consistently bisexual reproductive axes, bisexuality was a feature of some Bennettitales (possible Pan-Angiospermae) (Doyle 2008). The Gnetales are also thought to have potential precursors to a bisexual axis, with aborted male structures in the female-functional axis and aborted ovule(s) terminating the male-functional axis in *Gnetum*, *Ephedra*, and *Welwitschia*. In fact, the sharing of this bisexual axis was a key feature in the Anthophyte theory of floral evolution (see Frohlich 2006 for a detailed review) (**Figure 2**). Recent analyses of molecular and morphological data do not support a close relationship between Gnetales and Angiosperms, thus the potential for bisexuality in the Gnetales cannot be considered homologous to bisexuality found in angiosperms. If bisexuality originated in the ancestor of Bennettitales and angiosperms, it would have been independently lost in *Caytonia*. Recent studies of B- and C-class MADS-box gene evolution in gymnosperms indicate that the development of a bisexual axis was one of the first innovations during the evolution of the flower (see below).

Theories of Flower Origins

Recent theories of floral origins have evoked developmental genetics in combination with morphological analyses to help explain the bisexuality, condensation of strobilus axis, and development of a sterile perianth that are required to evolve the angiosperm flower (**Figure 2**). In their mostly male theory of flower origins, Frohlich & Parker (2000) propose that the origin of the flower was caused by an ectopic translocation of the ovules to the adaxial side of laminar microsporophylls following the loss of one *LEAFY* gene ortholog (*NEEDLY*) in the angiosperms (see Frohlich 2006 for a review). Although not stated in the original theory, these feminized microsporophylls would have then evolved into carpels, initially being ascidiate (urn shaped, not completely fused) as commonly observed in early diverging lineages of extant angiosperms (Endress & Igersheim 2000a) (**Figure 2**). Although this theory is testable, one potential pitfall is that the flower should be derived from a gymnospermous reproductive axis with laminar microsporophylls and adaxially borne ovules, yet *Caytonia*, sister to the angiosperms, does not have laminar microsporophylls (Sokoloff & Timonin 2007). The laminar microsporophylls would have to be lost in *Caytonia* or evolved following the divergence of *Caytonia* from the future angiosperm lineage. The actual function of the duplicated *LFY* gene, *NEEDLY*, has not been studied in detail for any of the gymnosperm taxa in which it has been identified. Such studies are necessary to assess the likelihood of the loss of *NEEDLY* explaining the morphological changes associated with flower origins.

Alternatively, bisexuality could have evolved from a unisexual axis via the "out-of-male" theory (Theissen et al. 2002). In this theory, flowers originated from a male cone via a reduction of B-class gene expression in the upper region of the cone, leading to the development of female structures at the apex (**Figure 2**). An alternative would be the "out-of-female" scenario in which flowers originated from a female cone via ectopic expression of B-class genes in the base of the cone, resulting in the development of male reproductive structures below the female apex (Theissen et al. 2002). Baum & Hileman (2006) built upon this theory, providing a testable hypothesis invoking, as did Frohlich, *LFY* as a major player in the origin of the flower (**Figure 2**). If reproductive shoots in the ancestor to angiosperms accumulated higher levels of LFY protein, B- and C-class genes would be activated. C-class genes are more responsive to *LFY* than are B-class genes; thus C-class expression would continue to increase while B-class expression would reach a plateau (or decline) as C- and E-class proteins outcompeted the B/C/E complexes. At the bottom of the cone, both B- and C-class genes are expressed and male organs develop, while at the apex of the cone with high *LFY* levels only C-class genes are expressed and female organs develop (Baum & Hileman 2006).

Theissen & Melzer (2007) agree that this scenario is plausible, attributing its functionality to their "quartet model"; cooperative binding involving tetramers of B- and C-class proteins with E-class (SEP1–4) proteins increases binding affinity and enables proteins to bind target gene promoters at lower critical threshold levels. With the increased binding affinity it is possible to decrease or eliminate a zone of ambiguous organ formation between male and female organs, allowing for condensation of the floral axis with greater precision in the male-to-female transition.

Quartet model: a theory that expands upon the ABCE model in which it is hypothesized that E-class proteins form complexes with the A-, B-, and C-class proteins for specification of petal, stamen, and carpel identity

According to their model, the close proximity of the angiosperm organs is enabled by co-operativity brought about by quartet DNA-binding affinity; thus, the invention of the quartets may be a crucial molecular step for the origin of the flower (Theissen & Melzer 2007). To test this model, it is necessary to study the origin of the proteins that form the tetramers and determine if the capacity for tetramer formation arose with the SEP/AP1 subfamilies along the stem lineage leading to angiosperms (Theissen & Melzer 2007). Unfortunately, the origins of the A- and E-class genes are not well resolved beyond their well-supported relationship with the AGL6-like genes (see Theissen & Melzer 2007 for a review).

ABCE model: an elaboration on the ABC model of floral organ identity in which A-class genes alone specify sepals, A-class plus B-class genes specify petals, B-class plus C-class genes specify stamens, and C-class genes alone specify carpels. The addition of E-class genes to this model came about with the finding that the SEPALLATA genes are required for the reproductive organ identity function of the B- and C-class genes

Duplications of certain lineages and subsequent diversification may have placed restrictions on protein interactions, as is seen with the B-class subfamily: obligate heterodimerization between B-class genes in *Arabidopsis* likely occurred following duplication in this lineage. Prior to the duplication event, homodimerization of the single protein was sufficient for function, but was perhaps not as effective as the heterodimer formed by the duplicated gene products. In early angiosperms, there seem to be more possible combinations of dimerization of B-function genes to form tetramers with *SEP1–4* genes, in effect creating the fuzzy expression domains inherent in the proposed models of shifting/sliding boundaries (Bowman 1997, Kramer et al. 2003) or fading borders (Buzgo et al. 2004; reviewed in Soltis et al. 2006). The ABCE model as described for eudicots is likely to have evolved from a more "fuzzy" system of fading borders of gene expression, characterized by gradual transitions in organ identity and perhaps more elongate floral axes (Theissen & Melzer 2007). If shifting boundaries of MADS-box genes occurred in the early angiosperm lineages, the solidification into canalized gene expression patterns, via either tetramer formation or other means, may have occurred multiple times in angiosperm evolution, resulting in multiple origins of the canonical flower.

It is possible that there is a bidirectional, homoplastic origin of the flower (Rudall et al. 2009). All structures we currently recognize as flowers originate from a uniaxial structure. This follows the euanthial model of flower evolution, which assumes that the first flower arose from the condensation of a single and unbranched axillary axis containing both mega- and microsporophylls. Alternatively, pseudanthial models derive the flower from a multiaxial structure where each organ was axillary and ultimately condensed into an unbranched axis. Whereas the euanthial interpretation requires homeosis in order to develop a bisexual flower (Frohlich & Parker 2000, Theissen et al. 2002), the pseudanthial model may require only simultaneous or consecutive suppression of branching and internodal elongation. However, as mentioned by Rudall et al. (2009) and detailed by Meyen (1988) in his work on gametoheterotopy, switches between unisexual and bisexual reproductive structures were frequent during the evolution of early angiosperms and may play a role in spatial changes and shifts in position of female and male organs. A pseudanthial hypothesis for the evolution of the flower does not necessarily mean that the flower itself evolved multiple times, but rather that current floral structures may be nonhomologous owing to heterochronic and heterotopic shifts in the boundary between the flower and the inflorescence, as seen in terminal structures of racemose inflorescences that resemble flowers but are ontogenetically demonstrated to be pseudanthal (Sokoloff et al. 2006). This same process could have occurred in seed plants such as the Gnetales, where the flower-like reproductive structures seem to be ontogenetically derived from (*a*) the reduction of compound and bisexual cones and (*b*) the loss of subtending bracts in the axils of which were borne male or female branched reproductive units (Mundry & Stutzel 2004).

Phyllotaxis and Inflorescence/Flower Boundaries

Phyllotaxis in the flowers of the earliest diverging lineages of angiosperms is much more flexible and subsequently more diverse and complex than in eudicot lineages (see Trends section).

Although many early flowering plant lineages such as some members of Magnoliales and Laurales have spiral floral phyllotaxis particularly in the androecium, it is proposed that this is derived rather than representative of the ancestral floral state (Endress & Doyle 2007). Most noneudicot angiosperms with whorled phyllotaxis are based on a trimerous (three-part) organization, although whorled polymery does occur in some Nymphaeales and Laurales (Endress & Doyle 2007). Unfortunately, it is difficult to discern what the state of the ancestral flower may have been. No fossil flowers that can be unequivocally identified as angiosperm relatives have been found as yet (Crepet 2008), so assessment of the ancestral state for phyllotaxis must rely on ancestral character state reconstructions (top-down approach). The perianth and androecium are both spiral in *Amborella* and Austrobaileyales, but are both whorled in Nymphaeales. Shifts from whorled to spiral phyllotaxis occur in Ranunculaceae and *Nelumbo* (perianth) (Endress & Doyle 2007). Perianth and androecium phyllotaxis appears to be decoupled evolutionarily, with the androecium becoming spiral in the common ancestor of Magnoliales and Laurales (evolved from a whorled common ancestor) while the perianth remains whorled only to become spiral later at least two times, once in *Degeneria* and once in the common ancestor of Laurales (Endress & Doyle 2007).

Hydatellaceae were recently found to be closely related to Cabombaceae plus Nymphaeaceae in the Nymphaeales (Saarela et al. 2007), and thus would be expected to have the whorled perianth and androecium phyllotaxis found in *Cabomba* and *Brasenia* as optimized by Endress & Doyle (2007). However, the reproductive units of *Trithuria*, the sole genus in the Hydatellaceae (Sokoloff et al. 2008), are interpreted as an aggregation of reduced unisexual and apetalous flowers (Rudall et al. 2007, 2009) although the bractlike involucres resemble a typical perianth with whorled, dimerous phyllotaxis (Rudall et al. 2009). Rudall et al. refer to these reproductive units as "nonflowers," structures in which loss of flower identity occurs and the boundary between the inflorescence and the flower becomes difficult to interpret. Such flowers are found in the monocot family Triuridaceae, where female or hermaphrodite reproductive units demonstrate reverse order (carpels are exterior to stamens) and inflorescence characteristics can be found within the reproductive unit itself, making it difficult to determine the flower/inflorescence boundary (Ambrose et al. 2006; Rudall et al. 2008). Although widely interpreted as flowers, male reproductive units in *Ceratophyllum* consist of up to 46 stamens and could be considered pseudanthia (Rudall et al. 2009) whereas *Hedyosmum* (Chloranthaceae) units have been interpreted as cone-like in structure due to possession of lateral stamens along an axis lacking bracts or tepals (see Endress & Doyle 2009), potentially representing an abracteate inflorescence (see Rudall et al. 2009 for a review). This concept of a nonflower also provides rationale for the interpretation of *Archaefructus*, considered to be either an evolutionary prefloral structure or an inflorescence (Friis et al. 2003, Sun et al. 2002). A prefloral condition may represent the condition of the reproductive unit that gave rise to the angiosperm flower, and could then reappear when secondary loss of floral organs and flower identity revert the unit to an inflorescence-like structure. Such evolutionary events may provide clues as to the inflorescence/flower boundary and the rise of the angiosperm flower.

Gene Duplication and Floral Evolution: A Floral Toolkit?

Gene and genome duplications followed by neo- or subfunctionalization, or perhaps more likely a combination of the two (Force et al. 2005), can lead to the formation of a large gene network that could enable the evolution of morphological novelties. Such mechanisms have been proposed (Mondragon-Palomino & Theissen 2007) and tested (Mondragon-Palomino & Theissen 2009) in such dynamic flowers as the orchids.

Although homologs of many genes known to be involved in the development of *Arabidopsis* and maize have been identified in early land plant lineages, their functions have not been fully tested and thus their role in development and developmental evolution remains speculative (Floyd & Bowman 2007). However, these potential homologs in gymnosperms and basal angiosperms can be used to develop an idea of the genetic toolkit that may have been present during the evolution of the flower. As the developmental genetic background for the flower has been recently reviewed (Baum & Hileman 2006, Irish & Litt 2005, Kramer 2007), we keep the discussion on each gene family to a minimum and focus on genes thought to be involved specifically in flower origin.

KANADI genes. KAN1 and KAN2 are involved in abaxial cell-fate determination in lateral organs, including those produced by floral meristems (reviewed in Floyd & Bowman 2007), and KAN1, KAN2, and KAN4 play a role in the development of ovule integuments (McAbee et al. 2006) that form a major innovation in the development of the angiosperm ovule and separate angiosperms from modern gymnosperms. It is impossible to determine the presence and function of these genes in the stem lineages leading up to the angiosperms; however, conservation of abaxial/adaxial polarity and the development of integuments from cupules are important evolutionary stages demonstrated by *Caytonia* and the glossopterids (Doyle 2008, Frohlich 2006). The KANADI genes may have thus played a role in the evolution of the angiosperm ovule.

APETALA2 family. *APETALA2* (*AP2*) and *AINTEGUMENTA* (*ANT*) are two of the *Arabidopsis* genes in the *AP2* subfamily of the AP2/ERF gene family. In *Arabidopsis*, *AP2* was first recognized as a class-A homeotic gene responsible for sepal and petal organ identity. It has since been shown to be expressed at various stages of plant development and in many plant tissues, playing a role in, among other functions, stem cell–lineage maintenance (Wurschum et al. 2006) and control of flowering time (Chen et al. 2001). *ANT* is involved in regulating cell division in lateral organs, including the lateral organs of the flower (Mizukami & Fischer 2000). Within the AP2 subfamily, phylogenetic analyses resolve *AP2* and *ANT* into separate lineages (Kim et al. 2006, Shigyo et al. 2006), but the gene trees are not easily reconciled with species trees without inferring multiple gene duplications and losses (Floyd & Bowman 2007). Both *AP2* and *ANT* are found in gymnosperm and angiosperms as well as in early diverging lineages of seed plants. The role in transitioning from vegetative to reproductive growth seems to be conserved across gymnosperms and angiosperms; however, the organ identity function found in *Arabidopsis* is likely derived and played no role in the origin and early evolution of the flower. Gymnosperm *AP2* genes are expressed in reproductive meristems and cone bud primordia (Shigyo and Ito 2004) and may be involved in reproductive organ identity.

The *ANT*-like genes have been implicated in the regulation of floral meristems and floral organ growth in *Arabidopsis* (Nole-Wilson et al. 2005). *ANT* genes are resolved into two separate clades, a basal ANT lineage and a euANT lineage comprising two well-supported clades (Floyd & Bowman 2007). Duplications in flowering plants occurring prior to the divergence of monocot and eudicot lineages and subsequently within both monocots and eudicots indicate the potential for a role in morphological evolution of the angiosperm flower. Sequences from *Ginkgo*, *Cycas revoluta*, and *Pinus taeda* have been identified in the euANT clade along with the *Arabidopsis ANT* sequence that has known function in lateral organ expansion (Floyd & Bowman 2007); to date, no gymnosperm sequences have been identified in the basal ANT clade. The role of these genes in gymnosperm reproductive structures and subsequent diversification in angiosperm lineages may shed light on the origin and diversification of lateral organ identity in flowers.

MADS-box genes. It was once thought that expression of genes responsible for organ identity would help define homologies across flowering plants, but this has since been proven to be much more complicated. Massive gene and genome duplications in all angiosperm lineages combined with the serial nature of plant development provide multiple opportunities for gene co-option and repeated evolution of similar phenomena, resulting in convergence rather than homology (Jaramillo & Kramer 2007). The MADS-box gene family, famous for its role in floral development, has undergone extensive duplications leading to complicated relationships of orthology, paralogy, and functional homology (Jaramillo & Kramer 2007).

Because of the identification of the MADS-box genes as the main homeotic genes involved in floral organ identity (Coen & Meyerowitz 1991), many papers and recent reviews have been written concerning these genes and their role in the origin and evolution of the angiosperm flower (e.g., Irish 2003, Soltis et al. 2006, Theissen & Melzer 2007). While it has become clear that the *Arabidopsis*- and *Antirrhinum*-based ABC(E) model of floral development is derived within eudicots but neither explains organ identity for all angiosperms nor helps infer mechanisms involved in the transition to flowers along the angiosperm stem lineage, the MIKC^c MADS-box genes in particular are likely to be involved in both reproductive organ identity and reproductive meristem specification in seed plants and thus in the ancestral flowering plant. Within the MADS-box genes involved in organ identity, the C- and B-class genes (*AGAMOUS*, *APETALA3*, *PISTILLATA*) and their functions appear to be conserved among angiosperms and gymnosperms, involved in reproductive specification, meristem determinancy, and male organ identity (Theissen & Becker 2004).

Presence of B- and C-class putative orthologs in gymnosperms implies that the MADS-box gene family had undergone duplication prior to the split of angiosperms from gymnosperms. In gymnosperms, C-class genes are expressed in both male and female reproductive organs and B-class genes are expressed mostly in male reproductive tissues. As mentioned, the differential spatial expression of B- and C-class genes is likely involved in the origin of bisexuality, regardless of which theory of floral origins is accepted. The early perianth could have evolved later with duplications in the MADS-box gene lineage leading to the origin and diversification of the E-class genes (*SEP1–SEP4*), possibly enabling more stringent control over spatial patterning of the B- and C-class genes (Theissen & Melzer 2007). E-class genes are unique to flowering plants and are required for the identity of all floral organs as well as meristem identity (Ditta et al. 2004). As such, they likely play a key role in the origin of the flower (Theissen & Melzer 2007). The eudicot perianth, or perhaps the perianth whorls of just a subset of eudicot lineages, would have evolved much later following subsequent duplication in the MADS-box lineage, leading to the A-class subfamily controlling sepal and petal development in *Arabidopsis*.

LEAFY. As discussed in the various theories of floral origin, *LEAFY* is a highly conserved activator of the A-, B-, C-, and E-class genes and plays a role in the specification of floral meristem identity. In both angiosperms and gymnosperms, *LFY* seems to mediate the transition from vegetative to reproductive growth (Dornelas & Rodriguez 2005, Frohlich & Parker 2000). A gymnosperm homolog, *NEEDLY*, is apparently lost in angiosperms and is proposed to be partly responsible for the condensation of male and female reproductive parts into a single axis (see Baum & Hileman 2006, Frohlich 2006).

WHY SO MANY SPECIES?

Perhaps a flower is best described as not a simple or single entity, but rather as a complex of innovations (Baum & Hileman 2006) that appears to have conferred evolutionary success on flowering plants, whether by efficient pollination enabling the successful maintenance of populations in lower densities without inbreeding depression or extinction (Regal 1977), or by increased reproductive isolation due to morphological innovations that altered pollinator specificity or flowering phenology (Grant 1971).

Certain attributes in the general form, both vegetative and reproductive, of angiosperms have been shown to favor high speciation rates, low extinction rates, or broad ecological tolerances (Crepet & Niklas 2009), all of which can individually or in combination lead to an extraordinary diversity of species. Several of these functions, such as annual growth form and propensity for hybrid polyploidy, are not necessarily functions of the flower itself. Other functions, however, are directly related to the flower. These include homeotic gene effects on floral trait evolution and duplications within the homeotic gene lineages leading to an expansion of floral morphospace upon which selection can act, leading to adaptive evolution, speciation, and diversification.

Plant-animal interactions have often been cited as a driving force in the evolution of flower morphology and in rapid diversification among angiosperm lineages. Although criticized for being "adaptationist" in nature, these theories have been empirically demonstrated in populations where a particular character can infer a shift in reproductive biology, leading to rapid loss of gene flow and subsequent isolation followed by character fixation (for recent reviews, see Fenster et al. 2004, Thomson & Wilson 2008). In the next sections we review some of the major trends in flower evolution and indicate how these trends have led to increased complexity and perhaps driven diversification over time.

ORGANIZATION AND EVOLUTIONARY TRENDS: ANCESTRAL TO DERIVED FEATURES

Below we detail various important trends in the evolution of the angiosperm flower (**Figure 3**), highlighting recent work in these areas and suggesting potential candidate genes that may be investigated to infer the roles of gene families and networks in the evolution of morphological form across flowering plants.

Phyllotaxis

Phyllotaxis, the geometry of lateral organ insertion, is defined by (*a*) the divergence angle formed by two successive primordia relative to the center of the flower and (*b*) the vertical displacement between initiation events of the two floral organs ("plastochron"). Phyllotaxis in reproductive meristems can be spiral, whorled, or random/chaotic (Endress & Doyle 2007). In spiral phyllotaxis, divergence angles and plastochrons are more or less equal. In whorled phyllotaxis, divergence angles and plastochrons are often equal (zero or very short) within each whorl but differ between whorls (Endress & Doyle 2007). In single flowers, phyllotaxis can differ between organ classes. Furthermore, organ initiation in flowers is often in a spiral whether phyllotaxis is whorled or spiral (Endress 1990). Within the basal angiosperms, spiral initiation has been recorded in the outer whorled organs of *Nuphar*, *Magnolia*, and several Annonaceae.

Ronse de Craene et al. (2003), and more recently Endress & Doyle (2009) mapped a broad swathe of floral characters onto a phylogenetic reconstruction of evolution in the basal angiosperms. With respect to phyllotaxy, Ronse de Craene demonstrated that a whorled perianth evolved concomitantly with a whorled androecium and that there were more reversions to spiral phyllotaxis in the androecium than in the perianth (Ronse de Craene et al. 2003). Floral phyllotaxis is much more labile in basal angiosperms than in the core eudicots and monocots (**Figure 3**). In the basal angiosperms, there are frequent transitions between whorled and spiral phyllotaxis in both the androecium and perianth, although whorled phyllotaxis predominates in the perianth (Endress & Doyle 2007). These frequent transitions between spiral and whorled phyllotaxis is perhaps because of open floral organization (Ronse de Craene et al. 2003). In the early diverging lineages, changes in floral phyllotaxis are uncomplicated owing to lack of synorganization, whereas

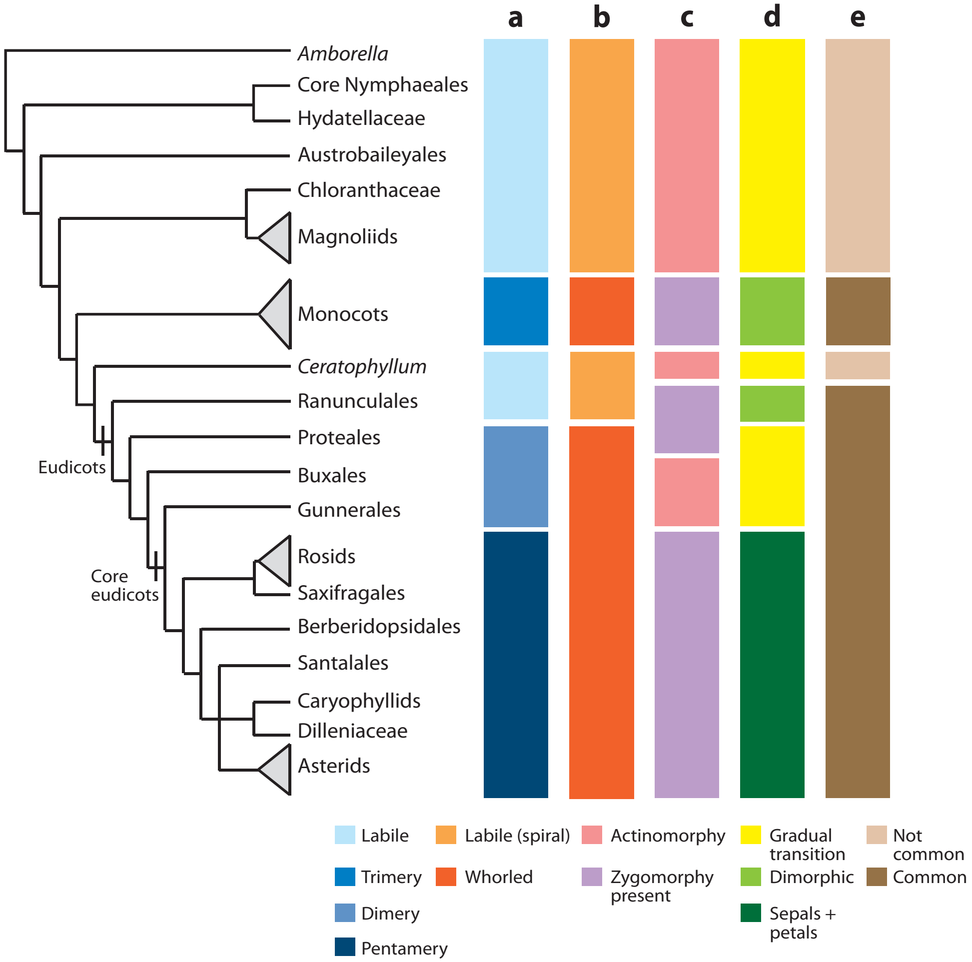

Figure 3

Major trends in angiosperm floral evolution. Except for symmetry and synorganization, character states in major angiosperm groups are colored according to the dominant state present in the categories of (*a*) merism, (*b*) phyllotaxis, (*c*) symmetry, (*d*) dimorphic perianth, and (*e*) synorganization. Basal angiosperms show far more lability in merosity (*a*) and phyllotaxis (*b*) than do more derived groups. Spiral phyllotaxis is also more common in the basal angiosperms. In terms of symmetry (*c*), zygomorphy is rare in the basal angiosperms, but is characteristic of many large and successful clades in the monocots and eudicots. Sharply delimited canonical sepals and petals are common in the core eudicots, but a dimorphic perianth (*d*) is common in both the monocots and the Ranunculales. A perianth with a gradual transition between outer and inner perianth organs or an undifferentiated perianth is common in the basal angiosperms and the basal eudicots. Synorganization (*e*) is rare in the basal angiosperms, but becomes an important trait in many monocot flowers and in the eudicots. Mapping such trends across the phylogeny, it becomes clear that certain characteristics held in common between monocots and eudicots (e.g., presence of zygomorphy, whorled phyllotaxis) are independently evolved and may involve the participation of different genes or gene networks in the major groups in which they occur. Other characteristics of the eudicots, such as pentamery and a perianth comprised of sepals + petals, are clearly unique to the eudicots, although similar, but likely nonhomologous, conditions may be found in other lineages (e.g., dimorphic perianth in monocots). Phylogeny adapted from **Figure 1**; references cited in text.

having numerous organs (rather than a fixed number) perhaps necessitates spiral phyllotaxis as a more efficient way of spacing (Endress & Doyle 2007).

Phyllotaxis in the eudicots and monocots is almost exclusively whorled (Ronse de Craene et al. 2003). The consolidation of whorled floral phyllotaxis is of extreme importance in floral evolution. Whorled phyllotaxis allows for greater synorganization of floral organs and subsequent floral diversification in derived angiosperm taxa, in both the eudicots (e.g., Asteraceae) and the monocots (e.g., Orchidaceae) (Endress 1990). Changes in phyllotaxis in vegetative shoots, however, do not appear to be as adaptive (Endress and Doyle 2007, Kuhlemeier 2007).

Progress has been made recently in elucidating the role of auxin in the generation of phyllotactic patterns of both leaf and flower initiation (Reinhardt et al. 2003). A conceptual model of how auxin transport regulates phyllotaxis was proposed based on results from molecular genetics (Reinhardt et al. 2003). PIN1 auxin efflux carrier orientation leads to localized regions of auxin accumulation in the shoot apical meristem, resulting in organ induction. Organ primordia act as auxin sinks, depleting auxin from neighboring cells. This ensures that new primordia are formed at a distance from already initiated primordia (Reinhardt et al. 2003). Various quantitative models of phyllotaxis have been proposed (e.g., Jonsson et al. 2006, Smith et al. 2006). The model of Jonsson et al. (2006) is of particular interest because it generates both spiral and whorled phyllotactic patterns, key for understanding floral phyllotaxis where both patterns frequently occur. [For a review of computer models of phyllotaxis, and a breakdown of general computer model structure for biologists, see Kramer (2008). For a more general review of phyllotaxis see Kuhlemeier (2007).]

Merosity

Merosity refers to the number of organs within floral organ classes, most often discussed in terms of the perianth (regardless of division into calyx and corolla) and the androecium. The gynoecium has undergone a series of reductions and secondary increases that often do not follow the trends observed in the perianth or androecium (Ronse de Craene et al. 2003).

Throughout the course of floral evolution there has been a trend toward fixation of a stable merosity in conjunction with whorled phyllotaxis (**Figure 3**). Along with whorled phyllotaxy and radial symmetry, a small fixed merosity is considered a prerequisite for the evolution of complex patterns of synorganization (Endress 1990). In basal angiosperms, perianth merosity is unstable with frequent transitions between variable merosity, dimery, trimery and pentamery. Although the ancestral character state for perianth merosity is equivocal (or trimerous if whorled; see Endress & Doyle 2009), both *Amborella* and the Austrobaileyales have variable perianth merosity. Throughout the basal angiosperms, androecium merosity corresponds largely to that of the perianth, although it is less stable than perianth merosity. Androecium merosity is variable for all three of the earliest diverging lineages—*Amborella*, Nymphaeales and Austrobaileyales—and is reconstructed as being ancestrally variable (Ronse de Craene et al. 2003).

Perianth merosity follows the same distribution as phyllotaxis: Spiral phyllotaxis is linked with an indefinite merosity. Pentamery has evolved at least three times in the basal angiosperms. Tetramery, thought to be derived from pentamery, is rare in basal angiosperms but is frequent where derived from trimery in Nymphaeaceae (Ronse de Craene et al. 2003). The number of perianth and androecium whorls also undergoes frequent changes in basal angiosperms, possibly because of low levels of synorganization and therefore less developmental constraint on organ and whorl number. Gynoecium merosity in the basal angiosperms is rarely higher than that of the perianth, and a reduction in carpel number to one has occurred multiple times (Ronse de Craene et al. 2003).

Stable merosity is a derived feature characteristic of the core eudicots and the monocots, with the majority of core eudicots displaying fixed pentamerous merosity and the majority of monocots fixed trimerous merosity (**Figure 3**). Pentamery in eudicots is thought to have evolved multiple times, as the branch leading to the core eudicots is consistently reconstructed as dimerous regardless of optimization method or scoring of problematic taxa (such as Proteaceae) (Soltis et al. 2003). The Gunnerales, moderately supported as sister to all other core eudicots, are dimerous (Soltis et al. 2003). Developmental work, however, suggests that the dimery in *Gunnera* is itself a derived feature (Wanntorp & Ronse de Craene 2005), thus confounding the ancestral state of merosity in the core eudicots. This interpretation, however, could be the result of a misconception in character optimization (see Endress & Doyle 2009).

Independent derivation of pentamery in the eudicots is supported by developmental work in *Meliosma* (Sabiaceae) and the Ranunculales. Sabiaceae are part of the basal grade of eudicots, but their exact position remains unclear (Ronse de Craene & Wanntorp 2008). Although organs are in whorls, floral development is spiral, resulting in atypical organ placement. Pentamerous flowers in *Meliosma* may have been derived from an ancestor with spirally arranged undifferentiated perianth parts (Ronse de Craene & Wanntorp 2008). Perianth pentamery associated with spiral phyllotaxis of stamens in Ranunculales is reconstructed to have evolved from a trimerous ancestor with whorled phyllotaxis (Damerval & Nadot 2007, Ronse de Craene et al. 2003). In both *Meliosma* and Ranunculales, derivation of pentamery is separate from the canalization of a pentamerous groundplan that occurred in core eudicots (**Figure 3**).

In addition to multiple transitions to pentamery, transitions from pentamery are not uncommon. Within the Asterids, eight independent transitions toward a variable perianth have occurred, often in the context of polyandry (Jabbour et al. 2008). In addition, the core eudicots are home to taxa with "encipient pentamery" such as that found in *Berberidopsis*. The Berberidopsidales may be sister to the Asterids plus Caryophyllales-Dilleniaceae and Santalales (Soltis et al. 2008). Floral phyllotaxis is spiral with a gradual transition from smaller outer tepals to larger inner tepals, traits typically associated with basal angiosperms but not most basal eudicots. Floral development, however, is much more regular than that found in basal angiosperm lineages (Ronse de Craene 2004). The transition from acyclic, spiral flowers such as those of *Berberidopsis* to whorled, pentamerous flowers characteristic of most core eudicots may have occurred within several eudicot lineages (Ronse de Craene 2004). Such "convergence" may indicate the release of cryptic variation in merosity, accumulated as a result of strict canalization into whorled pentamerous flowers (Flatt 2005). That is, the potential to be spiral and incipiently pentamerous may still exist in whorled, strictly pentamerous core eudicots and is realized multiple times independently. Alternatively, it may be the result of the repeated derivation of pentamery from an ancestor with spiral flowers within the core eudicots. The situation may not be as simple as that suggested by character state reconstructions, which indicate that the pentamerous flowers characteristic of the core eudicots were derived once from a dimerous ancestor (Magallon 2007, Soltis et al. 2003).

Trimery is reconstructed as ancestral in the monocots (Ronse de Craene et al. 2003) and is the most common state across monocots. Interesting deviations from trimery occur in the basal lineages of Asparagales. In Orchidaceae, a reduction of stamen number is associated with the development of zygomorphy although the monocot trimerous pattern is maintained by the position of the remaining stamens (Rudall & Bateman 2004). *Cucurligo* (Hypoxidaceae) displays polyandry, and it has been hypothesized that it may be a natural *ULT*, *SUPERMAN*, or *CARPEL FACTORY* mutant: All three genes manifest changes in floral organ number (Kocyan 2007). Pentamery and dimery, although rare, have both arisen in the monocots from trimery (Rudall et al. 2005). Orders such as Pandanales are particularly interesting for investigating evolution of merosity as the trait is relatively labile within this lineage and may occur through different developmental pathways.

Pentamery in *Pentastemona* (Stemonaceae: Pandanales) may occur via suppression of an outer tepal and stamen, and thus pentamery may be an intermediate between trimery and dimery, two states that do exist in the order: Pentamery, dimery, and tetramery are also present in the Triuridaceae (Rudall et al. 2005).

Mutants that control just floral organ merosity in *Arabidopsis* are rare. The majority of the floral organ number mutants identified in *Arabidopsis* are related to the control of meristem size. Many are in the *CLAVATA-WUSCHEL* (*CLV-WUS*) pathway and have pleiotropic effects on development. Evolution of floral meristem size regulation may well be key in the evolution of merosity, but this character is not very tractable for study in an evo-devo framework. One gene of possible interest in the *CLV-WUS* pathway is the SAND domain transcription factor *ULTRAPETALA* (Carles et al. 2005, Kocyan 2007). The loss-of-function *ult1 Arabidopsis* mutant shows an increase in the number of floral organs and flowers, presumably due to an increase in floral and inflorescence meristem size. Mutants also show a decrease in floral determinancy (Carles et al. 2005). It will be interesting to investigate this gene in basal angiosperms and naturally occurring oddities such as *Curculigo*. Perhaps there have been changes in copy number that have allowed for subfunctionalization and neofunctionalization of *ULT* genes. Another intriguing *Arabidopsis* gene is *PERIANTHA*. The loss-of-function mutant is pentamerous, a reversal from the derived tetramerous merosity characteristic of *Arabidopsis* (Chuang et al. 1999). *PERIANTHA* is a bZIP transcription factor and acts independently of pathways controlling meristem size and meristem identity (Chuang et al. 1999).

Symmetry

Three broad categories of floral symmetry can be defined: polysymmetry (actinomorphy), bilateral symmetry (zygomorphy, monosymmetry), disymmetry (two symmetry planes), and asymmetry (no symmetry plane). Symmetry is most often defined with respect to the perianth whorl alone, although by definition it should extend to all whorls. Perfect symmetry across all whorls and organ categories of the flower, that is, actinomorphy in its strictest sense, is not very common (Rudall & Bateman 2004). Floral zygomorphy, in which adaxial and abaxial sides of the flower differ, can result from differential elaboration, reduction, or suppression of organs in one or more whorls of the developing flower (Endress 1999). This change in floral bauplan has been termed "structural zygomorphy" (Rudall & Bateman 2004). Zygomorphy may also result from changes in color or organ orientation, but these more subtle changes to floral mode are not as deeply rooted in phylogeny (Rudall & Bateman 2004). Asymmetry is not widespread in flowers; it occurs most often in the form of either enantiostyly (stigma and style are curved to one side of the flower) or contort corolla aestivation (petals contorted to either the right or the left) (Endress 1999). Here we review the evolution of symmetry as it is most often discussed in the literature, in terms of the superficial appearance of the flower, which is typically due to modifications in the perianth and stamen whorls.

Zygomorphy is almost certainly a derived condition (**Figure 3**). The earliest known bisexual flowers are actinomorphic and appear in the fossil record around 120–125 Mya, whereas the first zygomorphic flowers do not appear until 30–40 million years later (Crane et al. 1995). Phylogenetic studies also indicate that zygomorphy is derived: There are very few zygomorphic flowers in the extant basal angiosperms, yet zygomorphy has arisen independently multiple times (at least 25) in the monocots and eudicots (reviewed in Endress 1999). The evolution of zygomorphy is considered a major trend in the evolutionary history of the angiosperms (Dilcher 2000). Zygomorphy is thought to promote reproductive isolation and concomitant speciation through encouraging pollinator specificity, and to have played a role in generating the diversity inherent in many large and successful angiosperm clades, such as Orchidaceae and Fabaceae (Dilcher 2000, Cubas 2004). Sister group comparisons confirm that zygomorphic lineages are more species-rich than are closely related actinomorphic lineages (Sargent 2004).

Closed floral ground plan: fixed organ number and arrangement

Zygomorphy is almost completely absent from basal angiosperms and is rare in early diverging eudicots (Endress 1999). Deviations from actinomorphy in basal angiosperms are often the result of extreme floral reduction (for example, *Chloranthus;* but note *Aristolochia*) (Ronse de Craene et al. 2003). Monocot flowers are also usually actinomorphic; complete radial symmetry is easier to achieve as floral organs are usually arranged in threes. Zygomorphy has, however, evolved at least four times in the monocots, occurring more in the Asparagales and commelinids than in other lineages (Rudall & Bateman 2004). Patterns of stamen expression and suppression are a major cause of differing symmetries and structural zygomorphy in monocots. Two patterns of structural zygomorphy occur: either adaxial (inner and outer) stamen suppression (pattern 1, often associated with labellum formation) or abaxial (outer) stamen suppression (pattern 2). Pattern 1 is more common, with pattern 2 occurring mostly in taxa embedded in pattern 1 clades (Rudall & Bateman 2004). In monocots and eudicots, structural zygomorphy is almost universally associated with oligandry (few stamens of a defined number) and fertile stamen suppression (either abortion or reduction to staminodes) (Endress 1999, Rudall & Bateman 2004).

In the early diverging eudicot lineage Ranunculales, zygomorphy is reconstructed to have evolved three times: once from disymmetry and twice from actinomorphy (Damerval & Nadot 2007). The case in the Ranunculales is unique in that perianth zygomorphy evolved in the context of both oligandry and polyandry (Damerval & Nadot 2007). The Ranunculales are one of the few orders where disymmetry exists: In the Fumarioideae, disymmetry evolved from actinomorphy (Damerval & Nadot 2007). Within the core eudicots, zygomorphy has evolved multiple times and is a characteristic of two extremely successful lineages, Fabaceae and Asteraceae. Using parsimony and a composite tree, zygomorphy in the asterids is reconstructed to have evolved 15 times independently from an actinomorphic ancestor, with 10 inferred reversals to actinomorphy (Jabbour et al. 2008). Surprisingly, zygomorphy evolved twice in the context of polyandry in two highly specialized genera, *Tupidanthus* (Araliaceae) and *Couroupita* (Lecythidaceae). Despite these two events, the evolution of zygomorphy in most asterids is most commonly associated with oligandry. Zygomorphy in most asterids and in the Ranunculales, two distantly related lineages, evolved in flowers with fixed perianth merism (Jabbour et al. 2008), supporting the hypothesis that the evolution of zygomorphy requires a fully integrated, closed floral ground plan (Endress 2001a, Jabbour et al. 2008).

It is in the eudicot clade that the developmental genetics of zygomorphy is best understood. Double mutants of the two class II TCP genes *CYCLOIDEA* (*CYC*) and *DICHOTOMA* (*DICH*) in *Antirrhinum majus* are actinomorphic, a change from the zygomorphic symmetry of wild-type flowers. *CYC* has different effects on different whorls of the *Antirrhinum* flower; it appears to promote growth of the dorsal petals while restricting growth of the dorsal stamen that aborts to become the staminode. CYC and the proteins acting in partnership with CYC (in particular RAD and DIV, two MYB domain transcription factors) control both floral symmetry on a large scale (the entire flower) and on a smaller scale (symmetry of individual organs) (Corley et al. 2005).

Correlations between changes in CYC-like gene expression patterns and evolutionary shifts in floral symmetry have been reported in many angiosperm taxa including *Mohavea* (Plantaginaceae), *Cadia purpurea* (Fabaceae), *Chirita hetrotricha* (Gesneriaceae), *Bournea* (Gesneriaceae), and *Iberis amara* (Brassicaceae) (Busch and Zachgo 2007, Citerne et al. 2006, Gao et al. 2008, Hileman et al. 2003, Zhou et al. 2008). Transgenic *Arabidopsis* plants overexpressing the closest *Iberis CYC* homolog, *IaTCP1*, had phenotypes that support a role for *IaTCP1* in controlling corolla zygomorphy in *Iberis* (Busch & Zachgo 2007).

Recently, it has been convincingly demonstrated that *CYC*-like genes also control symmetry in *Lotus* and *Pisum* (Fabaceae) (Feng et al. 2006, Wang et al. 2008), thus suggesting the role of the *CYC* family in the independent evolution of zygomorphy in *Antirrhinum* (Plantaginaceae) and Fabaceae. *Antirrhinum* has "lip" flowers in which the stamens are enclosed by the adaxial petal, wheras *Pisum* has "flag" flowers in which the pollination organs are enclosed by the abaxial keel (modified petals) (Endress 1996). In *Pisum*, floral symmetry is controlled by two TCP genes (*PsCYC2* and *PsCYC3*) and another uncharacterized single locus, *SYP1* (Wang et al. 2008). *PsCYC2* and *PsCYC3* appear to control adaxial-abaxial symmetry at the level of the entire flower, whereas *SYP1* controls individual organ asymmetry. The triple mutant is radially symmetric with all petals possessing an abaxialized identity (Wang et al. 2008). As in *Antirrhinum*, CYC-like genes in *Pisum* appear to control adaxial identity. *TCP1*, the closest *Arabidopsis* homolog, is likewise expressed in the adaxial side of the flower but does not appear to alter floral morphology. *TCP1* is also expressed asymmetrically in vegetative axillary meristems (Cubas et al. 2001). Genes with inherently asymmetric expression patterns may have been recruited throughout the course of evolution to generate asymmetric flowers along the adaxial-abaxial plane (Cubas 2004).

In Asteraceae, *CYC*-like genes seem to play a role not in controlling symmetry but in specifying floral identity across the inflorescence. In *Gerbera*, there are three distinct flower types: zygomorphic ray flowers, actinomorphic disk flowers, and intermediate trans flowers. One CYC-like gene (*GhCYC2*) is expressed only in ray flower primordia once the disk and ray flowers begin to differ morphologically and *GhCYC2* overexpresser lines have disk flowers with more ray-like characteristics (Broholm et al. 2008).

Asymmetry in *Senna* (Fabaceae) and Cannaceae and Marantaceae (Zingiberales) is derived from zygomorphy. Asymmetry in *Senna* may involve only the gynoecium (enantiostyly), but may also include the stamens and the petals. Changes in organ size, shape, and deflection are combined in various combinations to generate differing patterns of asymmetry (Marazzi & Endress 2008). In Cannaceae and Marantaceae one side of the single fertile stamen is petaloid and only one theca develops (Rudall & Bateman 2004).

Dimorphic Perianth

A perianth sharply delimited into morphologically distinct sepals and petals is a derived feature that has been gained and lost multiple times in angiosperms (**Figure 3**). The perianth of basal angiosperms is often described as "undifferentiated." More common than a truly undifferentiated perianth, however, is a gradual transition in morphology from inner to outer perianth organs (Ronse de Craene et al. 2003, Zanis et al. 2003). This perianth morphology is characteristic of *Amborella*, the Austrobaileyales, many magnoliids and the basal monocot lineages (Buzgo et al. 2004, Ronse de Craene et al. 2003, Staedler et al. 2007). The Nymphaeales are often described as possessing a dimorphic perianth (Ronse de Craene et al. 2003, Zanis et al. 2003), but detailed morphological studies suggest that despite some differences between inner and outer whorl organs, they are not typical sepals and petals (with the possible exception of *Nuphar*). In Nymphaeaceae a single perianth member can display both sepaloid (green coloration, nonpapillate flat cells, trichomes) and petaloid characteristics. Sepaloid features occur on regions of the perianth that are exposed in the developing bud (Warner et al. 2008).

All major clades of the core eudicots are reconstructed as biseriate and possessing both sepals and petals (Ronse de Craene 2008). The sharply differentiated perianth characteristic of most core eudicots is maintained by strictly controlled expression patterns of ABCE MADS-box genes. It has been hypothesized that the B-class genes (*AP3*, *PI*) are responsible for petaloidy in eudicots, as B-class mutants in *Arabidopsis* have an undifferentiated perianth of sepals (Coen & Meyerowitz

1991). Perhaps the diversification of this gene family has resulted in the evolution of petaloidy and perianth dimorphism. Suggestive evidence comes from work in the Ranunculales. In the majority of Ranunculaceae taxa examined and in all Berberidaceae taxa examined, *AP3-III*, the product of a putatively Ranunculales-specific gene duplication event, is expressed only in petals (Rasmussen et al. 2009). The case in the basal angiosperm *Persea* (Laurales), however, is different. *Persea borbonia* has inner and outer tepals of two different sizes, whereas *P. americana* has an undifferentiated perianth. The expression of C-class genes differs between the outer tepals of the two species, but B-class gene expression does not (Chanderbali et al. 2006). Hileman & Irish (2009) used functional and expression data to reconstruct ancestral *AP3* function, and perhaps elucidate *AP3*'s role in the evolution of the dimorphic perianth. Presumably due to a lack of sufficient data, no statistically significant relationships were found, but this is a potentially powerful technique that may be used to investigate the role of candidate genes in the evolution of morphology.

Synorganization

Synorganization has been recently reviewed (Endress 2006, Soltis et al. 2009) and so is only briefly discussed here. Synorganization is the result of either congenital or postgenital fusion of organs either in the same whorl (connation) or in two different whorls (adnation; much less common). Synorganization results in new functional "hyperorgans" and is hypothesized to be a key process in floral diversification (Endress 2006). The process has not been investigated in an evo-devo framework as yet, but there are several mutants in *Arabidopsis* and *Petunia* that could be of interest in investigating this phenomenon. Congenital fusion may be the result of confluent organ primordia or the failure of developing organs to separate from one another (Endress 2006). Separate organs in *Arabidopsis* are maintained by a complex network of cadastral genes that preserve the boundary regions of organs, characterized by a distinct set of cells (Aida & Tasaka 2006). The mutants of the transcription factors *PETAL LOSS* (*PTL*) and *RABBIT EARS* (*RBE*), either alone or in combination with other mutations, show varying degrees of sepal fusion (Brewer et al. 2004, Krizek et al. 2006). In *Petunia*, the NAC domain transcription factor *NO APICAL MERISTEM* (*NAM*) has mutants with extra petals fused to extra stamens (Souer et al. 1996). Another *Petunia* mutant of possible interest is *maewest*. This gene encodes a WOX-domain transcription factor, and mutants have both unfused petals and carpels (M. Vandenbussche A. Horstman, J. Zethof, R. Koes, A.S. Rijpkem, T. Gerats, submitted). It will be interesting to explore the function of these genes across angiosperms and investigate their potential role in the evolution of synorganization.

CONCLUSIONS AND FUTURE DIRECTIONS

While the origin and radiation of the angiosperms, and inherently therein the origin of the flower, are among the most widely addressed questions in plant biology using tools from paleobotany to molecular genetics, the major questions remain unresolved. The use of molecular genetics to investigate underlying homologies of organs has been widely cited as the key to resolving homology for which there are no morphological intermediates identified in extinct or extant lineages, but assignment of homology based on gene expression patterns is far from definitive and has been carried out in only a handful of groups.

Mode, mechanism, origin, and early diversification are still debated. The sudden appearance of angiosperm diversity that Charles Darwin so famously hailed as an "abominable mystery" in 1879 to a large extent remains a mystery today. Even as we learn more about the intricacies of molecular interactions that result in the development of individual flowers, we struggle to fully understand the evolution of those interactions and their role in creating the diversity of floral forms, both extant and extinct, that comprise the angiosperms.

It is intriguing to imagine a toolkit that existed in the common ancestor of angiosperms and gymnoperms that enabled the development of the flower (Floyd & Bowman 2007). Any changes in expression or regulation of the toolkit genes and their corresponding networks can be considered a potential venue for the evolution of floral form corresponding to shifts in meristematic activity, organogenesis, organ identity, and ultimately floral patterning. However, these developmental gene families have undergone massive amounts of duplication and diversification throughout the history of land plants, and orthologous genes found in modern representatives of early land plant lineages such as mosses, liverworts, and lycophytes (all nonflowering plants) may have had completely different roles in the reproductive or vegetative life cycles of these early lineages. Co-option of these genes and gene families to enable the development of the flower and subsequent diversification of function to enable the evolution of floral form remain exciting areas of research that are yet to be explored with the detail necessary to understand the developmental genetic origin and evolution of the flower. To study diversity at this level of detail, however, it seems prudent not to seek out full-blown model systems, but rather to look at natural floral diversity as a means of understanding floral evolution.

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*Erratum

LITERATURE CITED

Aida M, Tasaka M. 2006. Morphogenesis and patterning at the organ boundaries in the higher plant shoot apex. *Plant Mol. Biol.* 60:915–28

Ambrose BA, Espinosa-Matias S, Vazquez-Santana A, Vergara-Silva F, Martinez E, et al. 2006. Comparative floral developmental series of the Mexican triurids support a euanthial interpretation for the unusual floral structures of *Lacandonia schismatica* (Lacandoniaceae). *Am. J. Bot.* 93:15–35

APG. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linnean Soc.* 141:399–436

Arber EAN, Parkin J. 1907. On the origin of the angiosperms. *Bot. J. Linnean Soc.* 38:29–80

Bateman RM, Hilton J, Rudall PJ. 2006. Morphological and molecular phylogenetic context of the angiosperms: contrasting the "top down" and "bottom-up" approaches to inferring the likely characteristics of the first flowers. *J. Exp. Bot.* 57:3471–503

Baum DA, Hileman LC. 2006. A developmental genetic model for the origin of the flower. In *Flowering and its Manipulation*, ed. C Ainsworth, pp. 3–27. Sheffield, UK: Blackwell

Bowman JL. 1997. Evolutionary conservation of angiosperm flower development at the molecular and genetic levels. *J. Biosci.* 22:515–27

Brewer PB, Howles PA, Dorian K, Griffith ME, Ishida T, et al. 2004. PETAL LOSS, a trihelix transcription factor gene, regulates perianth architecture in the *Arabidopsis* flower. *Development* 131:4035–45

Broholm SK, Tahtiharju S, Laitinen RAE, Albert VA, Teeri TH, Elomaa P. 2008. A TCP domain transcription factor controls flower type specification along the radial axis of the *Gerbera* (Asteraceae) inflorescence. *Proc. Natl. Acad. Sci. USA* 105:9117–22

Busch A, Zachgo S. 2007. Control of corolla monosymmetry in the Brassicaceae *Iberis amara*. *Proc. Natl. Acad. Sci. USA* 104:16714–19

Buzgo M, Soltis PS, Soltis DE. 2004. Floral development and morphology of *Amborella trichopoda* (Amborellaceae). *Int. J. Plant Sci.* 165:925–47

Cantino PD, Doyle JA, Graham SW, Judd WS, Olmsted RG, et al. 2007. Towards a phylogenetic nomenclature of Tracheophyta. *Taxon* 56:822–46

Carles CC, Choffnes-Inada D, Reville K, Lertpiriyapong K, Fletcher JC. 2005. ULTRAPETALA1 encodes a SAND domain putative transcriptional regulator that controls shoot and floral meristem activity in *Arabidopsis*. *Development* 132:897–911

Chanderbali AS, Kim S, Buzgo M, Zheng Z, Oppenheimer DG, et al. 2006. Genetic footprints of stamen ancestors guide perianth evolution in *Persea* (Lauraceae). *Int. J. Plant Sci.* 167:1075–89

Chen JG, Ullah H, Young JC, Sussman MR, Jones AM. 2001. *ABP1* is required for organized cell elongation and division in *Arabidopsis* embryogenesis. *Genes Dev.* 15:902–11

Chuang C-F, Running MP, Williams RW, Meyerowitz EM. 1999. The *PERIANTHA* gene encodes a bZIP protein involved in the determination of floral organ number in *Arabidopsis thaliana*. *Genes Dev.* 13:334–44

Citerne HL, Pennington RT, Cronk QC. 2006. An apparent reversal in floral symmetry in the legume *Cadia* is a homeotic transformation. *Proc. Natl. Acad. Sci. USA* 103:12017–20

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

Corley SB, Carpenter R, Copsey L, Coen E. 2005. Floral asymmetry involves an interplay between TCP and MYB transcription factors in *Antirrhinum*. *Proc. Natl. Acad. Sci. USA* 102:5068–73

Crane PR. 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. *Ann. Missouri Bot. Garden* 72:716–93

Crane PR, Friis EM, Pedersen KR. 1995. The origin and early diversification of angiosperms. *Nature* 374:27–33

Crepet WL. 2008. The fossil record or angiosperms: requiem or renaissance. *Ann. Missouri Bot. Garden* 95:3–33

Crepet WL, Niklas KJ. 2009. Darwin's second "abominable mystery": Why are there so many angiosperm species? *Am. J. Bot.* 96:366–81

Cubas P. 2004. Floral zygomorphy, the recurring evolution of a successful trait. *BioEssays* 26:1175–84

Cubas P, Coen E, Zapater JM. 2001. Ancient asymmetries in the evolution of flowers. *Curr. Biol.* 11:1050–52

Damerval C, Nadot S. 2007. Evolution of perianth and stamen characteristics with respect to floral symmetry in Ranunculales. *Ann. Bot.* 100:631–40

Dilcher D. 2000. Toward a new synthesis: Major evolutionary trends in the angiosperm fossil record. *Proc. Natl. Acad. Sci. USA* 97:7030–36

Ditta G, Pinyopich A, Robles P, Pelaz S, Yanofsky MF. 2004. The *SEP4* gene of *Arabidopsis thaliana* functions in floral organ and meristem identity. *Curr. Biol.* 14:1935–40

Dornelas MC, Rodriguez APM. 2005. A *FLORICAULA/LFY* gene homolog is preferentially expressed in developing female cones of the tropical pine *Pinus caribaea* var. *caribaea*. *Genet. Mol. Biol.* 28:229–307

Doyle JA. 2008. Integrating molecular phylogenetic and paleobotanical evidence on the origin of the flower. *Int. J. Plant Sci.* 169:816–43

Doyle JA, Donoghue MJ. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. *Bot. Rev.* 52:321–431

Endress PK. 1990. Patterns of floral construction in ontogeny and phylogeny. *Biol. J. Linnean Soc.* 39:153–76

Endress PK. 1996. *Cambridge Tropical Biology Series; Diversity and Evolutionary Biology of Tropical Flowers*, pp. xiv+511 p. Cambridge, United Kingdom: Cambridge University Press

Endress PK. 1999. Symmetry in flowers: diversity and evolution. *Int. J. Plant Sci.* 160:S3–23

Endress PK. 2001a. Origins of flower morphology. *J. Exp. Zool.* 291:105–15

Endress PK. 2001b. The flowers in extant basal angiosperms and inferences on ancestral flowers. *Int. J. Plant Sci.* 162:1111–40

Endress PK. 2006. Angiosperm floral evolution: morphological developmental framework. *Adv. Bot. Res.* 44:1–61

Endress PK. 2008. Perianth biology in the basal grade of extant angiosperms. *Int. J. Plant Sci.* 169:844–62

Endress PK, Doyle JA. 2007. Floral phyllotaxis in basal angiosperms: development and evolution. *Curr. Opin. Plant Biol.* 10:52–57

Endress PK, Doyle JA. 2009. Reconstructing the ancestral angiosperm flower and its initial specializations. *Am. J. Bot.* 96:22–66

Endress PK, Igersheim A. 2000a. Gynoecium structure and evolution in basal angiosperms. *Int. J. Plant Sci.* 161:S211–23

Endress PK, Igersheim A. 2000b. The reproductive structures of the basal angiosperm *Amborella trichopoda* (Amborellaceae). *Int. J. Plant Sci.* 161:S237–48

Feng X, Zhao Z, Tian Z, Xu S, Luo Y, et al. 2006. Control of petal shape and floral zygomorphy in *Lotus japonicus*. *Proc. Natl. Acad. Sci. USA* 103:4970–75

Fenster CB, Armbruster WS, Wilson P, Dudash MR, Thomson JD. 2004. Pollination syndromes and floral specialization. *Annu. Rev. Ecol. Evol. Syst.* 35:375–403

Flatt T. 2005. The evolutionary genetics of canalization. *Q. Rev. Biol.* 80:287–316

Floyd SK, Bowman JL. 2007. The ancestral developmental tool kit of land plants. *Int. J. Plant Sci.* 168:1–35

Force A, Cresko WA, Pickett BF, Proulx SR, Amemiya C, Lynch M. 2005. The origin of subfunctions and modular gene regulation. *Genetics* 170:433–36

Friis EM, Crane PR, Raunsgaard Pedersen K, Bengtson S, Donoghue PCJ, et al. 2007. Phasecontrast X-ray microtomography links Cretaceous seeds with Gnetales and Bennettitales. *Nature* 450:549–52

Friis EM, Doyle JA, Endress PK, Leng Q. 2003. *Archaefructus*—Angiosperm precursor or specialized early angiosperm. *Trends Plant Sci.* 8:369–73

Friis EM, Pedersen KR, Crane PR. 2006. Cretaceous angiosperm flowers: innovation and evolution in plant reproduction. *Palaeogeogr. Paleoclimatol. Palaeoecol.* 232:251–93

Frohlich MW. 2006. Recent developments regarding the evolutionary origin of flowers. *Adv. Bot. Res.* 44:63–127

Frohlich MW, Parker DS. 2000. The Mostly Male theory of flower evolutionary origins: from genes to fossils. *Syst. Bot.* 25:155–70

Gao Q, Tao JH, Yan D, Wang YZ, Li ZY. 2008. Expression differentiation of CYC-like floral symmetry genes correlated with their protein sequence divergence in *Chirita heterotricha* (Gesneriaceae). *Dev. Genes Evol.* 218:341–51

Graham SW, Iles WJD. 2009. Different gymnosperm outgroups have (mostly) congruent signal regarding the root of flowering plant phylogeny. *Am. J. Bot.* 96:216–27

Graham SW, Olmsted RG. 2000. Utility of 17 chloroplast genes for inferring the phylogeny of the basal angiosperms. *Am. J. Bot.* 87:1712–30

Grant V. 1971. *Plant Speciation*. New York: Columbia Univ. Press

Hileman LC, Irish V. 2009. More is better: the uses of developmental genetic data to reconstruct perianth evolution. *Am. J. Bot.* 96:83–95

Hileman LC, Kramer EM, Baum DA. 2003. Differential regulation of symmetry genes and the evolution of floral morphologies. *Proc. Natl. Acad. Sci. USA* 100:12814–19

Irish V, Litt A. 2005. Flower development and evolution: gene duplication, diversification and redeployment. *Curr. Opin. Genet. Dev.* 15:454–60

Irish VF. 2003. The evolution of floral homeotic gene function. *BioEssays* 25:637–46

Jabbour F, Damerval C, Nadot S. 2008. Evolutionary trends in the flowers of Asteridae: Is polyandry an alternative to zygomorphy? *Ann. Bot.* 102:153–65

Jansen RK, Cai Z, Raubeson LA, Daniell H, dePamphilis CW, et al. 2007. Analysis of 81 genes from 64 chloroplast genomes resolves relationships in angiosperms and identifies genome-scale evolutionary patterns. *Proc. Natl. Acad. Sci. USA* 104:19369–74

Jaramillo MA, Kramer E. 2007. The role of developmental genetics in understanding homology and morphological evolution in plants. *Int. J. Plant Sci.* 168:61–72

Ji Q, Li B, Bowe LM, Liu Y, Taylor DW. 2004. Early Cretaceous *Archaefructus eoflora* sp. nov., with bisexual flowers from Beipiao, western Liaoning, China. *Acta Geol. Sin.* 78:883–96

Jonsson H, Heisler MG, Shapiro BE, Meyerowitz EM, Mjolsness E. 2006. An auxin-driven polarized transport model for phyllotaxis. *Proc. Natl. Acad. Sci. USA* 103:1633–38

Kim S, Soltis PS, Wall K, Soltis DE. 2006. Phylogeny and domain evolution in the APETALA2-like gene family. *Mol. Biol. Evol.* 23:107–20

Kinney MS, Columbus JT, Friar EA. 2008. Unisexual flower, spikelet, and inflorescence development in monoecious/dioecious *Bouteloua dimorpha* (Poaceae, Chloridoideae). *Am. J. Bot.* 95:123–32

Kocyan A. 2007. The discovery of polyandry in *Curculigo* (Hypoxidaceae): implications for androecium evolution of asparagoid monocotyledons. *Ann. Bot.* 100:241–48

Kramer EM. 2007. Understanding the genetic basis of floral diversity. *Bioscience* 57:479–87

Kramer EM. 2008. Computer models of auxin transport: a review and commentary. *J. Exp. Bot.* 59:45–53

Kramer EM, Di Stilio VS, Schluter PM. 2003. Complex patterns of gene duplication in the *APETALA3* and *PISTILLATA* lineages of the Ranunculaceae. *Int. J. Plant Sci.* 164:1–11

Krizek BA, Lewis MW, Fletcher JC. 2006. *RABBIT EARS* is a second-whorl repressor of *AGAMOUS* that maintains spatial boundaries in *Arabidopsis* flowers. *Plant J.* 45:369–83

Kuhlemeier C. 2007. Phyllotaxis. *Trends Plant Sci.* 12:143–50

Magallon S. 2007. From fossils to molecules: phylogeny and the core eudicot floral groundplan in Hamamelidoideae (Hamamelidaceae, Saxifragales). *Syst. Bot.* 32:317–47

Marazzi B, Endress PK. 2008. Patterns and development of floral asymmetry in *Senna* (Leguminosae, Cassiinae). *Am. J. Bot.* 95:22–40

McAbee JM, Hill TA, Skinner DJ, Izhaki A, Hauser BA, et al. 2006. *ABERRANT TESTA SHAPE* encodes a *KANADI* family member, linking polarity determination to separation and growth of *Arabidopsis* ovule integuments. *Plant J.* 46:522–31

Meyen SV. 1988. Origin of the angiosperm gynoecium by gametoheterotopy. *Bot. J. Linnean Soc.* 97:171–78

Mizukami Y, Fischer RL. 2000. Plant organ size control: *AINTEGUMENTA* regulates growth and cell numbers during organogensis. *Proc. Natl. Acad. Sci. USA* 97:942–47

Mondragon-Palomino M, Theissen G. 2007. MADS about the evolution of orchid flowers. *Trends Plant Sci.* 13:1360–85

Mondragon-Palomino M, Theissen G. 2009. Why are orchid flowers so diverse? Reduction of evolutionary constraints by paralogues of class B floral homeotic genes. *Ann. Bot.* 104:583–94

Moore MJ, Bell CD, Soltis PS, Soltis DE. 2007. Using plastid genomic-scale data to resolve enigmatic relationships among basal angiosperms. *Proc. Natl. Acad. Sci. USA* 104:19363–68

Mundry M, Stutzel T. 2004. Morphogenesis of the reproductive shoots of *Welwitschia mirabilis* and *Ephedra distachya* (Gnetales) and its evolutionary implications. *Org. Divers. Evol.* 4:91–108

Nixon KC. 2006. *Early flowering plants: evidence for and against aquatic habit and pollination syndromes*. Presented at Eur. Palaeobot. Palynol. Conf., 7th, Prague

Nole-Wilson S, Tranby TL, Krizek BA. 2005. AINTEGUMENTA-like (AIL) genes are expressed in young tissues and may specify meristematic or division-competent states. *Plant. Mol. Biol.* 57:613–28

Qiu Y-L, Li L, Hendry A, Li R, Taylor DW, et al. 2006. Reconstructing the basal angiosperm phylogeny: evaluating information content of mitochondrial genes. *Taxon* 55:837–56

Rasmussen DA, Kramer E, Zimmer EA. 2009. One size fits all? Molecular evidence for a commonly inherited petal identity program in Ranunculales. *Am. J. Bot.* 96:96–109

Regal PJ. 1977. Ecology and evolution of flowering plant dominance. *Science* 196:622–29

Reinhardt D, Pesce E-R, Stieger P, Mandel T, Baltensperger K, et al. 2003. Regulation of phyllotaxis by polar auxin transport. *Nature* 426:255–60

Ronse de Craene LP. 2004. Floral development of *Berberidopsis corallina*: a crucial link in the evolution of flowers in the core Eudicots. *Ann. Bot.* 94:741–51

Ronse de Craene LP. 2008. Homology and evolution of petals in the core eudicots. *Syst. Bot.* 33:301–25

Ronse de Craene LP, Soltis PS, Soltis DE. 2003. Evolution of floral structures in basal angiosperms. *Int. J. Plant Sci.* 164:S329–63

Ronse de Craene LP, Wanntorp L. 2008. Morphology and anatomy of the flower of *Meliosma* (Sabiaceae): implications for pollination biology. *Plant Syst. Evol.* 271:79–91

Rudall PJ, Bateman RM. 2004. Evolution of zygomorphy in monocot flowers: iterative patterns and developmental constraints. *New Phytol.* 162:25–44

Rudall PJ, Cunniff J, Wilkin P, Caddick LR. 2005. Evolution of dimery, pentamery and the monocarpellary condition in the monocot family Stemonaceae (Pandanales). *Taxon* 54:701–11

Rudall PJ, Remizowa MV, Beer A, Bradshaw E, Stevenson DW, et al. 2008. Comparative ovule and megagametophyte development in Hydatellaceae and water lilies reveal a mosaic of features among the earliest angiosperms. *Ann. Bot.* 101:941–56

Rudall PJ, Remizowa MV, Prenner G, Prychid CJ, Tuckett RE, Sokoloff DD. 2009. Nonflowers near the base of extant angiosperms? Spatiotemporal arrangement of organs in reproductive units of Hydatellaceae and its bearing on the origin of the flower. *Am. J. Bot.* 96:67–82

Rudall PJ, Sokoloff DD, Remizowa MV, Conran JG, Davis JI, et al. 2007. Morphology of Hydatellaceae, an anomalous aquatic family recently recognized as an early-divergent angiosperm lineage. *Am. J. Bot.* 94:1073–92

Saarela JM, Rai HS, Doyle JA, Endress PK, Mathews S, et al. 2007. A new branch emerges near the root of angiosperm phylogeny. *Nature* 446:312–15

Sargent RD. 2004. Floral symmetry affects speciation rates in angiosperms. *Proc. R. Soc. B* 271:603–8

Shigyo M, Hasebe M, Ito M. 2006. Molecular evolution of the *AP2* subfamily. *Gene* 366:256–65

Shigyo M, Ito M. 2004. Analysis of gymnosperm two-AP2-domain-containing genes. *Dev. Genes Evol.* 214:105–14

Smith RS, Guyomarc'h S, Mandel T, Reinhardt D, Kuhlemeier C, Prusinkiewicz P. 2006. A plausible model of phyllotaxis. *Proc. Natl. Acad. Sci. USA* 103:1301–6

Sokoloff DD, Remizowa MV, MacFarlane SA, Rudall PJ. 2008. Classification of the early-divergent angiosperm family Hydatellaceae: one genus instead of two, four new species, and sexual dimorphism in dioecious taxa. *Taxon* 57:179–200

Sokoloff DD, Rudall PJ, Remizowa MV. 2006. Flower-like terminal structures in racemose inflorescences: a tool in morphogenetic and evolutionary research. *J. Exp. Bot.* 57:3517–30

Sokoloff DD, Timonin AC. 2007. Morphological and molecular data on the origin of angiosperms: on a way to a synthesis. *J. Gen. Biol.* 68:83–97

Soltis DE, Bell CD, Kim S, Soltis PS. 2008. Origin and early evolution of angiosperms. *Ann. NY Acad. Sci.* 1133:3–25

Soltis DE, Senters AE, Zanis MJ, Kim S, Thompson JD, et al. 2003. Gunnerales are sister to other core eudicots: implications for the evolution of pentamery. *Am. J. Bot.* 90:461–70

Soltis PS, Brockington SF, Yoo M-J, Piedrahita A, Latvis M, et al. 2009. Floral variation and floral genetics in basal angiosperms. *Am. J. Bot.* 96:110–28

Soltis PS, Soltis DE, Kim S, Chanderbali A, Buzgo M. 2006. Expression of floral regulators in basal angiosperms and the origin and evolution of ABC-function. *Adv. Bot. Res.* 44:483–505

Souer E, vanHouwelingen A, Kloos D, Mol J, Koes R. 1996. The *NO APICAL MERISTEM* gene of *Petunia* is required for pattern formation in embryos and flowers and is expressed at meristem and primordia boundaries. *Cell* 85:159–70

Staedler YM, Weston PH, Endress PK. 2007. Floral phyllotaxis and floral architecture in Calycanthaceae (Laurales). *Int. J. Plant Sci.* 168:285–306

Sun G, Ji Q, Dilcher DL, Zheng SL, Nixon KC, Wang XF. 2002. Archaefructaceae, a new basal angiosperm family. *Science* 296:899–904

Theissen G, Becker A. 2004. Gymnosperm orthologues of class B floral homeotic genes and their impact on understanding flower origin. *Crit. Rev. Plant Sci.* 23:129–48

Theissen G, Becker A, Winter KU, Munster T, Kirchner C, Saedler H. 2002. How the land plants learned their floral ABCs: the role of MADS-box genes in the evolutionary origin of flowers. In *Developmental Genetics and Plant Evolution*, ed. QCB Cronk, RM Bateman, JA Hawkins, pp. 173–206. London: Taylor & Francis

Theissen G, Melzer R. 2007. Molecular mechanisms underlying origin and diversification of the angiosperm flower. *Ann. Bot.* 100:603–19

Thomson JD, Wilson P. 2008. Explaining evolutionary shifts between bee and hummingbird pollination: convergence, divergence, and directionality. *Int. J. Plant Sci.* 169:23–28

Wang Z, Luo YH, Li X, Wang LP, Xu SL, et al. 2008. Genetic control of floral zygomorphy in pea (*Pisum sativum* L.). *Proc. Natl. Acad. Sci. USA* 105:10414–19

Wanntorp L, Ronse de Craene LP. 2005. The *Gunnera* flower: key to eudicot diversification or response to pollination mode? *Int. J. Plant Sci.* 166:945–53

Warner KA, Rudall PJ, Frohlich MW. 2008. Differentiation of perianth organs in Nymphaeales. *Taxon* 57:1096–109

Wurschum T, Gross Hardt R, Laux T. 2006. *APETALA2* regulates the stem cell niche in the *Arabidopsis* shoot meristem. *Plant Cell* 18:295–307

Zanis M, Soltis DE, Soltis PS, Mathews S, Donoghue MJ. 2002. The root of the angiosperms revisited. *Proc. Natl. Acad. Sci. USA* 99:6848–53

Zanis MJ, Soltis PS, Qiu YL, Zimmer E, Soltis DE. 2003. Phylogenetic analyses and perianth evolution in basal angiosperms. *Ann. Mo. Bot. Garden* 90:129–50

Zhou X-R, Wang Y-Z, Smith JF, Chen R. 2008. Altered expression patterns of TCP and MYB genes relating to the floral developmental transition from initial zygomorphy to actinomorphy in *Bournea* (Gesneriaceae). *New Phytol.* 178:532–43

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