

Are Petals Sterile Stamens or Bracts? The Origin and Evolution of Petals in the Core Eudicots

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- **Background** The aim of this paper is to discuss the controversial origins of petals from tepals or stamens and the links between the morphological expression of petals and floral organ identity genes in the core eudicots.
- **Scope** I challenge the widely held classical view that petals are morphologically derived from stamens in the core eudicots, and sepals from tepals or bracts. Morphological data suggest that tepal-derived petals have evolved independently in the major lineages of the core eudicots (i.e. asterids, Santalales and rosids) from *Berberidopsis*-like prototypes, and that staminodial petals have arisen only in few isolated cases where petals had been previously lost (Caryophyllales, Rosales). The clear correlation between continuous changes in petal morphology, and a scenario that indicates numerous duplications to have taken place in genes controlling floral organ development, can only be fully understood within a phylogenetic context. B-gene expression plays a fundamental role in the evolution of the petals by controlling petaloidy, but it does not clarify petal homology.
- **Conclusions** An increased synorganization of the flower in the core eudicots linked with the establishment of floral whorls restricts the petaloid gene expression to the second whorl, reducing the similarities of petals with tepals from which they were originally derived. An increased flower size linked with secondary polyandry or polycarpely may lead to a breakdown of the restricted gene expression and a reversal to ancestral characteristics of perianth development. An altered 'sliding boundary' hypothesis is proposed for the core eudicots to explain shifts in petaloidy of the perianth and the event of staminodial petals. The repetitive changes of function in the perianth of the core eudicots are linked with shifts in petaloidy to the outer perianth whorl, or losses of petal or sepal whorls that can be secondarily compensated for by the inclusion of bracts in the flower. The origin and evolution of petals appears to be as complex on a molecular basis as it is from a morphological point of view.

Key words: *Apetala 3*, *Berberidopsis*, bract-derived petals, core eudicots, gene expression, perianth evolution, petaloidy, phylogeny, staminodial petals.

MORPHOLOGY AND GENES: TWO CONTRASTING APPROACHES?

The origin and evolution of the perianth has received increased interest in recent years from evolutionary developmental genetic studies (e.g. Jack *et al.*, 1992; Albert *et al.*, 1998; Kramer *et al.*, 1998, 2003; Kramer and Irish, 1999, 2000; Theissen *et al.*, 2002; Lamb and Irish, 2003; Kim *et al.*, 2004b; Zahn *et al.*, 2005). Thanks to a stable molecular phylogeny of the eudicot clade (e.g. Hoot *et al.*, 1999; Magallón *et al.*, 1999; Soltis *et al.*, 2000, 2003; Hilu *et al.*, 2003; Kim *et al.*, 2004a) it has become possible to test hypotheses regarding the evolution of floral structures in the angiosperms within a firm phylogenetic context (e.g. Zanis *et al.*, 2003; Ronse de Craene *et al.*, 2003, unpubl. res.; Endress and Matthews, 2006).

Most angiosperm flowers have an outer envelope enclosing the reproductive organs, called a perianth. The perianth can take a myriad of forms and shapes, ranging from undifferentiated (tepaloid) to differentiated into an outer calyx (sepals) and an inner corolla (petals). Unlike with stamens and carpels it is not possible to homologize the perianth in a satisfactory manner, as the perianth can have different origins and can take up different forms (Endress, 1994, 2006; Kramer *et al.*, 2003). Although different theories have been proposed in the past, the most commonly

accepted classical morphological theories have pointed out that petals in the majority of angiosperms have been derived either from bracts as are the sepals (*bracteopetals*), or from sterile stamens (*andropetals*) (e.g. Hiepkö, 1965; Takhtajan, 1991). Angiosperm sepals often have characteristics of leaves or bracts (i.e. persistent, protective organs with chlorophyll, a triangular shape with a broad base, three vascular traces and rapid growth), while petals often have characteristics morphologically common to stamens (i.e. deciduous, thin, coloured organs with a single vascular trace, a narrow base and retarded growth) (Hiepkö, 1965; see also Endress, 1994). The general consensus is that petals in the core eudicots have a staminodial nature. Because of the strong emphasis on Ranunculaceae petals that show obvious characteristics of staminodes (e.g. Tamura, 1965; Erbar *et al.*, 1998), the temptation is great to use this evidence as the driving force for petal evolution among all eudicots (Fig. 1A).

Evolutionary developmental genetics have presented models to understand perianth development and evolution on a molecular genetic basis. The differentiation of the flower rests on the ABC-model, in which identity of organs in each whorl is determined by a combination of three classes of MADS-box organ identity genes: A genes are responsible for sepal formation, A + B function determines petal identity, B + C function specifies stamens, and C-function determines carpel development. This model

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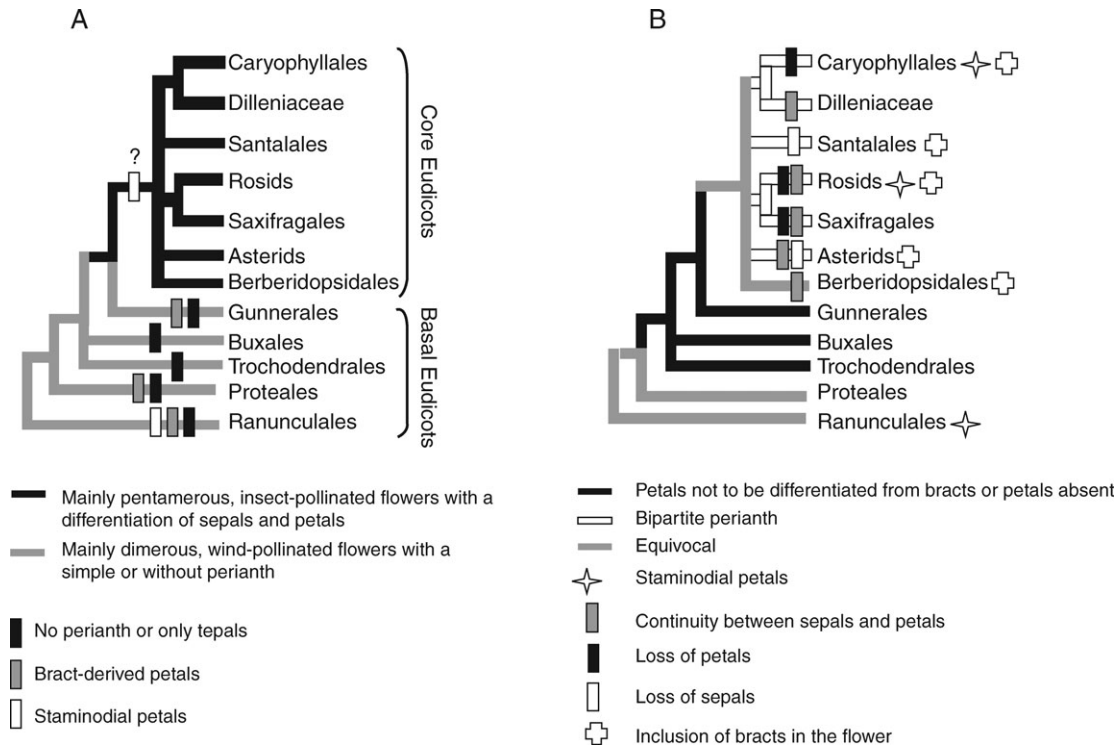


FIG. 1. Illustration of the phylogenetic relationship of the major clades of eudicots, based on APG (2003). (A) Reconstruction of perianth differentiation in the basal eudicot grade and Gunnerales, in contrast to the supposedly staminodial petals of the core eudicots. (B) Reconstruction of petal homologies in the eudicots. The distribution of characters has been mapped for the major lineages of the core eudicots, indicating cases where petals have a staminodial or a bract-derived origin.

has been subsequently extended to include D- and E-class genes that also play a role in floral organ development (reviewed in, for example, Ferrario *et al.*, 2004). Most genetic studies of petal identity have focused on the class B genes *APETALA3* (*AP3*) and *PISTILLATA* (*PI*) from *Arabidopsis* or their orthologues *DEFICIENS* (*DEF*) and *GLOBOSA* (*GLO*) from *Antirrhinum* (Weigel and Meyerowitz, 1994; Albert *et al.*, 1998; Gustaffson, 2000; Theissen *et al.*, 2002; Kramer *et al.*, 2003; Lamb and Irish, 2003; Litt and Irish, 2003; Kramer and Jaramillo, 2005; Zahn *et al.*, 2005). *AP3* or *DEF* interacts with the *PI* or *GLO* function in the formation of obligate heterodimers in conveying petal and stamen identity in both *Arabidopsis* and *Antirrhinum* (Jack *et al.*, 1992; Riechmann *et al.*, 1996). The ABC model was initially developed for core eudicot model flowers (i.e. *Arabidopsis*, *Antirrhinum*), which have a clearly differentiated bipartite perianth, but is becoming increasingly used to determine the genetic basis for undifferentiated organs (tepals) in all major groups of angiosperms and to understand the ‘true’ nature of the petals (cf. Kramer *et al.*, 2003; Soltis *et al.*, 2003; Di Stilio *et al.*, 2005; Zahn *et al.*, 2005). It is generally assumed that the original perianth of angiosperms was either sepaloid or petaloid and that a homeotic transition from sepaloid to petaloid organ identity or *vice versa* was responsible for a biseriate perianth (Albert *et al.*, 1998; Kramer and Irish, 2000; Kanno *et al.*, 2003; Hintz *et al.*, 2006). A shift of region in the expression of genes (the ‘sliding-boundary’ model) has

been put forward as a mechanism of flower evolution (e.g. Kanno *et al.*, 2003; Kramer *et al.*, 2003, 2006; Ochiai *et al.*, 2004; Kramer and Jaramillo, 2005; Hintz *et al.*, 2006). Shifts of gene expression towards sepals (A genes) would lead to a greater affinity of the petals with sepals or bracts (bracteopetals); ectopic expression of B-function genes *AP3* and *PI* in the first whorl leads to a replacement of sepaloid by petaloid organs. The presence or absence of petaloid tepals in monocots is correlated with *DEF*-gene expression (equivalent to *AP3*) in the first whorl or its absence (Kanno *et al.*, 2003; Ochiai *et al.*, 2004). However, other studies show that there is much more variation in petal gene expression than initially thought. For example, in *Asparagus* with undifferentiated petaloid tepals *GLO* B-genes are only expressed in the inner tepal whorl (Park *et al.*, 2004). In the orchid *Phalaenopsis* there is a differential expression of four different *DEF*-like paralogues in the perianth (Tsai *et al.*, 2004). In addition, petaloid tissue can be produced that does not express *AP3* and *PI* homologues, as was shown for *Aristolochia* by Jaramillo and Kramer (2004) and for Marcgraviaceae by Geuten *et al.* (2006). This indicates that a simple model with ectopic expression to provide a global explanation for petal origins and homology (e.g. Albert *et al.*, 1998; Kanno *et al.*, 2003; He *et al.*, 2004) needs to be used with moderation as it cannot be applied to all cases of ectopic petaloidy. Although there is a conserved petal identity programme common for all angiosperms, the explanation of petal derivations based on the

biseriate model of *Antirrhinum* and *Arabidopsis* does not take any historical or phylogenetic context into account and excludes any other origins of petals from multiple whorls or spirals. For example, the biseriata, tetramerous flower of *Arabidopsis* has been derived along an evolutionary pathway that is highly different from that of trimerous *Tulipa*. In between there is scope for much divergent evolution. Although the model explains how organs become petaloid (bear petal features) by a shift of genetic expression, it does not elucidate the homology of the petals. Assuming that *Arabidopsis* mutants in which sepals are replaced by petals can function as general models for petal evolution is clearly an oversimplification.

EVOLUTIONARY MODELS FOR THE ORIGIN OF PETALS IN THE CORE EUDICOTS

Several studies (e.g. Doyle, 1994; Kramer and Irish, 1999, 2000; Theissen *et al.*, 2000; Kramer *et al.*, 2003; Zahn *et al.*, 2005) have demonstrated that B-class gene expression is found in basal angiosperms as well as gymnosperms, and suggested that there is a single origin of petaloidy in the perianth, followed by many independent derivations of a bipartite perianth. This development rests on a variable but commonly inherited petal identity programme, and the acquisition of different gene lineages leading to different evolutionary pathways for perianth development in angiosperms, which closely follow the phylogeny of the angiosperms (e.g. Kramer and Irish, 1999; Lamb and Irish, 2003; Litt and Irish, 2003; Soltis *et al.*, 2004; Kim *et al.*, 2004b; Kramer and Jaramillo, 2005; Zahn *et al.*, 2005; Kramer *et al.*, 2006). While B-gene function is linked to the specification of male reproductive organs in both gymnosperms and angiosperms, its function became increasingly altered by multiple gene or genome duplications, followed by neofunctionalization events, leading to the core eudicots and derived monocots and this is linked with a higher degree of specialization of organs and the differentiation of a bipartite perianth. Kim *et al.* (2005a, b) investigated the expression of *AP3* and *PI* genes in several basal angiosperms. They found a broader expression pattern of these genes compared with the eudicots, and this appears to be correlated with the progressive transition from bracts to carpels in flowers, and with a lack of differentiation of the perianth. Kramer and co-workers (Kramer and Irish, 1999, 2000; Kramer *et al.*, 2003; Di Stilio *et al.*, 2005) extensively studied diversification of *AP3* and *PI* lineages in the Ranunculaceae of the lower eudicots. They demonstrated the presence of several duplication events and expression patterns not necessarily associated with petal development. Their results only confirm that petal expression in different whorls results from divergent pathways of *AP3* and *PI* genes, which at least for Ranunculaceae corresponds to the traditional distinction between tepals and nectar leaves (Hiepmo, 1965).

Recent molecular phylogenies have explicitly demonstrated that the core eudicots have been derived from a grade comprising the lower eudicots (e.g. Magallón *et al.*, 1999; Hilu *et al.*, 2003; Soltis *et al.*, 2003; Kim *et al.*, 2004a). One outstanding result of the molecular

phylogenetic studies is that Gunnerales with two monogeneric families Gunneraceae and Myrothamnaceae is the sister group of the remaining core eudicots, and this has important consequences for our understanding of petal evolution. There is an important floral morphological gap between lower and core eudicots. The lower eudicots immediately sister to the core eudicots (e.g. Tetracentraceae, Myrothamnaceae, Didymelaceae, Buxaceae) and the Gunnerales share small dimerous, often wind-pollinated flowers without perianth or with a perianth that is not clearly differentiated (Fig. 1A; Endress, 1986; von Balthazar and Endress, 2002; von Balthazar *et al.*, 2003; Drinnan *et al.*, 2004; Wanntorp and Ronse De Craene, 2005; Ronse De Craene and Wanntorp, 2006). The majority of core eudicots, by contrast, share well-developed pentamerous, insect-pollinated flowers with a differentiation of sepals and petals (Fig. 1A).

The morphological transition between lower and core eudicots appears to be an abrupt event, coinciding with the rapid radiation of the major lineages of the core eudicots and may be caused by different reasons, including a high extinction rate or an ancient explosive radiation at the base of the core eudicots (Soltis *et al.*, 2003; Ronse De Craene, 2004; Wanntorp and Ronse De Craene, 2005). However, the relationships between the main six lineages of core eudicots (i.e. Berberidopsidales, Santalales, Caryophyllales, rosids, Saxifragales and asterids) remain unresolved (Fig. 1; Magallón *et al.*, 1999; Soltis *et al.*, 2003; Judd and Olmstead, 2004). There is limited fossil evidence to provide transitional forms between lower and core eudicots. Most lower eudicots are not good candidates for understanding core eudicot floral evolution. Gunnerales, the sister group to all other core eudicots (Soltis *et al.*, 2003), are also dimerous and show a strong reductive trend linked with wind-pollination; therefore, they cannot help explain the evolution of core eudicot flowers (Wanntorp and Ronse De Craene, 2005; Ronse De Craene and Wanntorp, 2006).

One of the phylogenetic scenarios of basal core eudicot evolution has placed the Berberidopsidales, a small order with two families Berberidopsidaceae and Aextoxicaceae, as one of the basal core eudicot lineages but with relatively weak support (Soltis *et al.*, 2003; Judd and Olmstead, 2004; Kim *et al.*, 2004a). *Berberidopsis* has an atypical flower construction for the core eudicots in that the perianth is undifferentiated and spiral with several parts intergrading from outer bracts to inner petals (Ronse De Craene, 2004; Fig. 2A, B). The other genera in Berberidopsidales, such as *Streptothamnus* and *Aextoxicon*, have a clearly differentiated perianth. This points to a potential transformation event from the undifferentiated perianth to a biseriata perianth, which can function as a model for petal evolution in the core eudicots.

Because *Berberidopsis* has many intermediate features, Ronse De Craene (2004) suggested that the genus may help to understand how the transition between a spiral undifferentiated perianth and the common biseriata perianth in the core eudicots came about. *Berberidopsis* resembles other core eudicots at mid-developmental stage in an incipient pentamerous arrangement following a 2/5 sequence of

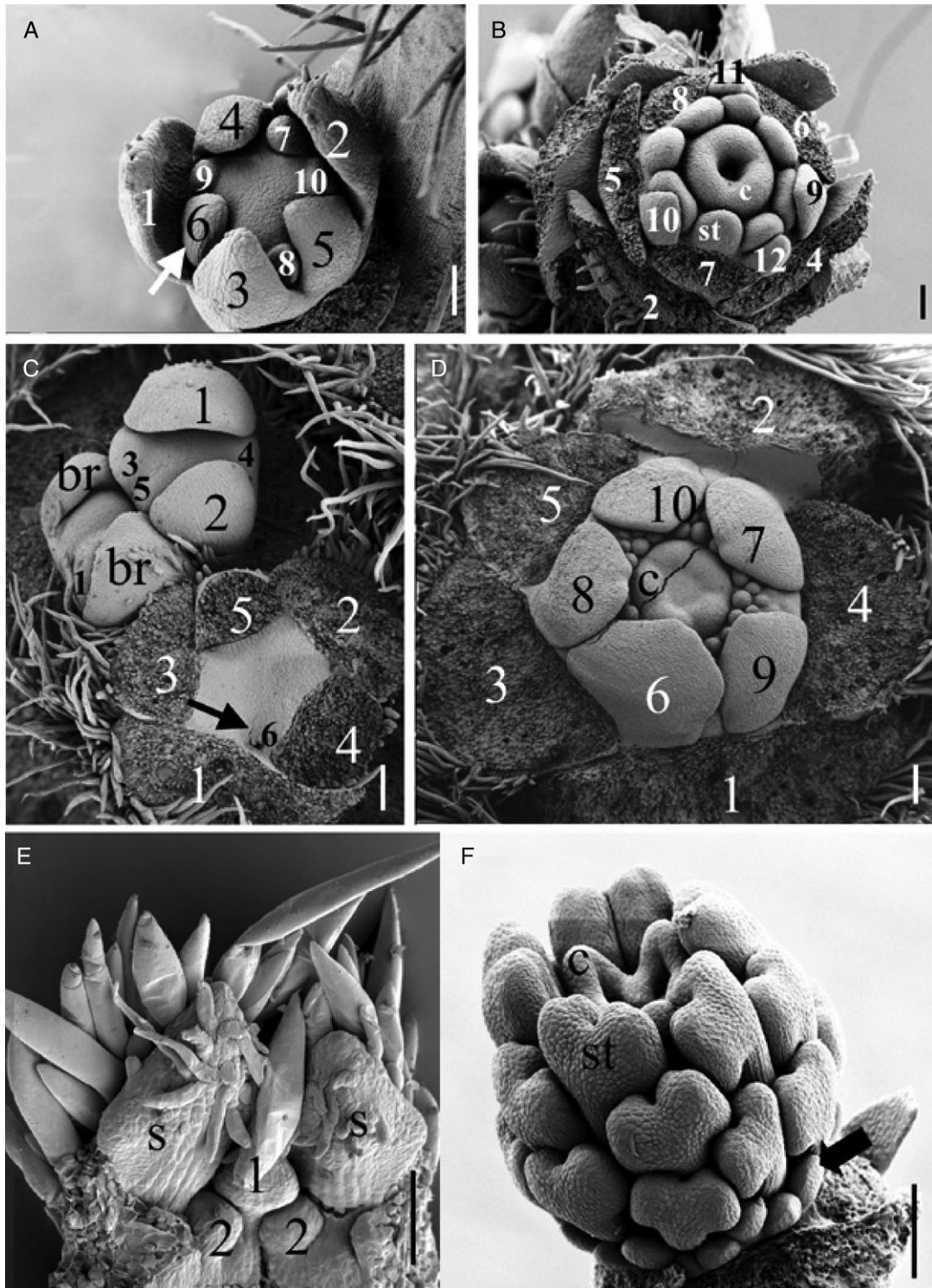


FIG. 2. (A,B) Stages of the floral development of *Berberidopsis corallina* (Berberidopsidaceae). (A) Early stage of perianth initiation showing two pentamerous whorls of tepals arising in a spiral sequence. The arrow points to the sixth tepal initiating a second 'whorl'. (B) Later stage of development of the flower at gynoecium development. The outer tepals have been removed. Numbers show the sequence of the 12 tepals; c, carpel; st, stamen. (C,D) Stages of the floral development of *Cochlospermum vitifolium* (Bixaceae – rosids). (C) Young inflorescence with three flowers at different stages of development. Numbers show the sequence of initiation of the sepals on individual flowers and first petal (arrow in front flower); br, bracteole. (D) Older bud at the initiation of the carpels (sepals removed); c, carpel primordium. (E) Section through young flower of *Potentilla* sp. (Rosaceae). Initiation of three primordia on a common primordium; the uppermost primordium develops as a petal and the lower as stamens. S, sepal. (F) Young flower primordium of *Corbichonia decumbens* (Lophiocarpaceae). The outer members of a centrifugal androecium develop into petaloid staminodes (arrow). St, stamen; c, carpel. Scale bars = 100 μ m.

initiation of outer and inner tepals (Fig. 2A). The pattern of development in *Berberidopsis* is not much different from the spiral initiation of sepals and petals found in several core eudicots (Fig. 2C, D). It could be suggested that the origin of the biseriate perianth of core eudicots is a matter of progressive readjustment (Fig. 3) by a strict arrangement of tepals in alternating whorls, the reduction of size of the inner tepals, and their nearly simultaneous initiation through shorter plastochrons. Increased synorganization of the petal whorl is responsible for a stronger differentiation of the petals as independent organs with specific attributes. An alternative hypothesis of the extension of petaloidy to the sepals appears improbable owing to the constraints of a spiral arrangement and the absence of similar cases in other core eudicots.

The node at the transition from basal to core eudicots has been identified with a large-scale gene duplication event at the level of Trochodendraceae–Buxaceae (*TM6* and *euAP3* arising from a *paleoAP3* lineage), and there is a concordant evolution of derived gene lineages with the abrupt evolution of different floral morphologies in the core eudicots, although sampling of genes did not include crucial groups such as Berberidopsidales (Lamb and Irish, 2003; Litt and Irish, 2003; Hernández-Hernández *et al.*, 2007; Kramer *et al.*, 2006). Whereas *TM6* and *paleoAP3* have a similar motif at the C-terminal, *euAP3* has a distinctive motif that has been shown to promote petal formation, unlike that of *paleoAP3* (Lamb and Irish, 2003). Although the function of *TM6* remains unclear, in Solanaceae it appears to have little or no role in petal development (e.g. Rijpkema *et al.*, 2006). The divergence of *euAP3* has therefore been implicated in the evolution of petals in the core eudicots (Lamb and Irish, 2003; Kramer and Jaramillo, 2005; Kramer *et al.*, 2006). A single nucleotide deletion was responsible for the transition of the *paleoAP3* motif into the *euAP3* motif after duplication (Kramer *et al.*, 2006). Kramer and Jaramillo (2005) questioned whether the petals in the core eudicots evolved by a restriction of the C-gene expression from an outer whorl of stamens (cf. andropetals) or by the expansion of the B-gene expression into previously sterile organs (cf. bracteopetals).

TRENDS IN THE DIFFERENTIATION OF THE PERIANTH IN THE CORE EU DICOTS: LINKS WITH EVO-DEVO

A study of the distribution of selected morphological characters related to petals on a recent morphological phylogeny of the core eudicots (Fig. 1B; L. P. Ronse De Craene, unpubl. res.) revealed that a number of characters traditionally associated with sepals are widely expressed in the petals of the core eudicots; these include a high frequency of broadly built, fast-growing, imbricate petals present in all main core eudicot clades. Thick petals of unequal size as well as the presence of three or more vascular bundles per petal also figure frequently among the major clades of the eudicots. Petals arising as a direct continuation of bracts are widespread in several of the higher lineages (Fig. 1B; Ronse De Craene, 2004). Although aestivation patterns are formed late in the floral development, an imbricate aestivation is usually a reflection of a spiral initiation sequence. These observations contradict the previously presented assumptions of a general staminodial origin of core eudicot petals. Several taxa scattered over the core eudicots possess large flowers with multiples of stamens and carpels and a variable number of sepals and petals arising in a helical order (e.g. Bixaceae, Dilleniaceae, Salicaceae, Clusiaceae, Theaceae: Fig. 2C, D; Ronse De Craene, 1989; Endress, 1997; Tsou, 1998; Bernhard and Endress, 1999; Gustaffson, 2000; Tucker and Bernhardt, 2000). These taxa are nested in clades having more regular flowers with fewer parts, and it remains uncertain whether large, helical flowers represent a truly plesiomorphic condition or a reversal.

It is clear that the general opinion that petals of the majority of angiosperms are derived from stamens is a myth that does not withstand closer scrutiny. The use of floral ontogenetic evidence within a reliable phylogenetic framework supports the derivation of petals by a differentiation of an inner series of tepals, leading to a bipartite perianth (Fig. 3; L. P. Ronse De Craene, unpubl. res.). Contrary to the common assumption of staminodial petals in *Arabidopsis* or *Antirrhinum*, distribution patterns based on floral developmental evidence, anatomy and morphology demonstrate that petals can be considered as of staminodial

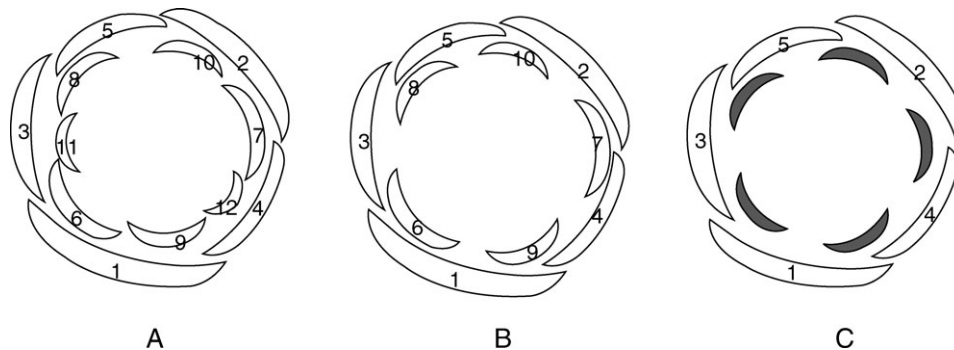


FIG. 3. Floral diagrams demonstrating the putative sequence for the origin of petals in the core eudicots. (A) Prototype such as *Berberidopsis* with a spiral perianth of 12 tepals. (B) Core eudicot flower with a bipartite perianth of five broad sepals and five petals arising in a spiral sequence. (C) Core eudicot flower with five sequentially arising sepals and five petals arising simultaneously (in grey).

origin on only a few occasions. They tend to be restricted to certain clades where petals have initially been lost and where a visual attraction had to be reinvented (e.g. Fig. 2E, F; Caryophyllales, Rosales: Hofmann, 1994; Ronse De Craene *et al.*, 1998; Leins *et al.*, 2001; Ronse De Craene and Smets, 2001; Ronse De Craene, 2003). Therefore, staminodial petals must be the result of a secondary readjustment of gene expression in an outer whorl of sterile stamens. The observations of a recruitment of a *TM6* homologue from the petal into the stamen of *Silene* (Caryophyllaceae: Zahn *et al.*, 2005) should be interpreted in this context.

The controversy regarding petal homology cannot be solved with gene expression studies alone. Some support for andropetals comes from the fact that *AP3* and *PI* genes in the eudicots are strongly expressed in the stamens as well as the petals (Kramer and Irish, 2000; Zahn *et al.*, 2005). Alternatively, the expression of *AP3* and *PI* homologues appears highly conserved across the angiosperms (e.g. Kramer and Irish, 2000; Stellari *et al.*, 2004; Kramer *et al.*, 2006), having different functions in some basal groups, and being expressed in different degrees across the eudicot phylogeny. All angiosperms are capable of the expression of petaloid features and this expression can run along a gradient (with little morphological distinction between sets of organs and with the expression of petaloid genes in the stamens), or it can be increasingly set as a distinction between strictly defined whorls. Litt and Irish (2003) argue that the molecular mechanisms responsible for floral development may be different outside the core eudicots, and this underlines the important gap that is seen in the morphology. Morphological evidence of petal development in the core eudicots adds more support for a bracteolar derivation of the petals in the majority of core eudicots, including the model systems, such as *Arabidopsis*, *Antirrhinum* and *Petunia*, and only for the possibility of a staminodial nature in some restricted clades (Caryophyllales, Rosales: Fig. 2E, F). This also implies that the independent derivation of petals from either stamens or bracts would either involve the recruitment of different kinds of genes in different lineages of the core eudicots, or the same genes can be recruited independently to the same effect. It will be one of the future challenges to determine how staminodial petals differ genetically from bracteolar petals.

A whorled arrangement of the flower is a fundamental prerequisite for a restricted differentiation of petaloid organs and is fundamental for canalizing the expression of genes towards specific organs. In basal angiosperms B-gene expression extends over all organs and this appears to be correlated with the progressive transition from bracts to carpels in flowers, with a lack of differentiation of the perianth (Kim *et al.*, 2005a). Already in the Ranunculales the expression of the MADS box genes *AP3* and *PI* in the nectar leaves of Ranunculaceae is different from the petaloid tepals, culminating in the strictly whorled genus *Aquilegia* (Kramer and Irish, 1999; Kramer *et al.*, 2003). The suggestion that new sequences in the C-terminal domain in *euAP3* genes in core eudicots is associated with the evolution of a differentiated perianth

(e.g. Kramer *et al.*, 1998; Lamb and Irish, 2003) does not clarify the whole picture of petal evolution. I postulate that a stricter synorganization of whorled flowers in the advanced clades of the core eudicots (Endress, 1990, 2006) is linked with a more restricted expression of A-genes in the second whorl and an incursion of C-genes in the developing petals, leading to an increased similarity of petals (and even sepals) with stamens.

However, one often finds massive multistaminate flowers scattered over different clades of the core eudicots which appear less synorganized and have a strong expression of bract features in the petals: spiral initiation sequence, large, unequal petals with rapid growth and imbricate aestivation. Although these flower types may represent a retained plesiomorphic condition (resembling the pattern in *Berberidopsis*), it is possible that the development of a ring meristem linked with an increase of stamens or carpels has caused a disruption of the regular whorled initiation pattern of floral organs, leading to a reversal to a more diffuse expression of petal-inducing genes.

PETALOIDY AND PETAL EVOLUTION IN THE CORE EUDICOTS

A bipartite perianth is commonly found in all major clades following the divergence of the Berberidopsidales. Although petals appear to have a bract origin in the core eudicots, it is not known whether the transition between tepals and petals occurred once or several times. Petaloidy can easily jump between different whorls, with the possible extension of gene influences in the adjoining whorls. For example, in tetramerous flowers of *Stachyurus sinensis* (Stachyuraceae), the two outer sepals are brownish as are the bracts, while the two inner sepals bear the same coloration as the four petals (L. P. Ronse De Craene, unpubl. obs.). The coloured staminodes of *Jacquinia macrocarpa* are morphologically very similar to the petals, although they represent an aborted stamen whorl (Caris and Smets, 2004). Similarly, organ identity can switch at the boundary of petals and stamens, as illustrated in the transition of petals into stamens and *vice versa* (e.g. Papaveraceae: Ronse De Craene, 2003; Brassicaceae: Nutt *et al.*, 2006). Sudden homeotic transformations may play an important role in the evolution of the perianth (known as hopeful monsters: see Theissen, 2006).

The number of species in the core eudicots with coloured petaloid sepals is very high (L. P. Ronse De Craene, unpubl. res.). Sepals often appear as an outer, pigmented whorl highly similar to the petal whorl. This phenomenon might be used as an indication that sepals and petals are functionally homologous structures but it affects flowers at maturity while sepals and petals maintain their distinct morphologies in earlier developmental stages. Examples of this are widespread, such as *Passiflora* (Passifloraceae), *Impatiens* (Balsaminaceae), Rhamnaceae, *Fuchsia* (Onagraceae), *Staphylea* (Staphyleaceae), *Gomphia* (Ochnaceae), *Moringa* (Moringaceae), *Ribes* (Grossulariaceae), *Clermontia* (Campanulaceae) and several Brassicaceae. Petaloidy of the calyx is often correlated with a reduction in size or variability in the presence or absence of the petals (e.g. Cunoniaceae,

Oliniaceae, Polygonaceae, Saxifragaceae, Thymelaeaceae). The combination of protection with attraction in the calyx has affected several clades. It would be interesting to know whether this shift has occurred concomitantly with a reduction of the petals (as observed in, for example, Fabaceae: Tucker, 2001; Oliniaceae: Schöenberger and Conti, 2003), or after petals have initially been lost (in wind-pollinated clades: e.g. Begoniaceae, Phytolaccaceae). Endress and Matthews (2006) found an evolutionary connection between reduced petals and lobate petals, as both are frequently associated in the same family. However, they did not observe whether this trend was correlated with petaloidy of the sepals.

Petaloidy in the sepals has arisen independently and on many different occasions, and is clearly a secondary phenomenon linked to a shifting pattern of gene expression. It is clear that this transference of function to the sepals is in no way a replacement of the sepals with the petals (Geuten *et al.*, 2006).

The sliding boundary model proposed by default for all angiosperms can be altered for the core eudicots, as it has been for other groups (Figs 4 and 5). However, this approach needs to be used cautiously as different genetic mechanisms can induce similar morphologies, or *vice versa* (Theissen, 2005; Zahn *et al.*, 2005; Geuten *et al.*, 2006). Starting with a floral model well established in the core eudicots such as *Arabidopsis* (Figs 4A and 5A), an ectopic shift of B-genes towards the sepals leads to increased petaloidy of the outer whorl (Figs 4B and 5B). As explained above, this trend is frequently found in several families of rosids, Caryophyllales and asterids. The secondary acquisition of petaloid organs by an extension of the B-gene expression in the stamen whorl, the addition of different B-genes, or the restriction of the C-gene expression in stamens may lead to staminodial petals as found in some taxa of the Caryophyllales and Rosales (Figs 2E, F, 4C and 5F; Ronse De Craene, 2003).

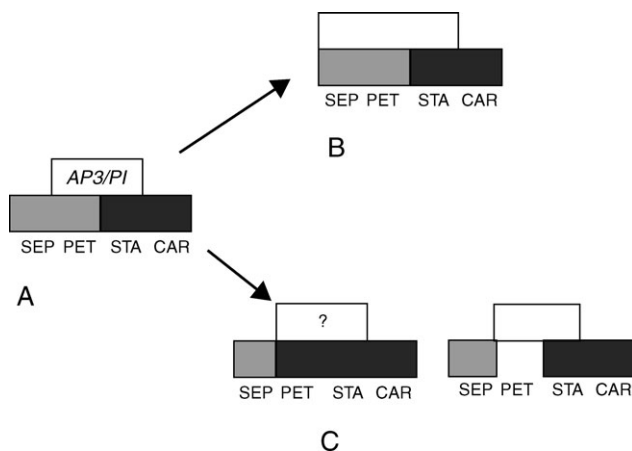


FIG. 4. Altered ‘sliding-boundary’ hypothesis for the core eudicots. (A) ABC model for flowers with well-differentiated sepals and petals; (B) flowers with petaloid calyx next to a corolla; (C) flowers with staminodial petals, either by an ectopic expression of C genes linked with different B-genes, or by a restriction of the C-gene activity.

Once the differentiation of a petal whorl has been firmly established there are certain clear patterns associated with the main clades of the core eudicots (Fig. 1B). In Santalales evidence for a bipartite perianth is only found in some Olacaceae *s.l.* (e.g. *Heisteria*, *Diogoa*: L. Wanntorp and L. P. Ronse De Craene, unpubl. res.). In most Santalales petals represent a well-developed valvate whorl and the calyx is reduced, or replaced by a calyculus of probably bracteolar origin (L. Wanntorp and L. P. Ronse De Craene, unpubl. res.). Asterids and rosids usually have a clear differentiation of sepals and petals, although the development of the petals is highly variable. Rosids (including Saxifragales) have a frequent tendency for petal loss (Endress and Matthews, 2006), linked with petaloidy of the sepals (e.g. Saxifragaceae, Grossulariaceae, Rosaceae, Malvaceae, Fabaceae, Thymelaeaceae). The core Caryophyllales represent a basically apetalous clade with probably wind-pollinated ancestors. Petals have been reinvented several times within the order, either by petaloidy of the sepal whorl (e.g. Nyctaginaceae, Cactaceae, Amaranthaceae), or by the development of petaloid staminodes (e.g. Caryophyllaceae, Stegnospermaceae, Aizoaceae, Molluginaceae p.p.: Fig. 2F; Hofmann, 1994; Ronse De Craene *et al.*, 1998). Asterids have the largest number of taxa with strongly developed, synorganized flowers, and the corolla is often sympetalous. The protective function is occasionally taken over by the corolla, or by the floral bracts, making the calyx redundant. As a result the calyx is repeatedly lost in several larger families (e.g. Rubiaceae, Acanthaceae, Asteraceae, Caprifoliaceae).

CONCLUSIONS

The model of a tepaline origin of the petals through *Berberidopsis*-like ancestors is supported by the widespread distribution of tepal attributes in the petals of the core eudicots (Fig. 1B) and links up with the assumption that an ancient exclusion of the B function from the outer petaloid whorl in early eudicots may be responsible for the sepal-petal distinction (Albert *et al.*, 1998). The core eudicot flower is a dynamic structure and the evolution of the perianth is reflected in the shifting balance between different gene expressions. The topographical limits of the flower, especially the perianth, are constantly altered during evolution. At this stage only broad lines can be traced regarding changes occurring in the differentiation of a perianth in the core eudicots (Fig. 5), but with better resolved phylogenies it will be possible to reconstruct the steps in perianth evolution more accurately on a morphological as well as a genetic basis. There are various evolutionary patterns possible in the development of the perianth from a prototype such as those present in *Antirrhinum* or *Arabidopsis* (Fig. 5A). Loss of petals in certain families has been compensated for by petaloidy of the sepals (Fig. 5B; e.g. Begoniaceae, Rhamnaceae, Saxifragaceae, Thymelaeaceae, Malvaceae); this has occurred before or after total petal loss. In other groups bracts can be included in the flower to produce a secondary calyx (Fig. 5C; e.g. Loranthaceae, Portulacaceae, Didiereaceae). Loss of sepals is also a frequent phenomenon in certain families, especially among

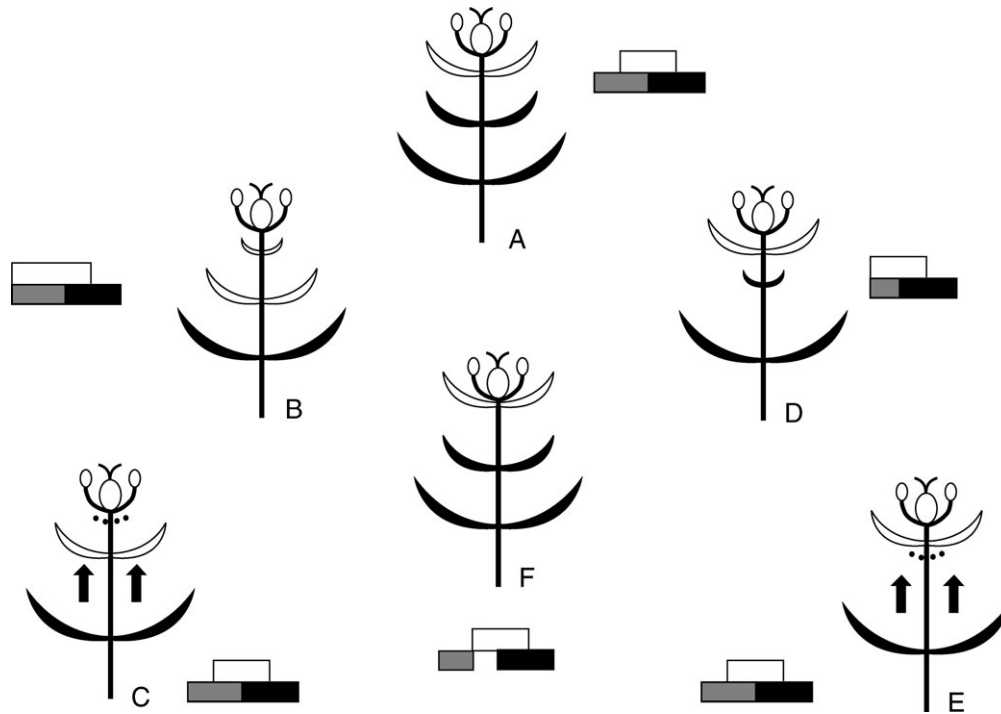


FIG. 5. Floral models showing different levels of perianth evolution in the core eudicots; phyllomes from bottom to top represent bracts, sepals and petals; black colour represents absence of petaloidy; white colour represents petaloidy; broken curves represent lost whorls. For each model the putative ABC-model is shown. (A) Flower with well-differentiated biseriate perianth; (B) reduction or loss of petals and petaloidy of the sepal whorl; (C) secondary insertion of bracts in an apetalous flower; (D) reduction or loss of sepals; (E) secondary insertion of bracts in an asepalous flower; (F) development of staminodial petals after the initial loss of petals.

asterids (Fig. 5D; e.g. Rubiaceae, Acanthaceae, Asteraceae). An insertion of bracts in the flower (possibly as an epicalyx) leads to a flower with a biseriate perianth with the same or a different gene expression (Fig. 5E). The derivation of petals from staminodes (Fig. 5F) remains a special case with a limited distribution. It will be interesting to discover the details of how different pathways of reduction and increase have evolved in different groups of core eudicots. However, it is important to understand how structural changes fit with changes in gene expression.

There is no strict correlation between the phylogeny of the core eudicots and gene duplications, although there is some concordance (e.g. Hernández-Hernández *et al.*, 2007; Kramer *et al.*, 2006). Genetic changes may reflect changes in morphology, but not necessarily: gene homologies do not necessarily correspond to morphological homologies. Neither is it possible to link gene phylogenies (different orthologues and paralogues arising through duplication events) with their function (Theissen, 2005; Zahn *et al.*, 2005). This makes it extremely difficult to assign a specific role in petal determination, as a reflection of the morphology of the petals. Neither can one unequivocally answer whether there is one origin of petals or several independent developments within the core eudicots. The numerous paralogues of *euAP3* and *TM6* in the core eudicots seem to indicate the latter scenario, although the duplication event pre-dates the diversification of the core eudicots. The general use of the term 'petal' appears

unfortunate as it does not convey any information on homology. We could use the terms 'sepaloid tepal' and 'petaloid tepal', as well as 'petaloid staminode' or 'staminopetal' (cf. Ronse De Craene and Smets, 2001) to describe petals in the core eudicots, depending on their origin.

The floral phyllotaxis is fundamentally linked to the expression of genes in flowers and this has not been addressed sufficiently in genetic studies (cf. Endress, 2006). An increased arrangement in whorls leads to a restricted petal gene expression. But what genes are responsible for this? It is also a question of whether changes in genetic expression trigger morphological novelties or whether plants have the ability to switch on/off gene activity in response to functional pressures. A breakdown of the strictly whorled arrangement is linked to stamen or carpel increases in the flower and this appears to dilute the strict genetic boundaries between whorls. As a result perianth differentiation becomes less clear with a gradual change between outer and inner organs and unsettled petal boundaries. How is this reflected at the genetic level?

However, sudden homeotic changes can also have an important impact on evolutionary changes. Ectopic petaloidy of the sepal whorl can go hand in hand with a progressive reduction of the petal whorl, involving different genes and processes.

These questions remain largely unanswered at the moment.

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