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REVIEW

Origin and evolution of petals in angiosperms

Louis P. Ronse De Craene[1,*] & Samuel F. Brockington[2]

[1]Royal Botanic Garden Edinburgh20A Inverleith Row, Edinburgh, EH3 5LR, United Kingdom
[2]Department of Plant Sciences, University of Cambridge, Cambridge, CB2 3EA, United Kingdom
*Author for correspondence: l.ronsedecraene@rbge.ac.uk

Background and aims – The term 'petal' is loosely applied to a variety of showy non-homologous structures, generally situated in the second whorl of a differentiated perianth. Petaloid organs are extremely diverse throughout angiosperms with repeated derivations of petals, either by differentiation of a perianth, or derived from staminodes. The field of evo-devo has prompted re-analysis of concepts of homology and analogy amongst petals. Here the progress and challenges in understanding the nature of petals are reviewed in light of an influx of new data from phylogenetics, morphology and molecular genetics.
Method and results – The complex web of homology concepts and criteria is discussed in connection to the petals, and terminology is subsequently defined. The variation and evolution of the perianth is then reviewed for the major clades of angiosperms. From this pan-angiosperm variation, we highlight and discuss several recurrent themes that complicate our ability to discern the evolution of the petal. In particular we emphasise the importance of developmental constraint, environmental stimuli, interrelationship between organs and cyclic patterns of loss and secondary gain of organs, and the development of a hypanthium or corona.
Conclusions – A flexible approach to understanding 'petals' is proposed requiring consideration of the origin of the floral organ (stamen-derived or tepal-derived, or other), the functional role (sepaloid or petaloid organs), evolutionary history of the organismal lineage, and consideration of developmental forces acting on the whole flower. The variety and complex evolutionary history of the perianth may necessitate the exploration of petal development within phylogenetically quite restricted groups, combining data from morphology with evo-devo.

Key words – andropetal, bracteopetal, corolla, calyx, evo-devo, perianth, reduction, staminode, tepal.

THE SEARCH FOR HOMOLOGY BETWEEN PETALS

'Petal' – an altogether awkward term

The term petal commonly refers to floral organs that are coloured or otherwise visually striking ('petaloid'), relative to sepals, which are usually dull and green ('sepaloid'). Endress (1994) defines petals in a narrow sense as organs sharing a narrow base, a single vascular bundle and a delayed development. However, these criteria cannot be universally applied (Ronse De Craene 2007). The term petal is closely linked to the concept of a *differentiated* perianth, which consists of two whorls comprising an outer *calyx* of sepals and an inner *corolla* of petals. In the differentiated perianth of most core eudicot flowers, outer sepals and inner petals can be easily distinguished. The recognition of petals becomes problematic in cases where no clear distinction can be made between greenish sepals and showy petals, such as when both whorls are sepaloid (e.g. Juncaceae) or when the outer perianth whorl is petaloid and similar in appearance to the inner whorl (e.g. the 'monocotyledonous' perianth of Passifloraceae). Therefore, in the instance of an undifferentiated perianth, the term *perigone* (comprised of *tepals*) is commonly applied, to avoid designating the perianth whorls or perianth members as corolla, calyx, petals, or sepals. The terms petal and sepal are also problematic in cases where a flower with a single whorl of perianth is derived from a flower with two perianth whorls through reduction or loss of one of the whorls. The resultant single perianth whorl may be of sepal origin and yet have a petaloid appearance, as in apetalous Saxifragaceae (*Rodgersia* or *Chrysosplenium*), Rhamnaceae (*Colletia*) and Myrsinaceae (*Glaux*); or the remaining perianth whorl may be of petal origin in instances when the sepals have been lost (e.g. Santalaceae, some Apiaceae). Differentiation between sepals and petals is essentially a division of function (Endress 1994), with sepals protecting young buds, and petals functioning as attractive organs for pollinators. However, the functions of sepals and petals can also be spatially combined in one set of organs (as in the tepals of Phytolaccaceae and

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Cactaceae), or temporally combined through transference of function during the maturation of the perianth (Ronse De Craene 2008a). Variable degrees and forms of perianth differentiation, in conjunction with complex histories of perianth organ loss and gain, challenge our ability to discern homologous perianth parts among divergent angiosperm lineages. In this context, if the term 'petal' is loosely applied to all visually striking coloured floral organs, there is potential to collectively label non-homologous floral organs as 'petals': this can erroneously imply homology or fail to pinpoint the nature of the homology. In part recognition of this problem comparative morphologists distinguish two classes of petals, *bracteopetals* and *andropetals*, to acknowledge that 'petals' may be derived from different evolutionary progenitors.

The different derivations of petals

Bracteopetals are petals with an obvious link to bracts and sepals, a connection established by Goethe (1790) who recognised the linear transformation between vegetative leaves, perianth and reproductive organs along the main axis of the plant. The term bracteopetal is commonly applied to the flowers of plant lineages in which this transformation can be readily observed e.g. in basal angiosperms, earlier described as 'Ranales', 'Polycarpicae', or Magnoliidae (Troll 1927, Eames 1961, Hiepko 1965, Bierhorst 1971, Weberling 1989, Takhtajan 1991). Flowers containing bracteopetals are rarely biseriate as the perianth parts are arranged in a spiral phyllotaxis. Differentiation along this phyllotaxis is generally gradual and clear boundaries between different perianth organ categories and subtending bracts are lacking. Aside from fuzzy boundaries between the perianth parts and bracts, additional bract-like characters of bracteopetals include the breadth of primordia, their vasculature, and cellular structure (Ronse De Craene 2008a).

In contrast, andropetals have been described as transformed outer stamens and were originally recognised based on studies of nectar leaves in Ranunculales, especially Ranunculaceae, which were presented as direct evidence of staminodial petals (e.g. Goebel 1933, Tamura 1993, Kosuge 1994, Endress 1995, Erbar et al. 1998, Ren et al. 2010). Evidence for a link between andropetals and stamens has been presented from anatomy, development and micromorphology, and andropetals are often identified based on this evidence. Andropetals are organs with a narrow base, a single vascular trace, with retarded growth compared to stamens, pigmentation of leucoplasts or chromoplasts with a lack of chloroplasts, an adaxial epidermis of conical or elongate cells, and presence of volatile oils (e.g. Weberling 1989, Endress 1994, Erbar et al. 1998, Ronse De Craene & Smets 2001, Ronse De Craene 2007, 2008a, Irish 2009).

Although the concept of bracteopetals and andropetals reflects an important feature of perianth evolution, it is difficult to apply in practice. The limitations of traditional criteria used to discern the derivation of petals are discussed in Ronse De Craene (2007). In a meta-analysis of sepal and petal morphology in core eudicots, Ronse de Craene (2008a) demonstrates that the petal/sepal distinction is often blurred. Furthermore characters used to differentiate andropetals from bracteopetals (e.g petal morphology, ontogeny, and number of vascular traces) are linked to functional requirements of flowers and are often unreliable indicators of homology. Despite these difficulties clear examples of bracteopetals and andropetals are recognisable across angiosperms e.g in the Ranunculales and Caryophyllales, and possibly Rosales (see Ronse De Craene 2003, 2007, 2008a). Previous loss of a perianth whorl can evidently trigger the transformation of outer stamens into petaloid structures linked with shifts in pollinator strategies (as has occurred in Aizoaceae, *Corbichonia*, and Caryophyllaceae), or the transformation of sepals in petaloid organs (as in Portulacinae, Nyctaginaceae) (Brockington et al. 2009).

Towards a molecular definition of the petal?

Petals have received much attention from an evo-devo perspective with a number of recent reviews of the molecular genetic control of petal development (e.g. Albert et al. 1998, Kramer et al. 1998, Lamb & Irish 2003, Ronse De Craene 2007, Rasmussen et al. 2009, Irish 2009). These studies have focussed on the canonical ABC(DE) model to explain the molecular control of floral organ identities. The ABC model was originally conceived based on studies conducted on the core eudicot model organisms *Arabidopsis thaliana* and *Antirrhinum majus* (Coen & Meyerowitz 1991, Weigel & Meyerowitz 1994). Accordingly, three classes of homeotic genes act in overlapping domains across the flower meristem: A-class genes alone control sepal identity, A- and B-class genes control petal identity, B- and C-class genes control stamen identity, and C-class genes alone control carpel identity. In addition two other gene classes have later been identified: D-class genes control ovule development and E-class genes act as mediators in the development of all floral organ identities (see Pelaz et al. 2000, Theissen 2001, Becker & Theissen 2003). With reference to petal development, the B-class MADS-box genes *PISTILLATA* (*PI*) and *APETALA3* (*AP3*) or *GLOBOSA* (*GLO*) and *DEFICIENS* (*DEF*) in *Arabidopsis* and *Antirrhinum* respectively have been shown to be of particular importance: (1) B-class MADS-box genes are generally expressed in the second whorl petals of a differentiated perianth in core eudicots (see Albert et al. 1998, Kim et al. 2004, 2005a, Ronse De Craene 2007). (2) In the absence of the C-class MADS-box gene *AGAMOUS* (*AG*) or its orthologs, activity of B-class MADS-box genes is necessary for development of the petal in the second whorl of the flower (Jack et al. 1992, Mizukami & Ma 1992, Bradley et al. 1993, Goto & Meyerowitz 1994). (3) Persistent activity of B-class MADS-box genes through late stages of petal development is necessary to maintain the expression of characteristic petal features (Bowman et al. 1991, Sommer et al. 1991, Zachgo et al. 1995). (4) Heterotopic expression of B-class MADS-box genes in the first-whorl sepals of the flower is sufficient to induce ectopic petal morphology (Coen & Meyerowitz 1991, Krizek & Meyerowitz 1996). Given these observations from distantly related core eudicot taxa, it has been proposed that a petal identity program regulated by B-class MADS-box gene homologs arose early in the evolution of angiosperms (Kramer & Jaramillo 2005). The concept of an ancestral petal identity program of angiosperms provides a developmental genetic criterion to homologise petals (pro-

cess homology) regardless of their position in the flower or derivation. For example the presence of petaloidy outside of the second floral whorl could be caused by ectopic expression of B-function genes outside the petal whorl resulting in petaloid sepals (i.e the 'shifting boundaries' model of Bowman 1997).

Numerous studies have looked for a genetic signature consistent with the concept of an ancestral petal identity program: i.e conserved B-class MADS-box gene activity in all petals and petaloid organs, regardless of phylogenetic lineage, derivation, or position within the flower. A considerable amount of data has been collected on the expression patterns and function of B-class MADS-box genes across angiosperms, although a collective interpretation of the data is inconclusive. It is clear that B-function MADS-box genes predate angiosperm evolution and are generally expressed during floral development across angiosperms (Kim et al. 2004, Zahn et al. 2005, Kramer et al. 1998) – observations that are consistent with the concept of an ancestral petal identity program. However, expression of B-class MADS-box genes can be highly variable with regard to the presence and absence of petaloidy. In basal angiosperms, B-gene expression is not restricted to the inner perianth members, but is broadly expressed across the floral meristem with an obvious gradient in the level of gene expression. It has been suggested that this gradient corresponds to gradual transitions between floral organ identities across the flower, in support of the correlation of petaloidy and gene expression patterns (Kramer et al. 2003, Kim et al. 2005a, 2005b, Shan et al. 2006, Chanderbali et al. 2009). However, in some taxa within the basal eudicot family Ranunculaceae, B-class MADS-box genes are expressed in petals, but their expression is rapidly turned off early in development (Kramer & Irish 1999). This is in contrast to core eudicot model taxa in which continuous expression is required to maintain normal petal development. Additionally there are numerous examples of petaloid organs whose development may not depend on B-class MADS-box genes. For example, homologs of *AP3* but not *PI* are expressed in late stages of petaloid organs of the asterid eudicot *Impatiens hawkeri* (Geuten et al. 2006); in the showy perianth of the magnoliid *Aristolochia*, the *AP3* homolog only is expressed late in the differentiation of perianth organs (Jaramillo & Kramer 2004); *AP3* and *PI* homologs are not expressed in the outermost petaloid perianth whorl in flowers of the monocot *Asparagus* (Park et al. 2003, 2004); a *PI* homolog is required for petal identity in the second whorl but not the petaloid first whorl in the basal eudicot *Aquilegia* (Kramer et al. 2007) despite expression in both whorls. The petaloid sepals of *Rhodochiton atrosanguineum* (Plantaginaceae) do not show any B-gene expression, although they superficially resemble the petals of the same species (Landis et al. 2012). Finally there are examples of B-gene expression in perianth parts that are not petaloid, e.g in the lodicules of grasses (Jaramillo & Kramer 2004, 2007, Whipple et al. 2007).

Differences in methods of gene expression analysis and patchy functional data make generalised interpretations difficult. But taken together these observations conspire to decouple petaloidy and the expression of B-class MADS-box genes. As a consequence, numerous additional hypotheses have been proposed either to explain the tendency for B-class MADS-box gene expression in the second floral whorl, or to explain variation in gene expression patterns. The 'mosaic theory' has been put forward to recognise the influence of environmental conditions, such as light, on the development of sepaloidy or petaloidy in basal angiosperms (Warner et al. 2009). Kramer & Jaramillo (2005) have explored the connection between variation in gene expression and complexity in petal morphology. Others have suggested that *AP3* and *PI* homologs show conserved expression primarily to specify regional domains in the flower rather than organ identity *per se* (Drea et al. 2007, Whipple et al. 2007). Finally it remains possible that the presence or absence of B-class MADS-box genes is a developmental legacy imposed by the progenitor organs from which a petal is derived – be it stamens or bracts. These models are not mutually exclusive as each may hold for different floral structures, taxonomic groups, phylogenetic levels, and episodes of evolutionary history. However at this point it seems that no collective molecular definition of the petal has been reached at the hierarchical level of all angiosperms.

The 'petal' as a functional and homology-neutral term

In the preceding sections we have explored the definition and homology of the angiosperm petal from the perspective of various criteria: topology, historical derivation, morphology, and developmental genetics. It is evident that none of these criteria, either alone or in combination, provide a unifying principle with which to homologise the petal. This is perhaps an unsurprising conclusion, because at the level of angiosperms, petals are probably non-homologous structures that have attained an analogous showy petaloid condition in order to perform a common function in the attraction of pollinators. Therefore for the remainder of this review we propose to use the terms petal, petaloidy, sepal and sepaloidy as purely functional *homology-neutral* terminology, i.e. we use these terms to refer to perianth parts purely on the basis of their perceived functions as sepals or petals within the perianth. Despite using the common terminology of sepals and petals to describe floral organs in different lineages of angiosperms, we do not imply that collectively termed floral organs are necessarily homologous – only that the organs perform similar functions and thus may appear similar. Regardless of this inability to homologise petals across all angiosperms, insight into the nature of petals can be obtained by examining the variation and evolution of the perianth at different taxonomic levels and in different clades within the angiosperm phylogeny. Therefore we will now examine various lineages of angiosperms and discuss the opportunities and insights they offer to our understanding of perianth evolution.

PERIANTH VARIATION ACROSS ANGIOSPERMS

The iterative differentiation of perianth across angiosperms

Walker & Walker (1984) present an interesting scheme of perianth evolution in the angiosperms with six evolutionary stages, called grades. Starting with a simple perianth of floral

bracts (grade 1), as in Austrobaileyaceae and Trimeniaceae, an entirely sepaloid or petaloid perianth was obtained (grade 2); this was followed by differentiation of a distinct calyx and corolla of tepalar origin (grade 3). A reversal to wind pollination led to the loss of petals (grade 4: primary apetaly). Staminodial petals were acquired secondarily from these apetalous precursors by a transformation of stamens (grade 5), but could be further lost (grade 6, secondary apetaly). It is by using the latest phylogenies of the angiosperms (e.g. Soltis et al. 2003, 2011, Chase et al. 2005, Brockington et al. 2009, Wang et al. 2009) that these proposed patterns of perianth differentiation can be explored in an evolutionary context. Although the scheme of Walker & Walker (1984) is premolecular in concept, there is broad agreement with perianth traits mapped across molecular phylogenies. In a broad statement regarding the evolution of perianth across angiosperms, it can be argued that the basalmost angiosperms (i.e. *Amborella*, ANITA grade) possess an undifferentiated bracteate perianth with a gradual transformation of outer bracts into inner tepals; a typical tepaline perianth or bracteopetaline perianth where the perianth is more clearly demarcated from bracts, is more common for magnoliids and monocots; apetalous, wind pollinated flowers are common for the basal eudicot grade; and a well differentiated perianth with a predominance of sepals with petals occurs in the core eudicots (Ronse De Craene et al. 2003, Zanis et al. 2003). However, as we will explore in the following sections, superimposed on this scaffold are numerous reiterative trends and convergences in perianth evolution.

Perianth in the basal angiosperms

In basal angiosperms, it is difficult to separate and distinguish the bracts and perianth. Petaloid structures have arisen several times in the basal angiosperms. The most common pattern is the progressive differentiation of tepals into bracteopetals (e.g. Amborellaceae, Calycanthaceae, Illiciaceae, Lauraceae: fig. 1A), a sharp distinction of outer sepaloid tepals and inner petaloid tepals (e.g. Magnoliaceae, Annonaceae, Winteraceae), or an intergradation of tepals with outer staminodes (Himantandraceae, Nymphaeaceae) (e.g. Endress 2001, 2004, 2008b, 2010, Ronse De Craene et al. 2003, Soltis et al. 2009, Yoo et al. 2010). The degree of perianth differentiation is linked with the phyllotaxis (spiral or whorled) and number of perianth parts. Based on evidence in *Eupomatia*, Endress (2003, 2005) and Kim et al. (2005b) discussed the difference between bracts and tepals in the basal angiosperms as categories with different levels of complexity. Endress demonstrated that the association of bracts (in the form of a calyptra) with tepals, in clades where petals have not yet evolved, could be considered analogous to the formation of sepals and petals. In some basal angiosperms we can see that bracts may become associated with the flower (Winteraceae, Monimiaceae) to form the outer parts of the perianth. In Chloranthaceae and Ceratophyllaceae the perianth is considered to be reduced or lost in relation with the diminutive size of the flowers, although character reconstructions remain controversial (Endress & Doyle 2009, Doyle & Endress 2011).

Genetic analyses of MADS-box genes in basal angiosperms reveal that the homologs of the ABC function genes are more broadly expressed than their eudicot counterparts. The 'fading borders' model proposes that this lack of defined expression domains is related to gradation in floral organ identity that often occurs across the flowers of basal angiosperms. The model implies that the broadly expressed floral developmental pathways became canalised in association with the differentiated and whorled perianth that is characteristic of the core eudicots. However perianth differentiation has become divergent in some lineages of basal angiosperms, such as Nymphaeaceae and Cabombaceae, where the latter have a whorled phyllotaxis and a differentiation of sepals and petals. But the differentiation is not strong and B-gene homologs expression is detected in both sepals and petals (see Kim et al. 2005a, Endress 2008b, Warner et al. 2009, Yoo et al. 2010). Yoo et al. (2010) suggested that inner petals of Nymphaeaceae originated from petaloid staminodes, as they are intermediate in morphology and have a different gene expression from outer perianth organs. The staminodes of *Nuphar* also develop in pairs (Endress 2001), which is suggestive of stamen initiation and is comparable to paired stamens of *Cabomba* (see Ronse De Craene et al. 2003). Yoo et al. (2010) preferred not to use 'sepals' and 'petals' for Nymphaeales, because they do not relate to structures described for core eudicots, but to refer to 'sepaloid' and 'petaloid' tepals instead.

Perianth in the magnoliids

The bipartite flower of magnoliids (e.g. Magnoliaceae, Annonaceae) is in many ways comparable to the bipartite perianth of core eudicots, although it certainly has a separate origin. In Myristicaceae, as in Aristolochiaceae and Lactoridaceae, the perianth is reduced to a single whorl with clear sepaloid characteristics (Ronse De Craene et al. 2003, Xu & Ronse De Craene 2010). The ancestral number of perianth whorls for the magnoliids is reconstructed as more than two by Endress & Doyle (2009), with a repetitive derivation of a single or two whorls of perianth parts. This reconstruction made no assumption about the mechanism of increase of whorls. More than two whorls can also be derived by the addition of staminodial organs as has been observed in Ranunculales. Regardless, there is a clear trend towards a reduction and stabilisation of the number of whorls, either in dimerous or trimerous flowers and this occurs in all extant clades of basal angiosperms such as magnoliids. In agreement with the 'fading borders' model of basal angiosperms, patterns of gene expression including homologs of *AP3*, *PI* and *AG* appear to be broader and less constrained than for core eudicots. As in the early lineages of angiosperms, this has been related to the more gradual transition in organ identity that can occur in many magnoliid flowers. Interestingly, in the more differentiated flowers of *Asimina*, the expression of the MADS-box gene homologs appears to be more constrained again suggesting a link between perianth differentiation and genetic canalisation (Kim et al. 2004). Kim et al. found that *AP3* and *PI* were expressed in petals and stamens of *Asimina* (Annonaceae), but with very limited expression in sepals (only *AP3*). In other basal angiosperms, such as *Magnolia grandiflora*, B-gene expression is strong in all perianth whorls (Kim et al. 2004). This suggests a progressive restric-

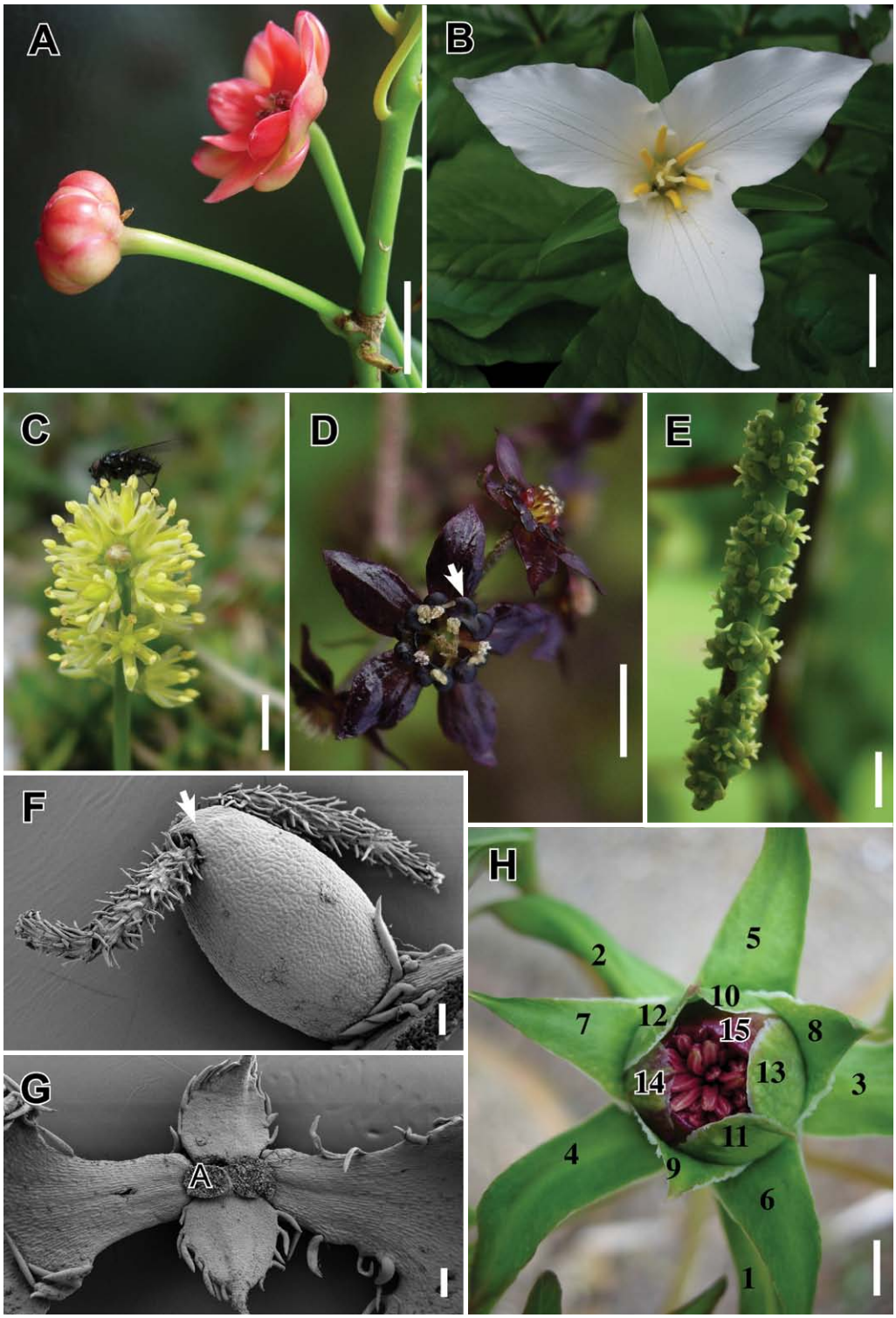

Figure 1 – Examples of perianth structure in angiosperms, flowers of basal angiosperms, monocots, basal eudicots and early diverging core eudicots: A, *Illicium henryi* Diels (Illiciaceae), lateral view of two flowers with undifferentiated perianth; B, *Trillium grandiflorum* (Michx.) Salisb. (Melanthiaceae), flower with differentiated perianth; C, *Tofieldia calyculata* (L.) Wahlenb. (Tofieldiaceae), inflorescence; note flowers with undifferentiated perianth; D, *Xanthorhiza simplicissima* Marshall (Ranunculaceae), flowers; note the coloured calyx and small nectar leaves (arrow); E, *Tetracentron sinense* Oliv. (Trochodendraceae), inflorescence with small dimerous flowers and undifferentiated perianth; F, *Gunnera prorepens* Hook.f. (Gunneraceae), pistillate flower with simple calyx (arrow); G, *Gunnera monoica* Raoul (Gunneraceae), staminate flower with calyx and corolla; stamens (A) removed. H, *Paeonia delavayi* Franch. (Paeoniaceae), flower bud; numbers give sequence of initiation of continuous spiral linking bracts, sepals and petals. Scale bars: A, C, E, H = 1 cm; B = 2 cm; D = 0.5 cm; F = 100 µm; G = 200 µm.

tion of gene expression linked with a stronger differentiation between sepal and petal whorls.

Laurales generally have an undifferentiated perianth, often as two trimerous or dimerous whorls of tepals. While some families have a spiral, undifferentiated perianth (e.g. Gomortegaceae, Calycanthaceae), a whorled perianth is generalized in Hernandiaceae, Monimiaceae, and Lauraceae (Staedler & Endress 2009). Chanderbali et al. (2006) interpreted the Lauraceae as having andropetals (based on a study of *Persea*, where *AG* expression was found in the tepals), and some Lauraceae (*Litsea*, *Lindera*) apparently have a homeotic transformation of tepals into stamens (Rohwer 1993). However, gene expression alone is insufficient to consider the perianth of Lauraceae as stamen-derived, as gene expression is generally diffuse in magnoliids and this may also be the case in the small flowers of Lauraceae. A staminodial origin of the simple perianth of *Persea* and Lauraceae (Chanderbali et al. 2006) is further doubtful because of the widespread biseriate and undifferentiated perianth in other families within the Laurales such as Hernandiaceae and Monimiaceae.

The primitive perianth of Aristolochiaceae is interpreted as unipartite in recent molecular analyses (e.g. Zanis et al. 2003), and this could apply to all Piperales, with possibly a secondary acquisition of petals from sterilized stamens (i.e. *Saruma*, *Asarum*: Leins & Erbar 1995, González & Stevenson 2000, Ronse De Craene et al. 2003, Jaramillo & Kramer 2004). *Saruma* is the only member of Aristolochiaceae with a fully developed petaloid second perianth whorl. In some species of *Asarum* (*A. caudatum*: Leins & Erbar 1985, Ronse De Craene 2010) there are small appendages that have been interpreted as staminodial on morphological evidence (discussed in Ronse De Craene 2010) and this may be a link with petals in *Saruma*. The fact that *Saruma* has a derived position in the family (Kelly & González 2003) and the generalized *AP3/PI* expression in the petals, which is different from the perianth of *Aristolochia* (where *AP3/PI* expression is restricted to non petaloid tissue of the tepals: Jaramillo & Kramer 2004) could arguably support a staminodial origin for the petals of *Saruma*. Note that in these case studies from both the Laurales and Aristolochiaceae, MADS-box gene expression patterns could be explained in relation to their progenitor organs rather than in connection to the extant organ function.

Perianth in the monocots

In monocots, with a stable configuration of two perianth whorls, two stamen whorls and one carpel whorl ("trimerous-pentacyclic flowers": Remizowa et al. 2010), the perianth can take one of three forms. Either both perianth whorls are petaloid and undifferentiated (e.g. Liliales, Asparagales: fig. 1C), both perianth whorls are sepaloid and undifferentiated (some Alismatales, Poales), or there is a clear differentiation of the inner whorl into coloured petals and the outer whorl into green sepals (e.g. Alismataceae, some Melanthiaceae, Commelinaceae, Bromeliaceae: fig. 1B). The three conditions are generally interchangeable. Phylogenetic reconstructions support a repeated derivation of a differentiated perianth in the monocots (Ronse De Craene et al. 2003, Zanis et al. 2003, Endress & Doyle 2009). The presence of coloured staminodes is restricted to Zingiberales (Zingiberaceae, Costaceae, Marantaceae, Cannaceae), where they play a specific role in pollination (Dahlgren et al. 1985, Walker-Larsen & Harder 2000, Bartlett & Specht 2010, Glinos & Coccucci 2011). In Zingiberaceae *GLO* (*PI*) and *AG* are expressed in labellum and stamens, supporting the staminodial nature of the former organ (Gao et al. 2006). Bartlett & Specht (2010) showed a repeated duplication and diversification event of *GLO* in Zingiberales, corresponding with the increased complexity of the androecium.

The delimitation of bracts and perianth is occasionally blurred in the monocots. In *Acorus* (Buzgo & Endress 2000), the bracts and outer median tepals of the perianth cannot be distinguished, and it is suggested that the bract 'invades' the flower as a merged organ. In Tofieldiaceae and several members of the Alismatales, perianth and subtending or preceding bracts often intergrade with intermediate structures (Remizova & Sokoloff 2003). There are several other cases where bracts and tepals cannot be distinguished and this is generally linked with strong flower reductions as in Cyperaceae (Remizowa et al. 2010).

The occurrence of two trimerous (rarely dimerous) perianth whorls is highly conservative in the clade and facilitates the understanding of perianth homology, although the genetic basis of petal differentiation can be variable and complex. In general, homologues of eudicot *AP3* and *PI* are found in monocots (Gao et al. 2006) and shifting boundaries in the expression of these B-class MADS-box genes have been hypothesised to explain the transition between a differentiated perianth and an undifferentiated perianth comprised of petaloid tepals (Albert et al. 1998, Kramer et al. 2003). This has been illustrated for Liliales (e.g. Kanno et al. 2003 for *Tulipa*) and some Asparagales (e.g. *Agapanthus*: Nakamura et al. 2005). The model postulates an expansion of B-gene activity to the outer perianth, indirectly implying that a differentiated perianth is ancestral in the monocots. However, as discussed by Ronse De Craene (2007) and Soltis et al. (2009), this model is not always supported by patterns of gene expression in Monocots. Indeed, it is challenging to compare the genetics of petal differentiation in monocots with core eudicots, as both clades have undergone highly different evolutionary pathways. One interpretation of the genetic data is that an undifferentiated perianth is basic in monocots and cases of differentiated perianth or restricted gene expression (e.g. *Asparagus*) are derived. Clear support for this has been provided by a study of three species of Commelinaceae by Preston & Hileman (2012). Contrary to the two other species with similar petaloid inner whorl tepals, the inner ventral tepal of *Commelina communis* is similar to the outer whorl tepals in morphology and absence of B-gene expression. The homeotic transformation of the inner ventral tepal indicates that the outer non-petaloid whorl has probably been derived by loss of B-gene expression, with a recurrent invasion of the inner whorl, possibly linked with bilateral symmetry. In a similar line earlier genetic studies have suggested that grass lodicules are analogous to petals of eudicots because they share similar B-gene expression (reviewed in Yoshida 2012). Whipple et al. (2007) compared the perianth development and B-gene expression in *Streptochaeta angustifolia*, a basal

grass that possesses tepals, and two species related to grasses, *Joinvillea ascendens* (Joinvilleaceae) and *Elegia elephas* (Restionaceae). They found that, similar to the lodicules of grasses, there was B-class gene expression in the inner tepal whorl of all investigated species possibly indicating homology of inner tepals with lodicules. Their conclusions suggest that there is a difference between the outer tepals and inner tepals and that B class genes control the identity of second whorl organs regardless of whether the second whorl organs are petal-like or lodicules. These shared gene expression patterns in whorl two constitute evidence of a shared deep homology of perianth parts, nonwithstanding their difference in morphology (Yoshida 2012). However, as suggested earlier, inner and outer perianth whorls in monocots are derived from an undifferentiated perianth where petaloidy was initially linked with B-class gene expression in both whorls. The gene expression patterns in lodicules may be a relict of petaloid developmental pathway that became restricted (in parallel to the eudicot restriction) to the inner whorl (as in some Commelinales); subsequently petaloidy was lost with the evolution of lodicules but the B-class genes were retained in regulation of lodicule development.

Perianth in the early diverging eudicots

Contrary to core eudicots but comparable to basal angiosperms, B-gene expression is often much broader in the basal eudicots, sometimes extending to sepals, bracts or carpels (Zahn et al. 2005, Shan et al. 2006, Wu et al. 2007, Rasmussen et al. 2009, Yoo et al. 2010). This perhaps links early diverging eudicots more strongly to basal angiosperms than core eudicots and is reflected by their variable floral morphology. Within the early diverging eudicots, petals have been derived independently on several occasions from non-homologous organs. Ranunculales present a plethora of evolutionary trends leading to a differentiated perianth (Drinnan et al. 1994, Endress 1995, Ronse De Craene et al. 2003, Soltis et al. 2003, Doyle & Endress 2011). The basic elaboration of petaloid organs is through the coloration of an undifferentiated perianth (e.g. *Nandina* and *Podophyllum* in Berberidaceae, *Anemone* in Ranunculaceae), the formation of outer bractlike sepals and two whorls of petals (e.g. Papaveraceae), or by the differentiation of the perianth into two types of petaloid organs: showy outer sepals and inner, variable nectar-leaves or petals (e.g. Ranunculaceae: fig. 1D, Berberidaceae, Lardizabalaceae, Menispermaceae: Erbar et al. 1998, Hoot et al. 1999, Endress 1995, 2010, Ronse De Craene et al. 2003, Kramer et al. 2003, Zanis et al. 2003, Jabbour et al. 2009, Rasmussen et al. 2009). In some cases, outer stamens are staminodial with aborted anthers (e.g. *Anemone* - *Pulsatilla* group), or outer stamens are interchangeable with petaloid staminodes (e.g. *Clematis*) (Ren et al. 2010). In both cases nectar may be produced at the base of the filaments. The fact that petal development is linked with a regression of outer stamens may signify that loss of fertility is compensated by the development of rewards and attractiveness in the sterile organs.

Variable forms of the differentiation of the perianth limits our ability to discern when petals correspond to sepals or stamens but this distinction is of fundamental importance for understanding the evolution of the perianth in the Ranunculales (cf. Ronse De Craene et al. 2003). It has been frequently suggested that inner whorl petals or nectar leaves represent a transformed stamen whorl (e.g. Kosuge 1994, Takhtajan 1991, Erbar et al. 1998). While this is supported by similarities in position and morphology, in some cases a staminodial nature of petals has been questioned (e.g. Lardizabalaceae: Zhang & Ren 2011). Within Ranunculales class B homologous genes *AP3* and *PI* have undergone several duplication events in different families, leading to multiple paralogs (Shan et al. 2006, Rassmussen et al. 2009, Sharma et al. 2011). Two duplication events in the *AP3* lineage took place before the divergence of Ranunculales, giving rise to three paralogous lineages (Kramer et al. 2003, Rasmussen et al. 2009, Hu et al. 2012). While *AP3-I* and *AP3-II* are linked to a limited extent with petaloidy of sepals, *AP3-III* tends to be a major player in the development of petals in Ranunculaceae and Berberidaceae but not necessarily in the stamens (Kramer et al. 2003, Rasmussen et al. 2009). The *AP3* and *PI* gene expression in all studied Ranunculales (e.g. Kramer et al. 2003, Drea et al. 2007, Rasmussen et al. 2009, Hu et al. 2012) appears remarkably similar and implies that nectar leaves share a similar gene regulatory program. According to Rasmussen et al. (2009) and Sharma et al. (2011), this restricted expression of *AP3-III* is compelling evidence for a common inherited petal identity program and contradicts earlier hypotheses of independently derived petals in the Ranunculales. However, the repeated duplications appear to be restricted to Ranunculales and genetic evidence, by specifically stressing characteristics of petaloidy leaves open the possible homology of the petals with nectar leaves of staminodial origin. Hu et al. (2012) demonstrated that the nectar leaves of *Sinofranchetia chinensis* (Lardizabalaceae) show a strong affinity with stamens in the shared expression of *AG* and B-genes, supporting the hypothesis of a derivation from stamens.

Contrary to Ranunculales, a perianth differentiated into sepals and petals is more the exception than the rule in the grade leading to the core eudicots. It is very difficult to distinguish bracts from a perianth in several taxa of the basal eudicot grade and flowers may in fact be truly perianthless in several cases. Nelumbonaceae and Sabiaceae are the only taxa with a clear differentiation of sepals and petals. *Nelumbo* has two bract-like sepals enclosing several helically arising petals with a comparable vascular supply (Moseley & Uhl 1985, Hayes et al. 2000), suggestive of bracteopetals. *AP3* and *PI* gene expression in *Nelumbo* resembles that of Ranunculaceae but also basal angiosperms in their broad expression patterns (Yoo et al. 2010). This may either reflect a retained ancestral petal identity program, or the fact that a defined program simply did not exist at that stage. In Sabiaceae the biseriate perianth shows a clear link between petals and sepals in ontogeny and anatomy (Wanntorp & Ronse De Craene 2007, Ronse De Craene & Wanntorp 2008).

Other early-diverging eudicots have a simple, bipartite, valvate perianth (Proteaceae), or the perianth is undifferentiated, reduced, or absent and the delimitation of flowers is often unclear (see Drinnan et al. 1994, von Balthazar & Endress 2002, Wanntorp & Ronse De Craene 2005, González & Bello 2009). In Platanaceae the perianth is probably in a

state of reduction linked to a shift from insect to wind pollination (e.g. Kubitzki 1993, von Balthazar & Schönenberger 2009), as supported by a greater variety in fossil flowers (e.g. Magallón-Puebla et al. 1997, Mindell et al. 2006). Flowers have at least two whorls of sterile organs, with the inner one closely linked to the androecium and arising after all other floral organs. Although the homology of the second whorl is debatable, it has been interpreted as staminodial on the basis of the basal adherence of the inner sterile organs to the stamens in a short tube and evidence from fossils (von Balthazar & Schönenberger 2009). A distinction between tepals and bracts is also controversial in *Trochodendron* and *Tetracentron*. *Tetracentron* has a subtending bract and two alternating pairs of tepals (fig. 1E), and the outer transverse pair occupies the position of the lateral bracteoles that are found in the sister genus *Trochodendron* (Endress 1986, Chen et al. 2007). In *Trochodendron* there are variable numbers of small scales between bracteoles and stamens. Wu et al. (2007) suggested on genetic evidence that a perianth was secondarily lost in *Trochodendron* with retention of some aspects of a petal identity in the remaining floral organs. As for Ranunculales, the expression of B-genes in perianth organs may be an indication of an ancestral petal identity program but does not necessarily help in understanding the homology of these organs at other hierarchical levels. The presence or absence of a perianth in *Didymeles* is also controversial (von Balthazar et al. 2003). The flowers of Buxaceae are preceded by various numbers of superficially similar bract-like phyllomes and tepals, and a distinction between both kinds of organs can only be made on differences of plastochron and degree of differentiation (von Balthazar & Endress 2002). The differentiation of bracts into tepals is more convincing in staminate flowers of Buxaceae than in pistillate flowers, which can either be interpreted as without perianth (being surrounded by empty bracts), or with undifferentiated bracts. Von Balthazar & Endress (2002) hypothesized that Buxaceae represent an early preliminary stage of perianth differentiation, leading to a later canalization of the bipartite perianth common to the core eudicots. Alternatively, the flowers of Buxaceae and Trochodendraceae can be seen as reduced and perianthless, with a secondary acquisition of a simple perianth linked with a reversal to insect pollination. This is in part enabled by development of nectary tissue on the back of the ovary (see also Ronse De Craene 2010).

Gunnerales have previously been considered as pivotal in the understanding of the origin and relationships of core eudicots (Soltis et al. 2003). Gunneraceae show a strong reductive trend in flowers linked with wind pollination (Wanntorp & Ronse De Craene 2005, Ronse De Craene & Wanntorp 2006; fig. 1F & G). Wanntorp & Ronse De Craene (2005) pointed out that sepals, petals, tepals or bracts designate organs of the same homology in the Gunneraceae. Interestingly Gunneraceae and Buxaceae (e.g. *Notobuxus* nested in *Buxus*) share the presence of median (outer) sepals (or bracteoles?) covering the rest of the flower. *Gunnera* shows the same tendency for reduction as the other taxa of the basal grade leading to the core eudicots, and it is not possible to consider the floral configuration in Gunneraceae to be the structural basis for the bipartite perianth of the core eudicots (Wanntorp & Ronse De Craene 2005, González & Bello 2009). The flowers of Gunneraceae may be the result of previous reductions and may become pseudanthial assemblages, which tend to culminate in some almost perianthless species, such as *Gunnera herteri* (Rutishauser et al. 2004). The arrangement of the perianth parts (ideally four in a dimerous-tetramerous decussate pattern opposite carpels or stamens) is strikingly similar in Buxaceae, *Tetracentron* and *Gunnera*, and there is no substantial difference between the perianth structures of *Gunnera* and its sister group *Myrothamnus* (Wanntorp & Ronse De Craene 2005, González & Bello 2009). However, unlike Gunneraceae, the perianth of *Myrothamnus* is only loosely integrated (described as functionally and morphologically transitional structures or 'Hochblätter' by Jäger-Zürn 1966). Gunneraceae represent a continuation of a line of dimerous, disymmetric flowers with a weak or no differentiation of a perianth. To visualize the floral arrangement of the grade as an early canalization to the well-established core eudicot flowers (e.g. Soltis et al. 2003) is structurally difficult because of highly different floral morphologies. However, either these flowers existed in the ancestors of core eudicots (e.g. Doyle & Endress 2011), or these flower types represent distinct evolutionary lines with little structural relation with the core eudicots (Wanntorp & Ronse De Craene 2005, Ronse De Craene & Wanntorp 2006, González & Bello 2009). This interpretation appears less parsimonious, although we may not have sufficiently filled in the 'missing links'.

Perianth transition in the core eudicots

The transition between early diverging eudicots and core eudicots (Gunneridae *sensu* Cantino et al. 2007) remains obscure, with pentamery and a well differentiated perianth as the main key innovations for core eudicots (see Ronse De Craene 2004, 2007, 2008a). Core eudicots are the group where a distinction between sepals and petals can be most easily made (Endress 2010), and this is expressed in the constrained expression of identity genes in adjacent whorls (Kim et al. 2004, Ronse De Craene 2007, Chanderbali et al. 2009). The origin of the pentamerous bipartite perianth of core eudicots remains a mystery. Ronse De Craene (2004) suggested that a flower such as *Berberidopsis* (Berberidopsidaceae-Berberidopsidales) could function as a prototypic model for the evolution of the perianth in the core eudicots. Based on evidence presented in *Berberidopsis*, it is argued that the biseriate perianth of core eudicots evolved from an undifferentiated perianth with spiral phyllotaxis by a gradual disruption of the plastochron and arrangement of tepals in two alternating whorls (Ronse De Craene 2007, Ronse De Craene & Stuppy 2010). Within Berberidopsidales *Aextoxicon* represents a clear transition to a pentamerous, bipartite flower. An alternative hypothesis is the derivation of the dicyclic pentamerous perianth of core eudicots from two dimerous whorls of reduced sepal-like organs (Endress & Doyle 2009, Doyle & Endress 2011), and while this is a more parsimonious alternative, it is more difficult to support on a structural basis.

Apart from Berberidopsidales, a biseriate pentamerous perianth is widespread and was acquired early in core eudicot evolution. In all observed cases, when the perianth is

uniseriate, this appears to be derived by loss of either the sepal whorl or the petal whorl.

Perianth in the rosids

Most rosids, including Saxifragales, have a pentamerous (or tetramerous) pentacyclic (or tetracyclic) flower with a clear differentiation between sepals and petals. Petals tend to be free in most taxa. Endress & Matthews (2012) mention several exceptions where petals are fused and usually connected by a hypanthium (cf. Ronse De Craene 2010). Petals are often clawed and can be retarded in their development. Petal shapes vary widely, and petals can be fringed, trilobed or often bear ventral appendages (Endress & Matthews 2006). In several clades (e.g. Saxifragaceae, Rhamnaceae, Thymelaeaceae), there is a tendency for petals to become smaller or to vanish altogether. In Saxifragales, several families have no petals, petals are small, strap-shaped or fimbriate, or they are absent (Haloragaceae, Hamamelidaceae, Grossulariaceae, Saxifragaceae: fig. 2A–B). Endress & Matthews (2006) found that petal lobation and petal reduction are connected as both conditions are often found in the same family, even the same genus. Within rosids, several apetalous clades have evolved independently, especially in fabids (e.g. Rosales, Fagales, Cucurbitales) and within each major order or family there are at least some apetalous members (e.g. *Buchholzia* in Capparaceae, *Ceratonia* in Fabaceae, *Deinbolia* in Sapindaceae, subfamily Sterculioideae in Malvaceae). The reduction of petals is generally linked with the development of a showy hypanthium with persistent petaloid sepals (fig. 2G). Schönenberger & Conti (2003) demonstrated that petals in the small families Penaeaceae, Oliniaceae, Rhynchocalycaceae and Alzateaceae (Myrtales) can be either present and small, or absent with a transfer of petaloidy to the hypanthium and sepals. A similar evolution characterizes Begoniaceae (Cucurbitales), where petals are lost except in the monotypic *Hillebrandia* (Matthews & Endress 2004). Apart from the well-studied *Arabidopsis thaliana*, relatively few evo-devo studies have been carried out in rosids (except some *Carica* and Polygalaceae). However, the diversity of petal morphologies is striking (e.g. Endress & Matthews 2006) and different morphologies could be linked with loosening of the restrictive confinement of B-gene activity to the second whorl (e.g. Paeoniaceae, Clusiaceae: Ronse De Craene 2008a, 2008b), or a secondary origin from staminodes (e.g. Rosaceae: Ronse De Craene 2003, 2007).

Perianth in the Caryophyllales

Caryophyllales appear in most recent phylogenies as placed in a grade with Santalales and Berberidopsidales at the base of asterids. The caryophyllid clade can be considered as the grouping of two sister clades, Polygonales and Caryophyllales (Judd et al. 2002, Brockington et al. 2009) or subclades (Judd et al. 2008). A differentiation of sepals and petals is widespread in different families of Polygonales, but petals are lost in Nepenthaceae and Polygonaceae, with a possible reinvention in Plumbaginaceae. The perianth in Polygonaceae is sepaline in nature, originally pentamerous in a single whorl, with a shift to a hexamerous or tetramerous perianth in two whorls. The shift to six sepals occurred at least three times (Lamb Frye & Kron 2003). The perianth is generally connected by a hypanthium and is often petaloid. In the hexamerous flower the sepals are arranged in two whorls of three and often become differentiated morphologically, especially at fruiting, closely resembling a trimerous flower (Ronse De Craene 2010). Ainsworth et al. (1995) found no B-gene expression in the perianth of *Rumex*, but confuse petals with sepals in suggesting that sepaloidy is the result of a secondary restriction of petaloidy in the 'petals'. However, the flower in Polygonaceae is basically apetalous. It can be assumed that in other Polygonaceae such as *Fagopyrum* (Logacheva et al 2008), B-gene expression is not present in the petaloid perianth, although this has not been verified. Plumbaginaceae have petaliferous flowers with petals arising as appendages from common stamen-petal primordia (De Laet et al. 1995). Further studies, including evo-devo evidence should confirm whether petals are staminodial in this family, in analogy with Caryophyllaceae (see below). This would include a combined expression of B- and C- genes in the petals as in the stamens. Polygonaceae and Plumbaginaceae share striking similarities with Caryophyllales (Ronse De Craene 2010) and the distance between both clades may appear greater by an absence or loss of intermediates.

Basal flowers of core Caryophyllales are generally pentamerous and apetalous with five sepals in a 2/5 arrangement and outer sepals often bear a dorsal crest (e.g. Caryophyllaceae, Aizoaceae, Amaranthaceae, Portulacaceae). At least thirteen families are fully apetalous or have some members without petals (Endress 2010). In some clades petaloid sepals are the main attractive parts of the flower (Phytolaccaceae, Nyctaginaceae, Cactaceae: fig. 3D & E). In other clades a bipartite perianth has evolved in parallel, either by insertion of a pair of bracts close to the petaloid sepals (e.g. Portulacinae), or by a differentiation of outer staminodes from common stamen rings (e.g. Caryophyllaceae, Aizoaceae, Lophiocarpaceae: fig. 3A–C).

Brockington et al. (2011) demonstrated that at least for some Caryophyllales petaloid structures in the flower can have a different gene expression from *AP3* and *PI*, supporting the hypothesis of a novel acquisition of petals in the clade (Ronse De Craene 2007, 2008a, 2010, Brockington et al. 2009). In Aizoaceae the perianth is either undifferentiated (e.g. *Sesuvium portulacastrum*) or differentiated into sepals and numerous (staminodial) petals (e.g. *Delosperma napiformа*). In *Delosperma* the staminodial petals behave as expected for stamens in the early expression of *AP3*, *PI* (B-genes) and *AG* (C-gene) before these genes are turned off. However, the petaloid tepals of *Sesuvium* do not show any expression of *AP3* and *PI*, suggesting a novel acquisition of petaloidy in the sepal-derived perianth. These findings support the initial loss of the inner perianth whorl in Caryophyllales and the correspondence of the single perianth whorl to sepals of other core eudicots (cf. Hofmann 1994, Ronse De Craene 2008a). It also demonstrates that evolution of a petaloid appearance is highly complex in Caryophyllales with repeated events of a novel acquisition of petaloid sepals and petaloid staminodes in different clades.

In Portulacaceae s.l. there is a progressive delay in the development of the petaloid sepals, culminating in Montiaceae, where sepals develop as appendages of the stamens

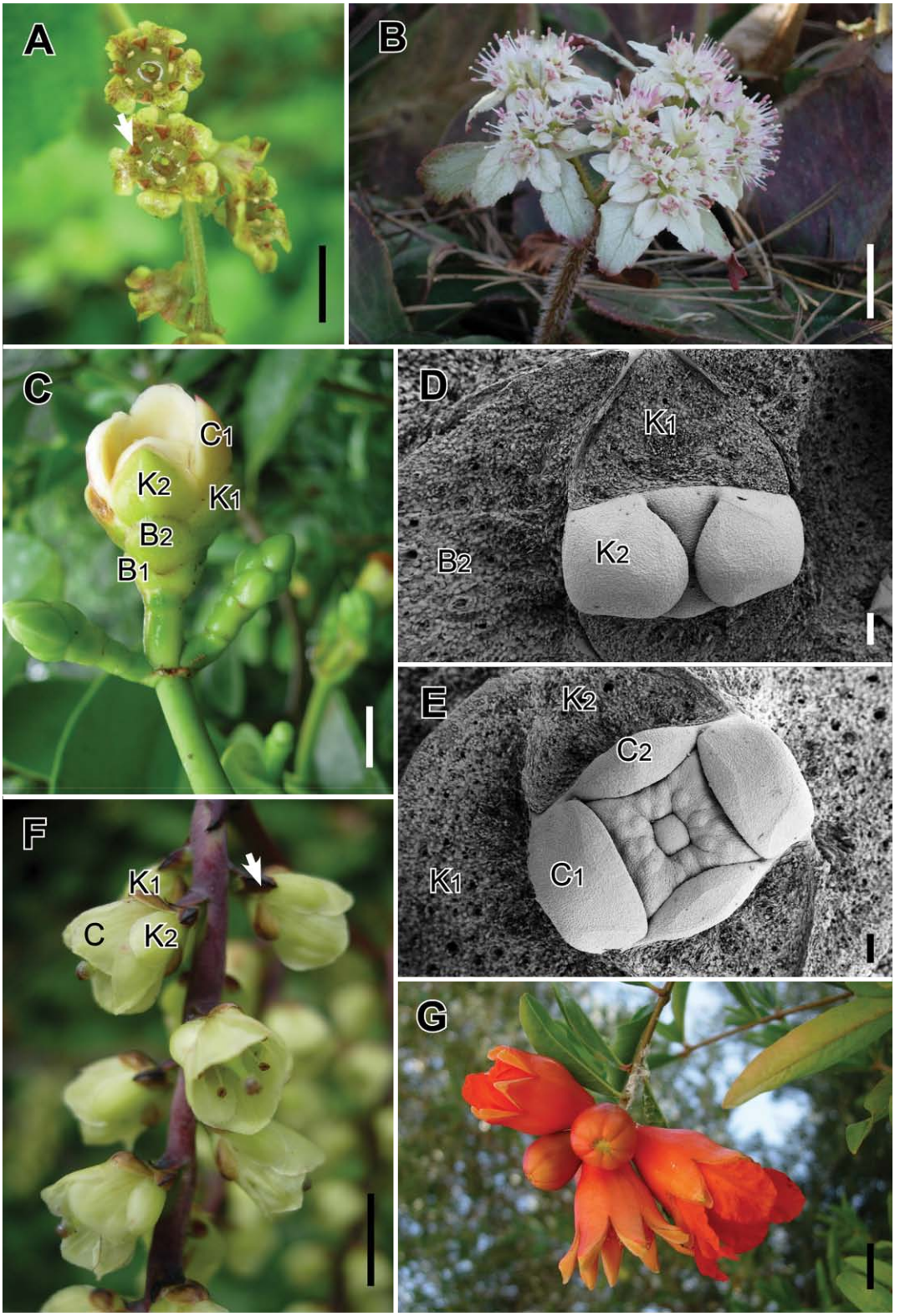

Figure 2 – Examples of perianth structure in angiosperms, flowers of rosids: A, *Ribes affine* Kunth (Grossulariaceae), group of flowers; note the small petals (arrow); B, *Chrysosplenium macrophyllum* Oliv. (Saxifragaceae), inflorescence; note the showy white bracts and absence of petals; C–E, *Clusia* sp. (Clusiaceae), male flowers: C, mature flowers showing succession of bracts (B), sepals (K) and petals (C); D, early initiation of sepals in decussate whorls; E, initiation of petals and androecium; F, *Stachyurus chinensis* Franch. (Stachyuraceae), partial view of inflorescence; note two-whorled sepals with the outer sepals (K1) similar to the bract (arrow) and the inner sepals (K2) similar to the petals (C); G, *Punica granatum* L. (Lythraceae), inflorescence with flowers at different stages; note the bright hypanthium which is indistinguishable from petals and sepals. Scale bars: A = 0.5 cm; B, C, F, G = 1 cm; D, E = 100 μm.

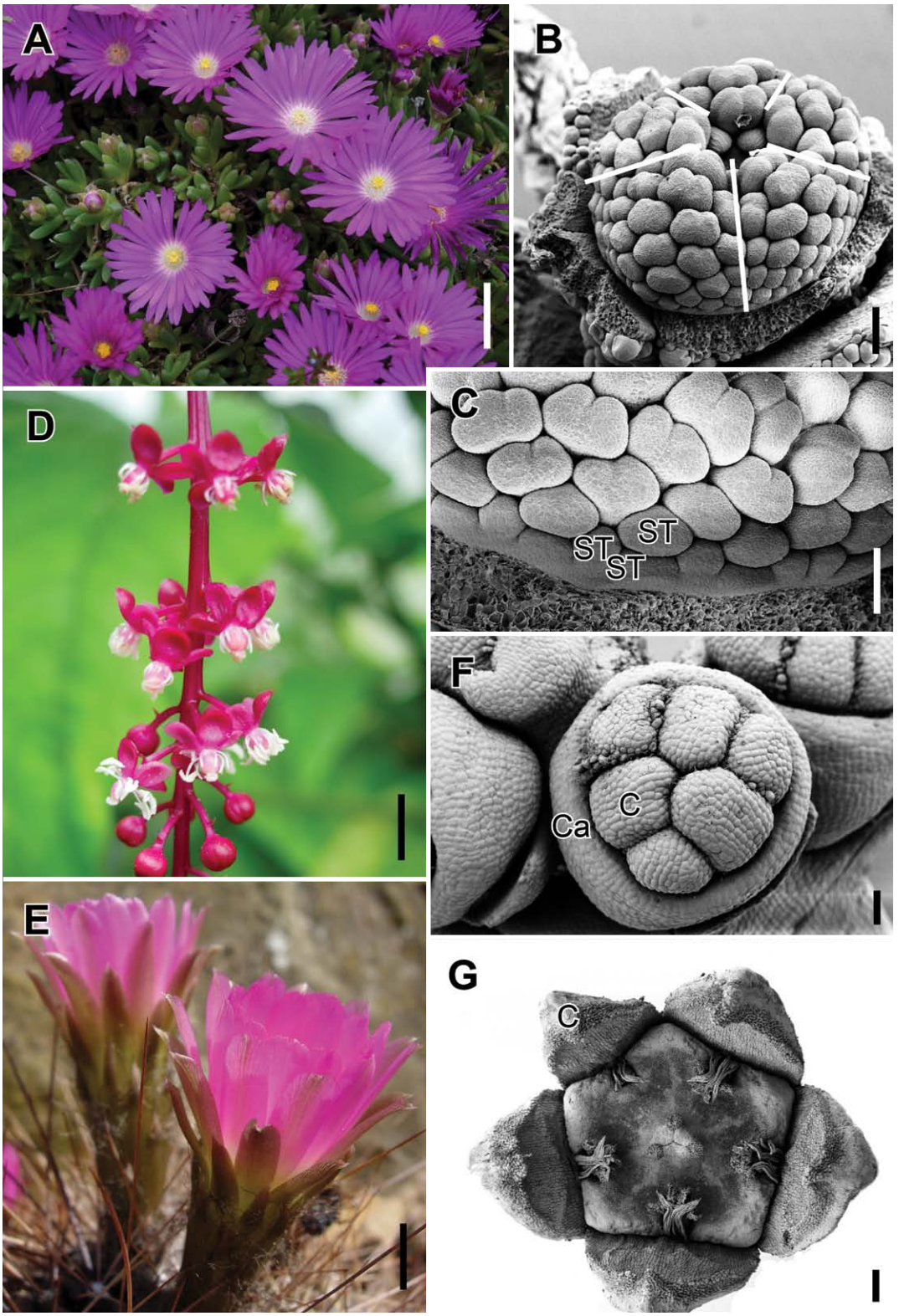

Figure 3 – Examples of perianth structure in angiosperms, flowers of Caryophyllales and Santalales: A, *Delosperma lavisiae* (L.) Bolus (Aizoaceae); B–C, *Mesembryanthemum* sp. (Aizoaceae): B, centrifugal initiation of stamens in five groups (delimited by lines); C, detail of outer stamens, with development of three whorls of sterile stamens (ST); D, *Trichostigma peruvianum* H.Walter (Phytolaccaceae): partial view of inflorescence with coloured sepals and peduncle; E, *Echinopsis pentlandii* (Hook.f) Salm-Dyck (Cactaceae): lateral view of flowers showing gradual transition of bracts and tepals; F, *Loranthus europaeus* Jacq. (Loranthaceae): Flowers in bud showing calyculus (Ca) and two whorls of three petals (C); G, *Colpoon compressum* Bergius (Santalaceae), mature flower from above. Note the large petals and nectary. Scale bars: A, E = 1.5 cm; B, C, F = 100 µm; D = 0.25 cm, G = 200 µm.

in a homoplasious fashion to staminodial petals of Caryophyllaceae (Dos Santos et al. 2012). It will be interesting to discover how other species in Caryophyllales behave in their gene expression, as staminodial petals arose approximately seven times in Caryophyllales (e.g. Caryophyllaceae, Aizoaceae, *Limeum*, *Glinus*, *Macarthuria*, *Asteropeia*, *Corbichonia*: Ronse De Craene 2007, 2010, Brockington et al. 2009). These findings also demonstrate that the suggestion that petaloidy can be switched on and off on a regular basis in the eudicots (e.g. Kramer & Jaramillo 2005, Irish 2009) cannot be applied to at least some Caryophyllales, where the disappearance of petals was linked with the complete loss of their genetic structure.

Perianth in the asterids (including Santalales)

Petal loss in rosids is commonly linked with the development of an attractive, tubular hypanthium taking over the function of petals and providing protection to the inside of the flower. In asterids an analogous tubular structure is provided by the association of petals and stamens in a stamen-petal tube (fig. 4C, E & F). Contrary to rosids, not the corolla but the calyx tends to be redundant, particularly in a number of clades of asterids and Santalales, often being reduced to a small rim or lobes or a tuft of hairs (Ronse De Craene 2010; figs 3F, 4D & G).

The development of a stamen-petal tube is one of the most conspicuous features of the asterids, although it is not present in all families. The nature of the tube is hypanthial and develops in a similar way as in monocots with tubular flowers. The tube has generally been described as a petal tube or corolla tube but it is two-parted and consists of a common meristematic zone for petals and stamens ('Stapet') and an upper corolla tube, which represents the fused petals (Erbar 1991, Ritterbusch 1991, Ronse De Craene & Smets 2000, Ronse De Craene et al. 2000, Endress & Matthews 2012). Growth of both zones is independent and leads to great variation in flower shapes. While the tube may be extremely long, it may fail to develop, leading to secondary apopetalous flowers (e.g. Apiaceae, Araliaceae, Montiniaceae, Plantaginaceae: Hufford 1995, Erbar & Leins 1997, Ronse De Craene 2010, Ronse De Craene et al. 2000; fig. 4G). The stamen-petal tube is frequent (but not generalized) in members of Ericales (e.g. Primuloid clade, Ebenaceae, Sapotaceae, Theaceae, Lecythidaceae; see also Endress & Matthews 2012). In Primulaceae and Theophrastaceae the tube may incorporate a staminodial whorl (e.g. Caris & Smets 2004, pers. obs. on *Soldanella*; fig. 4A).

Apetalous asterids are not common and are generally found in genera with highly reduced flowers (e.g. *Hydrostachys*, *Callitriche*, *Hippuris*: Leins & Erbar 1988). Apetalous insect pollinated flowers, such as *Glaux* (Myrsinaceae), are exceptional.

Within campanulids the reduction of sepals can take great proportions, in the development of virtually asepalous flowers in several Apiales (Araliaceae, Apiaceae: fig. 4G) or a replacement of the calyx by scales or hairs (Asterales, Dipsacales); in all cases petals take over the protective function in bud. These asepalous flowers generally have an inferior ovary, and it is possible that the sunken gynoecium is sufficiently protected by surrounding tissue, making sepals redundant. In these cases the corolla combines attraction with protection, or flowers are grouped in dense pseudanthia surrounded by bracts (e.g. Asteraceae, Caprifoliaceae). In several *Schefflera* species the loss of the calyx is linked with strong anastomoses of vascular bundles in the flower (Nuraliev et al. 2011). In some Rubiaceae, the calyx is reduced to a small rim or lost altogether (e.g. *Galopina*: Ronse De Craene & Smets 2000; *Theligonum*: Rutishauser et al. 1998; *Phyllis*: fig. 4D). In *Thunbergia* (Acanthaceae) loss of a calyx is accompanied by the development of large bracts in some species, taking over the role of sepals (Endress 2008a). In Caprifoliaceae the loss of a calyx is often accompanied by the development of an epicalyx with similar function (Donoghue et al. 2003).

In analogy with campanulids, perianth evolution in Santalales also favours the corolla over the calyx and the loss of a calyx is generally associated with an inferior ovary. While a calyx is well developed in basal clades (see Malécot & Nickrent 2008), there is a tendency for loss of the sepals (e.g. Santalaceae: fig. 3G) with their replacement by a calyculus of bracteolar origin in Loranthaceae and Opiliaceae (Wanntorp & Ronse De Craene 2009; fig. 3F). As in asterids a common stamen-petal tube may lift up stamens with petal lobes.

DIFFERENTIATING SEPALS AND PETALS – FURTHER CHALLENGES

In the preceding sections, we have explored perianth diversity across the angiosperm phylogeny. It is evident that recurrent themes in perianth evolution operate repeatedly across multiple phylogenetic levels and in different taxonomic groups. For monocots there is convincing evidence to consider the biseriate perianth as morphologically homologous (see Dahlgren et al. 1985, Remizowa et al. 2010). Furthermore, in several lineages of core eudicots, a distinction between sepals and petals is often straightforward, and this is linked to the restricted occurrence of petaloidy in the second whorl. Nonetheless, the distinction between sepals and petals is often difficult (Ronse De Craene 2007, 2008a) and is complicated by a number of factors. Thus we now explore how select trends challenge our ability to differentiate between, and homologise amongst, sepals and petals. Here we emphasise five factors: (1) developmental constraints; (2) environmental stimuli; (3) transference of petal function through secondary bract inclusion; (4) transference of petal function through stamen sterilisation; (5) novel appendage formation via the hypanthium.

Developmental constraints

The differentiation of petals and sepals may be influenced by developmental forces acting on the entire flower, or can be disrupted by changes in other aspects of floral morphology, such as floral symmetry. In many cases the alterations to perianth differentiation could be considered ancillary to other changes to floral morphology. For example, the strict distinction between sepals and petals has broken down in a number of derived lineages, apparently triggered by an increase in the size of the floral apex and secondary stamen and carpel

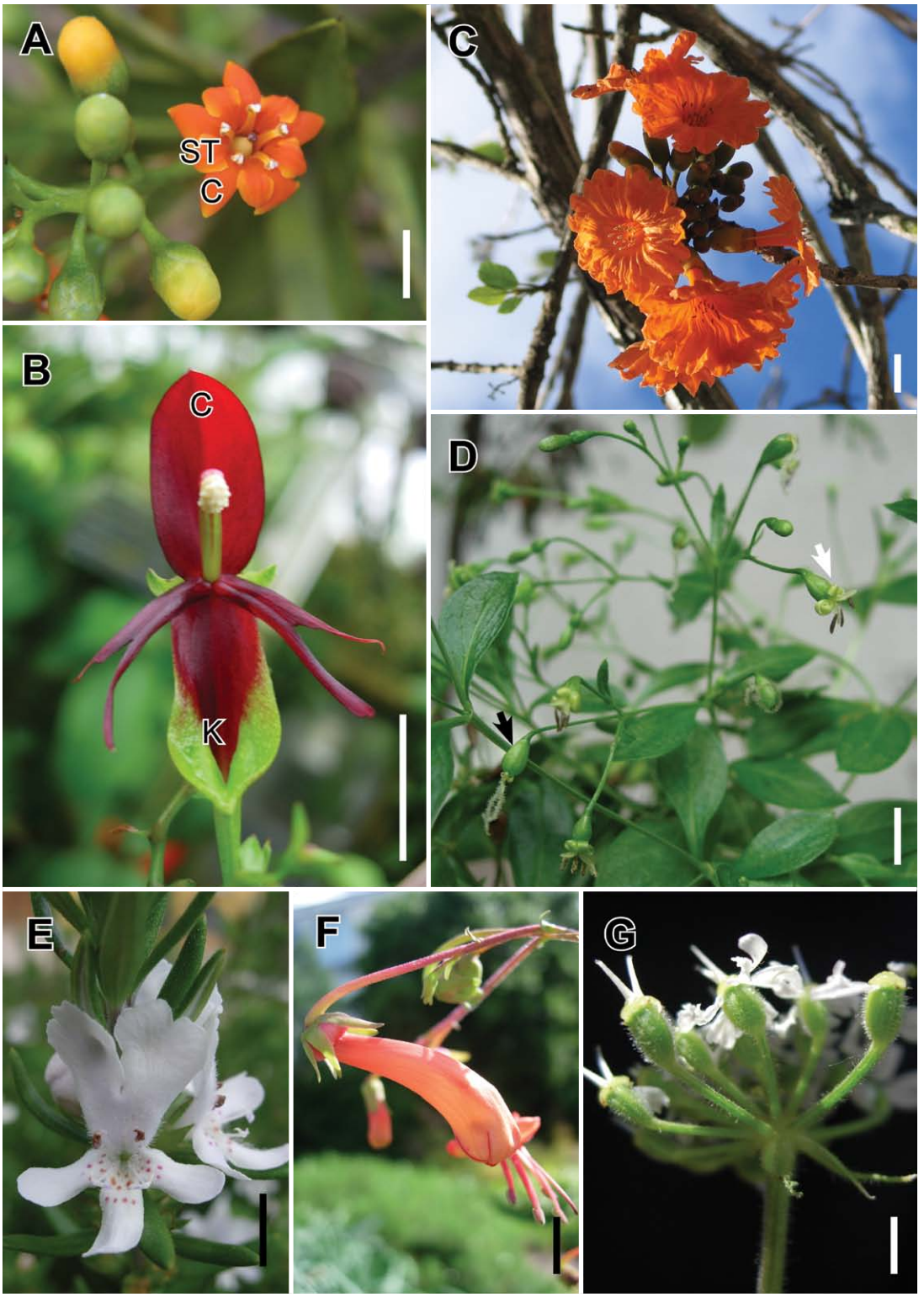

Figure 4 – Examples of perianth structure in angiosperms, flowers of asterids: A, *Bonellia macrocarpa* (Cavanilles) Ståhl & Källersjö (Theophrastaceae), flowers with staminodial whorl (ST) indistinguishable from the petals (C); B, *Impatiens hians* Hook.f. (Balsaminaceae), resupinate flower; note the large upper petal (C), lateral fused petals and the lower sepal which is partly coloured (K); C, *Cordia dodecandra* A.DC (Boraginaceae) with large stamen petal-tube; D, *Phyllis nobla* L. (Rubiaceae); reduced male (white arrow) and female flowers (black arrow) lacking a calyx; E, *Westringia fruticosa* (Willd.) Druce (Lamiaceae), view of zygomorphic flower with stamen-petal tube; F, *Phygelius capensis* E.Mey. ex Benth. (Scrophulariaceae), lateral view of flower; note long stamen-petal tube with exserted stamens; G, *Heracleum sphondylium* L. (Apiaceae), partial view of inflorescence; note absence of sepals and deciduous petals. Scale bars: A–C, E = 1 cm; D = 3 mm; F, G = 0.5 cm.

increases (e.g. Dilleniaceae, Clusiaceae, Theaceae, Lecythidaceae, Paeoniaceae: Ronse De Craene 2008a, 2008b; figs 1H & 2C). The resulting flowers have shifted to a spiral perianth with a progressive transition of petaloidy from sepals to petals through composite organs. Thus perianth differentiation can break down in the face of forces acting to increase meristem size. Another example is where petal primordia of core eudicots develop close to the stamen whorl and undergo important influences from the stamens during early development (e.g. initiation of stamen-petal primordia and fusions of petals to stamens in a tube, slow growth of petals: fig. 4C, E & F). This may also be reflected in a common genetic expression. Fusion may also occur between the sepals and petals as in *Impatiens* (Balsaminaceae), where the adaxial petal has a dual morphological nature, being green on the outside and with a dorsal crest, and petaloid on the inside (fig. 4B). Caris et al. (2006) suggested that a composite nature for the anterior petal is the result of a congenital fusion of the adaxial petal with reduced antero-lateral sepals. The antero-lateral sepals of *Impatiens* are often rudimentary or do not develop at all. Although this hypothesis appears attractive, it needs to be checked whether the correlation between visual absence of antero-lateral sepals and a mosaic petal morphology holds in a greater sample of species. In *Polygala*, the two inner sepals are larger and petaloid, contributing to the floral display in a comparable way to the wing petals of Leguminosae. Studies of B-gene expression in combination with developmental morphology suggest that the identity of the lateral sepals is strongly linked with the development of neighbouring organs, which leads to a mosaic identity of the lateral sepals (Bello et al. 2008, 2010). Thus in both Polygalaceae and Balsaminaceae flowers are highly monosymmetric with unequal development of organs within sepal or petal whorls. Ronse De Craene (2010) suggested that the strict boundaries between sepals and petals have broken down due to pressure of a monosymmetric development of the flower, with gene activity of the sepals invading the anterior petal. A similar interpretation could be put forward for *Commelina communis* (see before: Preston & Hileman 2012). Petals are highly susceptible to floral-wide developmental processes, with their fate regulated by their position and the influence exercised by neighbouring organs.

Environmental stimuli and developmental plasticity

Evidence in basal angiosperms has shown that characteristics of sepaloidy and petaloidy are not restricted in an organ specific manner, but that the development of these features depends on environmental factors, such as light and contact pressure (Warner et al. 2009). Similarly in some core eudicots, especially Caryophyllales, covered and uncovered sepals may show a mixture of green and coloured areas (e.g. Polygonaceae: pers. obs.; *Hypertelis*: Ronse De Craene & Brockington in prep.). Together these observations indicate that conditions at the bud stage may be crucial in the differentiation of petals and underline the importance of environmental factors in the development of petaloidy (Warner et al. 2009). The few cases where part of the calyx or corolla is half sepaloid and half petaloid (e.g. Polygalaceae, Balsaminaceae, Aizoaceae) show the importance of environmental control of chimeric organs and are of interest for further exploration outside of basal angiosperms. But in any case, the notion that petaloidy and sepaloidy are relatively plastic conditions, which can alternate through the maturation of organs and are influenced by environmental stimuli, undermines our ability to homologise these organs through processes alone.

Transference of function through secondary bract inclusion

The evolution of flowers in core eudicots must be seen as a continuous process with alternate losses and acquisitions of a differentiated perianth (Ronse De Craene 2007). This can evolve acropetally by inclusion of bracts in the confines of the flower, either as an epicalyx that may occasionally replace the existing calyx (e.g. *Scabiosa* in Caprifoliaceae, *Thunbergia* in Acanthaceae) or as an outer envelope in flowers where a petal whorl was lost earlier (e.g. Portulacaceae). It is known that bracts or bracteoles can become closely associated with flowers through the shortening of internodes and a compression of pedicels (Ronse De Craene 2008a). The result of this compression is a potential to increase the number of perianth parts and to ultimately develop a biseriate perianth (cf. Venkata Rao 1963, Drinnan et al. 1994, Albert et al. 1998, Ronse De Craene 2007, 2008a). A number of families in the core eudicots have flowers subtended by several whorls of bracts, without clear separation between bracts, sepals and petals (e.g. *Clusia* in Clusiaceae: Ronse De Craene 2010, fig. 2C–E; Strasburgeriaceae: Matthews & Endress 2005, *Reaumuria* in Tamaricaceae: Ronse De Craene 1990; *Stachyurus* in Stachyuraceae with half of the sepals similar to bracts and the other half similar to the corolla: fig. 3F) and bracts may occasionally fuse with sepals (e.g. *Macrocarpaea*: Albert et al. 1998). More examples are presented in Albert et al. (1998), but care must be taken not to confuse bract-derived epicalyces (e.g. Malvaceae) with stipular epicalyces (e.g. Rosaceae). Families such as Papaveraceae, Nelumbonaceae, Portulacaceae, Didiereaceae, and Basellaceae have a dimerous or pentamerous petaline perianth enclosed in a sepal-like envelope of two parts. In the Nyctaginaceae a bractlike pentamerous envelope can be mistaken for sepals (e.g., *Oxybaphus viscosus*, *Mirabilis jalapa*). However, the presence of lateral flower buds in the axil of the outer bracts of some species (*O. nyctagineus*) as well as typical sepaloid characters of the perianth excludes the possibility that the perianth in Nyctaginaceae is different from the undifferentiated perianth of other Caryophyllales (Rohweder & Huber 1974, Hofmann 1994, Brockington et al. 2009). Within core eudicots there are several cases where bracts invade the limits of the flower and this process is occasionally linked with the loss of the calyx. A calyculus of bracteolar origin is commonly found in Loranthaceae (Wanntorp & Ronse De Craene 2009; fig. 3F). In *Thunbergia*, bracteoles are closely associated with the flower at the expense of the calyx (Endress 2008a). An epicalyx can also develop at the expense of sepals and overtake their function (e.g. in Malvaceae, Caprifoliaceae).

Transference of function through stamen sterilisation

In contrast to the acropetal acquisition of bracts, a differentiated perianth can evolve through the basipetal differentia-

tion of staminodial petals. As discussed previously, evidence for staminodial petals is often poor and circumstantial, with some obvious exceptions. Ronse de Craene previously hypothesized that staminodial petals have arisen in a number of apetalous clades where a petal whorl had been present in ancestral forms, but became subsequently lost (see Ronse De Craene 2003, 2007, 2008a, 2010). In the core eudicots there are several candidates for this evolutionary trend. The case for staminodial petals in Caryophyllales has been discussed earlier. Larger apetalous clades tend to be generally wind-pollinated with secondary adaptations of the flowers including an absence of petals. The origin and evolution of such clades tends to be correlated with periods of increased aridity and seasonality in the history of the world favouring the expansion of wind pollination over insect pollination. (e.g. Whitehead 1969, Ehrendorfer 1976, Friis et al. 2006, Crepet 2008). This is particularly clear for Rosales and Fagales, which are mainly wind pollinated, and to a lesser extent for Caryophyllales. While Fagales are mainly wind-pollinated with small unisexual flowers associated with large or complex bract systems, the evolution of insect pollination is sporadic and not widespread (e.g. *Castanea* and *Lithocarpus* in Fagaceae and some fossil members: Stevens 2001). In Rosales, a large part of the order ('Urticales') is largely wind pollinated and apetalous. The remaining families are generally insect pollinated and possess petals (e.g. Rosaceae, Rhamnaceae, Dirachmaceae) or a coloured hypanthium with sepals (e.g. Elaeagnaceae). Ronse De Craene (2003, 2010) suggested that a loss of petals could have occurred in the immediate ancestors of Rosales or at the base of Rosaceae, with a subsequent differentiation of outer stamens into petals in the majority of Rosaceae. It is argued that petals arise as part of the androecium, through a process of homeosis (replacement of a stamen by a petal). Evidence for this interpretation is the close link of petals with stamens developing more or less as fascicles (e.g. Lindenhofer & Weber 1999a, 1999b, 2000) as well as the replacement of petals by stamens in some species. Some Rosaceae lack petals altogether, and their absence may be linked to flower reduction (tribe Sanguisorbeae) or replacement with stamens (*Neviusia*, *Maddenia*). However, the hypothesis of ancestral apetaly in Rosales is inconsistent with the basal position of Rosaceae in the clade and the presence of petals in associated orders. Further investigations, combining floral development with evo-devo, are necessary to clarify this hypothesis. In two other families, Rhamnaceae and Dirachmaceae, the identity of petals appears suspicious, as they generally develop from common primordia dividing into a stamen and a smaller petal. There is still a possibility that staminodial petals will be discovered in other clades of core eudicots, as the evolutionary flexibility of flowers is enormous with repeated transitions in the development of a perianth.

Coronas and pseudopetals

The study of petal evolution has been highly influenced by the concept of bracteo- and andropetals. However, this restricted transformational account of homology can fail to account for the diverse influences that act on petal evolution and development. This is well demonstrated by considering the influence of the hypanthium. It is clear that the hypanthium (expanded receptacle) plays a major role in late-stage development of flowers (Ronse De Craene 2010). Hypanthial outgrowths or extensions have arisen repeatedly in angiosperms and can occasionally attain great sizes, even exceeding the original organs (e.g. hypanthium of *Tropaeolum* and *Punica*: fig. 4G, corona or paracorolla of *Narcissus*, corona of *Passiflora*). Depending on their size and attachment to petals or stamens, appendages have been variously described as ligules, scales, staminodes or elaborations of petals or tepals (Endress & Matthews 2006). A corona can have different origins and is usually petaloid, either as part of the hypanthium (see above; e.g. Passifloraceae, Velloziaceae), or as an appendage of tepals (e.g. *Tulbaghia* in Alliacae), petals (e.g. Sapindaceae, Tamaricaceae), or stamens (e.g. Apocynaceae) (Ronse De Craene 2010). When the corona takes excessive proportions, it can develop as a pseudo-corolla. This is relatively rare in angiosperms and has often been interpreted as evidence of sterile organs (e.g. pseudostaminodes: Ronse De Craene & Smets 2001). Part of the androecium may contribute to the development of attractive petaloid structures, as the corona of *Pachynema* (Dilleniaceae) consisting of outer staminodes or the hood-like corona of Loasoideae (Endress & Matthews 2006). In *Napoleonaea* (Lecythidaceae), a complex corona develops as an amalgamation of two outer staminodial whorls with reflexed fused petals (Ronse De Craene 2011). The development of a staminal corona is also found in other members of Lecythidaceae and Scytopetalaceae (Endress 1994, Ronse De Craene 2011). Flowers with a staminal corona are generally strongly synorganized with a complex centrifugal androecium, and this delay in stamen development may be linked with an extension of petaloidy in the outer (usually sterile) stamens (e.g. some *Clusia* species, Lecythidaceae, *Pachynema* in Dilleniaceae). Staminodes may also be strongly similar to petals or even indistinguishable at maturity. In some Theophrastaceae (e.g. *Bonellia*), petals and staminodes are indistinguishable except in size (fig. 4A). As staminodes become connected with the petals in a tube (Caris & Smets 2004), organ identity genes probably become mixed. Another striking example of pseudopetals is *Sauvagesia* (Ochnaceae), where a whorl of antepetalous staminodes is indistinguishable from the real petals but functions as a specific buzz-pollination mechanism (Farrar & Ronse De Craene in prep.).

CONCLUSIONS

A biseriate perianth is the most common perianth configuration in angiosperms and a differentiation into outer sepals and inner petals is generally associated with this. It is essential to link evidence from phylogeny with comparative morphology and genetic studies, as a biseriate perianth may come and go in evolution, driven by internal and external forces. Different origins are at play here, as the biseriate perianth may arise either by restriction of B-gene expression to the outer whorl of a petaloid perianth, or by the intercalation of bracts at the base of the flower (e.g. Albert et al. 1998, Ronse De Craene 2007). Furthermore the difference between sepals and petals is often circumstantial to functional interactions and depends on developmental factors affecting the whole flower, making a strict distinction generally untenable. Petals and sepals

are often homologous at many levels and appear to transition easily with respect to function. Indeed, a distinction can only be discerned when there are physical differences between non-petaloid and petaloid tepals, where the expression of pigmentation (or its possible absence in white flowers) and lack of chlorophyll are crucial characters in the perception of petals. The traditional distinction between bracteopetals and andropetals has its value, but its importance may vary with phylogenetic context. Staminodial structures with petal characters are different from tepals and have a different origin thus their description as *andropetals*. Takhtajan (1991) underlines their special role as transformed staminodes (see Ronse De Craene & Smets 2001). It emphasizes their link with the androecium and their distinctness from other petals. Against a backdrop of considerable perianth variation, the incorporation of genetic data is challenging. Hypothesis formulation and interpretation of genetic data has by necessity been simplistic in the face of the diverse developmental and evolutionary forces that may influence the genetics of the perianth. Nonetheless considerable progress is being made in exploring the role of gene duplications in the evolution of morphological novelty in a family such as Ranunculaceae (Kramer et al. 2003, Rassmussen et al. 2009). Furthermore the difference between tepals and staminodes may become discernable on a genetic basis in some groups such as the Caryophyllales, where, in contrast to sepal-derived petals, petals derived from stamens can have different gene expression patterns (Brockington et al. 2011). Thus we may begin to be able to distinguish the genetic consequences of historical homology versus a genetic signature of petal identity.

The study of comparative gene expression and function in connection to petal evolution and development has been driven by two central tenets: the idea of evolutionary homeosis and the notion of bracteo- and andropetals. These are both important concepts of considerable value. However, they are unable to accommodate the full range of evolutionary variation exhibited by the angiosperm perianth. While there is considerable burden of proof associated with the demonstration of homeosis, it is startling that after close to twenty years of comparative investigations, there are still no clear examples of naturally occurring homeosis driven by the heterotopic expression of MADS-box genes. The lack of evidence for demonstrable homeosis at a genetic level within the perianth can in part be attributed to the fact that there are innumerable other forces that shape the evolution of the perianth, in addition to homeosis. These additional contributing forces are rarely incorporated in the hypotheses of contemporary evo-devo approaches, perhaps because we cannot hypothesise their effect at the molecular genetic level. Prudence is also necessary in interpreting organ origin and homology on gene expression alone, as recent studies have occasionally jumped to conclusions of homology that seem little justified (e.g. perianth of Lauraceae: Chanderbali et al. 2006: see above; corona of Passifloraceae: Hemingway et al. 2011; petals of Polygonaceae: Ainsworth et al. 1995). In our analysis of perianth variation we have sought to emphasise the complexity of perianth evolution with its continual cycles of organ loss and gain, as well as the diverse influences of different floral organs and developmental processes. It must be a future goal of evolutionary developmental biology to diversify its framework in order to explore these complex evolutionary processes at the comparative genetic level.

Finally, we believe that the use of the term 'petals' can generally be misleading when used to convey correspondence, in absence of a thorough exploration of homology at several hierarchical levels. The major distinction remains between petals derived from perianth leaves (bracts or perigone) and petals derived from stamens. This is reflected in our terminology where a distinction can be made between sepaloid and petaloid tepals, and in a relatively few cases – andropetals. As petals are situated between vegetative parts and the reproductive organs, they clearly are influenced by a variety of proximal and distal developmental processes. The continued exploration of these diverse influences will be a rich area of future research.

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