Evolution of Reproductive Morphology in the Papaveraceae s.l. (Papaveraceae and Fumariaceae, Ranunculales)

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ABSTRACT

Flower bearing branching systems are of major importance for plant reproduction, and exhibit significant variation between and within lineages. A key goal in evolutionary biology is to discover and characterize changes in the genetic programming of development that drive the modification and diversification of morphology. Here we present a synopsis of reproductive architecture in Papaveraceae s.l., a lineage in which the evolution of inflorescence determinacy, flower structure and symmetry, and effloration sequence produced unique reproductive syndromes. We discuss the potential of this group to study key issues on the evolution of reproductive structures, and refer to candidate gene families, choice of landmark species, and available tools for developmental genetic investigations.

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INTRODUCTION

The flower, the basic reproductive organ of angiosperms, is incomparably more diverse than equivalent structures found in any other group of organisms (Barrett 2002). This extraordinary reproductive variety is further increased by a wide range of specialized branching systems clustering flowers, the inflorescences (Weberling 1992), which expose flowers and then fruits with their seeds to ensure successful reproduction (Prusinkiewicz 2007). The evolution of flowers and inflorescences is logically tightly connected (Coen and Nugent 1994). The huge morphological diversity of flowers and inflorescences raises the question of its evolutionary origin through re-orchestration of genetic control elements. An integrated understanding of floral and inflorescence diversification constitutes a major task of plant evolutionary biology, and can also be expected to have a tremendous and economically relevant impact on plant breeding strategies. However, available evolutionary developmental (evo-devo) data on the topic remain so far mostly restricted to a few model systems widely dispersed within flowering plant lineages.

A great diversity of flowers and inflorescences is seen early in angiosperm history, a morphological radiation referred to as the "abominable mystery" by Darwin (Crepet 1998, 2000; Friedman 2009). In fact, principal trends such as floral symmetry shifts and synorganization, are already found in the fossil record and in extant basal angiosperms, but further appear recurrently throughout angiosperm phylogeny (Soltis *et al.* 2009). This makes it difficult to infer ancestral character states in the reconstruction of the "primitive" flower (for one of the most recent attempts, see Endress and Doyle 2009). The fundamental problem that evolutionary developmental biology addresses is the correspondence of morphological traits and their underlying developmental processes in the comparison of different lineages. A common approach is to study the genetic regulation of specific morphological traits in isolation. However, traits are often functionally linked and may exhibit coordinate evolution. Understanding the genetic basis of the evolution of such morphological syndromes requires a thorough examination of multiple traits that show interdependency. A prime example is the coordinated evolution of flower and inflorescence morphology. So far, studies have
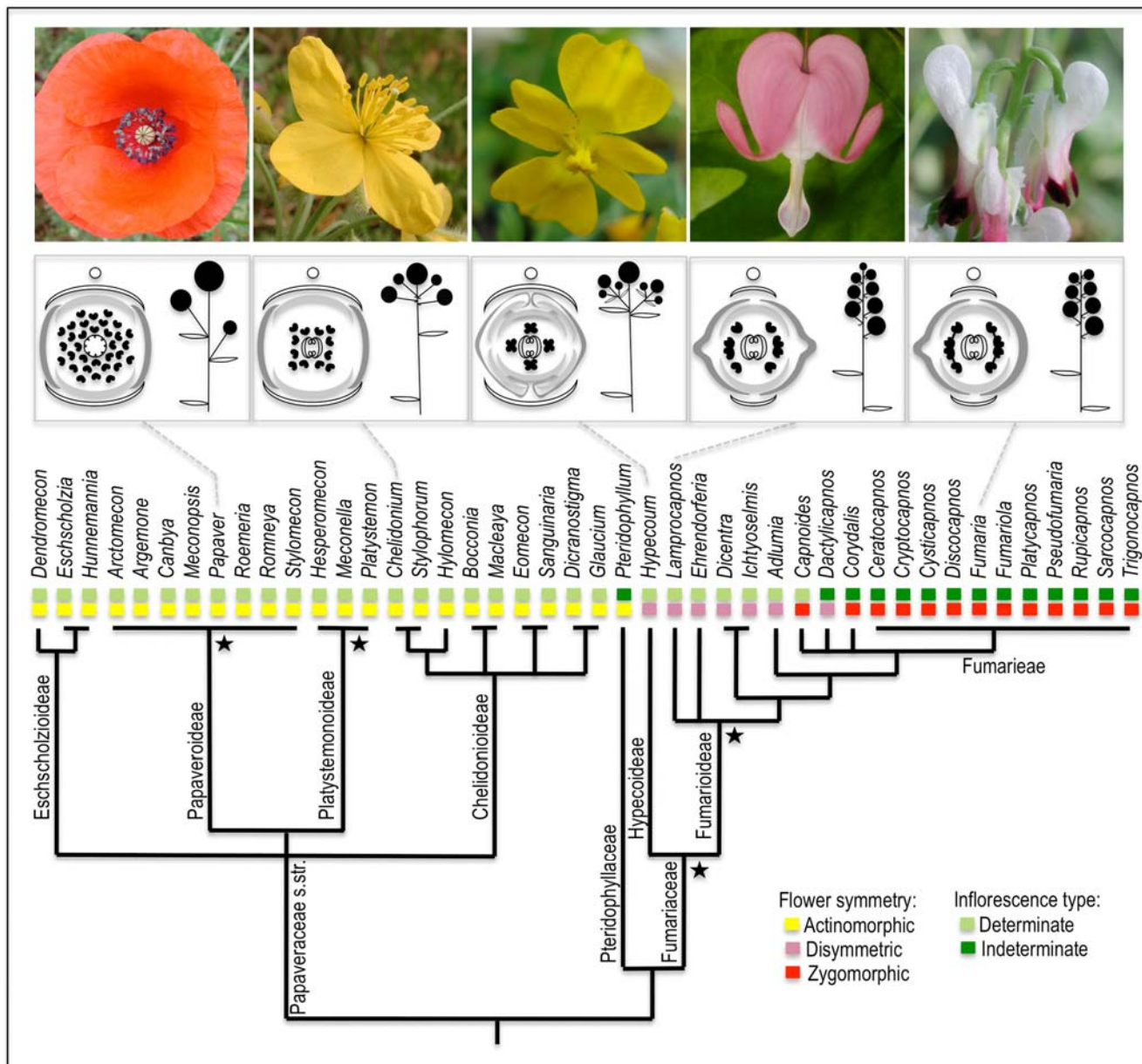
Invited Review

Fig. 1 Summarized phylogeny of the Papaveraceae s.l. based on molecular inferences and traditional classifications (Hoot *et al.* 1997; Lidén *et al.* 1997; Wang *et al.* 2009, and references therein). Flower symmetry and determinate/indeterminate inflorescence states are indicated for all genera. Flower picture, flower diagram and inflorescence type scheme are given for some selected representatives of the family throughout its phylogeny. ★: Taxonomic groups of traditional classifications for which monophyly is not confirmed by current molecular data.

revealed an astonishing degree of conservation of developmental mechanisms across flowering plants. Therefore, for non-model lineages, a candidate gene approach that uses the evidence from established model systems remains a straightforward and powerful strategy to address morphological evolution. Because the current major model systems are representatives of either core eudicots (e.g. *Antirrhinum* L., *Arabidopsis* (DC.) Heynh.) or monocots (e.g. *Oryza* L.), and efforts understandably concentrate on plants of economic importance, it has been realized that research in basal angiosperms and basal eudicots is especially needed, as it will be instrumental in deciphering major evolutionary transitions in the regulation of development (Soltis *et al.* 2002).

Research in the Papaveraceae s.l. may be a very useful response to this current need. This family belongs to the Ranunculales, the order which diverged first in the eudicot lineage (Soltis *et al.* 2007c; APG III 2009), and is early branched within the order (Kim *et al.* 2004a; Soltis *et al.* 2007c; Wang *et al.* 2009). The phylogenetic position of Ranunculales, between the core eudicot and grass model systems, makes the group suitable for evolutionary-deve-

lopmental studies in angiosperms (Kramer 2009). The poppy relatives in the broad circumscription (Papaveraceae s.l.), comprise around 760 species and 44 genera (Stevens 2001 onwards), and is constituted of two main groups, the Papaveraceae (poppies in the narrower sense) on the one hand, and the Fumariaceae on the other (the fumitory family; or Fumarioideae subfamily of Papaveraceae s.l.). An isolated taxon, *Pteridophyllum racemosum* Siebold & Zucc., often viewed as a separate family Pteridophyllaceae (or Pteridophylloideae subfamily of Papaveraceae s.l.), may be sister to Fumariaceae (Wang *et al.* 2009; **Fig. 1**). Papaveraceae s.l. has attracted researchers because various diversity patterns invite comparative studies. The family received much attention for its biochemical richness in alkaloids (Hesse 2002; Ziegler *et al.* 2006). Diversity in leaf shape (Gleissberg and Kadereit 1999) and inflorescence morphology (Günther 1975a, 1975b) has also been studied.

Therefore, Papaveraceae s.l. is a useful lineage to draw comparisons between major angiosperm clades such as eudicots and monocots, as well as to elucidate the emergence of diversity within a well-defined group. In recent years, the

Table 1 Overview of candidate gene studies related to flower and inflorescence development in Papaveraceae s.l. Sequencing, expression and functional aspects are taken into account.

Genes	Species	Papaveraceae homologs	Expression data														Functional data
			IM	FM	B1	B2	B3	B4	F	Fab	Fad	Se	P	St	C	O	
AGAMOUS	Eschscholzia californica	EScaAG1 [1]		+								-	-	++	++	++	
		EScaAG2 [1]		+								-	-	++	++	++	
		EScaAGL11 [1]															
	Sanguinaria canadensis	ScAG [2]															
AINTEGUMENTA	Eschscholzia californica	[3]															
APETALA1/ FRUITFULL	Chelidonium majus	CmFL1 [4]															
		CmFL2 [4]															
	Papaver nudicaule	PapnFL1 [4]															
		PapnFL2 [4]															
	Papaver somniferum	PapsFL1 [4]															
		PapsFL2 [4]															
APETALA3	Dicentra eximia	DeAP3 [5,6]										-	++	++	+		
	Papaver californicum	PcAP3 [5]															
	Papaver nudicaule	PnAP3-1 [5,6]										-	++	++	+		
		PnAP3-1 [5,6]										-	+	++	+		
	Papaver somniferum	PapsAP3-1 [7]										-	++	++	-		VIGS
		PapsAP3-2 [7]										-	++	++	-		VIGS
	Sanguinaria canadensis	ScAP3 [8]										+	++	++	++		
CRABS CLAW	Eschscholzia californica	EcCRC [9]		+								-	-	-	++	++	VIGS
CYCLOIDEA	Capnoides sempervirens	CsemTCP1 [10]															
		CsCYL1 [11]			+	-	-										
		CsCYL2 [11]			+	-	-										
	Chelidonium majus	CmajTCP1 [10]															
		CmCYL1 [11]			+	+	-										
		CmCYL2 [11]			+	+	+										
	Cysticapnos vesicarius	CvCYL1 [11]															
		CvCYL2A [11]															
		CvCYL2B [11]															
	Dactylicapnos torulosa	DtorTCP1 [10]															
		DtCYL1 [11]															
		DtCYL2 [11]															
	Eschscholzia californica	EcalTCP1 [10]				++	++		-	++	++						
		EcaTCP2 [10]				++	++		++	++	++						
	Fumaria vaillantii	FvaiTCP1 [10]															
		FvaiTCP2 [10]															
	Hypecoum imberbe	HimbTCP1 [10]															
		HimbTCP2 [10]															
		HimbTCP3 [10]															
	Hypecoum procumbens	HpCYL1 [11]															
		HpCYL2 [11]															
	Lamprocapnos spectabilis	LspeTCP1 [10]															
		LsCYL1 [11]			++	-	-	-									
		LsCYL2 [11]			+	-	-	-									
	Papaver rhoeas	PrCYL1 [11]															
		PrCYL2 [11]															
	Pseudofumaria alba	PalbTCP1 [10]							++	++	++						
	Ronmeya coulteri	RcouTCP1 [10]															
FLORICAULA	Eschscholzia californica	EcFLO [12,13]	++	++					++			-	++	++	-		
PISTILLATA	Dicentra eximia	DePI [5,6]										-	++	++	+		
	Papaver nudicaule	PnPI-1 [5,6]										-	++	++	+		
		PnPI-2 [5,6]										-	+/-	-	-		
	Papaver somniferum	PapsPI-1 [7]										-	++	++	-		VIGS
		PapsPI-2 [7]										-	+	+	+		VIGS
	Sanguinaria canadensis	ScPI [8]										+	++	++	-		
SEPALLATA	Papaver nudicaule	PapnSEP3 [4]															

[1] Zahn et al. (2006), [2] Kramer et al. (2003b), [3] Kim et al. (2006), [4] Litt and Irish (2003), [5] Kramer et al. (1998), [6] Kramer and Irish (1999), [7] Drea et al. (2007), [8] Kramer and Irish (2000), [9] Orashakova et al. (2009), [10] Kölsch and Gleissberg (2006), [11] Damerval et al. (2006), [12] Busch and Gleissberg (2003), [13] Becker et al. (2005).

establishment of developmental genetic tools in members of the family have opened new avenues of research. So far, developmental genetic work has focused on *Eschscholzia californica* Cham. (Busch and Gleissberg 2003; Becker *et al.* 2005; Groot *et al.* 2005; Carlson *et al.* 2006; Wege *et al.* 2007; Orashakova *et al.* 2009), and the economically important *Papaver somniferum* L., the opium poppy (Hileman *et al.* 2005; Drea *et al.* 2007). In fact, functional studies are until now exclusively carried out in these two species, using virus-induced gene silencing that was first developed by Hileman *et al.* (2005) in *P. somniferum*, and subsequently established by Wege *et al.* (2007) in *Eschscholzia californica*. Nevertheless, evo-devo questions on reproductive characters result in the need to enlarge the taxonomic representation of Papaveraceae s.l. to include species with different reproductive features (Kramer *et al.* 1998; Kramer and Irish 1999, 2000; Kramer *et al.* 2003b; Damerval *et al.* 2007; Kölsch and Gleissberg 2006; **Table 1**).

We discuss here the diversity of reproductive architecture in Papaveraceae s.l., paying special attention to inflorescence determinacy, flower structure and symmetry, and effloration (the blooming sequence). We suggest candidate

gene families that may help to elucidate how the developmental regulation of these traits underwent modifications that gave rise to the present diversity, and review work already done using this approach.

FLORAL AND INFLORESCENCE DIVERSITY IN PAPAVERACEAE S.L.

Floral diversity

The flower of Papaveraceae s.l. is bisexual and usually presents a dimeric ground plan, although trimerous flowers are also common in Papaveraceae. Trimery characterizes some taxonomic groups as a whole (the subfamily Platystemonoideae, *Canbya* Parry ex A.Gray, and *Romneya* Harv., Ernst 1962). Furthermore, some genera (*Arctomecon* Torr. & Frem., *Argemone* Tourn. ex L., *Papaver* L.) and even species (*Dendromecon rigida* Benth.) exhibit both dimeric and trimeric flowers (Ernst 1962). The perianth is generally triseriate consisting of one whorl of sepals and two alternating whorls of petals, with the exceptions of *Bocconia* Plum. ex L. and *Macleaya* R.Br. (apetalous), and some *Meconopsis* Vig. and *Sanguinaria* L. (polypetalous, Ernst 1962). Papaveraceae perianth parts are free (except in *Eomecon* Hance and *Eschscholzia* Cham., which are synsepalous), and not elaborate, whereas in Fumariaceae petals are fitted with different kinds of wings, joints and/or spurs, and the outer and inner whorls are dissimilar (Lidén 1986; Endress and Matthews 2006). Furthermore, petaloid sepals are found in all Fumarioideae. Stamens of Papaveraceae are usually numerous and arranged in several whorls, even though only two series are found in *Meconella californica* Torr., and one in *Canbya candida* Parry ex A. Gray, *Meconella denticulata* Greene and *M. oregana* Nutt. ex Torr. & A. Gray (Ernst 1962). The androecium of the remaining Papaveraceae s.l. develops four stamens in *Pteridophyllum* Siebold & Zucc. and *Hypecoum* L., and six stamens that are partially fused in two bundles within Fumarioideae (Ernst 1962; **Fig. 1**). The gynoecium is two- to many-carpelled in Papaveraceae, and two-carpelled in Fumariaceae and Pteridophyllaceae, and has parietal placentation throughout (Murbeck 1912).

Papaveraceae s.l. presents a unique case of evolutionary transitions in floral symmetry (Kölsch and Gleissberg 2006; Damerval *et al.* 2007). Papaveraceae and *Pteridophyllum* flowers are polysymmetric (or actinomorphic), which is thought to be the ancestral character state in the family (e.g. *Papaver* and *Chelidonium* Tourn. ex L., **Fig. 1**). Disymmetric flowers arose in the Fumariaceae through morphological differentiation of the two petal whorls, a process that can involve the formation of spurs in both outer petals (e.g. *Hypecoum* and *Lamprocapnos* Endl., **Fig. 1**). Disymmetry in Fumariaceae flowers also involves the androecium (Damerval and Nadot 2007). The reduction of symmetry planes can continue to monosymmetry (or zygomorphy), when only one of the two outer petals forms a spur (e.g. *Fumaria* L., **Fig. 1**). Monosymmetry in the Fumariaceae is quite peculiar because it develops in the transverse plane instead of the usual median plane. Interestingly, a 90 degree torsion of the pedicel before anthesis leads to a secondarily vertical orientation of the symmetry plane ("transverse zygomorphy", Weberling 1992; Endress 1999). Furthermore, some species present alternatively disymmetric or monosymmetric flowers depending on the environmental conditions (e.g. *Corydalis cheilanthifolia* Hemsl., Tebbitt *et al.* 2008).

Floral homeosis has evolved twice in Papaveraceae. In *Macleaya*, all the petals are replaced by stamens (**Fig. 2B**), whereas *Sanguinaria canadensis* L. shows additional petals in the location of the more external stamens (Lehmann and Sattler 1993, Ronse de Craene 2003; **Fig. 2C**).

Inflorescence diversity

The Papaveraceae s.l. flowers are aggregated in reproductive shoot systems usually formed by the primary shoot in which all meristems eventually develop into flowers. Vegetative renewal may occur from axillary meristems close to the base of the plant, allowing perennial growth. In a few exceptions to this rule, flowering shoots form only laterally while the main shoot remains vegetative. This is the case in the climbing fumitory *Adlumia* Raf. ex DC., where inflorescences occupy an axillary position while the main axis grows indeterminately (Lidén 1986). In *Dicranostigma lactucoides* Hook. f. & Thomson, the main shoot continues to grow as a vegetative rosette, and inflorescences form only laterally (Günther 1975a). Flowers often cluster in determinate inflorescences, in which the apical meristem of the primary shoot converts to a flower. Determinate (or closed) inflorescences may occur as cymes (e.g. *Hypecoum*, **Fig. 1**), botryoids (a raceme with a terminal flower, e.g. *Lamprocapnos*, **Fig. 1**), or panicles (*sensu* Weberling, 1992; e.g. *Macleaya*, **Fig. 2B**). Indeterminate (or open) inflorescences, in which the primary shoot meristem is aborted after formation of lateral flowers, are only found in Fumariaceae (e.g. racemes of *Fumaria*, **Fig. 1**), where they are associated with monosymmetric flowers. Therefore, characteristic reproductive syndromes are found in this family in which floral polysymmetry and disymmetry are associated with closed inflorescences, and monosymmetry with open inflorescences (Kölsch and Gleissberg 2006; **Fig. 1**). However, three interesting exceptions occur. Firstly, in *Capnoides* Mill., monosymmetric flowers form in a determinate inflorescence (**Fig. 1**). In angiosperms, monosymmetric flowers are almost always associated with indeterminate inflorescences because the lateral position of flower primordia is thought to provide a positional clue for adaxial-abaxial patterning. Exceptions are extremely rare, and besides *Capnoides* in the Fumariaceae, monosymmetric flowers in terminal position have only been reported for *Schizanthus* Ruiz & Pav. in the Solanaceae (Coen and Nugent 1994). Secondly, in *Dactylicapnos* Wall., disymmetric flowers are grouped in an open inflorescence. The phylogenetic positions of *Capnoides* and *Dactylicapnos* are not resolved (**Fig. 1**), so that it remains unclear if the unusual character combinations found in these genera arose through reversals or through parallel evolution. For example, disymmetry in *Dactylicapnos* may have evolved from monosymmetric ancestors. Lastly, the isolated *Pteridophyllum* has polysymmetric flowers born on an indeterminate inflorescence. While this character combination is common in other angiosperm lineages, and appears e.g. in *Arabidopsis*, it occurs singly in this isolated taxon within Papaveraceae s.l. Taken together, three characteristic and widespread floral syndromes that link inflorescence determinacy and flower symmetry are found in Papaveraceae s.l. (actinomorphic flowers/determinate inflorescence, disymmetric flowers/determinate inflorescence, zygomorphic flowers/indeterminate inflorescence). However, three taxa are interesting "rule-breakers" with unusual syndromes, making this family particularly suitable for studying the connection between inflorescence determinacy and floral symmetry (**Fig. 1**).

Inflorescences differ not only with regard to determinacy. Some Papaveraceae, such as members of *Eschscholzia*, *Papaver*, and *Meconopsis*, have solitary flowers born on elongated leaf-less end internodes. These "full rosette plants" (Günther 1975b) resemble "flowering rosettes" found in some Brassicaceae (Yoon and Baum 2004), but differ in that their primary shoot also forms a flower. In contrast to the more common half-rosette plants, leaves preceding the solitary flower in full rosette plants are not elevated by internodes and remain close to the ground (**Fig. 2D**). Solitary flowers also occur in rhizomateous genera such as *Sanguinaria*, a chelidonioid poppy, and are infrequently found in Fumariaceae (e.g. *Dicentra uniflora* Kellogg).

The blooming sequence, or effloration, is not a commonly documented character in plant groups, despite its probable great evolutionary significance (Sell 1969). This trait has been systematically studied in Papaveraceae (Gün-
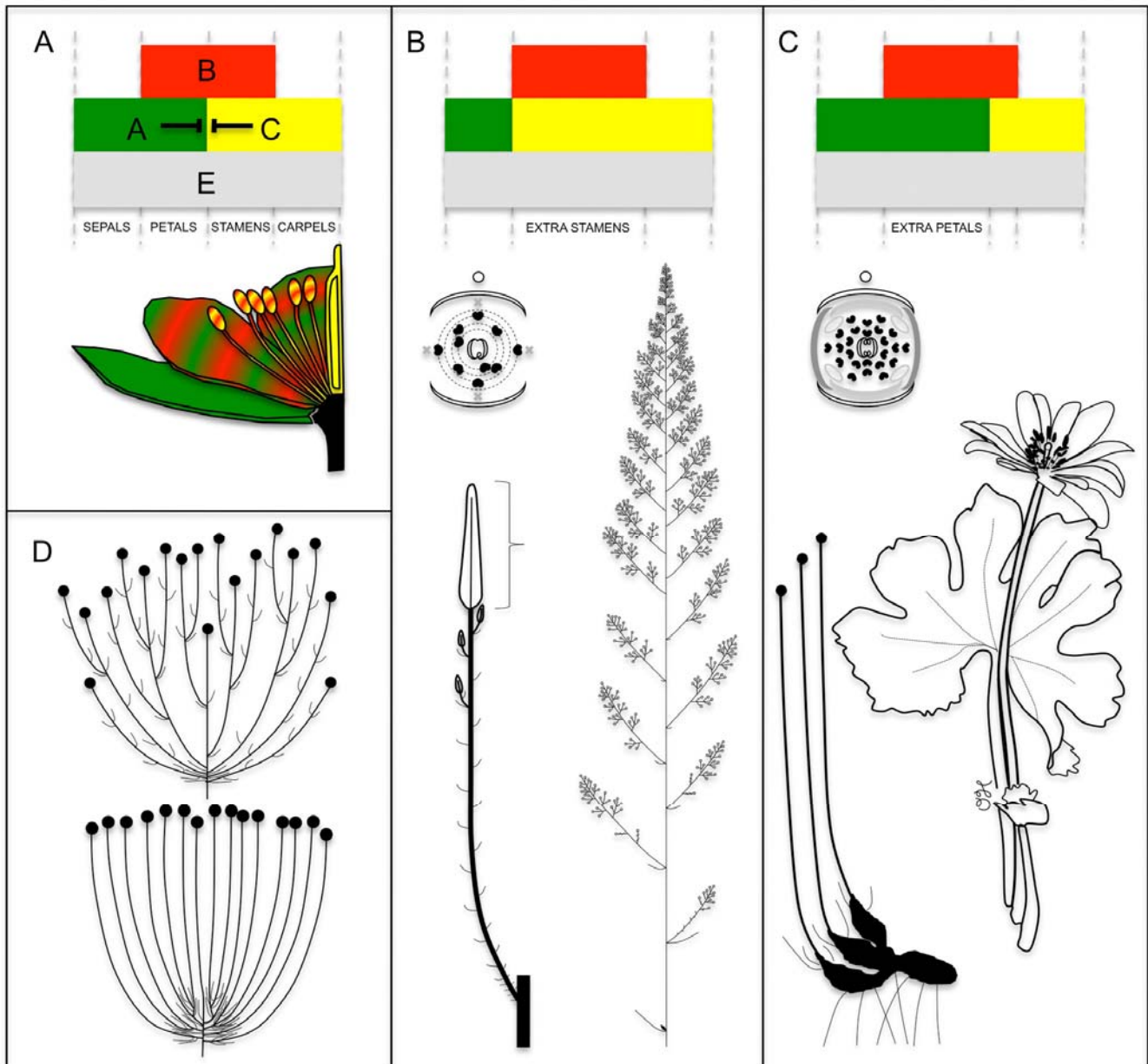
Fig. 2 The ABCE model of floral organ specification. Classic (**A**), as inferred for *Macleaya* (**B**), and *Sanguinaria* (**C**). Illustrations of floral and inflorescence features are provided for the two taxa. **D**. Architecture of *Eschscholzia caespitosa* Benth. (above) and *E. lobbii* Greene (below), illustrating the transition from half rosette to full rosette growth by restriction of elongation to the internode below the single flower (redrawn from Günther 1975a, 1975b). Floral diagram of *Macleaya microcarpa* Fedde in (**B**) from Karrer (1991) and *Sanguinaria canadensis* in (**C**) from Lehmann and Sattler (1993).

ther 1975a, 1975b), but is less well documented in Fumariaceae. Changes in effloration accompany evolutionary transitions in which the unit of pollinator attraction shifts from a single large flower to inflorescences of increasing orders (Sell 1969; Maresquelle 1970). In accordance with this trend, plants with large singly exposed flowers have a basipetal effloration, the terminal flower opening first, followed by lateral flowers that bloom in the order of their proximity to the terminal flower (e.g. *Papaver*, **Fig. 1**). The same sequence is found in the dichasium of *Hypecoum* (**Fig. 1**). An inverse effloration sequence occurs in plants in which the inflorescence constitutes an attraction unit. *Chelidonium* (**Fig. 1**) has a corymb-like determinate inflorescence in which the terminal flower blooms first, followed by acropetal effloration of the lateral flowers. Effloration in *Bocconia* and *Macleaya* is almost completely acropetal, with the terminal flower the last to bloom (Ernst 1962). In some Fumariaceae, such as *Lamprocapnos* (**Fig. 1**), effloration is completely acropetal even while a terminal flower persists. Acropetal effloration is also the rule in all species with indeterminate inflorescences, e.g. *Fumaria* (**Fig. 1**).

CANDIDATE GENE APPROACHES TO FLOWER AND INFLORESCENCE DIVERSITY IN PAPAVERACEAE S.L.: STATE-OF-THE-ART AND PROSPECTS

Floral organ identity genes

Papaveraceae, unlike other Ranunculales such as Ranunculaceae, has flowers with a distinct bipartite perianth, a pattern otherwise typical for core eudicots. This similarity with core eudicots makes the Papaveraceae particularly suitable for comparative studies of genetic pathways controlling floral organ identity.

Floral organs acquire their specific identity during development through the action of homeotic genes that act as major developmental switches between genetic programs specific for a particular organ (for an overview, see Theissen and Melzer 2007). Activity and interactions of floral homeotic genes have been summarized in the "ABC model" based on the observation of mutant phenotypes in *Arabidopsis* and *Antirrhinum* (Coen and Meyerowitz 1991). In this model, A class genes account for sepal formation, A and
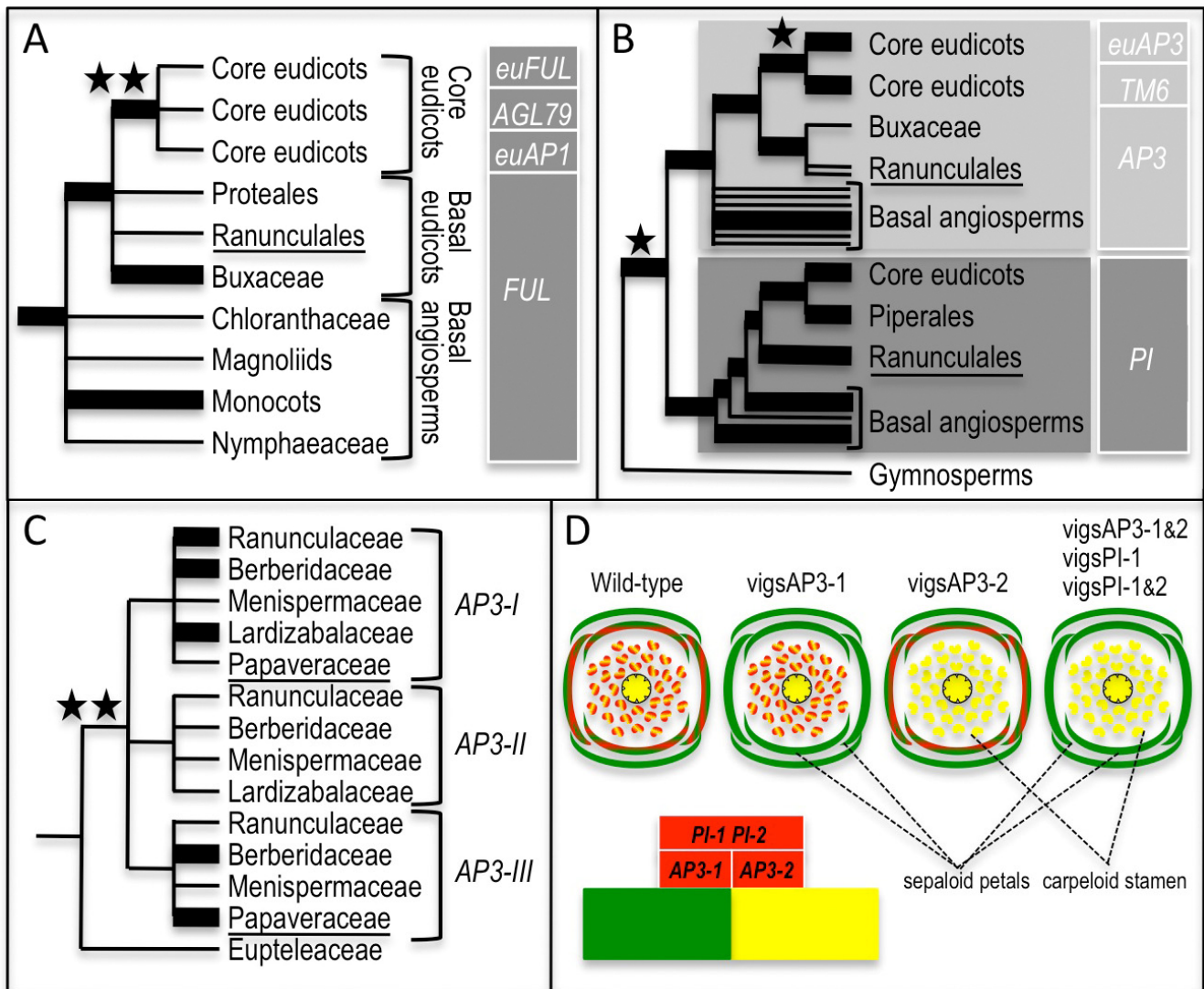
Fig. 3 Summarized phylogenies of some genes of the ABCE model. (**A**) *AP1/FUL* lineage in angiosperms (based on Shan *et al.* 2007), (**B**) *AP3/PI* lineage in angiosperms (based on Kim *et al.* 2004b), (**C**) detail of *AP3* lineage in Ranunculales (based on Rasmussen *et al.* 2009). Bold lines correspond to branches with significant statistical support (bootstrap values ≥70%, and/or posterior probabilities ≥95%). Stars indicate putative duplication events. **D**. Phenotypes obtained by VIGS of *AP3* and *PI* paralogs in *Papaver somniferum* (based on Drea *et al.* 2007), and deduced organization of these paralogs in the ABCE model.

B for petals, B and C for stamens and C for carpels (**Fig. 2A**). Class D genes implicated in ovule identity were proposed later (Angenent and Colombo 1996), however, a group of redundant genes active in all whorls, termed E class, became an essential part of the model that is now often referred to as the ABCE model (Theissen 2001; **Fig. 2A**). Most ABCE genes are members of the same family of transcription factors, type II MIKC MADS-box genes. In *Arabidopsis*, A function is specified by *AP1* and *APETALA2* (not a MADS-box gene), B function is specified by *AP3* and *PI*, C function by *AGAMOUS* (*AG*) and *SHATTER-PROOF1/2*, D function by *SEEDSTICK*, and E function by *SEPALLATA* (reviewed by Theissen and Melzer 2007; Soltis *et al.* 2009). Major duplication events affecting these genes are quite concurrent with major events in angiosperm phylogeny such as the evolution of core eudicots (Soltis *et al.* 2007b). These duplications generate new pools of genes for possible neo- and subfunctionalizations, and therefore they may have provided the "material" to construct novelties in flower architecture and to forge ahead its diversification (Soltis *et al.* 2007b).

AP1, which specifies A-function in *Arabidopsis*, provides an example of how lineage-specific duplications affect the use of the candidate gene approach in evo-devo studies. *AP1* results from a series of duplication events that occurred in core eudicots, and *Arabidopsis* possesses the three paralogs euAP1, AGL79 and euFUL (Shan *et al.* 2007; **Fig. 3A**). Basal eudicots and basal angiosperms share an ancestral copy of these paralogs, *FUL* (Litt and Irish 2003). Independent duplication events near the base of Ranunculales gave rise to two copies of *FUL*-like genes found in Papaveraceae s.l. (**Table 1**; Litt and Irish 2003; Shan *et al.* 2007). It is unclear whether any of these *FUL-like* genes have a sepal-specifying function as initially characterized for *AP1* in the core eudicot *Arabidopsis*. No *FUL* expression data are available in Papaveraceae s.l. (**Table 1**), and they are scarce in other basal eudicots. So far, A function has not been clearly documented outside the core eudicots (Soltis *et al.* 2007a, 2007b). In *Euptelea pleiospermum* Hook.f. & Thomson, a representative of the small but possibly first diverged family in Ranunculales (Kim *et al.* 2004a; Worberg *et al.* 2007), the two *FUL*-like copies show different expression patterns. One paralog is expressed in leaves, as well as in floral and inflorescence meristems, whereas the other is restricted to leaves (Shan *et al.* 2007). This may indicate neo- or sub-functionalization following the duplication. Regarding the copy expressed in flowers, no data on the precise location of the transcription product exist. In addition, functional analysis will be necessary to establish any A class role of these *FUL*-like genes.

Genes with B function are better documented in Papaveraceae s.l. *AP3* and *PI* lineages result from a duplication

event preceding – or coincident with – the advent of angiosperms, and consequently both genes are found in Ranunculales families (**Fig. 3B**). No duplication at supraspecific level is detected in the Ranunculales for *PI* (Shan *et al.* 2006), although one may have occurred within Ranunculaceae (Kim *et al.* 2004b). For the *AP3* lineage, three main duplication events have been inferred, leading to the *AP3-I*, *AP3-II* and *AP3-III* clades (Kramer *et al.* 2003a; **Fig. 3C**). Papaveraceae *AP3* paralogs are distributed between the *AP3-I* and *AP3-III* clades, and no *AP3-II* representative has been reported to date (**Fig. 3C**). It is possible that *AP3-II* genes are present in the family, but additional sequencing effort is required to detect them. Alternately, the *AP3-II* copy was lost after the duplication, or the duplication giving rise to *AP3-II* genes did not involve the Papaveraceae. Published gene trees would allow alternative topologies consistent with this last hypothesis without breaking any significantly supported branch (**Fig. 3C**). Expression data are consistent with the presumed function of *AP3* and *PI* in petal and stamen specification (**Table 1**), which has been supported by VIGS data of *AP3* and *PI* genes in *Papaver somniferum* (Drea *et al.* 2007). The results of these VIGS experiments show that *PI* paralogs of *P. somniferum* seem to have an additive and general B function (**Fig. 3D**). In contrast, *AP3* paralogs are subfunctionalized, with *AP3-1* implicated in petal, and *AP3-2* in stamen development (**Fig. 3D**).

The C function involves carpel organ identity specification as well as floral meristem determinacy. Expression data on *AGAMOUS* homologs in Papaveraceae s.l. are consistent with the putative C function documented for this gene throughout angiosperms (Zahn *et al.* 2006; **Table 1**). Another candidate gene for this function is *CRC*, a member of the *YABBY* gene family which has been shown to regulate aspects of carpel development in angiosperms, from *Oryza* to *Arabidopsis* (Orashakova *et al.* 2009, and references therein). A single-copy *CRC* ortholog was found for Papaveraceae, in *Eschscholzia californica* (Orashakova *et al.* 2009). VIGS experiments carried out to silence *EcCRC* resulted in carpels with reduced differentiation of abaxial cells, and multiple gynoecia interlocked as "Russian matrioshka dolls" (Orashakova *et al.* 2009). These results suggest that the Papaveraceae *CRC* ortholog may participate in both aspects of the C function, namely the specification of gynoecium identity, and the termination of the floral meristem.

Establishing the genetic pathways of floral organ specification is of fundamental importance, for its intrinsic interest but also because it represents a first essential step toward understanding floral traits superimposed onto the basic model. As mentioned before, homeotic changes have occurred in *Macleaya* and *Sanguinaria* (**Fig. 2**). Fixation of the number of floral parts, resulting in a "closed ground plan", permits subsequent organ elaboration and synorganization to take place through fusion or close connection of parts (Endress 1990). It also favors changes in symmetry, which are more frequent in a closed ground plan (Damerval and Nadot 2007). Compared to Papaveraceae, Fumariaceae flowers show a fixed number of stamens that may be partially fused. The Fumariaceae corolla is an example of synorganization through morphological differentiation of outer and inner petals. This creates a disymmetric flower, and evolution of monosymmetry represents a further step in flower synorganization. Congenital organ fusion outside the gynoecium is rare, but *Eschscholzia* and *Eomecon* are synsepalous.

Floral symmetry genes

In core eudicots, evolution of monosymmetric flowers is linked to *CYC*-like TCP transcription factors (Preston and Hileman 2009). These genes are characterized by a TCP and an R domain with a conserved ECE motif in between (Howarth and Donoghue 2006). In both asterids (Luo *et al.* 1996) and rosids (Feng *et al.* 2006), *CYC*-like genes act in the adaxial part of floral meristems to impose monosymmetry. In *Antirrhinum*, this function is accomplished through interaction with MYB genes (Corley *et al.* 2005). In addition, *CYC*-like genes play a role in the repression of lateral branching in both grasses (Doebley *et al.* 1997) and *Arabidopsis* (Aguilar-Martínez *et al.* 2007).

So far, Papaveraceae s.l. is the only group outside of core eudicots for which the implication of *CYC*-like genes in genetic mechanisms underlying floral symmetry has been addressed (for a review, see Jabbour *et al.* 2009). Independent duplications of *CYC*-like genes have occurred in basal eudicots, and these may be associated with flower symmetry evolution in Fumariaceae (Kölsch and Gleissberg 2006; Damerval *et al.* 2007; **Table 1**). Two *CYC*-like paralogs are present in both Papaveraceae and in Fumariaceae, including taxa with actinomorphic, disymmetric and monosymmetric flowers. Therefore, symmetry changes in Papaveraceae s.l. cannot be directly linked to differences in the number of *CYC*-like genes. However, expression data suggest a different temporal expression pattern during development that is related to symmetry (**Table 1**). In non-actinomorphic flowers the expression is limited to earlier stages (buds smaller than 2 mm), whereas transcripts are detected in later stages of actinomorphic flower buds (at least until the size 3-5 mm; Damerval *et al.* 2007). RT-PCR profiling also indicated some divergence in spatial expression patterns (Kölsch and Gleissberg 2006; Damerval *et al.* 2007; **Table 1**). Expression in disymmetric and zygomophic flowers is preferentially located in outer petals (Damerval *et al.* 2007), consistent with a role in spur formation and a morphological differentiation between outer and inner petals. In the disymmetric *Lamprocapnos spectabilis* (L.) T. Fukuhara, one of the two paralogs, *LsCyL1*, showed higher expression levels in floral buds smaller than 2 mm (Damerval *et al.* 2007). An orthologous gene in the zygomorphic *Capnoides sempervirens* Borkh., *CsCYL1*, exhibited asymmetric expression in the outer petals (Damerval *et al.* 2007). More comprehensive expression data, particularly from *in situ* hybridization, are needed to clarify to what extent organ- and stage-specific expression, as well as paralog-specific expression, is associated with symmetry changes in this group. The ability to modulate expression levels will be crucial to elucidate the function of these genes as suggested by their expression patterns. In the absence of transformation protocols, VIGS may provide a tool to study the role of *CYC*-like genes in flower symmetry diversification in Fumariaceae. Silencing of *CYC*-like genes may be expected to convert monosymmetric and disymmetric flowers into the ancestral polysymmetric state. Until now, VIGS technology is only available for two species of Papaveraceae, and needs to be developed in Fumariaceae representatives.

Floral meristem identity genes

In core eudicots, the acquisition of floral identity by the shoot apical meristem (SAM) and the development of inflorescence structures involve an antagonistic interaction between the flower meristem identity genes *FLO/LFY* and *AP1/FUL* on the one hand and *CEN/TFL1* on the other (Benlloch *et al.* 2007). Mutants in one or both of the floral meristem identity genes *FLO/LFY* and *AP1/FUL* partly or fully convert flowers into vegetative shoots. This function is widely conserved, while the degree of redundancy varies between species. For example, mutation of the *Antirrhinum FLO* gene alone is sufficient for a full conversion of flowers into vegetative shoots, while redundant action of *AP1/FUL* (and the paralog *CAL*) in *Arabidopsis lfy* plants maintains some floral characteristics of these meristems. The floral meristem identity genes *FLO/LFY* and *AP1/FUL* positively regulate each other. In both *Antirrhinum* and *Arabidopsis*, expression of *CEN* and *TFL1*, respectively, represses *FLO/LFY* and *AP1* activity and thus prevent flower formation from the terminal inflorescence meristem. Accordingly, this repression is released in *cen* and *tfl1* mutants.

Shifts between indeterminate and determinate inflores-

cences, at least in core eudicots, are accompanied by changes in expression domains of *TFL1* and its counterparts *FLO/LFY* and *AP1/FUL*. Absence of expression of *TFL1* homologs in terminal inflorescence meristems and presence of floral meristem identity genes in different species is correlated with determinate inflorescence architecture (Benlloch *et al.* 2007). We hypothesize that the transition from determinate (in Papaveraceae and basal Fumariaceae) to indeterminate architecture (in later branching Fumariaceae) may be associated with altered expression patterns and interactions between *FLO/LFY*, *FUL*, and *CEN/TFL1* genes. *FLO/LFY* genes are extensively studied and found in all land plants (Maizel *et al.* 2005). Only one copy has been found in *Eschscholzia californica* (Busch and Gleissberg 2003), even though this species, as well as the entire Papaveraceae family is known to be ancient tetraploid (Cui *et al.* 2006). This result is consistent with the assumption of rapid gene loss following duplication events for *FLO/LFY* genes, which are generally found as single copies in angiosperms (Maizel *et al.* 2005). This trend is suggested to be due to the low ability of recently generated *FLO/LFY* duplicates to experience subfunctionalization and neofunctionalization (Maizel *et al.* 2005). Expression studies in *Eschscholzia californica* show *FLO/LFY* transcripts restricted to the flanks of the SAM and in developing dissected leaves (Busch and Gleissberg 2003; Becker *et al.* 2005). The pattern of expression of *EcFLO* mRNA in the flanks of the shoot apex is maintained from late embryogenesis until flower initiation, indicating a continuous role of this gene in meristem function. As flower organs develop, *EcFLO* expression becomes more restricted to the petal and stamen primordia. Development of the gynoecium occurs without *EcFLO* expression, indicating that it may not be necessary for the activation of C-class genes. *EcFLO* is not upregulated during reproductive transition, as in core eudicot species with indeterminate inflorescences such as *Arabidopsis* and *Antirrhinum.* This may reflect its different, determinate inflorescence architecture. It is possible that *AP1/FUL* alone functions in the transition from vegetative to floral meristems in *Eschscholzia* and other Papaveraceae with determinate inflorescences. Functional analyses are needed to fully evaluate the roles of *FLO/LFY* and *AP1/FUL* genes as flower meristem identity genes. In Brassicaceae, *FLO/LFY* have been linked to the evolution of "flowering rosettes" (Yoon and Baum 2004), and therefore could also contribute to inflorescence diversification in Papaveraceae (**Fig. 2D**).

The major reproductive syndromes occurring in Papaveraceae s.l., determinate inflorescences with polysymmetric or disymmetric flowers and indeterminate inflorescences with monosymmetric flowers, provide a unique opportunity to study correlated traits in conjunction. *TFL1* may be important in the elucidation of that connection because it links inflorescence determinacy and flower symmetry. Mutations in *TFL1* result in a switch from indeterminate to determinate growth, but also affect the symmetry of the newly generated terminal flower. Such terminal flowers appear polysymmetric (a condition termed peloric) whereas the axillary flowers remain monosymmetric (Coen and Nugent 1994). In contrast, all flowers in *cyc* mutants are polysymmetric (Rudall and Bateman 2003, and references therein). Naturally occurring peloric flowers attracted interest from an evolutionary point of view, starting with Darwin (1868). The terminal peloric flower of *tfl1* mutants suggests a developmental constraint for generating monosymmetry, which could depend on a racemose condition. Coen and Nugent (1994) proposed that the terminal flower meristem, in contrast to axillary meristems, constitutes a symmetrical environment that lacks the cues required to activate *CYC* in an asymmetrical manner. This would explain why monosymmetric flowers are usually grouped in indeterminate inflorescences. The rare occurrence of monosymmetric terminal flowers, as in the monotypic Fumariaceae genus *Capnoides*, presents an additional incentive to study these reproductive syndromes in Fumariaceae.

Tools available for investigation

Two species in Papaveraceae, *Papaver somniferum* and *Eschscholzia californica*, can be considered emerging model systems, as functional studies based on VIGS have become available and have already been used to investigate developmental genes (Drea *et al.* 2007; Orashakova *et al.* 2009). These studies have demonstrated that VIGS is a powerful technique to study the role of meristem-expressed genes in morphogenesis. Protocols for stable transformation via *Agrobacterium* inoculation have also been reported for the two species (Park and Facchini 2000; Chitty *et al.* 2003) that should enormously increase future options for functional studies, by allowing overexpression, induced expression, and promoter-marker gene studies. However, since these protocols are based on time-consuming plant regeneration from callus culture, developmental genetic studies using *Agrobacterium*-mediated transformation have not yet surfaced. *Papaver somniferum* is a focus of pharmaceutical research that is reflected in a large number of publications (e.g. Zulak *et al.* 2007) and over 20,000 Expressed Sequence Tags available in GenBank. A moderate Expressed Sequence Tag collection of floral tissue is also available for *Eschscholzia californica* (Carlson *et al.* 2006), and developmentally important families of microRNAs have been identified in this species (Barakat *et al.* 2007). While these are important beginnings, no such tools are yet available for the Fumariaceae.

CONCLUDING REMARKS

The overview of flower and inflorescence diversity in Papaveraceae s.l. demonstrates the great potential of this family to study the evolution of reproductive syndromes. To explore the multiple morphological transitions in this lineage, it is necessary to broaden the taxonomic sampling, focusing on plants with distinct combination of characters for which their phylogenetic position is known. Such taxa need to be evaluated for their malleability for developmental-genetic studies. Functional studies, such as virus-induced gene silencing, are of particular importance in the elucidation of the changing role of developmental gene regulators in plant evolution.

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