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The Immense Diversity of Floral Monosymmetry and Asymmetry Across Angiosperms

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Abstract Floral monosymmetry and asymmetry are traced through the angiosperm orders and families. Both are diverse and widespread in angiosperms. The systematic distribution of the different forms of monosymmetry and asymmetry indicates that both evolved numerous times. Elaborate forms occur in highly synorganized flowers. Less elaborate forms occur by curvature of organs and by simplicity with minimal organ numbers. Elaborate forms of asymmetry evolved from elaborate monosymmetry. Less elaborate form come about by curvature or torsion of organs, by imbricate aestivation of perianth organs, or also by simplicity. Floral monosymmetry appears to be a key innovation in some groups (e.g., Orchidaceae, Fabaceae, Lamiales), but not in others. Floral asymmetry appears as a key innovation in Phaseoleae (Fabaceae). Simple patterns of monosymmetry appear easily "reverted" to polysymmetry, whereas elaborate monosymmetry is difficult to lose without disruption of floral function (e.g., Orchidaceae). Monosymmetry and asymmetry can be expressed at different stages of floral (and fruit) development and may be transient in some taxa. The two symmetries are most common in bee-pollinated flowers, and appear to be especially prone to develop in some specialized biological situations: monosymmetry, e.g., with buzz-pollinated flowers or with oil flowers, and asymmetry also with buzz-pollinated flowers, both based on the particular collection mechanisms by the pollinating bees. Floral monosymmetry has developed into a model trait in evo-devo studies, whereas floral asymmetry to date has not been tackled in molecular genetic studies.

Keywords Angiosperms · Asymmetry · Flower development · Flower evolution · Monosymmetry · Pollination biology

Introduction

Floral symmetry, which has long fascinated botanists (Sprengel, 1793; de Candolle, 1813; Wydler, 1844), continues to attract different fields of research more than ever, such as (1) floral developmental genetics (Coen et al., 1995; Coen, 1996; Cubas et al., 1999b; Hileman et al., 2003; Busch & Zachgo, 2009; Jabbour et al., 2009b; Preston & Hileman, 2009; Specht & Bartlett, 2010; Zhang et al., 2010; Bartlett & Specht, 2011; Preston et al., 2011), (2) comparative morphology with a special focus on diversity

(Endress, 1999, 2001a, 2006, 2010, 2011; Tucker, 1999; Endress & Matthews, 2006), (3) pollination ecology (Dafni & Kevan, 1996; Neal et al., 1998; Giurfa et al., 1999; Lehrer, 1999; Jesson & Barrett, 2003; Kalisz et al., 2006), and (4) evolution (Donoghue et al., 1998; Ree & Donoghue, 1999; Citerne et al., 2010; Zhang et al., 2012). Monosymmetry and asymmetry are of special evolutionary significance. In contrast to my former syntheses on floral symmetry (Endress, 1999, 2001a) this study goes more deeply into the diversity of monosymmetry and asymmetry expressions and more broadly into the systematic distribution.

The term monosymmetry is used here for flowers that have one symmetry plane (following Endress, 1999, 2001a). Developmental geneticists have sometimes called this asymmetry (e.g., Luo et al., 1996, 1999; Cubas et al., 2001). However, asymmetric flowers—without a symmetry plane—are different from monosymmetric flowers. Both monosymmetric and asymmetric flowers are of great interest in their own right. But truly asymmetric flowers have been largely neglected in floral developmental genetics so far, in contrast to asymmetry in animals (Levin, 2005; Raya & Belmonte, 2006; Levin & Palmer, 2007). An exceptional enantiomorphy that has been studied genetically in plants (but not in flowers) are helically growing mutants of *Arabidopsis* (Hashimoto, 2002; Buschmann et al., 2004). It is to be expected that asymmetry in flowers will be tackled soon, too.

Monosymmetric flowers with their single symmetry plane can be described as having two mirror symmetrical halves (divided by the symmetry plane) or as having two unequal sides (divided by a plane at right angles to the symmetry plane). Because the symmetry plane is mostly perpendicular, I will call the former the left and right half of the flower, and the latter the lower and upper side of the flower.

Monosymmetry and asymmetry are (immensely) diverse in two respects. First in structure, in the kinds of expression, and second in phylogeny, in the occurrence of these forms across the angiosperms. This paper will give a glimpse of both dimensions: the structural and the systematical and will also show some biological situations in which certain monosymmetry and asymmetry forms can be expected. For discussion of the distribution of different monosymmetry and asymmetry patterns primarily the classification in Stevens (2001 onwards) and APG (2009) is used.

Monosymmetric Flowers

If we think of monosymmetric flowers, some prominent large taxa come to mind, such as orchids, Lamiales, or papilionoids. They all have their own special clear-cut kinds of monosymmetry, if viewed in detail. However, if we consider monosymmetry across the entire angiosperms, we find an even greater diversity of forms. The situation is like an ocean of polysymmetry with a few large islands and a surprisingly great number of small islands of monosymmetry. Floral monosymmetry is an attractive topic for evo-devo studies. These studies have to date been concentrated on the big islands, whereas the small ones were not or rarely explored. The present study especially concentrates on the small islands to show what diversity of monosymmetry there really is. Thus the emphasis is not in how common monosymmetry is in the larger clades but whether it occurs at all in an order or family throughout the angiosperms and how it is expressed in morphology.

The attempt to consider the entire diversity is of much heuristic value to ask questions in evolutionary biology, and thus it is a contrast to the study of model species. Both approaches are complementary and therefore important. If we find certain patterns that appear again and again in unrelated groups, we should ask what this means in terms of evolution of developmental mechanisms and build our hypotheses to test based on this question.

Still 20 or 30 years ago there were only vague general ideas about evolution from polysymmetry to monosymmetry (e.g., Leppik, 1972). This is no longer the case, as now more or less detailed phylogenetic frameworks for the angiosperms and for many subgroups at various levels of angiosperm phylogeny (orders, families, genera) are available. They allow ever more precise reconstruction of where exactly and in which direction symmetry changes occurred (Ree & Donoghue, 1999). Specific case studies on secondary polysymmetry by pelorization are those on *Linaria* (Veroniaceae) by an epigenetic mutation (Cubas et al., 1999a), on some Gesneriaceae (Citerne et al., 2000), or on *Cadia* (Fabaceae) (Citerne et al., 2006).

A few angiosperm families or orders are prominent representatives of floral monosymmetry. Molecular developmental studies on monosymmetry have been carried out especially on such groups in eudicots, such as Fabaceae (Ree et al., 2004; Citerne et al., 2003, 2006; Feng et al., 2006; Wang et al., 2008), Lamiales (Cubas et al., 1999a, b; Möller et al., 1999; Citerne et al., 2000; Hileman & Baum, 2003; Reeves & Olmstead, 2003; Smith et al., 2004; Vincent & Coen, 2004; Aagaard et al., 2005; Davies et al., 2006; Baxter et al., 2007; Xiao & Wang, 2007; Du & Wang, 2008; Gao et al., 2008; Zhou et al., 2008), Asterales (Teeri et al., 2006; Broholm et al., 2008; Chapman et al., 2008; Kim et al., 2008), Dipsacales (Howarth & Donoghue, 2005, 2008). In contrast, in monocots, molecular developmental studies in large monosymmetric groups to date concentrated more on aspects of floral organ identity than symmetry, such as in Poaceae (Malcomber & Kellogg, 2004; Whipple & Schmidt, 2006), Orchidaceae (Tsai et al., 2008; Mondragón-Palomino & Theissen, 2009; Mondragón-Palomino et al., 2009), or Zingiberales (Specht et al., 2008; Bartlett & Specht, 2010, 2011). However, the present study does not especially focus on those large clades, but it aims to follow the occurrence of monosymmetry through all major angiosperm groups (orders and families; see also Endress, 2010, 2011).

Diverse Manifestations of Monosymmetry in Flowers

Monosymmetry has diverse expressions in flowers, which has been noticed since Wydler (1844). Floral monosymmetry is manifested in very different ways (Table 1). (1) Organ categories are affected in various combinations: all organs (in large groups with most conspicuous monosymmetry), or mainly calyx and corolla, or mainly only one organ category (calyx, corolla, androecium, or gynoecium). (2) Organs are affected to various degrees: by differential shape, curvature, reduction, loss, increase in number, or transfunctionalization (e.g., in stamens by heteranthery or in staminodes). (3) Monosymmetry by simplicity (when only a single organ of one kind is present, such as one stamen or one carpel). (4) Direction of monosymmetry (median, transverse, oblique) regarding the groundplan of ramification of the inflorescence. Thus, the notion of monosymmetry is somewhat vague and encompasses different kinds of forms, which may not be evolutionarily related.

Table 1 Diversity in the expression of floral monosymmetry

Organ categories are affected in various combinations

- All organs (corolla and androecium are generally the most obviously affected regions) (e.g., Lamiales, Fabaceae, Orchidaceae)
- Calyx and corolla (e.g., Balsaminaceae)
- Rarely only one organ category is (mainly) affected:
  - Calyx (e.g., *Mussaenda*, *Warszewiczia* of Rubiaceae)
  - Corolla (e.g., *Isonema*, *Rauvolfia* of Apocynaceae)
  - Androecium (e.g., *Lagerstroemia* p.p. of Lythraceae; *Solanum lidii* of Solanaceae)
  - Gynoecium (e.g., *Isolona*, *Monodora* of Annonaceae)

Organs are affected to various degrees

- Organs differentially shaped on both sides of symmetry plane (e.g., Lamiales)
- Organs curved to one direction (e.g., Cleomaceae)
- Organs reduced on upper or lower half (e.g., odd stamen in several families of Lamiales, e.g., Gesneriaceae)
- Organs lost on upper or lower half (e.g., stamen(s) in Lamiaceae)
- Organs increased in number on upper or lower half (e.g., stamens in Lecythidaceae)
- Degree of organ union different on upper or lower half (e.g., petals in *Teucrium* of Lamiaceae)
- Organs transfunctionalized (neofunctionalized) on upper or lower half (e.g., stamens in Lecythidaceae, odd stamen in *Jacaranda* of Bignoniaceae, *Penstemon* of Veronicaceae)

Monosymmetry by simplicity

- Flowers with a single stamen or a single carpel (stamen in Lacistemataceae, carpel in Lauraceae, both stamen and carpel in *Sarcandra*, Chloranthaceae)

Direction of monosymmetry with respect to the axis of the next higher order

- Median (predominant, e.g., Lamiales, Orchidaceae)
- Transversal (e.g., Fumarioideae of Papaveraceae; *Hibbertia* p.p., Dilleniaceae)
- Oblique (e.g., some Malpighiales, Brassicales, Sapindales, Solanales). Flowers with an organisationally transversal or oblique monosymmetry plane are commonly perpendicular at anthesis by adjustment of the pedicel.

Elaborate Monosymmetry. Elaborate monosymmetry especially occurs in flowers with highly synorganized organs (Endress, 2006). Classical cases of conspicuous monosymmetry are bilabiate flowers, which appear in two extreme forms: keel flowers and lip flowers, with the pollination organs more or less hidden in a container: either the keel (on the lower side) or the upper lip (on the upper side) (Endress, 1994; Westerkamp, 1997; Classen-Bockhoff et al., 2004; Classen-Bockhoff, 2007; Westerkamp & Classen-Bockhoff, 2007). Correspondingly, pollen transport is basically with the underside of the body in keel flowers and with the upper side in lip flowers (Fig. 1a, b).

In Lamiales, the largest angiosperm clade with almost exclusively monosymmetric flowers, corolla and androecium are greatly and differentially affected. The upper (posterior), median stamen of the five stamens is reduced, either present but not fertile or even absent, which was already noticed by de Candolle (1819). The paired stamens are much less affected. But in many taxa of different families, one of the two pairs is also reduced, either the upper or the lower (e.g., Endress, 1999). In other asterids (and

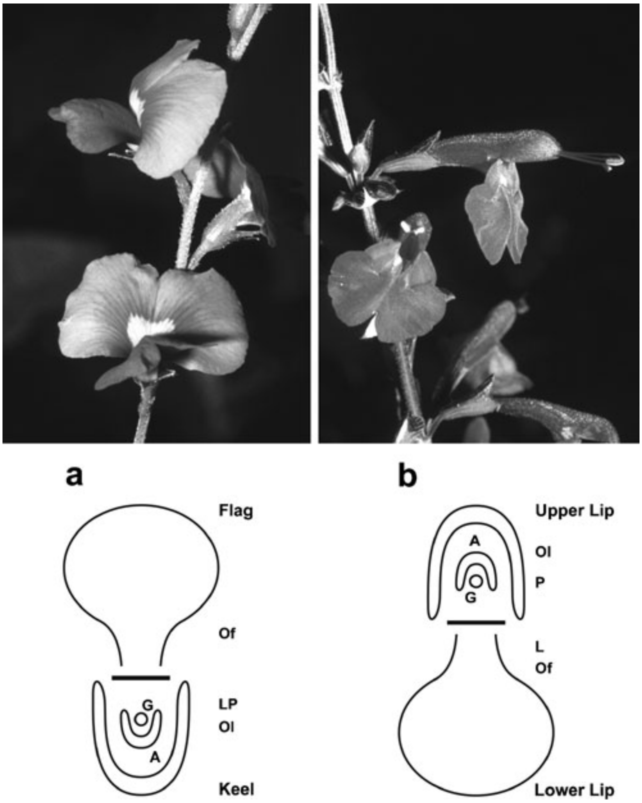

Fig. 1 Elaborate floral monosymmetry: two contrasting architectures. **a** Keel flower, lateral and frontal view (*Chorizema* sp., Fabaceae). **b** Lip flower, lateral and frontal view (*Salvia* sp., Lamiaceae). Diagrams showing frontal views of floral architecture (*A*: Androecium; *G*: Gynoecium; *L*: Landing platform; *Of*: Optical device, frontally exposed; *Ol*: Optical device, laterally exposed; *P*: Level of pollination organs; *Horizontal bar*: Divide of upper and lower part of floral architecture) (after Endress, 1994)

many rosids) floral monosymmetry is commonly concentrated on or restricted to the perianth and less or not expressed in the androecium (e.g. Balsaminaceae, Apocynaceae, Rubiaceae, Asteraceae).

Sigmoidal Curvature of Organs. A widespread, much less complex monosymmetric architecture is by sigmoidal curvature of the pollination organs and often also the perianth either up-down-up or down-up-down (Fig. 2a, b). The curvature commonly develops late in floral development. These two forms correspond in the direction of curvature to those of the keel and lip flowers. There are also flowers in which the curvature of the stamens and the style are in opposite directions (e.g., *Exacum*: stamens: down-up-down, style: up-down-up).

This kind of monosymmetry is directly influenced by the position of the flower. It can be experimentally reversed by positioning the plant with flower buds upside down as shown in classical experiments with the clinostat by Vöchting (1886), e.g. in *Sprekelia* (Amaryllidaceae). Such reversed flowers still have the stamens and style topographically up-down-up, but morphologically down-up-down.

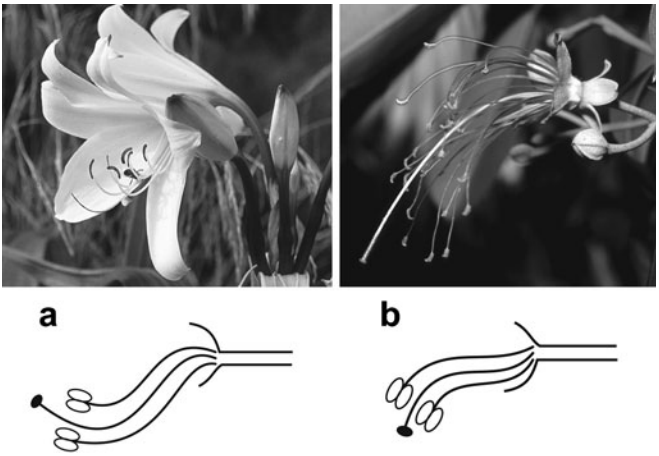

Fig. 2 Floral monosymmetry by sigmoidal curvature of organs: two contrasting directions of curvature. **a** Curvature up-down-up (*Crinum moorei*, Amaryllidaceae). **b** Curvature down-up-down (*Capparis cynophallophora*, Capparaceae)

Plasticity in Adjustment of Flowers to Final Position. In many plants the flowers have a relatively constant position or direction at the time of anthesis. This direction is based on the position of the flower in the ramification system and thus on flower initiation and early development, and, even more, in final adjustments of the position before and during anthesis. Mechanisms for such late adjustment are bending or torsion of pedicels and peduncles, as shown for *Aconitum*, *Antirrhinum*, *Scrophularia* and *Viola* by Noll (1888) and later also for many other plants (Cornehls, 1927; Zimmermann, 1933; Kaldewey, 1962; Huang et al., 2002). In this way monosymmetric flowers can be adjusted to a horizontal position with the symmetry plane perpendicular to the ground. In some cases, if a pedicel is lacking, bending or torsion can even take place in the middle of the flower (*Lonicera*; Noll, 1888), or in the inferior ovary ("resupination" in orchids). In orchid plants that are artificially reversed after flower resupination, the flowers attain again the right position (Noll, 1888). Such adjustment is not restricted to monosymmetric flowers, it also occurs in polysymmetric flowers that assume a constant final position. For example, in *Ceropegia* the corolla tube is bent (Bruyns, 1985). *Narcissus* is versatile as bending may involve only the pedicel or pedicel plus lowermost part of the flower (Church, 1908).

Minor Monosymmetry (Monosymmetry by Reduction or Simplicity). If a flower is reduced to one stamen or one carpel, it becomes strictly speaking monosymmetric (monosymmetry by simplicity or by reduction, passive monosymmetry). Even completely ascidiate carpels are monosymmetric (e.g., basalmost angiosperms; Endress, 1986b, 2005; or Araceae; Igersheim et al., 2001). Thus I have included also monocarpellate cases with an ascidiate carpel. Because such simplicity also occurs in some basal angiosperms (Chloranthaceae, Ceratophyllaceae, and the fossil *Archaefructus*) (e.g., Endress & Doyle, 2009), this kind of simple monosymmetry may have been present, besides polysymmetry, early in angiosperm evolution. In basal angiosperms it is safer to say monosymmetry by simplicity than by reduction. However, floral reduction can also have the opposite result: that monosymmetry becomes less strongly expressed, such as in some Amorpheae (Fabaceae) with reduced corolla (McMahon, 2005), or *Apostasia* (Orchidaceae) with reduced androecium (Kocyan & Endress, 2001b).

Minor monosymmetry is also present in flowers in which the floral whorls are not isomerous (or asymmetric if the symmetry plane is oblique). The most common cases are pentamerous flowers with a dimerous gynoecium (e.g. Saxifragaceae, Asteraceae), or pentamerous flowers with a trimerous gynoecium (e.g. Burseraceae, Cunoniaceae). I have not included these in the study, because they are much more frequent and widespread than those cases with a single stamen or carpel, and are thus too trivial.

Floral Organization and Architecture

Floral organisation (ground plan with initial disposition of young organs) and architecture (shape of the anthetic flower) are differentially affected by monosymmetry. Shallow (only architectural) monosymmetry is often present in a minority of taxa in largely polysymmetric groups (Meliaceae, Cleomaceae, Onagraceae). In contrast, organisational (or organisational plus architectural) monosymmetry often characterizes species-rich families or orders with complex monosymmetric flowers (Fabaceae, Lamiales, Orchidaceae, Zingiberales).

Such different degrees of monosymmetry were first discussed by Delpino (1887) who distinguished four levels of monosymmetry (zygomorphy): (1) very recent in evolutionary terms (deflection of styles and stigma), (2) recent, (3) old, and (4) very old (abortion of organs on one side). This discussion was taken up with new examples added by Robertson (1888).

Transient Early Floral Monosymmetry and Late Monosymmetry

There is also diversity in the timing of monosymmetry expression. Monosymmetry can have its strongest expression early in flower development or at anthesis or only in fruit (Table 2). Such changing or transient monosymmetry is poorly explored. This phenomenon may be especially interesting if it occurs in a polysymmetric group that is nested in a monosymmetric group.

A prominent example for such early monosymmetry in otherwise polysymmetric (disymmetric) flowers is *Arabidopsis* (Fig. 3a, b). In early development the lower side of the flower is more developed so that the flower bud is curved toward the inflorescence apex. Later in development this inequality disappears and anthetic flowers are no longer monosymmetric (see also Cubas et al., 2001). The same behavior is also present, e.g., in *Siparuna* (Siparunaceae; Endress, 1980), *Achlys* (Berberidaceae; Endress, 1989), *Trochodendron* (Trochodendraceae; Endress, 1986a), and *Batis* (Bataceae; Ronse De Craene, 2005). In contrast, in *Euptelea* (Eupteleaceae) (Endress, 1986a; Ren et al., 2007) and *Hypoxis* (Hypoxidaceae; Kocyan & Endress, 2001a) the upper side is more developed than the lower one.

The dimerous gynoecium in Apiaceae can have a superimposed pentamerous symmetry from the other floral whorls and thus be monosymmetric (instead of disymmetric). This monosymmetry is present in floral buds, and it may vanish during

Table 2 Changing expression of floral monosymmetry during development

	Early development	Anthesis	Fruit
Monosymmetry strongest in early development			
Arabidopsis	+	−	−
Monosymmetry strongest at anthesis (in species-rich families)			
Fabaceae	+	++	+ (1-carpellate)
Veronicaceae	+	++	−
Asteraceae/(Cichorioideae)	−/(+)	++	+ (1-ovulate)
Orchidaceae	+	++	−
Monosymmetry strongest in fruit			
Tiarella	+	+	++
Chrysosplenium sp.	+	−	++

++ monosymmetry strongly expressed; + monosymmetry weakly expressed; − monosymmetry lacking

Sources: Harris, 1995; Endress, 1998, 1999, 2001a; Tucker, 1999; Leins & Erbar, 2000; Cubas et al., 2001; Prenner, 2004a; personal observations

later flower and fruit development (*Stegotaenia*) or, in contrast, may become more pronounced (*Polemanniopsis*) (Liu et al., 2004). A similar kind of superimposed pentasymmetry is present in the bicarpellate Asclepiadeoideae (Apocynaceae) (Endress, 1994). In the likewise bicarpellate *Catharanthus* (Apocynaceae), thus with a basically disymmetric gynoecium, one of the two carpels is slightly larger in early development. This “leading” carpel induces meristematization of the epidermis of the smaller carpel for postgenital union of the carpel tips (unpublished results by Verbeke, reported by Mlot, 1998).

Tiarella and some *Chrysosplenium* species (Saxifragaceae) are of special interest because there are two changes in monosymmetry expression. Monosymmetry is strongest in early flower development (see also Endress, 1999) and at the mature fruit stage but least expressed at anthesis (see next chapter).

Floral Monosymmetry Associated with Special Biological Situations

Flower Direction and Expression of Monosymmetry—Differential Monosymmetry in Flat Inflorescences. Floral monosymmetry has long been recognized to have evolved in

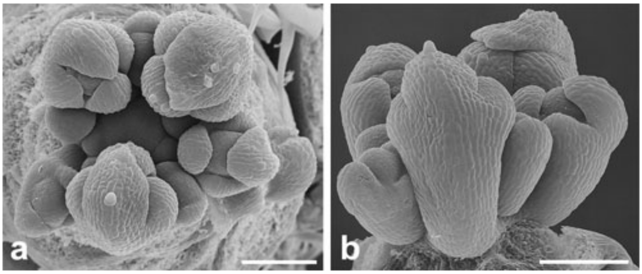

Fig. 3 Early monosymmetry in flowers that are disymmetric at anthesis: *Arabidopsis thaliana*. **a** Monosymmetric young flowers from above. **b** Monosymmetric young flowers from the side. Magnification bars=100 µm

the interaction with pollinating hymenopters (Delpino, 1887; Robertson, 1888). There are also more specific conditions that favour monosymmetry or certain kinds of monosymmetry.

Flowers with elaborate monosymmetry are commonly horizontally directed, i.e., the longitudinal axis of the part of the flower that is visited by pollinators is parallel to the ground, thus conforming to the normal position (posture) of the pollinators (Sprengel, 1793; Ushimaru & Hyodo, 2005; Fenster et al., 2009). In contrast, in monosymmetric flowers that have a vertical upright position, monosymmetry is often only expressed in the perianth. Such flowers are often positioned at the periphery of umbel-like inflorescences (certain Brassicaceae, Rubiaceae, Asteraceae, Apiaceae, Dipsacaceae). In this second case, the entire inflorescence has a unified signalling effect with the radiating monosymmetric flowers at its periphery, and the flowers are less likely to be visited in the direction of their monosymmetry than the horizontally directed flowers. In such inflorescences polysymmetric and monosymmetric flowers tend to co-exist. And even more, different degrees of monosymmetry may be present in the same inflorescence. Thus there is differential monosymmetry. The peripheral most flowers are most strongly monosymmetric. The central flowers are the least strongly monosymmetric ones. There may be a fine gradation of morphs in the intermediate flowers. Such graded morphs occur in some Brassicaceae (*Iberis*) (Busch & Zachgo, 2007), Apiaceae (*Orlaya*) (Froebe, 1980; Classen-Bockhoff, 1992), Asteraceae (*Hieracium*), and Dipsacaceae (*Scabiosa*) (Kunze, 1976) (Fig. 4a–d). Such differential expression of monosymmetry with several flower morphs is being studied in *Gerbera* (Asteraceae), where a TCP domain transcription factor is responsible for this gradation (Broholm et al., 2008). Chapman et al. (2008) "identified ten members of the *CYC*/*TBI* family in sunflower, which is more than found in any other species investigated to date."

Buzz Pollination and Heteranthery. A conspicuous trend of change to monosymmetry is present in some buzz-pollinated groups. This is especially impressive when they are nested in a large clade of mainly polysymmetric flowers. Examples are *Pseudocorchorus* (Malvaceae; Bayer & Kubitzki, 2003), *Exacum* (Gentianaceae; Klackenberg, 2002), and *Solanum* sect. *Androceras* (Solanaceae; Whalen, 1978). This trend is often further emphasized by the evolution of a division of function in stamens (heteranthery), with cryptic pollinating stamens and optically attractive feeding stamens (Vogel, 1978). If the flowers are monosymmetric, the enlarged feeding anthers in the median plane may especially contribute to pronounced monosymmetry, such as in *Senna* (Fabaceae; Marazzi & Endress, 2008), *Solanum* (Solanaceae; Whalen, 1978), *Commelina* (Commelinaceae; Faden, 1998), or *Cyanella* (Tecophilaeaceae; Simpson & Rudall, 1998).

Oil Flowers. Oil flowers tend to be more pronouncedly monosymmetric than their closest relatives that do not produce oil. In Cucurbitaceae, conspicuously monosymmetric flowers are restricted to the oil flowers of *Momordica* and *Thladiantha* (Vogel, 1990). The same applies for *Krameria* in Zygophyllales (Simpson, 1982). The oil-producing pseudanthia of species of *Dalechampia* (Euphorbiaceae) are strongly monosymmetric. The South American Malpighiaceae, which commonly have oil flowers, are slightly monosymmetric in contrast to the polysymmetric non-oil flower Malpighiaceae of the Old World (Davis & Anderson, 2010) and the polysymmetric sister family Elatinaceae (Davis & Chase, 2004; Davis et al., 2005). Some other

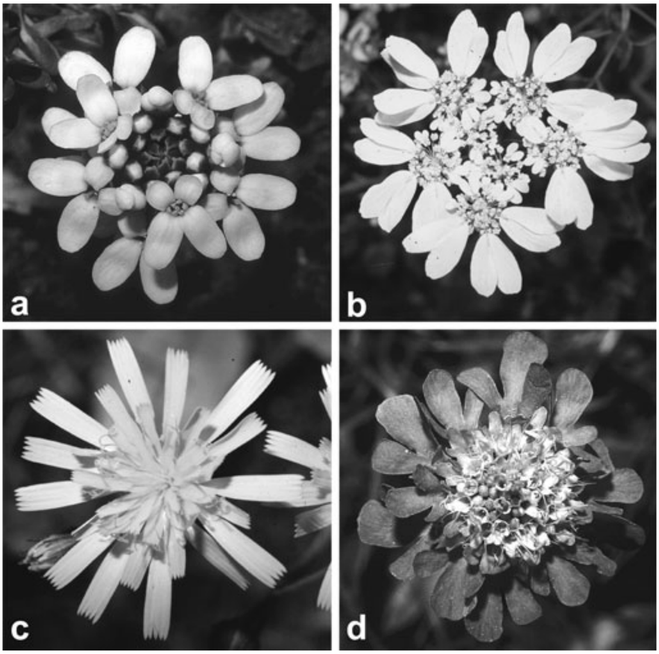

Fig. 4 Differential monosymmetry of upright flowers in flat inflorescences. Flowers are monosymmetric to different degrees, the most peripheral flowers show the strongest monosymmetry. **a** *Iberis sempervirens* (Brassicales). **b** *Orlaya grandiflora* (Apiales). **c** *Hieracium murorum* (Asterales). **d** *Scabiosa lucida* (Dipsacales)

groups with oil flowers are phylogenetically embedded in already strongly monosymmetric clades. The basis for this pronounced trend to monosymmetry in oil flowers may be that the pollinating bees take up oil from the flower with the two forelegs (Vogel, 1974), which is a more intimately “monosymmetric” activity than taking nectar with the proboscis.

Wind-Pollinated Flowers. In wind-pollinated plants there is a trend to reduction of floral organs in number, which may result in floral monosymmetry by simplicity or decay of elaborate monosymmetry (Preston et al., 2011). In a number of wind-pollinated groups among Fagales the flowers, especially the male flowers, are densely arranged in catkins and fill the (monosymmetric or even asymmetric) space created by neighboring bracts (e.g., Endress, 1967, 2008b).

Bird-Pollinated Flowers in Hawaii. In Hawaii some bird-pollinated flowers have evolved into monosymmetric shapes in clades with otherwise consistently polysymmetric flowers. The genus *Geranium* with more than 380 species world-wide has only one species with a monosymmetric corolla: the Hawaiian *Geranium arboreum* (Albers & Van der Walt, 2007). Likewise the genus *Hibiscadelphus* is—to my knowledge—the only genus in Malvaceae-Malvoideae with a consistently monosymmetric corolla and androecium. The conspicuous monosymmetry of these flowers may be functionally linked with the pronouncedly curved beaks of some Hawaiian flower-visiting birds.

Fruits with Rain-Dispersed Seeds. In some rain-dispersed plants of otherwise polysymmetric groups (with disymmetric gynoecium) the fruits (and the gynoecium at anthesis) are pronouncedly monosymmetric, such as *Tiarella* and some *Chrysosplenium* species of Saxifragaceae. The same applies for some species of *Begonia* (Begoniaceae, Cucurbitales) (Matthews & Endress, 2004; Tebbitt et al., 2006). In *Tiarella* the gynoecium is horizontally exposed with two broad, shovel-shaped carpels. When the seeds are mature, the upper, smaller carpel acts as a lid to cover the seeds lying on the lower carpel. Rain drops falling on the gynoecium cause the lower carpel to elastically move downwards. This movement opens the container with the seeds for a moment and sets free a small proportion of them (Savile, 1979); thus the fruit functions like a censer. In *Chrysosplenium* the seeds are also rain drop-dispersed but differently in detail. The gynoecium has an upright position but the two carpels commonly diverge at an angle of 180°. The two mature carpels are open and contain the seeds like a bowl. They can easily be washed out by rain drops (Savile, 1953). In most species both carpels are equally developed and the likewise bicarpellate gynoecium therefore disymmetric. However, in some Chinese species the two carpels are unequal (Pan & Ohba, 2001), thus the gynoecium is monosymmetric. One of the two carpels remains closed (personal observation), probably acting as a reservoir for seeds (the ovary is unilocular), which are thus dispersed more slowly than from a completely open fruit.

Systematic Distribution of Floral Monosymmetry Across Angiosperms

This chapter provides a survey of the widespread occurrence, almost ubiquity of monosymmetry in angiosperms, although with peaks in some groups and unequal distribution of different kinds of monosymmetry (Fig. 5). It appears that in many clades monosymmetry evolved multiple times.

Basal Angiosperms. Floral monosymmetry, although unusual, is not absent. It is mostly monosymmetry by simplicity, by the presence of only one carpel and/or only one stamen, such as in **Hydatellaceae** (Hamann, 1975; Saarela et al., 2007; Rudall et al., 2007), **Trimeniaceae** (Endress, 2001b), **Chloranthaceae** (Endress, 1987; Kong et al., 2002), **Ceratophyllaceae** (Endress, 2001b, 2004), some **Winteraceae** (Igersheim & Endress, 1997), **Piperaceae** (Tucker, 1984; Tucker et al., 1993), **Degeneriaceae**, **Myristicaceae** (Igersheim & Endress, 1997), **Lauraceae** (Endress, 1972), and **Hernandiaceae** (Endress & Lorence, 2004). Among **Annonaceae** flowers with one carpel have evolved several times as shown by their distribution in the phylogenetic tree by Doyle et al. (2004). Unique are *Isolona* and *Monodora* (**Annonaceae**) with a pluricarpellate monosymmetric gynoecium, which appears to begin development like a single carpel (Leins & Erbar, 1982) but is clearly pluricarpellate at anthesis (Deroin, 1985). The unusual case of *Glossocalyx* (**Siparunaceae**) with its onesided tongue is possibly not monosymmetry of the flower proper, but formed by the floral subtending bract which is fused with the flower (Staedler & Endress, 2009), comparable with similar flowers in *Steganthera* in the related **Monimiaceae** (Takeuchi, 2001). The most prominently monosymmetric group here is *Aristolochia* sensu lato (**Aristolochiaceae**), in which the single perianth whorl is greatly monosymmetric (González & Stevenson, 2000).

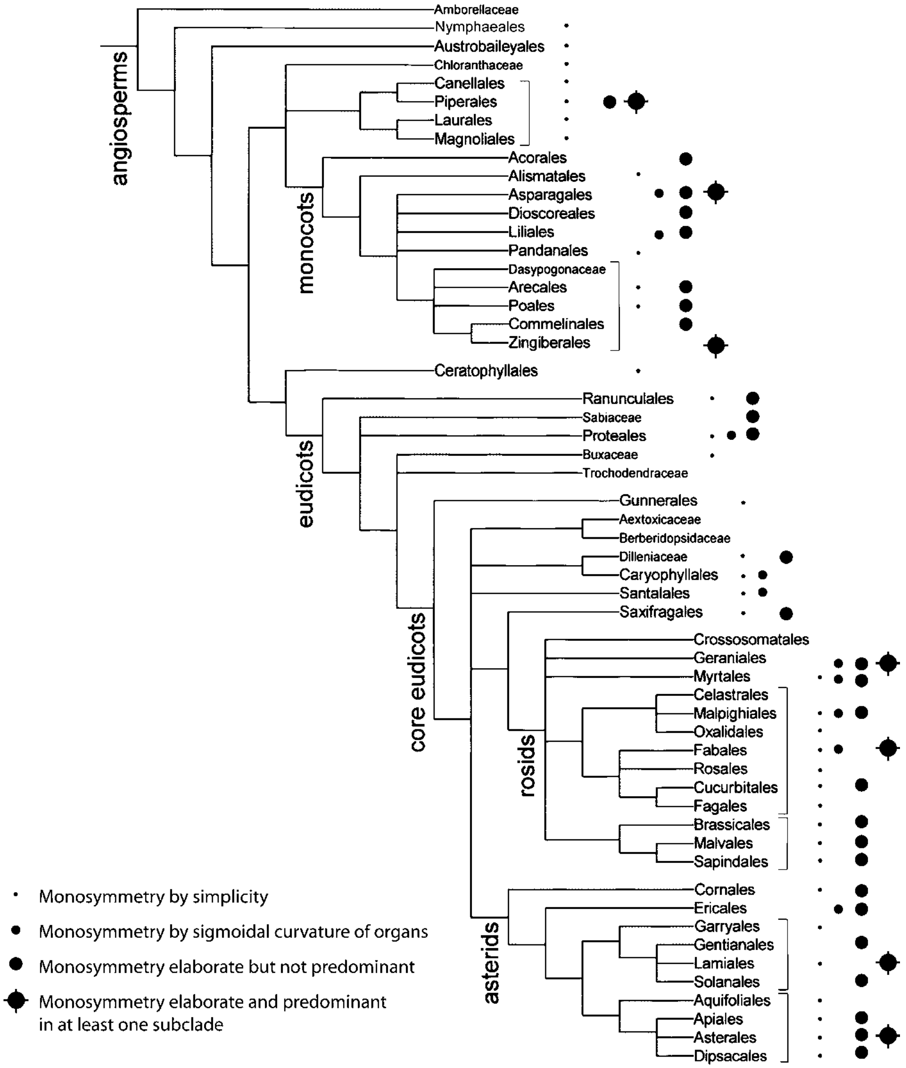

Fig. 5 Occurrence of different floral monosymmetry patterns across angiosperms (cladogram from APG, 2003, with change of "Nymphaeaceae" to "Nymphaeales", to include Hydatellaceae, according to Saarela et al., 2007). Each kind of monosymmetry is plotted only once in a clade where it occurs, even in cases where multiple origins are probable

Basal Eudicots. Elaborate monosymmetric flowers have evolved several times, at least once in **Papaveraceae** (Murbeck, 1912; Lidén, 1993; Damerval & Nadot, 2007) and at least once in **Ranunculaceae** (Mair, 1977; Jabbour et al., 2009a), both families in **Ranunculales**, and also in **Sabiaceae** (Ronse De Craene & Wanntorp, 2008), and more or less elaborate in **Proteaceae** (**Proteales**; Douglas, 1997; Weston, 2007). As in basal angiosperms, there are several cases of monosymmetry by simplicity with only one carpel, such as in **Berberidaceae** and some **Ranunculaceae** (**Ranunculales**), **Proteaceae** (**Proteales**), and **Didymelaceae** (von Balthazar et al., 2003); and there are also a few cases with one stamen as, e.g., *Cissampelos* (**Menispermaceae**)

(Puri, 1978; Kessler, 1993) (**Ranunculales**), *Placospermum* (**Proteaceae**) (Douglas & Tucker, 1996), and *Didymeles* (**Didymelaceae**). **Papaveraceae**-Fumarioideae (**Ranunculales**) are twofold unusual because monosymmetry evolved from disymmetry and because the monosymmetry plane is transversal and not median. There is also fluctuation between disymmetry and monosymmetry, such as in *Corydalis* (Endress, 1999). In addition, in **basal eudicots** there are several completely perianthless genera, which have pronounced early monosymmetry. Either the abaxial side of the young flower is delayed (in **Eupteleaceae**, **Ranunculales**) or the adaxial side (in *Achlys* of **Berberidaceae**, **Ranunculales**, and in *Trochodendron* of **Trochodendraceae**, **Trochodendrales**) (see above).

Core Eudicots

Gunnerales. Some *Gunnera* species (**Gunneraceae**) may have a single stamen and thus monosymmetry by simplicity (reduction) (Rutishauser et al., 2004; Wilkinson & Wanntorp, 2007).

Berberidopsidales. Monosymmetric flowers are lacking in **Berberidopsidaceae** (Ronse De Craene, 2004).

Dilleniales. Hibbertia (**Dilleniaceae**) has different kinds of monosymmetry: some species have a single carpel, some species have a monosymmetric androecium, this monosymmetry being median or transversal (Tucker & Bernhardt, 2000; Horn, 2006, 2007, 2009).

Rosid Alliance (see also Endress, 2010)

Saxifragales. In Saxifragales floral monosymmetry is scarce, and two of these cases have an unusual pollination biology. In **Hamamelidaceae**, the bird-pollinated *Rhodoleia* has flat inflorescences with peripherally radiating (enlarged) petals (Bogle, 1989). In **Saxifragaceae**, the monosymmetric flowers of *Tolmiea* have a lateral entrance by a onesided floral cup and are pollinated by fungus gnats (Goldblatt et al., 2004). A number of *Saxifraga* species have a monosymmetric corolla and nectary (Engler, 1930). *Tiarella* and some *Chrysosplenium* species have a monosymmetric gynoecium giving rise to fruits with rain dispersal (see above). In **Crassulaceae** the long-tubed flowers of *Tylecodon grandiflorus* are curved (van Jaarsveld, 2003). In **Cercidiphyllaceae**, the unicarpellate female flowers are monosymmetric by reduction and the male flowers by congestion in dense inflorescences (Endress, 1986a).

Vitales. Floral monosymmetry appears to be lacking.

Rosids. The distribution of floral monosymmetry is uneven. **Myrtales**, **Geraniales**, **Fabales**, and, to some extent, **malvids** are most conspicuous for monosymmetric flowers, with a peak of elaboration in **Fabales**. Other orders only have monosymmetry by reduction or none at all.

Eurosids 1 (Fabids). **Fabales** are distinguished by large clades with elaborate monosymmetric flowers. In the other orders monosymmetry is much less conspicuous.

Zygophyllales. In **Zygophyllaceae**, the flowers of *Bulnesia* and *Porlieria* are slightly monosymmetric (Sheahan, 2007). *Krameria* (**Krameriaceae**) has pronounced monosymmetry in its oil flowers (Vogel, 1974; Simpson, 1982).

Fabales. Monosymmetric flowers are predominant. Those of many subclades in **Fabaceae** (e.g., Endress, 1994; Westerkamp, 1997; Tucker, 2002; Prenner, 2004a, c, d) and in most **Polygalaceae** (e.g., Westerkamp & Weber, 1997; Prenner, 2004b) are especially elaborate. The two families are unusual by the convergent evolution of pronounced keel flowers (Westerkamp, 1999). They have been relatively widely studied and are not further treated here. In the small family **Surianaceae** there is monosymmetry by reduction (*Guilfoylia*; Schneider, 2007; *Stylobasium*; Carlquist, 1978).

Rosales. Elaborate floral monosymmetry is lacking. However, there are several families with monosymmetry by reduction to a single stamen or carpel. This is present in **Barbeyaceae** (Dickison & Sweitzer, 1970), **Cecropiaceae** (Kubitzki, 1993), **Moraceae** (Rohwer, 1993a), **Urticaceae** (Friis, 1993), and **Rosaceae** (e.g., *Prunus*, *Alchemilla*, *Aphanes*, *Margyricarpus*; Murbeck, 1941). Gynoecial pseudomonomery also occurs and is sometimes difficult to distinguish from monomery (**Elaeagnaceae**; Bartish & Swenson, 2004; **Moraceae**; **Ulmaceae**, and **Celtidaceae**; Eckardt, 1937).

Fagales. The situation is similar as in Rosales, with merely monosymmetry by reduction. In **Betulaceae**, the perianth is affected in *Betula* (Abbe, 1935), and male flowers are monosymmetric by dense arrangement between bracts in *Carpinus* (e.g., Endress, 2008b). Male flowers are monosymmetric by reduction to a single stamen in **Casuarinaceae** (Flores & Moseley, 1990), and some **Juglandaceae** (Abbe, 1974; personal observation) and **Myricaceae** (Abbe, 1972).

Cucurbitales. Floral monosymmetry is rare. In **Begoniaceae**, some species of *Begonia* have a monosymmetric (or even asymmetric) inferior ovary, which acts in rainballistic seed dispersal (Tebbitt et al., 2006). In **Cucurbitaceae**, the oil flowers of some *Momordica* species are monosymmetric (or asymmetric) (Vogel, 1990). A pseudomonomerous gynoecium is present in *Cyclanthera* (Leins & Galle, 1971). **Corynocarpaceae** flowers are monosymmetric by reduction because of their monomerous or pseudomonomerous gynoecium (Philipson, 1987; Matthews & Endress, 2004).

Celastrales. Monosymmetric flowers appear to be lacking (Matthews & Endress, 2005a)

Oxalidales. Floral monosymmetry by reduction is present in unicarpellate flowers of some **Connaraceae** (Matthews & Endress, 2002).

Malpighiales. Floral monosymmetry does not play an important role in this large order. However, because of its sheer size (over 40 families, Wurdack & Davis, 2009), a number of families are to be listed here. Elaborate monosymmetry is mainly known from **Chrysobalanaceae** s.l., where it is predominantly expressed in the floral cup, androecium and gynoecium (Prance & White, 1988; Matthews & Endress, 2008), some **Ochnaceae**, where it occurs together with buzz pollination (Amaral, 1991), and some **Violaceae**, in which the anterior petal has a spur, which surrounds the nectaries formed by two stamens, and the stigma has a monosymmetric pollen collection mechanism (Melchior, 1925; Beattie, 1969). In **Malpighiaceae** monosymmetry is especially present in the perianth as an adaptation to oil collection by oil bees (Vogel, 1974; Wurdack & Davis, 2009; Davis & Anderson, 2010; Zhang et al., 2010) (see also above). In some *Passiflora* species (**Passifloraceae**) sigmoid curvature of the pollination organs is present, and may be an adaptation to bat pollination (Sazima & Sazima, 1978). In **Lacistemataceae** (Endress, 1999), some **Euphorbiaceae** (Radcliffe-Smith, 2001; Prenner & Rudall, 2007; Prenner et al., 2008), some **Podostemaceae** (Cook & Rutishauser, 2007), and some cleistogamous flowers of **Violaceae** (Weibel, 1941), monosymmetry by reduction is present. In **Erythroxylaceae** and some **Linaceae** only one of the three carpels is fertile, which makes the flowers monosymmetric by reduction (Matthews & Endress, 2011).

Eurosids II (Malvids). The large core orders **Sapindales**, **Brassicales**, and **Malvales** have some monosymmetric cases in almost every family, even if polysymmetry is dominant in each order (Endress & Matthews, 2006). This is also true for the newly here positioned orders **Myrtales** and **Geraniales**. In most cases the shape of the organs but not their number is affected. Thus malvids are more strongly characterised by monosymmetry than fabids (measured by the occurrence of monosymmetry in percentage of families). In Brassicales and Sapindales several families have oblique monosymmetry.

Myrtales. Floral monosymmetry is widespread in **Melastomataceae** (Krasser, 1893), and extreme in **Vochysiaceae** with transitions to asymmetry (Litt & Cheek, 2002; Litt & Stevenson, 2003a, b; Kawasaki, 2007). Some **Combretaceae** have slightly monosymmetric flowers based on unequal development of the floral base, which, in *Quisqualis*, results in an inner spur in the floral tube (Brandis, 1893; Engler & Diels, 1899); in *Terminalia paniculata* the fruit is monosymmetric by a large wing (Brandis, 1893). Monosymmetry is present in various expressions in some **Lythraceae** (mainly perianth; Graham, 2007) and **Onagraceae** (mainly sigmoid curvature of pollination organs; Raimann, 1893; Mabberley, 2000; Wagner, et al. 2007). In the genus *Lagerstroemia* (**Lythraceae**) there is polysymmetry and monosymmetry side by side; some species have heterantherous flowers with conspicuous pollinating stamens and cryptic feading stamens; in some of the latter the cryptic stamens are turned to one side (personal observations). Lopezieae (**Onagraceae**) are strongly monosymmetric in corolla and androecium (Eyde & Morgan, 1973; Wagner et al., 2007). In **Lythraceae** monosymmetry by reduction occurs in some *Rotala* species with low stamen number (Eichler, 1878). In **Myrtaceae**, Chamaelaucieae and *Fenzlia* have a monosymmetric ovary by a one-sided placenta (Niedenzu, 1893); it is unclear whether these gynoecia are unicarpellate or pseudomonomerous.

Geraniales. **Geraniaceae** exhibit different gradations between polysymmetry and monosymmetry. *Geranium* is polysymmetric, in a few species the pollination organs are sigmoidally curved, and in the Hawaiian *Geranium arboreum* also the corolla is monosymmetric (Albers & Van der Walt, 2007), *Erodium* is weakly monosymmetric, and *Pelargonium* strongly monosymmetric (Vogel, 1998). **Melianthaceae** also have strongly monosymmetric representatives, in addition to polysymmetric ones (Ronse de Craene et al., 2001; Linder, 2007).

Crossosomatales. In **Aphloiaceae** and some *Glossopetalon* species (**Crossosomataceae**), which are unicarpellate, there is monosymmetry by reduction (Matthews & Endress, 2005b).

Sapindales. In some representatives of at least five families floral monosymmetry has been found. Monosymmetry is common in **Sapindaceae** (Eichler, 1878; Ronse de Craene et al., 2000) but less so in the other families. In various **Anacardiaceae** (especially Anacardioideae), there is monosymmetry by reduction to one functional stamen or one functional carpel (Bachelier & Endress, 2007, 2009). In **Meliaceae**, *Nymania* is monosymmetric in androecium and gynoecium, with sigmoidal curvature (Harms, 1940). In **Rutaceae**, a group of genera (Cusparieae, Galipeae) has a monosymmetric androecium by reduction of stamens to staminodes on one side (Eichler, 1878; Engler, 1931; Kallunki & Pirani, 1998; Mabberley, 2000; Pirani & Kallunki, 2007; Groppo et al., 2008); *Calodendrum* and *Dictamnus* have sigmoidally curved pollination organs (Engler, 1931), and *Cneoridium* and *Empleuridium* are monosymmetric by reduction (Engler, 1931). In **Simaroubaceae**, *Leitneria* is monosymmetric by reduction (Abbe & Earle, 1940).

Huerteales. There are no obvious monosymmetric flowers in this small order (Worberg et al., 2009).

Brassicales. In at least 13 families floral monosymmetry has been recorded. In very few **Brassicaceae** monosymmetry is expressed in the perianth: the calyx in *Streptanthus* (Rollins, 1993), and the corolla in *Iberis*, *Teesdalia*, and *Erysimum* (Appel & Al-Shehbaz, 2003; Gómez et al., 2006; Busch & Zachgo, 2007). In **Bataceae** the calyx is monosymmetric (Ronse De Craene, 2005). In some **Capparaceae** and **Cleomaceae** the pollination organs are sigmoidally curved (Hildebrand, 1886; Vöchting, 1886; Kers, 2003). In more extreme cases the nectary is one-sided (**Capparaceae**; *Capparis*, *Euadenia*, *Cadaba*; Kers, 2003), or the androecium is unequal (**Cleomaceae**; *Cleome*, *Dactylaena*, *Polanisia*; Endress, 1992). In **Cleomaceae** two distinct pathways to monosymmetry were found, one starting development with disymmetry, and the other with monosymmetry (Patchell et al. 2011). Several smaller families are partly or completely characterized by floral monosymmetry (Ronse de Craene & Haston, 2006), such as **Bretschneideraceae** (Ronse De Craene et al., 2002a), **Emblingiaceae** (Leins, 1969), **Moringaceae** (Ronse de Craene et al., 1998; Olson, 2003), **Resedaceae** (Sobick, 1983), and **Tropaeolaceae** (Ronse De Craene & Smets, 2001). Oblique monosymmetry was found in **Bretschneideraceae**, and **Moringaceae**. In **Gyrostemonaceae**, *Gyrostemon* may be unicarpellate, thus there is monosymmetry by reduction (George, 2003). The same is true for some **Salvadoraceae** (Kubitzki, 2003).

Malvales. Almost each subfamily of **Malvaceae** sensu lato has some monosymmetric representatives. In Bombacoideae, the gynoecium is affected in *Adansonia*, the androecium in *Chiranthodendron* (Endress, 1994, 1999). In Grewioideae

Pseudocorchorus has a monosymmetric androecium (Bayer & Kubitzki, 2003). In Helicteroideae, *Helicteres* and *Mansonia* are monosymmetric (Cheek & Dorr, 2007). In Byttnerioideae, *Kleinhovia* has elaborate monosymmetry (personal observation), in *Melochia* sigmoid curvature occurs (Machado & Sazima, 2008), and the unicarpellate *Waltheria* and *Plagianthus* are monosymmetric by reduction (Bayer & Kubitzki, 2003). In Malvoideae, species of *Hibiscus* and *Hibiscadelphus* may have curved pollination organs (and corolla) (Fryxell, 1983; Endress, 1999). In Sterculioideae, *Sterculia* species may have a curved staminal column (personal observation). In **Cochlospermaceae**, the androecium in *Amoreuxia* is onesided, with staminodes on one side (Poppendieck, 2003). In some **Dipterocarpaceae** the fruits are monosymmetric by differential further growth of the sepals (Ashton, 2003). The flowers of a number of **Thymelaeaceae** are monosymmetric by reduction: some *Pimelea* species have a single stamen, in other genera the gynoecium is pseudomonomerous (Eckardt, 1937; Herber, 2003).

Asterid Alliance (see also Endress, 2010)

Caryophyllales. Conspicuous monosymmetry is present in some bird-pollinated **Cactaceae** (Barthlott, 1993), and monosymmetry by sigmoid curvature in moth-pollinated *Mirabilis* (**Nyctaginaceae**, Correll & Correll, 1982) and *Silene* (**Caryophyllaceae**, Mabberley, 2000). Monosymmetry by reduction of the gynoecium to a single carpel is present in **Rhabdodendraceae** (Prance, 2003), in some **Molluginaceae** (Endress & Bittrich, 1993), in **Nyctaginaceae** (Rohweder & Huber, 1974; Bittrich & Kühn, 1993), and some **Phytolaccaceae** (Rohwer, 1993b); monosymmetry by reduction of stamen number occurs in some **Amaranthaceae** (including **Chenopodiaceae**) (Kühn, 1993), **Caryophyllaceae** (Bittrich, 1993), and **Portulacaceae** (Carolin, 1993). Cases with a single (curved) ovule in a bi- or tricarpellate gynoecium are present in **Basellaceae** (Eckardt, 1955), **Sarcobataceae** (Behnke, 1997), **Plumbaginaceae** (De Laet et al., 1995; see also under Asymmetry), and part of **Polygonaceae**, **Amaranthaceae** (including **Chenopodiaceae**), and **Caryophyllaceae**.

Santalales. Monosymmetry by sigmoid curvature of the pollination organs is present in a number of **Loranthaceae**. These flowers are bird-pollinated and have an explosive opening mechanism. Such explosive flowers evolved more than once in the family (Feehan, 1985; Wilson & Calvin, 2006; Kuijt, 2007). In **Eremolepidaceae**, *Antidaphne* has monosymmetry or disymmetry by reduction (Kuijt, 1988).

Asterids. Monosymmetric flowers are prominent in both large subclades, **lamiids** and **campanulids**. In some orders they are highly elaborate.

Ericales. Although most families have predominantly polysymmetric flowers, monosymmetric taxa occur in several of them. **Balsaminaceae** are all pronouncedly monosymmetric, especially in the perianth (Fischer, 2004; Caris et al., 2006; Geuten et al., 2006). In **Ericaceae** monosymmetry with sigmoid curvature of the pollination organs occurs in *Pyrola* and *Rhododendron* (Stevens et al., 2004). In **Lecythidaceae**, Lecythidoideae have predominantly monosymmetric flowers, mainly with different stamen (staminode) shapes (Tsou & Mori, 2007). In **Myrsinaceae** some buzz-pollinated taxa have a monosymmetric androecium (*Ardisia speciosa*, personal observation), and *Coris* has a bilabiate corolla (Stahl & Anderberg, 2004). In **Polemoniaceae**, *Cobaea* species and *Loeseliastrum* are pronouncedly monosymmetric (Grant & Grant, 1965; J. Schönenberger, personal communication), other genera have slighly monosymmetric flowers, either in the perianth or by curvature of the style (Grant & Grant, 1965; Wilken, 2004). In *Fouquieria* of **Fouquieriaceae**, the floral tube is slightly curved in long-tubed species (J. Schönenberger, personal communication).

Cornales. Flowers are largely polysymmetric, more rarely monosymmetric by reduction. In **Cornaceae** the gynoecium is sometimes pseudomonomerous and the flowers monosymmetric by reduction, such as in *Nyssa* and *Mastixia* (Eyde, 1963), and *Alangium* (Eyde, 1968). In **Hydrangeaceae**, *Schizophragma* has pronouncedly monosymmetric, onesided sterile flowers at the periphery of the inflorescences (Hufford, 2004), and *Kirengeshoma* has flowers with sigmoidally curved pollination organs. In **Loasaceae**, *Petalonyx* is monosymmetric (or asymmetric) by reduction of the fertile stamens to two or three and curvature of the pseudomonomerous gynoecium (Hufford, 1989; Weigend, 2004).

Euasterids I (Lamiids). Among the unplaced families in lamiids, **Boraginaceae** have a few genera with monosymmetric flowers. In *Echium* and relatives the corolla and androecium are (obliquely) monosymmetric (Gürke, 1893), and in some *Echiochilon* species the corolla is strongly monosymmetric (Langström & Oxelman, 2003). In *Lycopsis* flowers have a slightly curved floral tube (Gürke, 1893). In *Rochelia* the gynoecium is unicarpellate and monosymmetric (Hilger, 1984), in *Wigandia* the two carpels are of unequal size and thus slightly monosymmetric (Hilger, 1987). Some genera are pronouncedly monosymmetric only in fruit (*Asperugo*, *Harpagonella*) (Gürke, 1893). In **Metteniusaceae** the gynoecium is monosymmetric by pseudomonomery (González & Rudall, 2010).

Garryales. In **Eucommiaceae** the female flowers of *Eucommia* are pseudomonomerous and thus monosymmetric by reduction (Eckardt, 1957). In **Aucubaceae** female flowers have a (pseudo)monomerous gynoecium and are monosymmetric by reduction, whereas the male flowers are polysymmetric (Philipson, 1967). **Icacinaceae** (which may be included in an expanded Garryales; Karehed, 2001; Stevens, 2001 onwards) have a monosymmetric unilocular and biovulate gynoecium, and the flowers may be monosymmetric by reduction (Sleumer, 1942; Fagerlind, 1945; Karehed, 2001).

Gentianales. Gentianales have largely polysymmetric flowers but most families have one or few monosymmetric taxa. In **Gentianaceae** the buzz-pollinated *Exacum* and *Orphium* have a curved androecium and gynoecium (Klackenberg, 2002); in *Exacum dipterum* also the calyx is monosymmetric (Klackenberg, 2002). In the bat-pollinated *Irlbachia alata* the corolla tube is sigmoidally curved (Machado et al., 1998). In the likewise bat-pollinated *Fagraea racemosa* the pollination organs are sigmoidally curved (Endress, 1994). In *Canscora roxburghii*, corolla and androecium (heteromorphic anthers) are monosymmetric (Thiv & Kadereit, 2002b). In *Macrocarpaea marahuacae* corolla, androecium and gynoecium are slightly monosymmetric (Struwe & Albert, 2002). In some species of *Gentiana* (e.g. *G. lutea*) the calyx is basically polysymmetric but it splits on one side ("spathaceous" calyx) (Ho & Liu, 2001). In **Apocynaceae** the corolla is slightly monosymmetric in *Isonema* and *Rauvolfia vomitoria*, or the flowers adjust to the final position by bending of the corolla tube (e.g., *Allamanda*, *Beaumontia*, *Ceropegia*, *Tavaresia* (Bruyns, 1985; personal observation). In **Rubiaceae**, although polysymmetry is by far predominant, there are a number of monosymmetric taxa. Mainly calyx and corolla are affected (survey in Robbrecht, 1988). The most conspicuous cases are flowers in which one of the five sepals is higly enlarged and acts as a flag (*Mussaenda*, *Warszewiczia*) (Weber, 1955; Classen-Bockhoff, 1996). Rarely also the androecium is affected (*Posoqueria*; Robbrecht, 1988). Among **Loganiaceae**, in *Spigelia splendens* the floral tube is slightly curved upwards (Erbar & Leins, 1999).

Lamiales. Lamiales are a huge clade in terms of species, genera and families with monosymmetric, often elaborate bilabiate flowers (Kampny, 1995). Monosymmetry is differentially expressed in the different families. The most common pattern is pentamerous flowers with an upper lip of two and a lower lip with three petals, and the odd stamen posterior (adaxial) (Donoghue et al., 1998). Commonly the odd stamen is more or less reduced to a staminode or even lacking. It is still present as a staminode in **Gesneriaceae**, many **Bignoniaceae**, and many **Veronicaceae**, but lacking in, e.g., **Lamiaceae**, **Orobanchaceae**, and many **Acanthaceae** (Endress, 1998, 1999). **Scrophulariaceae** sensu stricto are diverse in this respect. In **Calceolariaceae**, the flowers are tetramerous (and may almost look dimerous) (Endress, 1999; Mayr & Weber, 2006). In a few groups flowers became secondarily polysymmetric, such as *Ramonda* (Endress, 1998) and some Gloxinieae (Clark et al. 2011) (**Gesneriaceae**), and *Sibthorpia* (**Veronicaceae**) (Endress, 1998). In other groups a change from pentamery to tetramery by complete reduction of the median adaxial floral sector led to approximate polysymmetry (e.g. *Veronica*, *Aragoa*, *Plantago*, **Veronicaceae**; Donoghue et al., 1998; Reeves & Olmstead, 1998; Endress, 1999; Bello et al., 2004; or in the former **Buddlejaceae**, which are now in **Scrophulariaceae**; Olmstead et al., 2001; Oxelman et al., 2005; Tank et al., 2006). Such cases of lost monosymmetry were especially investigateded in molecular developmental studies (Citerne & Cronk, 1999; Cubas et al., 1999a; Möller et al., 1999; Citerne et al., 2000; Wang et al., 2006; Preston et al., 2011)). Pseudomonomerous gynoecia occur scattered in several groups. They add another dimension to the monosymmetry already present in corolla and androecium (e.g. *Globularia*, *Hippuris*, *Litorella*, **Veronicaceae**; *Phryma*, **Phrymaceae**; *Stachytarpheta*, **Verbenaceae**; Eckardt, 1937). In the largely tetramerous and dimerous **Oleaceae**, *Jasminum* species with increased number of petals are polysymmetric (Torgard, 1924).

Solanales. Monosymmetry is rare in **Convolvulaceae**, most pronounced in *Ipomoea lobata*, with the corolla, androecium, and gynoecium bent, and *Humbertia*, with the androecium and gynoecium bent (Deroin, 1992). But it is more common in **Solanaceae**, with peaks in the keel flowers of *Schizanthus* and in the buzz-pollinated, heterantherous flowers of *Solanum* sect. *Androceras* (Whalen, 1978, 1979), which in the extreme have only one fertile stamen left (e.g., *Solanum citrullifolium*). Other nectariferous flowers less extremly monosymmetric than *Schizanthus* are, e.g., *Browallia*, *Brunfelsia*, *Nierembergia*, *Petunia*, *Reyesia*, *Salpiglossis*, *Schwenkia*, *Solandra*, and *Triguera*. In those mostly the corolla and androecium are affected; often only four or two of the five stamens are fertile (Robyns, 1930; Huber, 1980; Cocucci, 1991; Hunziker, 2001; Ampornpan & Armstrong, 2002).

Euasterids II (Campanulids)

Brunelliales. Monosymmetric flowers occur in *Columellia*, which have two stamens but otherwise pentamerous whorls (Stern et al., 1969), and in *Desfontainia* (both in **Brunelliaceae**), which have a slightly monosymmetric corolla tube (Endress, 2002).

Apiales. Monosymmetric flowers are rare. The most conspicuous monosymmetric flowers are in **Apiaceae**: In *Orlaya*, the peripheral flowers of the umbels have conspicuously enlarged petals on their peripheral side (Froebe, 1980; Classen-Bockhoff, 1992). Unequal petals are also present in a number of other genera, such as *Ammi*, *Heracleum*, and *Scandix* (Drude, 1897; Froebe, 1980). In some groups the two carpels are unequal, one with two main ribs and one with three main ribs (e.g., *Elaeoselinum*; Drude, 1897; *Polemanniopsis*; Burtt, 1988; Liu et al., 2004). In this case features of the pentamerous symmetry of the other floral whorls are superimposed on the gynoecium (see also chapter “Transient monosymmetry”). In *Griselinia* of **Griseliniacae**, the female flowers are monosymmetric by their pseudomonomerous gynoecium (Kubitzki, 1963; Philipson, 1967). This is also true for *Aralidium* (**Aralidiaceae**; Philipson & Stone, 1980).

Aquifoliales. **Cardiopteridaceae** and **Stemonuraceae** have a unilocular gynoecium with two ovules (Sleumer, 1942; Fagerlind, 1945; Karehed, 2001; Tobe, 2012), and the flowers are probably monosymmetric by reduction.

Asterales. In **Argophyllaceae**, *Corokia* has a bi- or unilocular gynoecium with one ovule per locule and the unilocular flowers are monosymmetric (Philipson, 1967). A unilocular, uniovulate gynoecium is constantly present in **Asteraceae** (Anderberg et al., 2007) and **Calyceraceae** (Hellwig, 2007). However, **Asteraceae** also have another, more conspicuous kind of monosymmetry, which has found much more attention: the pronouncedly onesided differentiation of the corolla forming the radiating part of flat inflorescences (Harris, 1995; Leins & Erbar, 2000; Anderberg et al., 2007; Jeffrey, 2007). In **Campanulaceae**, Lobelioideae have elaborate monosymmetric flowers, with all four whorls of floral organs involved (Brantjes, 1983; Ayers, 1990; Leins & Erbar, 2005). This is also true for **Stylidiaceae** (Erbar, 1992) and **Goodeniaceae** (Carolin, 1959). In the three last mentioned families, in addition, a few taxa with pseudomonomerous, uniovulate gynoecia occur (Carolin, 2007a, b; Lammers, 2007).

Dipsacales. The families of Dipsacales have partially or consistently monosymmetric flowers, such as **Adoxaceae**, **Caprifoliaceae**, **Diervillaceae**, **Dipsacaceae**,

Linnaeaceae, **Morinaceae**; only in **Valerianaceae** are they asymmetric) (Fukuoka, 1972; Roels & Smets, 1996; Donoghue et al., 2003; Howarth & Donoghue, 2005; Howarth et al., 2011). Monosymmetry comes about in various ways. In **Caprifoliaceae** the corolla is sometimes monosymmetric (especially *Lonicera*), also in **Diervillaceae** and **Dipsacaceae**, and in **Linnaeaceae** and **Morinaceae**, in addition, the androecium. Furthermore, in some **Adoxaceae** (*Sinadoxa*) and in **Dipsacaceae** the gynoecium is unilocular and uniovulate (Donoghue et al., 2003).

Basal Monocots. In basal monocots there is no elaborate monosymmetry, but monosymmetry by simplicity is more common. In *Acorus* (**Acoraceae**, **Acorales**), the putative sister to all other monocots, the perianth is more developed abaxially than adaxially (Buzgo & Endress, 2000). What looks like the subtending bract is in reality the outer median tepal. Among **Alismatales**, many **Araceae** (including **Lemnaceae**) have unicarpellate flowers (also the basal genus *Gymnostachys*; Buzgo, 2001), and some have unistaminate flowers (Mayo et al., 1997, 1998; Landolt, 1998). In **Aponogetonaceae**, flowers are often monosymmetric by the loss of the adaxial petal (*Aponogeton distachyus*) (van Bruggen, 1998). As an extreme, the spicate inflorescence may be condensed into a pseudanthium composed of several monosymmetric flowers as in *Aponogeton ranunculiflorus* (personal observation). In **Cymodoceaceae** flowers have one stamen or one carpel (Kuo & McComb, 1998a). In **Hydrocharitaceae**, similar reduction is known from several genera (Cook, 1998a), and the same applies for **Juncaginaceae** (Haynes et al., 1998a), **Najadaceae** (Haynes et al., 1998b), **Posidoniaceae** (Kuo & McComb, 1998b), **Potamogetonaceae** (Haynes et al., 1998c), **Zannichelliaceae** (Haynes et al., 1998d), and **Zosteraceae** (Kuo & McComb, 1998c).

Dioscoreales. In **Burmanniaceae**, *Afrothismia* and some *Thismia* have a bent floral tube (Maas-van de Kamer, 1998). In **Dioscoreaceae**, *Rajania* has fruits with a wing (Correll & Correll, 1982), which are then monosymmetric.

Asparagales. **Orchidaceae** are a monosymmetric family with highly elaborate flowers par excellence, with all floral whorls strongly involved (e.g., Endress, 1994; Kurzweil & Kocyan, 2002; Rudall & Bateman, 2002); if the frequent floral resupination is considered, orchid flowers are strictly speaking asymmetric (see below). All other families are not or only partly monosymmetric. In **Alliaceae**, *Gilliesia* is strongly monosymmetric involving the inner perianth whorl, androecium and gynoecium, the related *Gethyum* only androecium and gynoecium (Rahn, 1998; Rudall et al., 2002; Fay & Hall, 2007). In several families a slight monosymmetry is present in the form of sigmoidal curvature of the floral tube and/or pollination organs; this is true for a number of **Agapanthaceae** (Kubitzki, 1998a), **Agavaceae** (Verhoek, 1998), **Amaryllidaceae** (Vöchting, 1886; Church, 1908; Correll & Correll, 1982; Meerow & Snijman, 1998; Meerow, 2010), **Anthericaceae** (Conran, 1998), **Asphodelaceaae** (Vöchting, 1886; Correll & Correll, 1982; Smith & Van Wyk, 1998), **Blandfordiaceae** (Clifford & Conran, 1998), **Convallariaceae** (Conran & Tamura, 1998), **Doryanthaceae** (Clifford, 1998), **Hemerocallidaceae** (Vöchting, 1886; Clifford et al., 1998), **Hostaceae** (Vöchting, 1886; Kubitzki, 1998b), **Iridaceae** (mainly Ixioideae; Goldblatt et al., 1998), and **Tecophilaeaceae** (Simpson & Rudall, 1998). Other cases with stronger monosymmetry are: *Sprekelia* (**Amaryllidaceae**), in which, in addition to mere curvature, the perianth is conspicuously monosymmetric (Vöchting, 1886); *Haworthia* and *Chortolirion* (**Asphodelaceae**) with bilabiate perianth (Smith & Van Wyk, 1998); *Daubenya* with three enlarged petals in basal flowers of the inflorescence, and *Lachenalia* (**Hyacinthaceae**) with a bilabiate perianth (Speta, 1998); *Melasphaerula*, *Sparaxis*, *Chasmanthe* and perhaps other **Iridaceae-Ixioideae** with bilabiate or otherwise monosymmetric perianth (Vogel, 1954; Goldblatt et al., 1998); *Conanthera*, *Cyanella*, *Tecophilaea* (**Tecophilaeaceae**) with strongly monosymmetric androecium (Simpson & Rudall, 1998).

Liliales. Most Liliales have polysymmetric or only slightly monosymmetric flowers, commonly involving sigmoidal curvature of perianth and/or pollination organs, thus similar as in Asparagales. More conspicuously monosymmetric are **Alstroemeriaceae** with monosymmetric nectar guides in *Alstroemeria* (Bayer, 1998), **Colchicaceae** with sharply angled style in *Gloriosa* (Werth, 1956; Endress, 1994, Nordenstam, 1998), **Corsiaceae** with a strongly monosymmetric perianth (Neinhuis & Ibisch, 1998), **Liliaceae** with a spur in one of the six tepals in *Fritillaria* sect. *Theresia* (Tamura, 1998a), and **Melanthiaceae** with the perianth developed more strongly on one side in some *Chionographis* (Tamura, 1998b; Tanaka, 2003).

Pandanales. Pandanales generally have polysymmetric flowers. Slight monosymmetry is present in some flowers of *Pandanus* (**Pandanaceae**), in which a unicarpellate gynoecium occurs (Endress, 1995; Stone et al., 1998). In **Triuridaceae** the androecium is rarely reduced to one stamen (Maas-van de Kamer & Weustenfeld, 1998).

Commelinids. In general, in commelinids floral monosymmetry is more prominent than in the other suprafamilial clades of monocots.

Arecales. **Arecaceae** are supposed to have largely polysymmetric flowers as floral symmetry is not considered in Uhl & Dransfield (1987) and Dransfield & Uhl (1998). However, weak monosymmetry is present in at least some palms: in *Geonoma* the gynoecium is pseudomonomerous (Stauffer et al., 2002; Stauffer & Endress, 2003); some other Geonomeae have a dorsiventrally flattened gynoecium and the (sterile) androecium in female flowers is monosymmetric (Stauffer & Endress, 2003). Some coryphoid palms are unicarpellate (Rudall et al., 2011).

Commelinales. In **Commelinaceae** many genera have monosymmetric flowers, often with heteranthery involved (e.g., *Aëtheolirion*, *Tinantia*, *Floscopa*, *Polyspatha*, *Aneilema*, *Rhopalephora*, *Commelina*) (Faden, 1998). In *Plowmanianthus* the lower three stamens are strongly reduced (Hardy & Faden, 2004; Hardy et al., 2004). In *Dichorisandra* the stamens are sigmoidally curved (Hardy et al., 2000). In *Tapheocarpa*, one of the three carpels is sterile (Faden, 1998). **Haemodoraceae** have some monosymmetric genera in both subfamilies, such as *Pyrrorhiza* (with one stamen), *Schiekia*, *Wachendorfia* in Haemodoroideae, and the conspicuously bilabiate *Anigozanthos* in Conostylidoideae (Simpson, 1990, 1998). In **Philydraceae** the flowers of all genera are conspicuously monosymmetric (sometimes asymmetric) (Hamann, 1966, 1998).

In **Pontederiaceae** all genera are monosymmetric to some degree (Cook, 1998b; Strange et al., 2004).

Poales. **Bromeliaceae** have largely polysymmetric flowers. In a few genera weakly monosymmetric flowers occur, such as *Pitcairnia* or *Bilbergia* (Smith & Till, 1998). In **Centrolepidaceae**, the unisexual flowers are monosymmetric by reduction in having a single stamen or (probably) an unilocular and uniovulate gynoecium (Hamann, 1975; Sokoloff et al., 2009). In **Cyperaceae**, delimitation of flowers is unclear in Hypolytreae and Chrysitricheae. If the apparent flowers are pseudanthia, the male flowers are unistaminate and thus monosymmetric by reduction. Monosymmetry by reduction is also common in Cyperoideae, in which many genera have flowers with 1–3 stamens (e.g. *Scirpus*, *Eriophorum*, *Eleocharis*, *Cyperus*) or only one stamen (*Becquerelia*, *Diplacrum*, *Bisboeckelera*, *Calyptrocarya*); in female flowers the gynoecium is unilocular and uniovulate (Goetghebeur, 1998). In many **Eriocaulaceae** the median sepal is smaller than the other two or even lacking, and in several Eriocauloideae the united sepals form a one-sided spathe-like structure (Stützel, 1984). In **Poaceae**, floral monosymmetry by reduction is common; the petals ("lodicules") are reduced to two in most groups, some of the stamens may be reduced, and the gynoecium is unilocular and uniovulate (Dahlgren et al., 1985; Cocucci & Anton, 1988; Rudall & Bateman, 2004). In **Rapateaceae**, flowers of *Kunhardtia* have a monosymmetric corolla (Stevenson et al., 1998). In **Restionaceae**, floral monosymmetry by gynoecium reduction to one (uniovulate) locule has evolved several times (Linder et al., 1998; Ronse De Craene et al., 2002b). In **Sparganiaceae** floral monosymmetry by reduction is present by a unilocular ovary and sometimes reduction of perianth and androecium to one organ (Müller-Doblies, 1970; Kubitzki, 1998c). In **Xyridaceae** the calyx is monosymmetric in *Abolboda* and *Xyris*, the corolla is bilabiate in *Orectanthe*, and the ovary is dorsiventrally compressed in *Aratitiyopea* (Kral, 1998).

Zingiberales. All Zingiberales have pronouncedly monosymmetric (or even asymmetric) flowers (Kress, 1990). In **Musaceae** (Andersson, 1998b), **Strelitziaceae** (Andersson, 1998c), **Heliconiaceae** (Andersson, 1998a), and **Lowiaceae** (Larsen, 1998b) the median posterior stamen is reduced to a staminode or is missing, and the flowers are more or less conspicuously bilabiate. In **Zingiberaceae** (Larsen et al., 1998) and **Costaceae** (Larsen, 1998a), in contrast, only the median posterior stamen is fertile; in **Costaceae** the other five stamens are transformed into the lower lip, in **Zingiberaceae** only two to four of them form the lower lip, while the remaining ones may form separate petaloid organs (Endress, 1995; Specht et al., 2008).

Asymmetric Flowers

Real floral asymmetry, the lack of any symmetry plane, is much less studied than monosymmetry and is also much less common than monosymmetry, although subtle forms of asymmetry, in addition to fluctuating asymmetry, are widespread. Like monosymmetry, asymmetry is also expressed at different structural levels.

Asymmetry in flowers, if taken in a strict sense is, like monosymmetry, a mixed bag of forms that are likely not all homologous because this asymmetry comes about for different reasons. In the literature floral asymmetry is mostly addressed for cases of basically monosymmetric flowers that have lost their monosymmetry by unequal development of the two mirror symmetrical halves. The most well known cases are enantiostyly or enantiomorphy. More subtle cases of asymmetry are those in which the symmetry planes of the different organ whorls are not congruent.

Diverse Manifestations of Asymmetry in Flowers

Asymmetry as a Modification of Elaborate Monosymmetry (Enantiomorphy). Floral asymmetry is best known in enantiostylous flowers, which are basically monosymmetric but have the style deflected to the right or the left side (Jesson & Barrett, 2003; Jesson et al., 2003a, b). In such flowers with a deflected style often also other floral whorls are involved in this onesidedness (Marazzi et al., 2006; Marazzi & Endress, 2008). For those, the more inclusive term enantiomorphy is used. Enantiostyly and enantiomorphy express the presence of two mirror-image like morphs (either on the same individual or on different individuals). If only one morph exists in a species or higher group, it is non-enantiomorphic asymmetry. The latter tends to be the case in the most elaborate asymmetric flowers (e.g., Phaseoleae of Fabaceae; Endress, 1999, 2001a; Etcheverry et al., 2008). The presence of only one morph may make it easier for bees to exploit the flowers always from the same side (Endress, 1999; see also Schmucker, 1931; Woodward & Laverty, 1992; and Gegear & Laverty, 1995). In vertebrates the organisational internal asymmetry is not conspicuous externally; however, some specialized groups also have an external non-enantiomorphic asymmetry, such as snail-eating snakes with asymmetric jaws (Hoso et al., 2007). If enantiomorphic flowers occur on one individual, they are often components of a system with pendulum symmetry (Goebel, 1908; Endress, 1999; Kirchoff, 2003; Hardy et al., 2004).

A variant of curvature is torsion, such as resupination in orchids (inferior ovary), torsion in *Platystigma* (superior ovary), mimosoids (superior ovary), *Medicago* (superior ovary), *Helicteres* (superior ovary), *Cajophora* (inferior ovary), *Pedicularis* (corolla) (Goebel, 1920). In *Haemaria* (Orchidaceae) the torsion encompasses the entire flower and makes it conspicuously asymmetric (Goebel, 1920). Torsion is often a mechanism for resupination, the reorientation of otherwise monosymmetric flowers into a perpendicular position, best known from orchids. However, resupination may also be based on adjustments outside of the flower proper. Thus not all resupinated flowers are asymmetric. Besides orchids, resupination is less well studied but occurs in a number of families here and there (Papaveraceae-Fumarioideae, Melianthaceae, Leguminosae, Violaceae, Balsaminaceae, Acanthaceae, Lamiaceae, Scrophulariaceae sensu lato, Campanulaceae-Lobelioideae, Alstroemeriaceae, Zingiberaceae; Goebel, 1920).

At another level is fluctuating asymmetry, small irregularities resulting from incompletely balanced development (Möller, 2000). This is a widespread phenomenon and is not discussed here.

Asymmetry by Spiral or Irregular Phyllotaxis and by Imbricate Perianth Organ Aestivation. A kind of minor asymmetry is provided by spiral and irregular phyllotaxis. These cases are not considered in this study because the former are common and scattered through the basal angiosperms and basal eudicots, and the latter are common in flowers with an increased number of stamens throughout the angiosperms.

Likewise, all kinds of imbricate aestivation (contort, quincuncial, cochlear) of the calyx or corolla of a flower with pentamerous or otherwise odd-merous whorls lead to a kind of floral asymmetry (Reinsch, 1927). For instance, in Commelinaceae there is a cochlear aestivation in both perianth whorls (Hardy et al., 2000; Hardy et al., 2004). As imbricate aestivation of sepals and petals is the most common aestivation type in angiosperms, it is diffcult to record all these taxa. The most conspicuous asymmetric pattern among imbricate aestivations is contort aestivation. Thus among the imbricate aestivations only taxa with a contort pattern were recorded in this study. Contort petal aestivation is present in a number of angiosperm groups, especially in core eudicots. Whereas in many rosids, contort petal aestivation is enantiomorphic, in almost all asterids contort aestivation is fixed to one of the two possible morphs at genus or even family level (Endress, 1999, 2001a).

Ironically, contort aestivation is strongly correlated with polysymmetric flowers (Schoute, 1935; Endress, 1994, 1999). However, the contortion superimposes on the flowers an asymmetry pattern.

Contort aestivation in many cases also results in asymmetric petals: *Sida*, *Malva*, *Hibiscus*, *Kielmeyera*, *Dombeya*, *Linum austriacaum*, *Oxalis floribunda*, *O. ortgiesii*, *Plumbago capensis* (Schoute, 1935), and especially conspicuous in some Apocynaceae, such as *Vinca* (Endress, 1999). However, others have perfectly symmetrical petals: *Linum usitatissimum*, *L. flavum*, *Gypsophila paniculata*, *Geranium sanguineum*, *Plumbago larpentae* (Schoute, 1935).

In many groups of eudicots with an imbricate (quincuncial) calyx, inner and outer sepals are of somewhat difference size and/or shape, which also results in a minor floral asymmetry. Such cases are not considered here.

Transient Asymmetry

Monochasial partial inflorescences in which the angles of successive branches are not 180° are asymmetric systems. This asymmetry may influence the shape of the young flowers and they may also be slightly asymmetric. Later in development this asymmetry is equalized and the anthetic flowers are monosymmetric or polysymmetric. Such transient slight early asymmetry was observed in *Tradescantia* (Commelinaceae) (personal observation; Hardy & Stevenson, 2000b).

Asymmetry in Special Biological Situations

Buzz Pollination and Floral Enantiostyly. Interestingly, most enantiostylous flowers are buzz-pollinated pollen flowers (Buchmann, 1983), such as *Chamaecrista* and *Senna* (Fabaceae; Gottsberger & Silberbauer-Gottsberger, 1988; Marazzi et al., 2007), *Cyanella* (Tecophilaeaceae; Dulberger & Ornduff, 1980), *Heteranthera* (Pontederiaceae), *Philydrum* (Philydraceae), *Solanum* (Solanaceae), and *Paraboea* (Gao et al. 2006) and *Saintpaulia* (Gesneriaceae). It has been argued that the lateral position of the style, away from the buzzing bee, is favorable for not obstructing this special kind of pollination (Dulberger, 1981; Barrett et al., 2000; Marazzi & Endress, 2008).

Tubular Nectar Flowers with Anthers at Different Levels. Anthers of basically polysymmetric pentamerous, tubular flowers may be presented at three or five different levels, based on either different levels of stamen insertion or different length of filaments. These levels are linked with the spiral direction of the sepals (Endress, 1999) so that the result is, strictly speaking, floral asymmetry. Such cases were reported from Ericaceae (personal observation), Polemoniaceae (Grant & Grant, 1965; Mabberley, 2000), Gentianaceae (Thiv & Kadereit, 2002a), Rubiaceae (Robbrecht, 1988), Boraginaceae (Taroda & Gibbs, 1986), Convolvulaceae (Wagner, 1989; Deroin, 1996), and Solanaceae (Robyns, 1930; Hunziker, 2001). These families are all in asterids I (lamiids), except for Ericaceae and Polemoniaceae, which are in the more isolated Ericales (basal asterids).

Flowers in Agamospermous Plants. Another source of asymmetry is irregular petal formation, associated with reduction, which is known from some taxa with agamospermous (apomictic) flowers (*Potentilla aurea*; Heinricher, 1907; *Ranunculus auricomus*; Zimmermann, 1975). This may be seen as an extreme case of fluctuating asymmetry that is not constrained if pollination of flowers is not required.

Systematic Distribution of Floral Asymmetry Across Angiosperms

Also the occurrence of floral asymmetry is relatively widespread, although it is less common than monosymmetery. Different forms of asymmetry are not equally distributed across the angiosperms (Fig. 6). In contrast to the corresponding chapter on monosymmetric flowers in most cases only those larger taxa that contain asymmetric flowers are listed.

Basal Angiosperms. Asymmetric flowers are lacking, except for flowers with spiral or irregular floral phyllotaxis (here not considered), and flowers with contort aestivation in each perianth whorl (*Cabomba*, **Cabombaceae**) (Endress, 2008a).

Basal Eudicots. Floral asymmetry is rare and never conspicuous. It comes about by spiral or irregular phyllotaxis (here not considered), or by contort aestivation of petals (some Papaveraceae, Schoute, 1935), or with irregularity superimposed on monosymmetry (**Eupteleaceae**, Endress, 1986a, 2008b; Ren et al., 2007). Slight enantiomorphy occurs in otherwise monosymmetric flowers and fruits of *Banksia* (**Proteaceae**) (Renshaw & Burgin, 2008).

Saxifragales. Some **Crassulaceae** and **Haloragaceae** have contort petals (Eichler, 1878, Schoute, 1935).

Zygophyllales. In **Zygophyllaceae** the petals are contort in *Tribulus* (Correll & Correll, 1982).

Cucurbitales. In **Begoniaceae** the perianth and/or the inferior, winged ovary is often asymmetric (Eichler, 1878; Fang et al., 2006), and in some species of *Momordica* (**Cucurbitaceae**) corolla and androecium are asymmetric (Vogel, 1974).

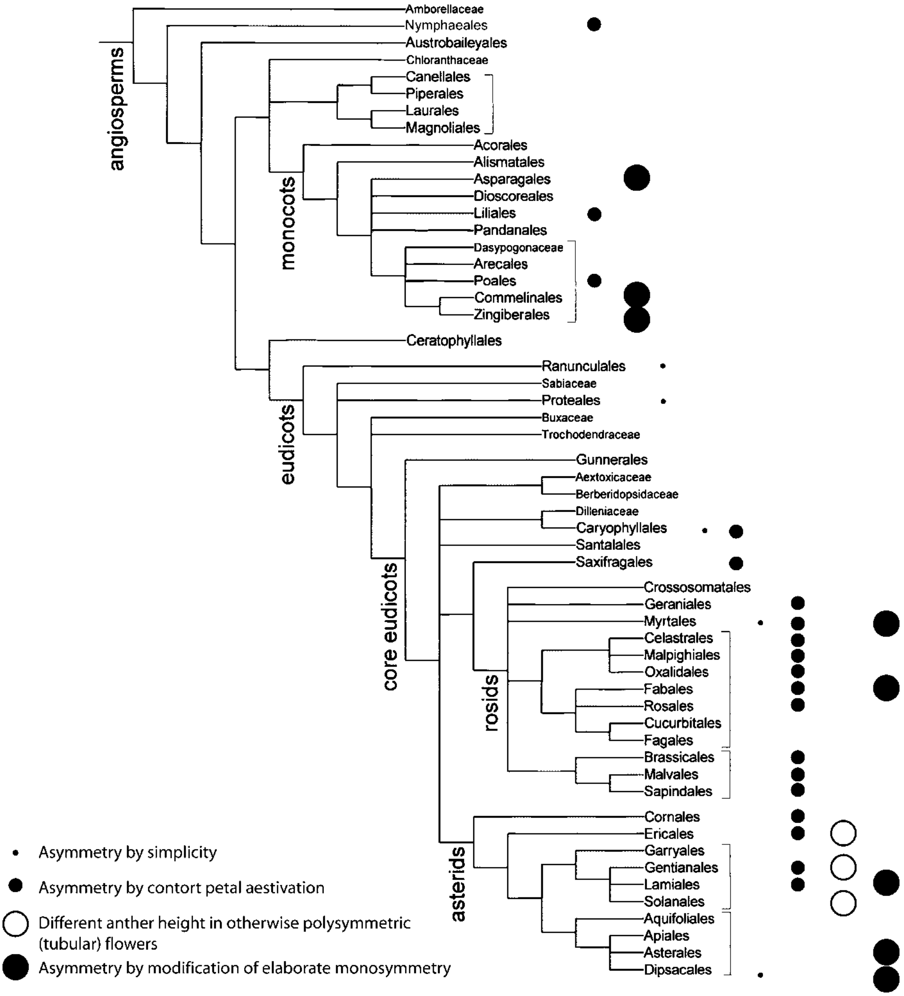

Fig. 6 Occurrence of different floral asymmetry patterns across angiosperms (cladogram from APG, 2003, with change of "Nymphaeaceae" to "Nymphaeales", to include Hydatellaceae, according to Saarela et al., 2007). Each kind of asymmetry is plotted only once in a clade where it occurs, even in cases where multiple origins are probable

Fabales. Floral asymmetry is characteristic for some larger clades of **Fabaceae**, such as *Senna* and *Chamaecrista* in caesalpinioids, in which the flowers are more or less open but corolla, androecium and gynoecium (enantiostyly) can be involved in asymmetry (Tucker, 1996; Gottsberger & Silberbauer-Gottsberger, 1988; Marazzi et al., 2006, 2007; Marazzi & Endress, 2008), and *Delonix*, in which the androecium base with the access to the nectar is asymmetric (Troll, 1951; Endress, 1994); in Papilionoideae the flowers of Phaseoleae are largely asymmetric by sometimes extensive torsion of the keel (Troll, 1951; Brizuela et al., 1993; Endress, 1994; Etcheverry et al., 2008), or in certain Vicieae the keel is asymmetric without torsion (the asymmetry arising late in development), as in *Lathyrus* species (Teppner, 1988; Westerkamp, 1993; Prenner, 2003) and *Ottleya* (Ottley, 1944; Sokoloff, 1999; Sokoloff et al., 2007); asymmetry in the androecium is present in early development of various Papilionoideae (Prenner, 2004e). Among basal Fabaceae, *Duparquetia* (Prenner & Klitgaard, 2008) and *Gleditsia* (Tucker, 1991) are asymmetric by loss of one or more sepals. Late asymmetry of the keel is also present in **Polygalaceae** (some *Polygala* species; Brantjes, 1982; Westerkamp & Weber, 1997, Prenner, 2004b). In **Quillajaceae** and *Suriana* (**Surianaceae**) the petals are contort (Bello et al., 2007).

Rosales. Petals are contort in *Gillenia* and *Raphiolepis* (**Rosaceae**) (Eichler, 1878).

Malpighiales. A number of families have representatives with contort petal aestivation, such as **Bonnetiaceae** (Lleras, 1972; Maguire, 1972; Kubitzki. 1978), **Clusiaceae** (Eichler, 1878; Schoute, 1935; de Oliveira & Sazima, 1990; Gill et al., 1998; Stevens, 2007), **Ctenolophonaceae** (Narayana & Rao, 1971; Matthews & Endress, 2011), **Erythroxylaceae** (Eichler, 1878), **Euphorbiaceae** (Schoute, 1935; Rao, 1972; Endress, 1999), **Euphroniaceae** (Matthews & Endress, 2008), **Humiriaceae** (Rao & Narayana, 1965; Narayana & Rao, 1969), **Hypericaceae** (Eichler, 1878; Ronse De Craene & Smets, 1991), **Ixonanthaceae** (Steyermark & Luteyn, 1980), **Linaceae** (Eichler, 1878; Schoute, 1935; Narayana, 1963; Endress, 1999; Matthews & Endress, 2011), **Medusagynaceae** (Dickison, 1990), **Ochnaceae** (Eichler, 1878), **Quiinaceae** (Schneider et al., 2006), **Rhizophoraceae** (Matthews & Endress, 2011; **Trigoniaceae** (Schoute, 1935; Matthews & Endress, 2008), and **Turneraceae** (Eichler, 1878; Rao, 1949; González, 1993).

Celastrales. Brexia (**Celastraceae**) has contort petals (Eichler, 1878; Matthews & Endress, 2005a).

Oxalidales. **Oxalidaceae** have contort petals (Narayana, 1966; Matthews & Endress, 2002).

Geraniales. The petals are contort in those genera of **Geraniaceae** that have otherwise polysymmetric flowers (*Geranium*, *Monsonia*) (Eichler, 1878), and also in **Hypseocharitaceae** (Devi, 1991) and **Ledocarpaceae** (Knuth, 1931).

Myrtales. Flowers with contort petals are present in some **Combretaceae** (Schoute, 1935; Tiagi, 1969), *Punica* (**Lythraceae**) (Eichler, 1878), **Melastomataceae** (Renner, 1993), and **Onagraceae** (Eichler, 1878). In **Vochysiaceae** the spurred flowers are strongly monosymmetric and in some taxa asymmetric (enantiomorphic) (Oliveira, 1996; Litt & Stevenson, 2003a, b; Kawasaki, 2007).

Brassicales. Contort petals occur regularly or occasionally in various families, such as **Akaniaceae** (Ronse De Craene et al., 2002a), **Capparaceae** (Correll & Correll, 1982; Ronse De Craene et al., 2002a; Rankin-Rodríguez & Greuter, 2004), **Caricaceae** (Eichler, 1878; Schoute, 1935; Devi, 1952; Ronse De Craene & Smets, 1999), **Cleomaceae** (Hildebrand, 1886), **Koeberliniaceae** (Mehta & Moseley, 1981), **Limnanthaceae** (Eichler, 1878), and **Moringaceae** (Olson, 2003).

Malvales. Contort petals occur in **Cistaceae** (Eichler, 1878), **Cochlospermaceae** (Poppendieck, 2003), **Dipterocarpaceae** (Rao, 1962; Ashton, 2003), **Malvaceae**

sensu lato (Eichler, 1878; Rao, 1952; Bayer, & Kubitzki, 2003), and **Sarcolaenaceae** (Bayer, 2003).

Sapindales. Taxa with contort petals are scattered in various families, e.g. **Anacardiaceae** (Bachelier & Endress, 2009), **Burseraceae** (Lam, 1932), **Meliaceae** (Narayana, 1958; Murty & Gupta, 1978; Correll & Correll, 1982; Castañeda-Posadas & Cevallos-Ferriz, 2007), **Nitrariaceae** (Eichler, 1878; Nair & Nathawat, 1958; Ronse De Craene et al., 1996), **Rutaceae** (Eichler, 1878; Engler, 1931; Tilak & Nene, 1978; Correll & Correll, 1982), **Sapindaceae** (Weckerle & Rutishauser, 2003), and **Simaroubaceae** (Nair & Joseph, 1957; Correll & Correll, 1982).

Caryophyllales. In several clades contort petal aestivation occurs, such as in some Lychnideae of **Caryophyllaceae** (Schoute, 1935), some **Droseraceae** (Eichler, 1878), **Plumbaginaceae** (Schoute, 1935), and **Tamaricaceae** (Eichler, 1878; Correll & Correll, 1982). In some **Caryophyllaceae** asymmetry by reduction also occurs, in flowers with only one stamen that is not in a symmetry plane (*Mniarum*, Eichler, 1878).

Cornales. Contort petals occur in *Philadelphus* of **Hydrangeaceae** (de Candolle, 1827; Eichler, 1878).

Ericales. In several families there are representatives with contort petals, such as in **Ebenaceae** (Schoute, 1935), **Ericaceae** (Eichler, 1875; Schoute, 1935), **Myrsinaceae** (Schoute, 1935), **Polemoniaceae** (Eichler, 1875; Schoute, 1935), **Samolaceae** (Schoute, 1935), and **Sapotaceae** (Eichler, 1875). The anthers are at different levels within a flower in *Erica fastigiata* (**Ericaceae**) (personal observation) and some **Polemoniaceae** (Grant & Grant, 1965; Mabberley, 2000; Wilken, 2004).

Boraginaceae. In several genera the petals are contort (Eichler, 1875; Schoute, 1935). Some species of *Cordia* have the stamens inserted at different levels in the corolla tube (Taroda & Gibbs, 1986).

Gentianales. Contort petals are common in **Gentianaceae** and **Apocynaceae** (Endress, 1999; Endress & Bruyns, 2000) and also occur in some **Loganiaceae** and **Rubiaceae** (Schoute, 1935; Robbrecht, 1988). In the otherwise monosymmetric *Exacum* (**Gentianaceae**) enantiostyly is present (Lloyd & Webb, 1992). In some **Gentianaceae** stamens are inserted at different levels within a flower (*Canscora*, *Hoppea*, *Schinziella*) or the stamen filaments are of different length (*Duplipetala*, *Phyllocyclus*) (Thiv & Kadereit, 2002a). Also in some **Rubiaceae** stamens are of different length within a flower (*Wittmackanthus*) (Robbrecht, 1988).

Solanales. Petals are contort in **Convolvulaceae** and some **Solanaceae** (Eichler, 1875; Schoute, 1935; Endress, 1999). Anthers positioned at different levels in a flower, either by different filament length or different insertion height occur in taxa of both families, such as *Convolvulus*, *Hildebrandtia* in **Convolvulaceae** (Wagner, 1989; Deroin, 1996) and many genera in **Solanaceae** (Robyns, 1930; Hunziker, 2001). In **Solanaceae**, species of *Solanum* sect. *Androceras* are enantiostylous (Whalen, 1979).

Lamiales. Contort petals are present in a number of **Acanthaceae** (Scotland et al., 1994; Schönenberger & Endress, 1998) and **Oleaceae** (Schoute, 1935). *Saintpaulia* and species of *Streptocarpus* (**Gesneriaceae**) are enantiostylous (Harrison et al., 1999; Jesson & Barrett, 2003). In a number of *Pedicularis* species (**Orobanchaceae**) the basically monosymmetric flowers have a twisted corolla (Endress, 1999). Among **Acanthaceae**, in *Brachystephanus glaberrimus*, flowers with a long and a short stamen were reported (Champluvier, 1997).

Asterales. No conspicuous floral asymmetries were found.

Dipsacales. In **Valerianaceae** the flowers are conspicuously asymmetric in *Kentranthus* because the monosymmetry planes of the corolla, androecium and gynoecium are not congruent (Eichler, 1875; Endress, 1999); in other genera this asymmetry is also present but less strong (Eichler, 1875; Goebel, 1908; Endress, 1999; Donoghue et al., 2003). A similar kind of asymmetry is also present in *Viburnum* (**Adoxaceae**), and *Abelia* and *Linnaea* (**Linnaeaceae**) (Eichler, 1875).

Basal Monocots. Asymmetric flowers appear to be lacking.

Asparagales. In **Orchidaceae**, many flowers have a twisted inferior ovary, which results in a superposed asymmetry (Ernst & Arditti, 1994); in a few genera, such as *Haemaria* (Goebel, 1920) and *Tipularia* (Stoutamire, 1978), also the upper parts of the flower are twisted. In **Iridaceae**, *Iris* and *Tigridia* have contort petals (Schoute, 1935). In **Tecophilaeaceae**, *Cyanella* has enantiostylous flowers (Dulberger & Ornduff, 1980; Simpson & Rudall, 1998).

Liliales. Contort petals are present in *Philesia* (**Philesiaceae**) (Conran & Clifford, 1998); both sepals and petals are contort in some **Trilliaceae** (Schoute, 1935; Tamura, 1998c).

Commelinales. The flowers of *Cochliostema* (**Commelinaceae**) are conspicuously asymmetric (Troll, 1961; Hardy & Stevenson, 2000a). In **Haemodoraceae**, some genera are enantiostylous, either based on otherwise polysymmetric or monosymmetric flowers (Simpson, 1990; Jesson & Barrett, 2002; Jesson et al., 2003b). Enantiostyly is also present in *Philydrum* (**Philydraceae**) (Simpson, 1990; Jesson et al., 2003b), and *Heteranthera* and *Monochoria* (**Pontederiaceae**) (Graham & Barrett, 1995; Jesson et al., 2003b).

Poales. Sepals and petals are contort in **Bromeliaceae** (Eichler, 1875; Smith & Till, 1998) and **Rapateaceae** (Pilger, 1930).

Zingiberales. **Marantaceae** and **Cannaceae** consistently have conspicuously asymmetric flowers with corolla, androecium and gynoecium involved, especially elaborate in **Marantaceae** (Kirchoff, 1983; Kress, 1990; Classen-Bockhoff & Heller, 2008). They may be seen as an elaboration of monosymmetric flowers as in the other six families of the order, of which a few **Zingiberaceae** also have asymmetric flowers (*Hedychium*) (Kress, 1990).

Summary: Evolution of Floral Monosymmetry and Asymmetry

Floral monosymmetry and asymmetry come in different forms. They may be based on complexity or on simplicity. The first case is based on evolutionary elaboration, mostly as a further step from elaborate polysymmetry or monosymmetry, respectively, the second commonly on evolutionary reduction. Imbricate organ aestivation is an additional kind of asymmetry but was not considered here, except for contort petal aestivation, which may lead to relatively conspicuous asymmetry. Monosymmetry or asymmetry may also appear in cryptic forms, if only early stages of floral development are affected.

These different kinds of floral monosymmetry and asymmetry are not necessarily all homologous, even if taken in the sense of biological homology (Wagner, 1989, 2007), i.e. based on the same genetic system, even if not all components of a clade have the particular symmetry feature. The same is true for asymmetry.

The systematic survey of the occurrence of floral monosymmetry shows that it is widespread and is present in one or the other form in almost every larger angiosperm clade (Fig. 5). The basalmost clade with monosymmetry by simplicity are Hydatellaceae (Nymphaeales) (Saarela et al., 2007). Basal angiosperms with relatively elaborate monosymmetry are *Aristolochia* (Piperales, magnoliids) and some Papaveraceae and Ranunculaceae (Ranunculales; basal eudicots) (Damerval et al., 2007). In monocots, the basalmost clade, *Acorus*, is monosymmetric by a stronger development of the lower half of the flower (Buzgo & Endress, 2000). More elaborate monosymmetry is present in Orchidaceae of Asparagales. Despite its almost ubiquitous occurrence among angiosperms at order level, monosymmetry also shows special concentration in some suprafamilial clades: among rosids especially in Fabales of fabids and in malvids (Endress & Matthews, 2006), among asterids especially in Lamiales, Asterales and Dipsacales, and among monocots especially in commelinids. Oblique monosymmetry is relatively widespread in angiosperms. However, it is especially concentrated in Sapindales, Brassicales, and Solanales. It is correlated with monochasial branching systems.

Among the asymmetry forms here considered, contort perianth organ aestivation is the most common in angiosperms (Fig. 6). Among basal angiosperms it is present in *Cabomba* (Nymphaeales) (Endress, 2008a). It is especially common in malvids and in Malpighiales of fabids. This may be an apomorphic tendency for malvids or malvids plus the COM clade (Endress & Matthews, 2006), if both together should turn out to form a clade (Endress & Matthews, 2006; Zhu et al., 2007; Qiu et al., 2010). Asymmetry based on modification of elaborate monosymmetry is present in some monocots (among Asparagales, Commelinales, and Zingiberales), some rosids (among Myrtales, and Fabales), and some asterids (among Lamiales, Asterales, and Dipsacales), and asymmetry by different anther height in otherwise polysymmetric, tubular flowers appears restricted to asterids (some Ericales, Gentianales, and Solanales).

In the fossil record monosymmetry by simplicity appears with *Chloranthus*-like flowers in the Santonian-Campanian (Doyle et al., 2003), whereas elaborate monosymmetric flowers are known since the Turonian (Crepet, 2008). Thus the evolution of elaborate monosymmetry began at least in the Late Cretaceous if not earlier.

Floral monosymmetry is predominant in some highly species-rich clades (Sargent, 2004). This suggests that the evolution of monosymmetry was a key innovation. However, from its distribution across angiosperms it appears that there are many clades in which it was not (yet) a key innovation (Endress, 2011). Thus, a differentiated statement is that monosymmetry appears to be a key innovation for several clades, but not for many other clades.

Why so many origins of monosymmetric flowers? It can be expected that monosymmetry is easy to evolve in terms of genetics and that it conveys a selective advantage over polysymmetry under certain circumstances. The genetic system responsible for monosymmetry in Lamiales was at least partly established much before the origin of Lamiales, at least at the level of basal eudicots (Coen & Nugent, 1994; Cubas et al., 2001; Cubas, 2004; Howarth & Donoghue, 2006; Kölsch & Gleissberg, 2006; Damerval et al., 2007). The selective advantage is related to more precise and thus more economical pollination by reduction of the pollination space from three to two dimensions. Movements of floral organs involved in herkogamy and dichogamy are restricted to the symmetry plane. Such movements may either be autonomous (herkogamy by differential elongation of stamens and styles; Webb & Lloyd, 1986; or curvature by flexistyly; Li et al., 2001; or inversostyly; Pauw, 2005) or they may be mediated by pollinators (movement of anthers in *Salvia*; Classen-Bockhoff et al., 2004; *Calceolaria*; Vogel, 1974; or *Roscoea*, Troll, 1929). Not only position and movement of floral organs but also movement of pollinators is canalized into the monosymmetry plane. Restriction not only of the stamens and stigma but also of the nectary into the monosymmetry plane are common. This may be accentuated by the repeated evolution of a single nectar spur (e.g. some Papaveraceae, Ranunculaceae, Geraniaceae, Tropaeolaceae, Balsaminaceae, Acanthaceae, Veronicaceae, Campanulaceae, Goodeniaceae, Orchidaceae) (Jabbour et al., 2008). In oil flowers, instead, two collateral spurs may be present in the monosymmetry plane (*Diascia*, Scrophulariaceae; Vogel, 1974).

Asymmetry appears much less common than monosymmetry, but not if imbricate perianth organ aestivation and floral torsions are also included. The only larger clades with consistently or predominantly elaborate asymmetric flowers are Phaseoleae (Fabaceae) and Cannaceae plus Marantaceae (Zingiberales). Elaborate asymmetric flowers with precise pollination may have even more restricted areas of pollen deposition on the bee body, as shown in *Macroptilium* (Fabaceae) (Brizuela et al., 1993), and thus even more economic pollination. But there may be structural restrictions for evolutionary diversification of such flowers.

Conclusions

Floral monosymmetry and asymmetry originated many times in angiosperms. In some groups, monosymmetry appears to be a key innovation (e.g., Fabaceae, Lamiales, Orchidaceae), but not in others. Asymmetry may be a key innovation in Phaseoleae (Fabaceae). Unelaborate forms of monosymmetry and asymmetry are easily lost again in evolution. Elaborate forms can also be lost but are more prone to persist. How much this trend to persist is based on developmental and how much on functional constraints, is unknown.

Advancement in our knowledge of floral symmetry will continue to be based on advances in phylogenetic reconstruction, molecular developmental genetics, and function of flowers of different monosymmetry and asymmetry types. The more the molecular developmental basis of structures is becoming elucidated the more intricate it becomes to use the terms homology (Wagner, 2007) and evolutionary innovation (Wagner, 2008).

Questions that have been asked are: Do monosymmetry genes respond to a common dorsoventral prepattern in the apex (Clark & Coen, 2002)? How is the evolution of regulatory interactions controlling floral monosymmetry (Costa et al., 2005)? How are different genes co-opted in the evolution of floral monosymmetry (Baxter et al., 2007)? What other functions in flowers do monosymmetry genes have (Baum, 1998)? New (evolutionary) aspects are also expected by comparison of symmetry types with other features, such as genetics of breeding systems via dichogamy (Kalisz et al., 2006), or with floral variability (Herrera et al., 2008). As generally in evolutionary biology, it seems important to combine the levels of macroevolution and microevolution (Wagner, 1986; Friedman et al., 2008).

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Literature Cited

Aagaard, J. E., R. G. Olmstead, J. H. Willis & P. C. Phillips. 2005. Duplication of floral regulatory genes in Lamiales. American Journal of Botany 92: 1284–1293.

Abbe, E. C. 1935. Studies in the phylogeny of the Betulaceae. I. Floral and inflorescence anatomy and morphology. Botanical Gazette (Crawfordsville) 97: 1–67.

——— 1972. The inflorescence and flower in male *Myrica esculenta* var. *farquhariana*. Botanical Gazette (Crawfordsville) 133: 206–213.

——— 1974. Flowers and inflorescences of the “Amentiferae”. Botanical Review 40: 159–261.

——— **& T. T. Earle.** 1940. Inflorescence, floral anatomy and morphology of *Leitneria floridana*. Bulletin of the Torrey Botanical Club 67: 173–193.

Albers, F. & J. J. A. Van der Walt. 2007. Geraniaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 9: 157–167. Springer, Berlin.

Amaral, M. C. E. 1991. Phylogenetische Systematik der Ochnaceae. Botanische Jahrbücher für Systematik 113: 105–196.

Ampornpan, L. & J. E. Armstrong. 2002. Floral ontogeny of *Salpiglossis* (Solanaceae) and the oblique gynoecium. Journal of the Torrey Botanical Society 129: 85–95.

Anderberg, A. A., B. G. Baldwin, R. G. Bayer, I. Breitwieser, C. Jeffrey, M. O. Dillon, P. Eldenäs, V. Funk, N. Garcia-Jacas, D. J. N. Hind, P. O. Karis, H. W. Lack, G. Nesom, B. Nordenstam, C. Oberprieler, J. L. Panero, C. Puttock, H. Robinson, T. F. Stuessy, A. Susanna, E. Urtubey, R. Vogt, J. Ward & L. E. Watson. 2007. Compositae. *In:* J. W. Kadereit & C. Jeffrey (eds). The families and genera of vascular plants, 8: 61–588. Springer, Berlin.

Andersson, L. 1998a. Heliconiaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 226–230. Springer, Berlin.

——— 1998b. Musaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 296–301. Springer, Berlin.

——— 1998c. Strelitziaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 451–455. Springer, Berlin.

APG (Angiosperm Phylogeny Group). 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Botanical Journal of the Linnean Society 141: 399–436.

———. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Botanical Journal of the Linnean Society 161: 105–121.

Appel, O. & I. A. Al-Shehbaz. 2003. Cruciferae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 5: 75–174. Springer, Berlin.

Ashton, P. S. 2003. Dipterocarpaceae. *In:* K. Kubitzki & C. Bayer (eds). The families and genera of vascular plants, 5: 182–197. Springer, Berlin.

Ayers, T. J. 1990. Systematics of *Heterotoma* (Campanulaceae) and the evolution of nectar spurs in the New World Lobelioideae. Systematic Botany 15: 296–327.

Bachelier, J. B. & P. K. Endress. 2007. Development of inflorescences, cupules, and flowers in *Amphipterygium*, and comparison with *Pistacia* (Anacardiaceae). International Journal of Plant Sciences 168: 1237–1253.

——— & ———. 2009. Comparative floral structure of Anacardiaceae and Burseraceae (Sapindales), with a special focus on gynoecium structure and evolution. Botanical Journal of the Linnean Society 159: 499–571.

Barrett, S. C. H., L. K. Jesson & A. M. Baker. 2000. The evolution and function of stylar polymorphisms in flowering plants. Annals of Botany 85(Supplement A): 253–265.

Barthlott, W. 1993. Cactaceae. *In:* K. Kubitzki, J. G. Rohwer, & V. Bittrich (eds). The families and genera of vascular plants, 2: 161–196. Springer, Berlin.

Bartish, I. V. & U. Swenson. 2004. Elaeagnaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 6: 131–134. Springer, Berlin.

Bartlett, M. E. & C. D. Specht. 2010. Evidence for the involvement of *GLOBOSA*-like gene duplications and expression divergence in the evolution of floral morpholgoy in the Zingiberales. New Phytologist 187: 521–541.

——— & ———. 2011. Changes in expression pattern of the *TEOSINTE BRANCHED1*-like genes in the Zingiberales provide a mechanism for evolutionary shifts in symmetry across the order. American Journal of Botany 98: 227–243.

Baum, D. A. 1998. The evolution of plant development. Current Opinion in Plant Biology 1: 79–86.

Baxter, C. E. L., M. M. R. Costa & E. S. Coen. 2007. Diversification and co-option of RAD-like genes in the evolution of floral asymmetry. Plant Journal 52: 105–113.

Bayer, C. 2003. Sarcolaenaceae. *In:* K. Kubitzki & C. Bayer (eds). The families and genera of vascular plants, 5: 345–352. Springer, Berlin.

——— & K. Kubitzki. 2003. Malvaceae. *In:* K. Kubitzki & C. Bayer (eds). The families and genera of vascular plants, 5: 225–311. Springer, Berlin.

Bayer, E. 1998. Alstroemeriaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 79–82. Springer, Berlin.

Beattie, A. J. 1969. Studies in the pollination ecology of *Viola*. I. The pollen-content of stigmatic cavities. Watsonia 7: 142–156.

Behnke, H.-D. 1997. Sarcobataceae—a new family of Caryophyllales. Taxon 46: 495–507.

Bello, M. A., P. J. Rudall, F. González & J. L. Fernándo-Alonso. 2004. Floral morphology and development in *Aragoa* (Plantaginaceae) and related members of the order Lamiales. International Journal of Plant Sciences 165: 723–738.

———, J. A. Hawkins & P. J. Rudall. 2007. Floral morphology and development in Quillajaceae and Surianaceae (Fabales), the species-poor relatives of Leguminosae and Polygalaceae. Annals of Botany 1000: 1491–1505.

Bittrich, V. 1993. Caryophyllaceae. *In:* K. Kubitzki, J. G. Rohwer, & V. Bittrich (eds). The families and genera of vascular plants, 2: 206–236. Springer, Berlin.

——— & U. Kühn. 1993. Nyctaginaceae. *In:* K. Kubitzki, J. G. Rohwer, & V. Bittrich (eds). The families and genera of vascular plants, 2: 473–486. Springer, Berlin.

Bogle, A. L. 1989. The floral morphology, vascular anatomy, and ontogeny of the Rhodoleioideae (Hamamelidaceae) and their significance in relation to the 'lower' hamamelids. *In:* P. R. Crane & S. Blackmore (eds). Evolution, systematics, and fossil history of the Hamamelidae, 1: 201–226. Clarendon, Oxford.

Brandis, D. 1893. Combretaceae. *In:* A. Engler & K. Prantl (eds). Die natürlichen Pflanzenfamilien, III, 7: 106–130. Engelmann, Leipzig.

Brantjes, N. B. M. 1982. Pollen placement and reproductive isolation between two Brazilian *Polygala* species (Polygalaceae). Plant Systematics and Evolution 141: 41–52.

——— 1983. Regulated pollen issue in *Isotoma*, Campanulaceae, and evolution of secondary pollen presentation. Acta Botanica Neerlandica 32: 213–222.

Brizuela, M. M., P. S. Hoc, V. S. Di Stilio, M. A. Agulló & R. A. Palacios. 1993. Biología floral de *Macroptilium bracteatum* (Leguminosae, Phaseoleae). Darwiniana 32: 41–57.

Broholm, S. K., S. Tähtiharju, R. A. E. Laitinen, V. A. Albert, T. H. Teeri & P. Elomaa. 2008. A TCP domain transcription factor controls flower type specification along the radial axis of the *Gerbera* (Asteraceae) inflorescences. Proccedings of the National Academy of Sciences of the U. S. A. 105: 9117–9122.

Bruyns, P. V. 1985. Notes on ceropegias of the Cape Province. Bradleya 3: 1–47.

Buchmann, S. L. 1983. Buzz pollination in angiosperms. Pp 73–113. *In:* C. E. Jones & R. J. Little (eds). Handbook of experimental pollination biology. Scientific and Academic Editions, New York.

Burtt, B. L. 1988. A new shrubby genus of African Umbelliferae. Notes Royal Botanic Garden Edinburgh 45: 493–501.

Busch, A. & S. Zachgo. 2007. Control of corolla monosymmetry in the Brassicaceae *Iberis amara*. Proceedings of the National Academy of Sciences of the U. S. A. 104: 16714–16719.

——— & ———. 2009. Flower symmetry evolution: Towards understanding the abominable mystery of angiosperm radiation. BioEssays 31: 1181–1190.

Buschmann, H., C. O. Fabri, M. Hauptmann, P. Hutzler, T. Laux, C. W. Lloyd & A. R. Schäffner. 2004. Helical growth of the *Arabidopsis* mutant *tortifolia1* reveals a plant-specific microtubule-associated protein. Current Biology 14: 1515–1521.

Buzgo, M. 2001. Flower structure and development of Araceae compared with alismatids and Acoraceae. Botanical Journal of the Linnean Society 136: 393–425.

——— & P. K. Endress. 2000. Floral structure and development of Acoraceae and its systematic relationships with basal angiosperms. International Journal of Plant Sciences 161: 23–41.

Caris, P. L., K. P. Geuten, S. B. Janssens & E. F. Smets. 2006. Floral development in three species of *Impatiens* (Balsaminaceae). American Journal of Botany 93: 1–14.

Carlquist, S. 1978. Wood anatomy and relationships of Bataceae, Gyrostemonaceae, and Stylobasiaceae. Allertonia 1: 297–330.

Carolin, R. C. 1959. Floral structure and anatomy in the family Goodeniaceae Dumort. Proceedings of the Linnean Society of New South Wales 84: 242–255.

——— 1993. Portulacaceae. *In:* K. Kubitzki, J. G. Rohwer, & V. Bittrich (eds). The families and genera of vascular plants, 2: 544–555. Springer, Berlin.

——— 2007a. Goodeniaceae. *In:* J. W. Kadereit & C. Jeffrey (eds). The families and genera of vascular plants, 8: 589–598. Springer, Berlin.

——— 2007b. Stylidiaceae. *In:* J. W. Kadereit & C. Jeffrey (eds). The families and genera of vascular plants, 8: 614–619. Springer, Berlin.

Castañeda-Posadas, C. & S. R. S. Cevallos-Ferriz. 2007. *Swietenia* (Meliaceae) flower in Late Oligocene—Early Miocene amber from Simojovel de Allende, Chiapas, Mexico. American Journal of Botany 94: 1821–1827.

Champluvier, D. 1997. *Brachystephanus glaberrimus* (Acanthaceae), espèce nouvelle gynomonoïque de la dorsale Congo-Nil (Congo, Rwanda, Uganda). Bulletin du Jardin Botanique de Belgique 66: 187–200.

Chapman, M. A., J. H. Leebens-Mack & J. M. Burke. 2008. Positive selection and expression divergence following gene duplication in the sunflower *CYCLOIDEA* gene family. Molecular Biology and Evolution 25: 1260–1273.

Cheek, M. & L. Dorr. 2007. Sterculiaceae. Pp 1–134. *In:* H. J. Beentje & S. A. Ghazanfar (eds). Flora of tropical East Africa. Royal Botanic Gardens, Kew.

Church, A. H. 1908. Types of floral mechanism. Clarendon, Oxford.

Citerne, H. & Q. C. B. Cronk. 1999. The origin of the peloric *Sinningia*. The New Plantsman 6: 219–222.

Citerne, H. L., M. Möller & Q. C. B. Cronk. 2000. Diversity of *cycloidea*-like genes in Gesneriaceae in relation to floral symmetry. Annals of Botany 86: 167–176.

———, R. T. Pennington & Q. C. B. Cronk. 2006. An apparent reversal in floral symmetry in the legume *Cadia* is a homeotic transformation. Proceedings of the National Academy of Sciences of the United States of America 103: 12017–12020.

———, D. Luo, R. T. Pennington, E. Coen & Q. C. B. Cronk. 2003. A phylogenomic investigation of *CYCLOIDEA*-like TCP genes in the Leguminosae. Plant Physiology 131: 1042–1053.

Citerne, H., F. Jabbour, S. Nadot & C. Damerval. 2010. The evolution of floral symmetry. Advances in Botanical Research 54: 86–137.

Clark, J. & E. Coen. 2002. The *cycloidea* gene can respond to a common dorsoventral prepattern in *Antirrhinum*. Plant Journal 30: 639–648.

Clark, J. L., E. H. Roalson, R. A. Pritchard, C. L. Coleman, V.-H. Teoh & J. Matos. 2011. Independent origin of radial floral symmetry in the Gloxinieae (Gesnerioideae: Gesneriaceae) is supported by the rediscovery of *Phinaea pulchella* in Cuba. Systematic Botany 36: 757–767.

Classen-Bockhoff, R. 1992. (Prä-)Disposition, Variation und Bewährung am Beispiel der Infloreszenzblumenbildung. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 89. Ergänzungsband 1: 37–72.

——— 1996. A survey of flower-like inflorescences in the Rubiaceae. Opera Botanica Belgica 7: 329–367.

——— 2007. Floral construction and pollination biology in Lamiaceae. Annals of Botany 100: 359–360.

——— **& A. Heller.** 2008. Floral synorganization and secondary pollen presentation in four Marantaceae from Costa Rica. International Journal of Plant Sciences 169: 745–760.

———**, T. Speck, E. Tweraser, P. Wester, S. Thimm & M. Reith.** 2004. The staminal lever mechanism in *Salvia* L. (Lamiaceae): a key innovation for adaptive radiation? Organisms. Diversity and Evolution 4: 189–205.

Clifford, H. T. 1998. Doryanthaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 236–238. Springer, Berlin.

——— **& J. G. Conran.** 1998. Blandfordiaceae. *In:* K. Kubitzki (ed). Families and genera of vascular plants, 3: 148–150. Springer, Berlin.

Clifford, H. A. T., R. J. F. Henderson & J. G. Conran. 1998. Hemerocallidaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 245–253. Springer, Berlin.

Cocucci, A. A. 1991. Pollination biology of *Nierembergia* (Solanaceae). Plant Systematics and Evolution 174: 17–35.

Cocucci, A. E. & A. M. Anton. 1988. The grass flower: suggestions on its origin and evolution. Flora 181: 353–362.

Coen, E. S. 1996. Floral symmetry. EMBO Journal 15: 6777–6788.

——— **& J. M. Nugent.** 1994. Evolution of flowers and inflorescences. Development 120 (Suppl.): 107–116.

———**,** ———**, D. Luo, D. Bradley, P. Cubas, M. Chadwick, L. Copsey & R. Carpenter.** 1995. Evolution of floral symmetry. Philosophical Transactions of the Royal Society of London B 350: 35–38.

Conran, J. G. 1998. Anthericaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 114–121. Springer, Berlin.

——— **& H. T. Clifford.** 1998. Philesiaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 409–411. Springer, Berlin.

——— **& M. N. Tamura.** 1998. Convallariaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 186–198. Springer, Berlin.

Cook, C. D. K. 1998a. Hydrocharitaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 234–248. Springer, Berlin.

——— 1998b. Pontederiaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 395–403. Springer, Berlin.

——— **& R. Rutishauser.** 2007. Podostemaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 9: 304–344. Springer, Berlin.

Cornehls, G. 1927. Über Orientierungsbewegungen dorsiventraler Blüten. Jahrbücher für Wissenschaftliche Botanik 67: 174–221.

Correll, D. S. & H. B. Correll. 1982. Flora of the Bahama archipelago. Cramer, Vaduz.

Costa, M. M. R., S. Fox, A. I. Hanna, C. Baxter & E. Coen. 2005. Evolution of regulatory interactions controlling floral asymmetry. Development 132: 5093–5101.

Crepet, W. L. 2008. The fossil record of angiosperms: requiem or renaissance? Annals of the Missouri Botanical Garden 95: 3–33.

Cubas, P. 2004. Floral zygomorphy, the recurring evolution of a successful trait. Bioessays 26: 1175–1184.

———**, C. Vincent & E. Coen.** 1999a. An epigenetic mutation responsible for natural variation in floral symmetry. Nature 401: 157–161.

———**, N. Lauter, J. Doebley & E. Coen.** 1999b. The TCP domain: a motif found in proteins regulating plant growth and development. Plant Journal 18: 215–222.

———**, E. Coen & J. F. Martinez-Zapater.** 2001. Ancient asymmetries in the evolution of flowers. Current Biology 11: 1050–1052.

Dafni, A. & P. G. Kevan. 1996. Floral symmetry and nectar guides: ontogenetic constraints from floral development, colour pattern rules and functional significance. Botanical Journal of the Linnean Society 120: 371–377.

Dahlgren, R. M. T., H. T. Clifford & P. F. Yeo. 1985. The families of the monocotyledons. Structure, evolution and taxonomy. Springer, Berlin.

Damerval, C. & S. Nadot. 2007. Evolution of perianth and stamen characteristics with respect to floral symmetry in Ranunculales. Annals of Botany 100: 631–640.

———**, M. L. Guilloux, M. Jager & C. Charon.** 2007. Diversity and evolution of *CYCLOIDEA*-like TCP genes in relation to flower development in Papaveraceae. Plant Physiology 143: 759–772.

Davies, B., M. Cartolano & Z. Schwarz-Sommer. 2006. Flower development: the *Antirrhinum* perspective. Advances in Botanical Research 44: 280–321.

Davis, C. C. & W. R. Anderson. 2010. A complete generic phylogeny of Malpighiaceae inferred from nucleotide sequence data and morphology. American Journal of Botany 97: 2031–2048.

——— **& M. W. Chase.** 2004. Elatinaceae are sister to Malpighiaceae; Peridiscaceae belong to Saxifragales. American Journal of Botany 91: 262–273.

———**, C. O. Webb, K. J. Wurdack, C. A. Jaramillo & M. J. Donoghue.** 2005. Explosive radiation of Malpighiales supports a mid-Cretaceous origin of modern tropical rain forests. American Naturalist 165: E36–E65.

de Candolle, A.-P. 1813. Théorie élémentaire de la botanique ou exposition des principes de la classification naturelle et de l'art de décrire et d'étudier les végétaux. Déterville, Paris.

——— 1819. Théorie élémentaire de la botanique. Déterville, Paris.

——— 1827. Organographie végétale, Vol. II. Déterville, Paris.

De Laet, J., D. Clinckemaillie, S. Jansen & E. Smets. 1995. Floral ontogeny in the Plumbaginaceae. Journal of Plant Research 108: 289–304.

de Oliveira, P. E. & M. Sazima. 1990. Pollination biology of two species of *Kielmeyera* (Guttiferae) from the Brazilian cerrado vegetation. Plant Systematics and Evolution 172: 35–49.

Delpino, F. 1887. Zigomorfia florale e sue cause. Malpighia 1: 245–262.

Deroin, T. 1985. Contribution à la morphologie comparée du gynécée des Annonaceae-Monodoroideae. Bulletin du Muséum National d'Histoire Naturelle, Pairs, Sér 4, 7, B, Adansonia: 167–176.

——— 1992. Anatomie florale de *Humbertia madagascariensis* Lam. Contribution à la morphologie comparée de la fleur et du fruit des Convolvulaceae. Bulletin du Muséum National de l'Histoire Naturelle, Paris, Sér. 4, B, Adansonia, 14: 235–255.

——— 1996. Deux espèces malgaches nouvelles du genre *Hildebrandtia* Vatke (Convolvulaceae). Candollea 51: 147–155.

Devi, D. R. 1991. Floral anatomy of *Hypseocharis* (Oxalidaceae) with a discussion on its systematic position. Plant Systematics and Evolution 177: 161–164.

Devi, S. 1952. Studies in the order Parietales III. Vascular anatomy of the flower of *Carica papaya* with special reference to the structure of the gynoecium. Proceedings of the Indian Academy of Sciences B 36: 59–69.

Dickison, W. C. 1990. The morphology and relationships of *Medusagyne* (Medusagynaceae). Plant Systematics and Evolution 171: 27–55.

——— **& E. M. Sweitzer.** 1970. The morphology and relationship of *Barbeya oleoides*. American Journal of Botany 57: 468–476.

Donoghue, M. J., R. H. Ree & D. A. Baum. 1998. Phylogeny and the evolution of flower symmetry in the Asteridae. Trends in Plant Science 3: 311–317.

———**, C. D. Bell & R. C. Winkworth.** 2003. The evolution of reproductive characters in Dipsacales. International Journal of Plant Sciences 164(Suppl): S453–S464.

Douglas, A. W. 1997. The developmental basis of morphological diversification and synorganization in flowers of Conospermeae (*Stirlingia* and Conosperminae: Proteaceae). International Journal of Plant Sciences 158(Suppl): S13–S48.

——— **& S. C. Tucker.** 1996. Comparative floral ontogenies among Persoonioideae including *Bellendena* (Proteaceae). American Journal of Botany 83: 1528–1555.

Doyle, J. A., H. Eklund & P. S. Herendeen. 2003. Floral evolution in Chloranthaceae: implications of a morphological phylogenetic analysis. International Journal of Plant Sciences 164(Suppl): S365–S382.

———**, H. Sauquet, T. Scharaschkin & A. Le Thomas.** 2004. Phylogeny, molecular and fossil dating, and biogeographic history of Annonaceae and Myristicaceae (Magnoliales). International Journal of Plant Sciences 165(Suppl): S55–S67.

Dransfield, J. & N. W. Uhl. 1998. Palmae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 306–389. Springer, Berlin.

Drude, O. 1897. Umbelliferae (Apiaceae, Doldengewächse). *In:* A. Engler & K. Prantl (eds). Die natürlichen Pflanzenfamilien, III, 8: 63–250. Engelmann, Leipzig.

Du, Z. Y. & Y. Z. Wang. 2008. Significance of RT-PCR patterns of *CYC*-like genes in *Oreocharis benthamii* (Gesneriaceae). Journal of Systematics and Evolution 46: 23–31.

Dulberger, R. 1981. The floral biology of *Cassia didymobotrya* and *C. auriculata* (Caesalpiniaceae). American Journal of Botany 68: 1350–1360.

——— **& R. Ornduff.** 1980. Floral morphology and reproductive biology of four species of *Cyanella* (Tecophilaeaceae). New Phytologist 86: 45–56.

Eckardt, T. 1937. Untersuchungen über Morphologie, Entwicklungsgeschichte und systematische Bedeutung des pseudomonomeren Gynoeceums. Nova Acta Leopoldina, neue Folge, 5, 26: 1–112.

——— 1955. Nachweis der Blattbürtigkeit ("Phyllosporie") grundständiger Samenanlagen bei Centrospermen. Berichte der Deutschen Botanischen Gesellschaft 68: 167–182.

——— 1957. Zur systematischen Stellung von *Eucommia ulmoides*. Berichte der Deutschen Botanischen Gesellschaft 69: 487–498.

Eichler, A. W. 1875. Blüthendiagramme. I. Engelmann, Leipzig.

——— 1878. Blüthendiagramme. II, Engelmann, Leipzig.

Endress, M. E. & V. Bittrich. 1993. Molluginaceae. *In:* K. Kubitzki, J. G. Rohwer, & V. Bittrich (eds). The families and genera of vascular plants, 2: 419–426. Springer, Berlin.

——— **& P. V. Bruyns.** 2000. A revised classification of the Apocynaceae s.l. Botanical Review 66: 1–56.

Endress, P. K. 1967. Systematische Studie über die verwandtschaftlichen Beziehungen zwischen den Hamamelidaceen und Betulaceen. Botanische Jahrbücher für Systematik 87: 431–525.

——— 1972. Zur vergleichenden Entwicklungsmorphologie, Embryologie und Systematik bei Laurales. Botanische Jahrbücher für Systematik 92: 331–428.

——— 1980. Ontogeny, function and evolution of extreme floral construction in Monimiaceae. Plant Systematics and Evolution 134: 79–120.

——— 1986a. Floral structure, systematics and phylogeny in Trochodendrales. Annals of the Missouri Botanical Garden 73: 297–324.

——— 1986b. Reproductive structures and phylogenetic significance of extant primitive angiosperms. Plant Systematics and Evolution 152: 1–28.

——— 1987. The Chloranthaceae: reproductive structures and phylogenetic position. Botanische Jahrbücher für Systematik 109: 153–226.

——— 1989. Chaotic floral phyllotaxis and reduced perianth in *Achlys* (Berberidaceae). Botanica Acta 102: 159–163.

——— 1992. Evolution and floral diversity—The phylogenetic surroundings of *Arabidopsis* and *Antirrhinum*. International Journal of Plant Sciences 153(Suppl): S106–S122.

——— 1994. Diversity and evolutionary biology of tropical flowers. Cambridge University Press, Cambridge.

——— 1995. Major evolutionary traits of monocot flowers. Pp 43–79. *In:* P. J. Rudall, P. J. Cribb, D. F. Cutler, & C. J. Humphries (eds). Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew.

——— 1998. *Antirrhinum* and Asteridae—evolutionary changes of floral symmetry. Symposium Series, Society of Experimental Biology 53: 133–140.

——— 1999. Symmetry in flowers: diversity and evolution. International Journal of Plant Sciences 160 (Suppl, 6): S3–S23.

——— 2001a. Evolution of floral symmetry. Current Opinion in Plant Biology 4: 86–91.

——— 2001b. The flowers in extant basal angiosperms and inferences on ancestral flowers. International Journal of Plant Sciences 162: 1111–1140.

——— 2002. Morphology and angiosperm systematics in the molecular era. Botanical Review 68: 545–570.

——— 2004. Structure and relationships of basal relictual angiosperms. Australian Systematic Botany 17: 343–366.

——— 2005. Carpels of *Brasenia* (Cabombaceae) are completely ascidiate despite a long stigmatic crest. Annals of Botany 96: 209–215.

——— 2006. Angiosperm floral evolution: morphological developmental framework. Advances in Botanical Research 44: 1–61.

——— 2008a. Perianth biology in the basal grade of extant angiosperms. International Journal of Plant Sciences 169: 844–862.

——— 2008b. The whole and the parts: relationships between floral architecture and floral organ shape, and their repercussions on the interpretation of fragmentary floral fossils. Annals of the Missouri Botanical Garden 95: 101–120.

——— 2010. Flower structure and trends of evolution in eudicots and their major subclades. Annals of the Missouri Botanical Garden 97: 541–583.

——— 2011. Evolutionary diversification of the flowers in angiosperms. American Journal of Botany 98: 370–396.

——— **& J. A. Doyle.** 2009. Reconstructing the ancestral angiosperm flower and its initial specializations. American Journal of Botany 96: 22–66.

——— **& D. H. Lorence.** 2004. Heterodichogamy of a novel type in *Hernandia* (Hernandiaceae) and its structural basis. International Journal of Plant Sciences 165: 753–763.

——— **& M. L. Matthews.** 2006. First steps towards a floral structural characterization of the major rosid subclades. Plant Systematics and Evolution 260: 223–251.

Engler, A. 1930. Saxifragaceae. *In:* A. Engler & K. Prantl (eds). Die natürlichen Pflanzenfamilien, ed. 2, 18a: 74–226. Engelmann, Leipzig.

——— 1931. Rutaceae. *In:* A. Engler & K. Prantl (eds). Die natürlichen Pflanzenfamilien, ed. 2, 19a: 187–359. Engelmann, Leipzig.

——— **& L. Diels.** 1899. Monographien afrikanischer Pflanzenfamilien und—gattungen III. Combretaceae, Engelmann, Leipzig.

Erbar, C. 1992. Floral development of two species of *Stylidium* (Stylidiaceae) and some remarks on the systematic position of the family Stylidiaceae. Canadian Journal of Botany 70: 258–271.

——— **& P. Leins.** 1999. Secondary pollen presentation and a curious rupture of the style in *Spigelia* (Spigeliaceae, Gentianales). Plant Biology 1: 389–402.

Ernst, R. & J. Arditti. 1994. Resupination. *In:* J. Arditti (ed). Orchid biology. Reviews and perspectives, VI: 135–188. Wiley, New York.

Etcheverry, A. V., M. M. Alemán & T. F. Fleming. 2008. Flower morphology, pollination biology and mating system of the complex flower of *Vigna caracalla* (Fabaceae: Papilionoideae). Annals of Botany 102: 305–316.

Eyde, R. H. 1963. Morphological and palaeobotanical studies on the Nyssaceae. I. A survey of the modern species and their fruits. Journal of the Arnold Arboretum 44: 1–54.

——— 1968. Flowers, fruits, and phylogeny of Alangiaceae. Journal of the Arnold Arboretum 49: 167–192.

——— **& J. T. Morgan.** 1973. Floral structure and evolution in Lopezieae (Onagraceae). American Journal of Botany 60: 771–787.

Faden, R. B. 1998. Commelinaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 109–128. Springer, Berlin.

Fagerlind, F. 1945. Bau des Gynöceums, der Samenanlage und des Embryosackes bei einigen Repräsentanten der Familie Icacinaceae. Svensk Botanisk Tidskrift 39: 346–364.

Fang, D., S.-M. Ku, Y.-G. Wei, D.-H. Qin & C.-I. Peng. 2006. Three new taxa of Begonia (sect. Coelocentrum, Begoniaceae) from limestone areas in Guangxi, China. Botanical Studies 47: 97–110.

Fay, M. F. & T. Hall. 2007. *Gethyum atropurpureum*. Alliaceae. Curtis's Botanical Magazine 24: 121–126.

Feehan, J. 1985. Explosive flower opening in ornithophily: a study of pollination mechanisms in some Central African Loranthaceae. Botanical Journal of the Linnean Society 90: 129–144.

Feng, X. Z., Z. Zhao, Z. X. Tian, S. Xu, Y. Luo, Z. Cai, Y. Wang, J. Yang, Z. Wang, L. Weng, J. Chen, L. Zheng, X. Guo, J. Luo, S. Sato, S. Tabata, W. Ma, X. Cao, X. Hu, C. Sun & D. Luo. 2006. Control of petal shape and floral zygomorphy in *Lotus japonicus*. Proceedings of the National Academy of Sciences of the United States of America 103: 4970–4975.

Fenster, C. B., W. S. Armbruster & M. R. Dudash. 2009. Specialization of flowers: is floral orientation an overlooked first step? New Phytologist 183: 502–506.

Fischer, E. 2004. Balsaminaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 6: 20–25. Springer, Berlin.

Flores, E. M. & M. F. Moseley. 1990. Anatomy and aspects of development of the staminate inflorescences and florets of seven species of *Allocasuarina* (Casuarinaceae). American Journal of Botany 77: 795–808.

Friedman, W. E., S. C. H. Barrett, P. K. Diggle, V. F. Irish & L. Hufford. 2008. Whither plant evo-devo? New Phytologist 178: 468–472.

Friis, I. 1993. Urticaceae. *In:* K. Kubitzki, J. G. Rohwer, & V. Bittrich (eds). The families and genera of vascular plants, 2: 612–630. Springer, Berlin.

Froebe, H. A. 1980. Randmusterbildung und Synorganisation bei strahlenden Apiaceendolden. Plant Systematics and Evolution 133: 223–237.

Fryxell, P. A. 1983. Floral symmetry and zygomorphy in Malvaceae. American Journal of Botany 70, 5, 2: 58.

Fukuoka, N. 1972. Taxonomic study of the Caprifoliaceae. Memoirs of the Faculty of Science, Kyoto University, Ser Biol 6: 15–58.

Gao, J.-Y., P.-Y. Ren, Z.-H. Yang & Q.-J. Li. 2006. The pollination ecology of *Paraboea rufescens* (Gesneriaceae): a buzz-pollinated tropical herb with mirror-image flowers. Annals of Botany 97: 371–376.

Gao, Q., J.-H. Tao, Y.-Z. Wang & Z.-H. Li. 2008. Expression differentiation of *CYC*-like floral symmetry genes correlated with their protein sequence divergence in *Chirita heterotricha* (Gesneriaceae). Development, Genes and Evolution 218: 341–351.

Gegear, R. J. & T. M. Laverty. 1995. Effect of flower complexity on relearning flower-handling skills in bumble bees. Canadian Journal of Zoology 73: 2052–2058.

George, A. S. 2003. Gyrostemonaceae. *In:* K. Kubitzki & C. Bayer (eds). The families and genera of vascular plants, 5: 213–217. Springer, Berlin.

Geuten, K., A. Becker, K. Kaufmann, P. Caris, S. Janssens, T. Viaene, G. Theissen & E. Smets. 2006. Petaloidy and petal identy MADS-box genes in the balsaminoid genera *Impatiens* and *Marcgravia*. Plant Journal 47: 501–518.

Gill, G. E., Jr., R. T. Fowler & S. A. Mori. 1998. Pollination biology of *Symphonia globulifera* (Clusiaceae) in Central French Guiana. Biotropica 30: 139–144.

Giurfa, M., A. Dafni & P. R. Neal. 1999. Floral symmetry and its role in plant-pollinator systems. International Journal of Plant Sciences 160(Suppl): S41–S50.

Goebel, K. 1908. Über Symmetrieverhältnisse in Blüten. Pp 151–166. *In:* K. Linsbauer (ed). Wiesner-Festschrift. Konegen, Wien.

——— 1920. Die Entfaltungsbewegungen der Pflanzen und deren teleologische Deutung. Fischer, Jena.

Goetghebeur, P. 1998. Cyperaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 141–190. Springer, Berlin.

Goldblatt, P., J. C. Manning & P. Rudall. 1998. Iridaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 295–333. Springer, Berlin.

———, P. Bernhardt, P. Vogan & J. C. Manning. 2004. Pollination by fungus gnats (Diptera: Mycetophilidae) and self-recognition sites in *Tolmiea menziesii* (Saxifragaceae). Plant Systematics and Evolution 244: 55–67.

Gómez, J. M., F. Perfectti & J. P. M. Camacho. 2006. Natural selection on *Erysimum mediohispanicum* flower shape: insights into the evolution of zygomorphy. American Naturalist 168: 531–545.

González, A. M. 1993. Anatomia y vascularizacion floral de *Piriqueta racemosa*, *Turnera hassleriana* y *Turnera joelii* (Turneraceae). Bonplandia 7: 143–184.

González, F. & D. W. Stevenson. 2000. Perianth development and systematics of *Aristolochia*. Flora 195: 370–391.

——— & P. J. Rudall. 2010. Flower and fruit characters in the early-divergent lamiid family Metteniusaceae, with particular reference to the evolution of pseudomonomery. American Journal of Botany 97: 191–206.

Gottsberger, G. & I. Silberbauer-Gottsberger. 1988. Evolution of flower structures and pollination in Neotropical Cassiinae (Caesalpiniaceae) species. Phyton (Austria) 28: 293–320.

Graham, S. A. 2007. Lythraceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 9: 226–246. Springer, Berlin.

Graham, S. W. & S. C. H. Barrett. 1995. Phylogenetic systematics of the Pontederiales: implications for breeding-system evolution. Pp 415–441. *In:* P. J. Rudall, P. J. Cribb, D. F. Cutler, & C. J. Humphries (eds). Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew.

Grant, V. & K. A. Grant. 1965. Flower pollination in the phlox family. Columbia University Press, New York.

Groppo, M., J. R. Pirani, M. L. F. Salatino, S. R. Blanco & J. A. Kallunki. 2008. Phylogeny of Rutaceae based on two noncoding regions from cpDNA. American Journal of Botany 95: 985–1005.

Gürke, M. 1893. Borraginaceae. *In:* A. Engler & K. Prantl (eds). Die natürlichen Pflanzenfamilien, IV, 3a: 71–131. Engelmann, Leipzig.

Hamann, U. 1966. Embryologische, morphologisch-anatomische und systematische Untersuchungen an Philydraceen. Willdenowia Beihefte 4: 1–178.

——— 1975. Neue Untersuchungen zur Embryologie und Systematik der Centrolepidaceae. Botanische Jahrbücher für Systematik 96: 154–191.

——— 1998. Philydraceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 389–394. Springer, Berlin.

Hardy, C. R. & R. B. Faden. 2004. *Plowmanianthus*, a new genus of Commelinaceae with five new species from tropical America. Systematic Botany 29: 316–333.

——— & D. W. Stevenson. 2000a. Development of the gametophytes, flower, and floral vasculature in *Cochliostema odoratissimum* (Commelinaceae). Botanical Journal of the Linnean Society 134: 131–157.

——— & ———. 2000b. Floral organogenesis in some species of *Tradescantia* and *Callisia* (Commelinaceae). International Journal of Plant Sciences 161: 551–562.

———, ——— & H. G. Kiss. 2000. Development of the gametophytes, flower, and floral vasculature in *Dichorisandra thyrsiflora* (Commelinaceae). American Journal of Botany 87: 1228–1239.

———, J. I. Davis & D. W. Stevenson. 2004. Floral organogenesis in *Plowmanianthus* (Commelinaceae). International Journal of Plant Sciences 165: 511–519.

Harms, H. 1940. Meliaceae. *In:* A. Engler & K. Prantl (eds). Die natürlichen Pflanzenfamilien, ed. 2, 19b1: 1–172. Engelmann, Leipzig.

Harris, E. M. 1995. Inflorescences and floral ontogeny in Asteraceae: A synthesis of historical and current concepts. Botanical Review 61: 93–278.

Harrison, C. J., M. Möller & Q. C. B. Cronk. 1999. Evolution and development of floral diversity in *Streptocarpus* and *Saintpaulia*. Annals of Botany 84: 49–60.

Hashimoto, T. 2002. Molecular genetic analysis of left-right handedness in plants. Philosophical Transactions of the Royal Society of London B 357: 799–808.

Haynes, R. R., D. H. Les & L. B. Holm-Nielsen. 1998a. Juncaginaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 260–263. Springer, Berlin.

———, L. B. Holm-Nielsen & D. H. Les. 1998b. Najadaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 301–306. Springer, Berlin.

———, D. H. Les & L. B. Holm-Nielsen. 1998c. Potamogetonaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 408–415. Springer, Berlin.

———, ——— & ———. 1998d. Zannichelliaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 470–474. Springer, Berlin.

Heinricher, E. 1907. *Potentilla aurea* L. mit zygomorphen oder auch asymmetrischen Blüten und Vererbbarkeit dieser Eigentümlichkeit. Zeitschrift des Ferdinandeums, III Folge 52: 281–286.

Hellwig, F. H. 2007. Calyceraceae. *In:* J. W. Kadereit & C. Jeffrey (eds). The families and genera of vascular plants, 8: 19–25. Springer, Berlin.

Herber, B. E. 2003. Thymelaeaceae. *In:* K. Kubitzki & C. Bayer (eds). The families and genera of vascular plants, 5: 373–396. Springer, Berlin.

Herrera, J., M. Arista & P. L. Ortiz. 2008. Perianth organization and intra-specific floral variability. Plant Biology 10: 704–710.

Hildebrand, F. 1886. Die Beeinflussung durch die Lage zum Horizont bei den Blüthentheilen einiger *Cleome*-Arten. Berichte der Deutschen Botanischen Gesellschaft 4: 329–337.

Hileman, L. C. & D. A. Baum. 2003. Why do paralogs persist? Molecular evolution of *CYCLOIDEA* and related floral symmetry genes in Antirrhineae (Veronicaceae). Molecular Biology and Evolution 20: 591–600.

———, E. M. Kramer & D. A. Baum. 2003. Differential regulation of symmetry genes and the evolution of floral morphologies. Proceedings of the National Academy of Sciences of the United States of America 100: 12814–12819.

Hilger, H. H. 1984. Wachstum und Ausbildungsformen des Gynoeceums von *Rochelia* (Boraginaceae). Plant Systematics and Evolution 146: 123–139.

——— 1987. Flower and fruit development in *Wigandia caracasana* (Hydrophyllaceae). American Journal of Botany 74: 250–259.

Horn, J. W. 2006. Evolution of floral symmetry and foliar organs in *Hibbertia* (Dilleniaceae). Botany 2006. Abstract (on-line).

——— 2007. Dilleniaceae. *In:* K. Kubitzki (ed). Families and genera of vascular plants, 9: 132–154. Springer, Berlin.

——— 2009. Phylogenetics of Dilleniaceae using sequence data from four plastid loci (*rbcL*, *infA*, *rps4*, *rpl16* intron). International Journal of Plant Sciences 170: 794–813.

Ho, T. N. & S. W. Liu. 2001. A world-wide monograph of *Gentiana*. Science Press, Beijing.

Hoso, M., T. Asami & M. Hori. 2007. Right-handed snakes: convergent evolution of asymmetry for functional specialization. Biology Letters 3: 169–172.

Howarth, D. G. & M. J. Donoghue. 2005. Duplications in *CYC*-like genes from Dipsacales correlate with floral form. International Journal of Plant Sciences 166: 357–370.

——— & ———. 2006. Phylogenetic analysis of the "ECE" (*CYC*/*TB1*) clade reveals duplications predating the core eudicots. Proceedings of the National Academy of Sciences of the U. S. A. 103: 9101–9106.

——— & ———. 2008. Phylogeny and expression of *DIV*-like and *RAD*-like genes (MYB transcription factors) and their role in floral symmetry shifts in Dipsacales and core eudicots. Botany 2008, Abstracts (on-line).

———, T. Martins, E. Chimney & M. J. Donoghue. 2011. Diversification of *CYCLOIDEA* expression in the evolution of bilateral flower symmetry in Caprifoliaceae and *Lonicera* (Dipsacales). Annals of Botany 107: 1521–1532.

Huang, S.-Q., Y. Takahashi & A. Dafni. 2002. Why does the flower stalk of *Pulsatilla cernua* (Ranunculaceae) bend during anthesis? American Journal of Botany 89: 1599–1603.

Huber, K. A. 1980. Morphologische und entwicklungsgeschichtliche Untersuchungen an Blüten und Blütenständen von Solanaceen und von *Nolana paradoxa* Lindl. (Nolanaceae). Dissertationes Botanicae 55: 1–252.

Hufford, L. D. 1989. Structure of the inflorescence and flower of *Petalonyx linearis* (Loasaceae). Plant Systematics and Evolution 163: 211–226.

Hufford, L. 2004. Hydrangeaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 6: 202–215. Springer, Berlin.

Hunziker, A. 2001. Genera Solanacearum. The genera of Solanaceae illustrated, arranged according to a new system. Gantner, Ruggell.

Igersheim, A. & P. K. Endress. 1997. Gynoecium diversity and systematics of the Magnoliales and winteroids. Botanical Journal of the Linnean Society 124: 213–271.

———, M. Buzgo & P. K. Endress. 2001. Gynoecium diversity and systematics in basal monocots. Botanical Journal of the Linnean Society 136: 1–65.

Jabbour, F., C. Damerval & S. Nadot. 2008. Evolutionary trends of Asteridae: Is polyandry an alternative to zygomorphy? Annals of Botany 102: 153–165.

———, L. P. Ronse De Craene, S. Nadot & C. Damerval. 2009a. Establishment of zygomorphy on an ontogenetic spiral and evolution of perianth in the tribe Delphinieae (Ranunculaceae). Annals of Botany 104: 809–822.

———, S. Nadot & C. Damerval. 2009b. Evolution of floral symmetry: A state of the art. Comptes Rendus Biologies 332: 219–231.

Jeffrey, C. 2007. Compositae. Introduction with key to tribes. *In:* J. W. Kadereit & C. Jeffrey (eds). The families and genera of vascular plants, 8: 61–87. Springer, Berlin.

Jesson, L. K. & S. C. H. Barrett. 2002. Enantiostyly in *Wachendorfia* (Haemodoraceae): the influence of reproductive systems on the maintenance of the polymorphism. American Journal of Botany 89: 253–262.

——— & ———. 2003. The comparative biology of mirror-image flowers. International Journal of Plant Sciences 164(Suppl.): S237–S249.

———, ——— & T. Day. 2003a. A theoretical investigation of the evolution and maintenance of mirror-image flowers. American Naturalist 161: 916–930.

———, J. Kang, S. L. Wagner, S. C. H. Barrett & N. G. Dengler. 2003b. The development of enantiostyly. American Journal of Botany 90: 183–195.

Kaldewey, H. 1962. Plagio- und Diageotropismus der Sprosse und Blätter, einschliesslich Epinastie, Hyponastie, Entfaltungsbewegungen. *In:* W. Ruhland (ed). Encyclopedia of plant physiology, XVII, 2: 200–321. Springer, Berlin.

Kalisz, S., R. H. Ree & R. D. Sargent. 2006. Linking floral symmetry genes to breeding system evolution. Trends in Plant Science 11: 568–573.

Kallunki, J. A. & J. R. Pirani. 1998. Synopses of *Angostura* Roem. & Schult. and *Conchocarpus* J.C. Mikan (Rutaceae). Kew Bulletin 53: 257–334.

Kampny, C. M. 1995. Pollination and flower diversity in Scrophulariaceae. Botanical Review 61: 350–366.

Karehed, J. 2001. Multiple origin of the tropical forest tree family Icacinaceae. American Journal of Botany 88: 2259–2274.

Kawasaki, M. L. 2007. Vochysiaceae. *In:* K. Kubitzki (ed). Families and genera of vascular plants, 9: 480–487. Springer, Berlin.

Kers, L. E. 2003. Capparaceae. *In:* K. Kubitzki & C. Bayer (eds). The families and genera of vascular plants, 5: 36–56. Springer, Berlin.

Kessler, P. J. A. 1993. Menispermaceae. *In:* K. Kubitzki, J. G. Rohwer, & V. Bittrich (eds). The families and genera of vascular plants, 2: 402–418. Springer, Berlin.

Kim, M., M.-L. Cui, P. Cubas, A. Gillies, K. Lee, M. A. Chapman, R. J. Abbott & E. Coen. 2008. Regulatory genes control a key morphological and ecological trait transferred between species. Science 322: 1116–1119.

Kirchoff, B. K. 1983. Floral organogenesis in five genera of the Marantaceae and in *Canna* (Cannaceae). American Journal of Botany 70: 508–523.

——— 2003. Shape matters: Hofmeister's rule, primordium shape, and flower orientation. International Journal of Plant Sciences 164: 505–517.

Klackenberg, J. 2002. Section Exaceae. Pp 66–94. *In:* L. Struwe & V. A. Albert (eds). Gentianaceae: Systematics and natural history. Cambridge University Press, Cambridge.

Knuth, R. 1931. Geraniaceae. *In:* A. Engler & K. Prantl (eds). Die natürlichen Pflanzenfamilien, ed. 2, 19a: 43–66. Engelmann, Leipzig.

Kocyan, A. & P. K. Endress. 2001a. Floral structure and development and systematic aspects of some 'lower' Asparagales. Plant Systematics and Evolution 229: 187–216.

——— & ———. 2001b. Floral structure and development of *Apostasia* and *Neuwiedia* (Apostasioideae) and their relationships to other Orchidaceae. International Journal of Plant Sciences 162: 847–867.

Kölsch, A. & S. Gleissberg. 2006. Diversification of *CYCLOIDEA*-like TCP genes in the basal eudicot families Fumariaceae and Papaveraceae s.str. Plant Biology 8: 680–687.

Kong, H.-Z., A.-M. Lu & P. K. Endress. 2002. Floral organogenesis in *Chloranthus sessilifolius* (Chloranthaceae): with special emphasis on the morphological nature of the androecium of *Chloranthus*. Plant Systematics and Evolution 232: 181–188.

Kral, R. 1998. Xyridaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4, 461–469. Springer, Berlin.

Krasser, F. 1893. Melastomataceae. *In:* A. Engler & K. Prantl (eds). Die natürlichen Pflanzenfamilien, III, 7: 130–199. Engelmann, Leipzig.

Kress, W. J. 1990. The phylogeny and classification of the Zingiberales. Annals of the Missouri Botanical Garden 77: 698–721.

Kubitzki, K. 1963. Zur Kenntnis des unilokularen Cornaceen-Gynözeums (Cornaceen-Studien I). Berichte der Deutschen Botanischen Gesellschaft 76: 33–39.

——— 1978. *Caraipa* and *Mahurea* (Bonnetiaceae). Memoirs of the New York Botanical Garden 29: 82–138.

——— 1993. Cecropiaceae. *In*: K. Kubitzki, J. G. Rohwer & V. Bittrich (eds.), The families and genera of vascular plants, 2: 243–246. Springer, Berlin.

——— 1998a. Agapanthaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 58–60. Springer, Berlin.

——— 1998b. Hostaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 256–260. Springer, Berlin.

——— 1998c. Typhaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 457–461. Springer, Berlin.

——— 2003. Salvadoraceae. *In:* K. Kubitzki & C. Bayer (eds). The families and genera of vascular plants, 5: 342–344. Springer, Berlin.

Kühn, U. 1993. Chenopodiaceae. *In:* K. Kubitzki, J. G. Rohwer, & V. Bittrich (eds). The families and genera of vascular plants, 2: 253–280. Springer, Berlin.

Kuijt, J. 1988. Monograph of the Eremolepidaceae. Systematic Botany Monographs 18: 1–60.

——— 2007. 105b. Loranthaceae. *In:* M. J. Jansen-Jacobs (ed). Flora of the Guianas A, 25: 7–69. Royal Botanic Gardens, Kew.

Kunze, G. 1976. Die Bildung von Pseudanthien bei den Angiospermen in morphologischer, ökologischer und phylogenetischer Hinsicht. Unpublished "Staatsexamens" thesis, University of Freiburg, Germany.

Kuo, J. & A. J. McComb. 1998a. Cymodoceaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 133–140. Springer, Berlin.

——— & ———. 1998b. Posidoniaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 404–408. Springer, Berlin.

——— & ———. 1998c. Zosteraceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 496–502. Springer, Berlin.

Kurzweil, H. & A. Kocyan. 2002. Ontogeny of orchid flowers. *In:* T. Kull & J. Arditti (eds). Orchid biology: reviews and perspectives, 8: 83–138. Kluwer, Dordrecht.

Lam, H. J. 1932. Beiträge zur Morphologie der Burseraceae, insbesondere der Canarieae II. Weitere Tendenzen in Blütenstand, Blüte, Frucht und Vegetationsorganen; Anatomisches; Schlussbetrachtung und Zusammenfassung. Annales du Jardin Botanique de Buitenzorg 43: 97–226.

Lammers, T. G. 2007. Campanulaceae. *In:* J. W. Kadereit & C. Jeffrey (eds). The families and genera of vascular plants, 8: 26–56. Springer, Berlin.

Landolt, E. 1998. Lemnaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 264–270. Springer, Berlin.

Langström, E. & B. Oxelman. 2003. Phylogeny of *Echiochilon* (Echiochileae, Boraginaceae) based on ITS sequences and morphology. Taxon 52: 725–735.

Larsen, K. 1998a. Costaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 128–132. Springer, Berlin.

——— 1998b. Lowiaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 275–277. Springer, Berlin.

———, J. M. Lock, H. Maas & P. J. M. Maas. 1998. Zingiberaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 474–495. Springer, Berlin.

Lehrer, M. 1999. Shape perception in the honeybee: symmetry as a global framework. International Journal of Plant Sciences 160(Suppl): S51–S65.

Leins, P. 1969. The flower morphology of *Emblingia*. Botanical Journal of the Linnean Society 62: 172–175.

——— **& C. Erbar.** 1982. Das monokarpellate Gynoeceum von *Monodora crispata* (Annonaceae). Beiträge zur Biologie der Pflanzen 57: 1–13.

——— **&** ———. 2000. Die frühesten Entwicklungsstadien der Blüten bei den Asteraceae. Botanische Jahrbücher für Systematik 122: 503–515.

——— **&** ———. 2005. Floral morphological studies in the South African *Cyphia stenopetala* Diels (Cyphiaceae). International Journal of Plant Sciences 166: 207–217.

——— **& P. Galle.** 1971. Entwicklungsgeschichtliche Untersuchungen an Cucurbitaceen-Blüten. Österreichische Botanische Zeitschrift 119: 531–548.

Leppik, E. E. 1972. Origin and evolution of bilateral symmetry in flowers. Evolutionary Biology 5: 49–85.

Levin, M. 2005. Left-right asymmetry in embryonic development: a comprehensive review. Mechanisms of Development 122: 3–25.

——— **& A. R. Palmer.** 2007. Left-right patterning from the inside out: widespread evidence for intracellular control. BioEssays 29(3): 271–287.

Li, Q.-J., Z.-F. Xu, W. J. Kress, Y.-M. Xia, L. Zhang, X.-B. Deng, J.-Y. Gao & Z.-L. Bai. 2001. Flexible style that encourages outcrossing. Nature 410: 432.

Lidén, M. 1993. Fumariaceae. *In:* K. Kubitzki, J. G. Rohwer, & V. Bittrich (eds). The families and genera of vascular plants, 2: 310–318. Springer, Berlin.

Linder, H. P. 2007. Melianthaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 9: 250–259. Springer, Berlin.

———**, B. G. Briggs & L. A. S. Johnson.** 1998. Restionaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 425–445. Springer, Berlin.

Litt, A. & M. Cheek. 2002. *Korupodendron songweanum*, a new genus and species of Vochysiaceae from West-Central Africa. Brittonia 54: 13–17.

——— **& D. W. Stevenson.** 2003a. Floral development and morphology of Vochysiaceae. I. The structure of the gynoecium. American Journal of Botany 90: 1533–1547.

——— **&** ———. 2003b. Floral development and morphology of Vochysiaceae. II. The position of the single fertile stamen. American Journal of Botany 90: 1548–1559.

Liu, M., B.-E. Van Wyk & P. M. Tilney. 2004. Ontogeny of the fruits of two anomalous African woody genera, *Polemanniopsis* and *Steganotaenia* (Apiaceae), and their phylogenetic relationship. Edinburgh Journal of Botany 60: 249–257.

Lleras, E. 1972. Review of the genus *Haploclathra* (Bonnetiaceae). Memoirs of the Nerw York Botanical Garden 22: 129–136.

Lloyd, D. G. & C. J. Webb. 1992. The evolution of heterostyly. Pp 179–208. *In:* S. C. H. Barrett (ed). Evolution and function of heterostyly. Springer, Berlin.

Luo, D., R. Carpenter, C. Vincent, L. Copsey & E. Coen. 1996. Origin of floral asymmetry in *Antirrhinum*. Nature 383: 794–799.

———**,** ———**,** ———**, J. Clark & E. Coen.** 1999. Control of organ asymmetry in flowers of *Antirrhinum*. Cell 99: 367–376.

Maas-van de Kamer, H. 1998. Burmanniaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 154–164. Springer, Berlin.

——— **& T. Weustenfeld.** 1998. Triuridaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 452–458. Springer, Berlin.

Mabberley, D. 2000. Arthur Henry Church. The anatomy of flowers, Merrell, London.

Machado, I. C. & M. Sazima. 2008. Pollination and breeding system of *Melochia tomentosa* L. (Malvaceae), a keystone floral resource in the Brazilian Caatinga. Flora 203: 484–490.

Machado, I. C. S., I. Sazima & M. Sazima. 1998. Bat pollination of the terrestrial herb *Irlbachia alata* (Gentianaceae) in northeastern Brazil. Plant Systematics and Evolution 209: 231–237.

Maguire, B. 1972. Bonnetiaceae. Memoirs of the New York Botanical Garden 23: 131–165.

Mair, O. 1977. Zur Entwicklungsgeschichte monosymmetrischer Dicotylen-Blüten. Dissertationes Botanicae 38: 1–90.

Malcomber, S. T. & E. A. Kellogg. 2004. Heterogeneous expression patterns and separate roles of the *SEPALLATA* gene *LEAFY HULL STERILE1* in grasses. Plant Cell 16: 1692–1706.

Marazzi, B. & P. K. Endress. 2008. Patterns and development of floral asymmetry in *Senna* (Leguminosae, Cassiinae). American Journal of Botany 95: 22–40.

———**,** ———**, L. Paganucci de Queiroz & E. Conti.** 2006. Phylogenetic relationships within *Senna* (Leguminosae, Cassiinae) based on three chloroplast DNA regions: patterns in the evolution of floral symmetry and extrafloral nectaries. American Journal of Botany 93: 288–303.

———**, E. Conti & P. K. Endress.** 2007. Diversity in anthers and stigmas in the buzz-pollinated genus *Senna* (Leguminosae, Cassiinae). International Journal of Plant Sciences 168: 371–391.

Matthews, M. L. & P. K. Endress. 2002. Comparative floral structure and systematics in Oxalidales (Oxalidaceae, Connaraceae, Cephalotaceae, Brunelliaceae, Cunoniaceae, Elaeocarpaceae, Tremandraceae). Botanical Journal of the Linnean Society 140: 321–381.

——— & ———. 2004. Comparative floral structure and systematics in Cucurbitales (Corynocarpaceae, Coriariaceae, Datiscaceae, Tetramelaceae, Begoniaceae, Cucurbitaceae, Anisophylleaceae). Botanical Journal of the Linnean Society 145: 129–185.

——— & ———. 2005a. Comparative floral structure in Celastrales (Celastraceae, Parnassiaceae, Lepidobotryaceae). Botanical Journal of the Linnean Society 149: 129–194.

——— & ———. 2005b. Comparative floral structure in Crossosomatales (Crossosomataceae, Stachyuraceae, Staphyleaceae, Aphloiaceae, Geissolomataceae, Ixerbaceae, Strasburgeriaceae). Botanical Journal of the Linnean Society 147: 1–46.

——— & ———. 2008. Comparative floral structure and systematics in Chrysobalanaceae sensu lato (Chrysobalanaceae, Dichapetalaceae, Euphroniaceae, and Trigoniaceae; Malpighiales). Botanical Journal of the Linnean Society 157: 249–309.

——— & ———. 2011. Comparative floral structure and systematics in Rhizophoraceae, Erythroxylaceae, and the potentially related Ctenolophonaceae, Linaceae, Irvingiaceae, and Caryocaraceae (Malpighiales). Botanical Journal of the Linnean Society 166: 331–416.

Mayo, S. J., J. Bogner & P. C. Boyce. 1997. The genera of Araceae. Royal Botanic Gardens, Kew.

———, ——— & ———. 1998. Araceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 26–74. Springer, Berlin.

Mayr, E. M. & A. Weber. 2006. Calceolariaceae: floral development and systematic implications. American Journal of Botany 93: 327–343.

McMahon, M. M. 2005. Phylogenetic relationships and floral evolution in the papilionoid legume clade Amorpheae. Brittonia 57: 397–411.

Meerow, A. W. 2010. Convergence or reticulation? Mosaic evolution in the canalized American Amaryllidaceae. Pp 145–168. *In:* O. Seberg, G. Petersen, A. S. Barfod, & J. I. Davis (eds). Diversity, phylogeny, and evolution in the monocotyledons. Aarhus University Press, Aarhus.

——— **& D. A. Snijman.** 1998. Amaryllidaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 83–110. Springer, Berlin.

Mehta, I. J. & M. F., Jr. Moseley. 1981. The floral anatomy of *Koeberlinia* Zucc.: Systematic implications. American Journal of Botany 68: 482–497.

Melchior, H. 1925. Violaceae. *In:* A. Engler & K. Prantl (eds). Die natürlichen Pflanzenfamilien, ed. 2, 21: 329–377. Engelmann, Leipzig.

Mlot, C. 1998. Plant biology in the genome era. Science 281: 331–332.

Möller, A. P. 2000. Developmental stability and pollination. Oecologia 123: 149–157.

Möller, M., M. Clokie, P. Cubas & Q. Cronk. 1999. Integrating molecular phylogenies and developmental genetics: a Gesneriaceae case study. Pp 375–402. *In:* P. M. Hollingsworth, R. J. Bateman, & R. J. Gornall (eds). Molecular systematics and plant evolution. Taylor & Francis, London.

Mondragón-Palomino, M. & G. Theissen. 2009. Why are orchid flowers so diverse? Reduction of evolutionary constraints by paralogues of class B floral homeotic genes. Annals of Botany 104: 583–594.

———, L. Hiese, A. Härter, M. A. Koch & G. Theissen. 2009. Positive selection and ancient duplications in the evolution of class B floral homeotic genes of orchids and grasses. BMC Evolutionary Biology 2009, 9:1.

Müller-Doblies, D. 1970. Über die Verwandtschaft von *Typha* und *Sparganium* im Infloreszenz- und Blütenbau. Botanische Jahrbücher für Systematik 89: 451–562.

Murbeck, S. 1912. Untersuchungen über den Blütenbau der Papaveraceen. Kungliga Svenska Vetenskapsakademiens Handlingar 50(1): 1–168.

——— 1941. Das Androeceum der Rosaceen. Lunds Universitets Arsskrift, n.F, Avd. 2, 37, 7: 1–56.

Murty, Y. S. & S. Gupta. 1978. Morphological studies in Meliaceae II. A reinvestigation of floral anatomy of members of Swietenieae and Trichilieae. Proceedings of the Indian Academy of Sciences B 87: 55–64.

Nair, N. C. & K. S. Nathawat. 1958. Vascular anatomy of some flowers of Zygophyllaceae. Journal of the Indian Botanical Society 10: 175–180.

——— **& T. C. Joseph.** 1957. Floral morphology and embryology of *Samadera indica*. Botanical Gazette (Crawfordsville) 119: 104–115.

Narayana, L. L. 1958. Floral anatomy of Meliaceae—I. Journal of the Indian Botanical Society 37: 365–374.

——— 1963. A contribution to the floral anatomy and embryology of Linaceae. Journal of the Indian Botanical Society 43: 343–357.

——— 1966. A contribution to the floral anatomy of Oxalidaceae. Journal of Japanese Botany 41: 321–328.

——— **& D. Rao.** 1969. Contributions to the floral anatomy of Humiriaceae 1. Journal of Japanese Botany 44: 328–335.

——— **& ———.** 1971. Contributions to the floral anatomy of Linaceae II. Phytomorphology 21: 64–67.

Neal, P. R., A. Dafni & M. Giurfa. 1998. Floral symmetry and its role in plant-pollinator systems: terminology, distribution, and hypotheses. Annual Review of Ecology and Systematics 29: 345–373.

Neinhuis, C. & P. L. Ibisch. 1998. Corsiaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 198–201. Springer, Berlin.

Niedenzu, F. 1893. Myrtaceae. *In:* A. Engler & K. Prantl (eds). Die natürlichen Pflanzenfamilien, III, 7: 57–105. Engelmann, Leipzig.

Noll, F. 1888. Über die normale Stellung zygomorpher Blüten und ihre Orientirungsbewegungen zur Erreichung derselben. Arbeiten des Botanischen Instituts in Würzburg 3: 189–252. 315–371. Engelmann, Leipzig.

Nordenstam, B. 1998. Colchicaceae. *In:* K. Kubitzki (ed). Families and genera of vascular plants, 3: 175–185. Springer, Berlin.

Oliveira, P. E. 1996. Biologia floral de *Salvertia convallariodora* (Vochysiaceae): uma espécie de cerrado polinizada por mariposas. Revista Brasileira de Botanica 19: 49–53.

Olmstead, R. G., C. W. dePamphilis, A. D. Wolfe, N. D. Young, W. J. Elisens & P. A. Reeves. 2001. Disintegration of the Scrophulariaceae. American Journal of Botany 88: 348–361.

Olson, M. E. 2003. Ontogenetic origins of floral bilateral symmetry in Moringaceae (Brassicales). American Journal of Botany 90: 49–71.

Ottley, A. M. 1944. The American loti with special consideration of a proposed new section, *Simpeteria*. Brittonia 5: 81–123.

Oxelman, B., P. Kornhall, R. G. Olmstead & B. Bremer. 2005. Further disintegration of Scrophulariaceae. Taxon 54: 411–425.

Pan, J. & H. Ohba. 2001. *Chrysosplenium*. *In:* Z. Wu & P. H. Raven (eds). Flora of China, 8: 346–358. Science Press, Beijing and Missouri Botanical Garden, St. Louis, Missouri.

Patchell, M. J., M. C. Bolton, P. Mankowski & J. C. Hall. 2011. Comparative floral development in Cleomaceae reveals two distinct pathways leading to monosymmetry. International Journal of Plant Sciences 172: 352–365.

Pauw, A. 2005. Inversostyly: a new stylar polymorphism in an oil-secreting plant, *Hemimeris racemosa* (Scrophulariaceae). American Journal of Botany 92: 1878–1886.

Philipson, W. R. 1967. *Griselinia* Forst. fil.—anomaly or link. New Zealand Journal of Botany 5: 134–165.

——— 1987. *Corynocarpus* J.R. and G. Forst.—an isolated genus. Botanical Journal of the Linnean Society 95: 9–18.

——— **& B. C. Stone.** 1980. The systematic position of *Aralidium* Miq.—a multidisciplinary study. 1. Introduction and floral and general anatomy. Taxon 29: 391–403.

Pilger, R. 1930. Rapateaceae. *In:* A. Engler & K. Prantl (eds). Die natürlichen Pflanzenfamilien, ed. 2, 15a, 59–65. Engelmann, Leipzig.

Pirani, J. R. & J. A. Kallunki. 2007. Two new species of *Galipea* (Rutaceae, Galipeae) from Bolivia, Ecuador, and Peru. Brittonia 59: 343–349.

Poppendieck, H.-H. 2003. Cochlospermaceae. *In:* K. Kubitzki & C. Bayer (eds). The families and genera of vascular plants, 5: 71–74. Springer, Berlin.

Prance, G. T. 2003. Rhabdodendraceae. *In:* K. Kubitzki & C. Bayer (eds). The families and genera of vascular plants, 5: 339–341. Springer, Berlin.

——— **& F. White.** 1988. The genera of Chrysobalanaceae: a study in practical and theoretical taxonomy and its relevance to evolutionary biology. Philosophical Transactions of the Royal Society of London B 320: 1–184.

Prenner, G. 2003. Floral ontogeny in *Lathyrus latifolius* (Fabaceae-Vicieae). Phyton 43: 392–400.

——— 2004a. Floral development in *Daviesia cordata* (Leguminosae: Papilionoideae: Mirbelieae) and its systematic implications. Australian Journal of Botany 52: 285–291.

——— 2004b. Floral development in *Polygala myrtifolia* (Polygalaceae) and its similarities with Leguminosae. Plant Systematics and Evolution 249: 67–76.

——— 2004c. Floral ontogeny in *Lespedeza thunbergii* (Leguminosae: Papilionaceae: Desmodieae): Variations from the unidirectional mode of organ formation. Journal of Plant Research 117: 297–302.

——— 2004d. New aspects in floral development of Papilionoideae: Initiated but suppressed bracteoles and variable initiation of sepals. Annals of Botany 93: 537–545.

——— 2004e. The asymmetric androecium in Papilionoideae (Leguminosae): Definition, occurrence, and possible systematic value. International Journal of Plant Sciences 165: 499–510.

——— **& B. B. Klitgaard.** 2008. Towards unlocking the deep nodes of Leguminosae: Floral development and morphology of the enigmatic *Duparquetia orchidacea*. American Journal of Botany 95: 1349–1365.

——— **& P. J. Rudall.** 2007. Comparative ontogeny of the cyathium in *Euphorbia* and its allies: exploring the organ-flower-inflorescence boundary. American Journal of Botany 94: 1612–1629.

———**, S. D. Hopper & P. J. Rudall.** 2008. Pseudanthium development in *Calycopeplus paucifolius*, with particular reference to the evolution of the cyathium in Euphorbieae (Euphorbiaceae-Malpighiales). Australian Systematic Botany 21: 153–161.

Preston, J. C. & L. C. Hileman. 2009. Developmental genetics of floral symmetry evolution. Trends in Plant Science 14: 147–154.

———**, C. C. Martinez & L. C. Hileman.** 2011. Gradual disintegration of the floral symmetry gene network is implicated in the evolution of a wind-pollination syndrome. Proceedings of the National Academy of Sciences of the USA 108: 2343–2348.

Puri, V. 1978. On some peculiarities of angiosperm carpel. Acta Botanica Indica 6(Suppl): I–XIV.

Qiu, Y.-L., L. Li, B. Wang, J.-Y. Xue, T. A. Hendry, R.-Q. Li, J. W. Brown, Y. Liu, G. T. Hudson & Z.-D. Chen. 2010. Angiosperm, phylogeny inferred from sequences of four mitochondrial genes. Journal of Systematics and Evolution 48: 391–425.

Radcliffe-Smith, A. 2001. Genera Euphorbiacearum. Royal Botanic Gardens, Kew.

Rahn, K. 1998. Alliaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 70–78. Springer, Berlin.

Raimann, R. 1893. Onagraceae. *In:* A. Engler & K. Prantl (eds). Die natürlichen Pflanzenfamilien, III, 7: 199–223. Engelmann, Leipzig.

Rankin-Rodríguez, R. & W. Greuter. 2004. A study of differentiation patterns in *Capparis* sect. *Breyniastrum* in Cuba, with a nomenclatural and taxonomic survey of Cuban *Capparis* (Capparaceae). Willdenowia 34: 259–276.

Rao, A. N. 1962. Floral anatomy and gametogenesis in *Hopea racophloea* Dyer. Journal of the Indian Botanical Society 41: 557–562.

Rao, C. V. 1952. Floral anatomy of some Malvales and its bearing on the affinities of families included in the order. Journal of the Indian Botanical Society 31: 171–203.

——— 1972. Floral anatomy of *Ricinocarpus pinifolius* Desf. with some observations on the phylogeny and centre of origin of Euphorbiaceae. Pp 85–91. *In:* Y. S. Murty, B. M. Johri, H. Y. Mohan Ram, & T. M. Vargese (eds). Advances in plant morphology. Sarita Prakashan, Nauchandi, India.

Rao, D. & L. L. Narayana. 1965. Vascular anatomy of Humiriaceae. Current Science 34: 383–384.

Rao, V. S. 1949. The morphology of the calyx-tube and origin of perigyny in Turneraceae. Journal of the Indian Botanical Society 21: 153–161.

Raya, Á. & J. C. I. Belmonte. 2006. Left-right asymmetry in the vertebrate embryo: from early information to higher-level integration. Nature Reviews Genetics 7: 283–293.

Ree, R. H. & M. J. Donoghue. 1999. Inferring rates of change in flower symmetry in asterid angiosperms. Systematic Biology 48: 633–641.

———**, H. L. Citerne, M. Lavin & Q. C. B. Cronk.** 2004. Heterogeneous selection on *LEGCYC* paralogs in relation to flower morphology and the phylogeny of *Lupinus* (Leguminosae). Molecular Biology and Evolution 21: 321–331.

Reeves, P. A. & R. G. Olmstead. 1998. Evolution of novel morphological and reproductive traits in a clade containing *Antirrhinum majus* (Scrophulariaceae). American Journal of Botany 85: 1047–1056.

——— **&** ———**.** 2003. Evolution of the TCP gene family in Asteridae: cladistic and network approaches to understanding regulatory gene family diversification and its impact on morphological evolution. Molecular Biology and Evolution 20: 1997–2009.

Reinsch, J. 1927. Über die Entstehung der Ästivationsformen von Kelch und Blumenkrone dikotyler Pflanzen und über die Beziehungen der Deckungsweisen zur Gesamtsymmetrie der Blüte. Flora 121: 77–124.

Ren, Y., H.-F. Li, L. Zhao & P. K. Endress. 2007. Floral morphogenesis in *Euptelea* (Eupteleaceae, Ranunculales). Annals of Botany 100: 185–193.

Renner, S. S. 1993. Phylogeny and classification of the Melastomataceae and Memecylaceae. Nordic Journal of Botany 13: 519–540.

Renshaw, A. & S. Burgin. 2008. Enantiomorphy in *Banksia* (Proteaceae): flowers and fruits. Australian Journal of Botany 56: 342–346.

Robbrecht, E. 1988. Tropical woody Rubiaceae. Opera Botanica Belgica 1: 1–272.

Robertson, C. 1888. Zygomorphy and its causes. I/II/III. Botanical Gazette (Crawfordsville) 13: 146–151/203–208/224–230.

Robyns, W. 1930. L'organisation florale des Solanacées zygomorphes. Mémoires de l'Académie Royale Belgique, Cl. Sci, 11, 8: 1–96.

Roels, P. & E. Smets. 1996. A floral ontogenetic study in the Dipsacales. International Journal of Plant Sciences 157: 203–218.

Rohweder, O. & K. Huber. 1974. Centrospermen-Studien 7. Beobachtungen und Anmerkungen zur Morphologie und Entwicklungsgeschichte einiger Nyctaginaceae. Botanische Jahrbücher für Systematik 94: 327–359.

Rohwer, J. G. 1993a. Moraceae. *In:* K. Kubitzki, J. G. Rohwer, & V. Bittrich (eds). The families and genera of vascular plants, 2: 438–453. Springer, Berlin.

——— 1993b. Phytolaccaceae. *In:* K. Kubitzki, J. G. Rohwer, & V. Bittrich (eds). The families and genera of vascular plants, 2: 506–515. Springer, Berlin.

Rollins, R. C. 1993. The Cruciferae of continental North America. Stanford University Press, Stanford.

Ronse De Craene, L. P. 2004. Floral development of *Berberidopsis corallina*: a crucial link in the evolution of flowers in the core eudicots. Annals of Botany 94: 741–751.

——— 2005. Floral developmental evidence for the systematic position of *Batis* (Bataceae). American Journal of Botany 92: 752–760.

——— **& E. Haston.** 2006. The systematic relationships of glucosinolate-producing plants and related families: a cladistic investigation based on morphological and molecular characters. Botanical Journal of the Linnean Society 151: 453–494.

——— **& E. F. Smets.** 1991. Androecium and floral nectaries of *Harungana madagascariensis* (Clusiaceae). Plant Systematics and Evolution 178: 179–194.

——— **&** ———**.** 1999. The floral development and anatomy of *Carica papaya* L. (Caricaceae). Canadian Journal of Botany 77: 582–598.

——— **&** ———**.** 2001. Floral developmental evidence for the systematic relationships of *Tropaeolum* (Tropaeolaceae). Annals of Botany 88: 879–892.

——— **& L. Wanntorp.** 2008. Morphology and anatomy of the flower of *Meliosma* (Sabiaceae): implications for pollination biology. Plant Systematics and Evolution 271: 79–91.

———**, J. De Laet & E. F. Smets.** 1998. Floral development and anatomy of *Moringa oleifera* (Moringaceae): what is the evidence for a capparalean or sapindalean affinity? Annals of Botany 82: 273–284.

———**,** ——— **&** ———**.** 1996. Morphological studies in Zygophyllaceae II. The floral development and vascular anatomy of *Peganum harmala*. American Journal of Botany 83: 201–215.

———**, E. Smets & D. Clinckemaillie.** 2000. Floral ontogeny and anatomy in *Koelreuteria* with special emphasis on monosymmetry and septal cavities. Plant Systematics and Evolution 223: 91–107.

———**, H. P. Linder, E. F. Smets & T. Dlamini.** 2001. Evolution and development of floral diversity of Melianthaceae, an enigmatic southern African family. International Journal of Plant Sciences 162: 59–82.

———**, T. Y. A. Yang, P. Schols & E. F. Smets.** 2002a. Floral anatomy and systematics of *Bretschneidera* (Bretschneideracaee). Botanical Journal of the Linnean Society 139: 29–45.

———**, H. P. Linder & E. F. Smets.** 2002b. Ontogeny and evolution of the flowers of South African Restionaceae with special emphasis on the gynoecium. Plant Systematics and Evolution 231: 225–258.

Rudall, P. J. & R. M. Bateman. 2002. Roles of synorganisation, zygomorphy and heterotopy in floral evolution: the gynostemium and labellum of orchids and other lilioid monocots. Biological Reviews 77: 403–441.

——— **&** ———**.** 2004. Evolution of zygomorphy in monocot flowers: iterative patterns and developmental constraints. New Phytologist 162: 25–44.

———**, R. F. Bateman, M. F. Fay & A. Eastman.** 2002. Floral anatomy and systematics of Alliaceae with particular reference to *Gilliesia*, a presumed insect mimic with strongly zygomorphic flowers. American Journal of Botany 89: 1867–1883.

———**, D. D. Sokoloff, M. V. Remizowa, J. G. Conran, J. I. Davis, T. D. Macfarlane & D. W. Stevenson.** 2007. Morphology of Hydatellaceae, an anomalous aquatic family recently recognized as an early-divergent angiosperm lineage. American Journal of Botany 94: 1073–1092.

———**, R. A. Ryder & W. J. Baker.** 2011. Comparative gynoecium structure and multiple origins of apocarpy in coryphoid palms (Arecaceae). International Journal of Plant Sciences 172: 674–690.

Rutishauser, R., L. Wanntorp & E. Pfeifer. 2004. *Gunnera herteri*—developmental morphology of a dwarf from Uruguay and S Brazil (Gunneraceae). Plant Systematics and Evolution 248: 219–241.

Saarela, J. M., H. S. Rai, J. A. Doyle, P. K. Endress, S. Mathews, A. D. Marchant, B. G. Briggs & S. W. Graham. 2007. Hydatellaceae identified as a new branch near the base of the angiosperm phylogenetic tree. Nature 446: 312–315.

Sargent, R. D. 2004. Floral symmetry affects speciation rates in angiosperms. Proceedings of the Royal Society of London B 271: 603–608.

Savile, D. B. O. 1953. Splash-cup dispersal mechanism in *Chrysosplenium* and *Mitella*. Science 117: 250–251.

——— 1979. Dispersal by falling water drops in Saxifragaceae. Davidsonia 10: 65–69.

Sazima, M. & I. Sazima. 1978. Bat pollination of the passion flower, *Passiflora mucronata*, in south-eastern Brazil. Biotropica 10: 100–109.

Schmucker, T. 1931. Über asymmetrisches Verhalten von Hymenopteren an Blüten. Biologisches Zentralblatt 51: 15–18.

Schneider, J. V. 2007. Surianaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 9: 449–455. Springer, Berlin.

———, U. Swenson, R. Samuel, T. F. Stuessy & G. Zizka. 2006. Phylogenetics of Quiinaceae (Malpighiales): evidence from *trnL-trnF* sequence data and morphology. Plant Systematics and Evolution 257: 189–203.

Schönenberger, J. & P. K. Endress. 1998. Structure and development of the flowers in *Mendoncia*, *Pseudocalyx*, and *Thunbergia* (Acanthaceae) and their systematic implications. International Journal of Plant Sciences 159: 446–465.

Schoute, J. C. 1935. On corolla aestivation and phyllotaxis of floral phyllomes. Koninklijke Akademie van Wetenschappen, Verhandeling, Tweede Sectie, 34, 4: 1–77.

Scotland, R. W., P. K. Endress & T. J. Lawrence. 1994. Corolla ontogeny and aestivation in the Acanthaceae. Botanical Journal of the Linnean Society 114: 49–65.

Sheahan, M. C. 2007. Zygophyllaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 9: 488–500. Springer, Berlin.

Simpson, B. B. 1982. *Krameria* (Krameriaceae) flowers: orientation and elaiophore morphology. Taxon 31: 517–528.

Simpson, M. G. 1990. Phylogeny and classification of the Haemodoraceae. Annals of the Missouri Botanical Garden 77: 722–784.

——— 1998. Haemodoraceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 212–222. Springer, Berlin.

——— & P. J. Rudall. 1998. Tecophilaeaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 429–436. Springer, Berlin.

Sleumer, H. 1942. Icacinaceae. *In:* A. Engler & K. Prantl (eds). Die natürlichen Pflanzenfamilien, ed. 2, 20b: 322–396. Engelmann, Leipzig.

Smith, G. F. & B.-E. Van Wyk. 1998. Asphodelaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 130–140. Springer, Berlin.

Smith, J. F., L. C. Hileman, M. P. Powell & D. A. Baum. 2004. Evolution of *GCYC*, a Gesneriaceae homolog of *CYCLOIDEA*, within Gesnerioideae (Gesneriaceae). Molecular Phylogenetics and Evolution 31: 765–779.

Smith, L. B. & W. Till. 1998. Bromeliaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 74–99. Springer, Berlin.

Sobick, U. 1983. Blütenentwicklungsgeschichtliche Untersuchungen and Resedaceen unter besonderer Berücksichtigung von Androeceum und Gynoeceum. Botanische Jahrbücher für Systematik 104: 203–248.

Sokoloff, D. D. 1999. *Ottleya*, a new genus of Papilionaceae-Loteae from North America. Feddes Repertorium 110: 89–97.

———, G. V. Degtjareva, P. K. Endress, M. V. Remizowa, T. H. Samigullin & C. M. Valiejo-Roman. 2007. Inflorescence and early flower development in Loteae (Leguminosae) in a phylogenetic and taxonomic context. International Journal of Plant Sciences 168: 801–833.

———, M. V. Remizova, H. P. Linder & P. J. Rudall. 2009. Morphology and development of the gynoecium in Centrolepidaceae: The most remarkable range of variation in Poales. American Journal of Botany 96: 1925–1940.

Specht, C. D. & M. E. Bartlett. 2010. Flower evolution: The origin and subsequent diversification of the angiosperm flower. Annual Review of Ecology, Evolution and Systematics 40: 217–243.

Specht, C., M. E. Bartlett & T. Renner. 2008. Evolution of the stamen whorl in the Zingiberales. Botany 2008. Abstract (on-line).

Speta, F. 1998. Hyacinthaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 261–285. Springer, Berlin.

Sprengel, C. K. 1793. Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen. Vieweg, Berlin.

Staedler, Y. M. & P. K. Endress. 2009. Diversity and lability of floral phyllotaxis in the pluricarpellate families of core Laurales (Gomortegaceae, Atherospermataceae, Siparunaceae, Monimiaceae). International Journal of Plant Sciences 170: 522–550.

Stahl, B. & A. Anderberg. 2004. Myrsinaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 6: 266–281. Springer, Berlin.

Stauffer, F. W. & P. K. Endress. 2003. Comparative morphology of female flowers and systematics in Geonomeae (Arecaceae). Plant Systematics and Evolution 242: 171–203.

———, R. Rutishauser & P. K. Endress. 2002. Morphology and development of the female flowers in *Geonoma interrupta* (Arecaceae). American Journal of Botany 89: 220–229.

Stern, W. L., G. K. Brizicky & R. H. Eyde. 1969. Comparative anatomy and relationships of Columelliaceae. Journal of the Arnold Arboretum 50: 36–75.

Stevens, P. F. 2001 onwards. Angiosperm Phylogeny Website. Version 9, June 2008 [and more or less continuously updated since]. http:/www.mobot.org/MOBOT/research/APweb/.

——— 2007. Clusiaceae-Guttiferae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 9: 48–66. Springer, Berlin.

———, J. Luteyn, E. G. H. Oliver, T. L. Bell, E. A. Brown, R. K. Crowden, A. S. George, G. J. Jordan, P. Ladd, K. Lemson, C. B. McLean, Y. Menadue, J. S. Pate, H. M. Stace & C. M. Weiler. 2004. Ericaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 6: 145–194. Springer, Berlin.

Stevenson, D. W., M. Colella & B. Boom. 1998. Rapateaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 415–424. Springer, Berlin.

Steyermark, J. A. & J. L. Luteyn. 1980. Revision of the genus *Ochthocosmus* (Linaceae). Brittonia 32: 128–143.

Stone, B. C., K.-L. Huynh & H.-H. Poppendieck. 1998. Pandanaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 397–404. Springer, Berlin.

Stoutamire, W. 1978. Pollination of *Tipularia discolor*, an orchid with modified symmetry. American Orchid Society Bulletin 33: 413–415.

Strange, A., P. J. Rudall & C. J. Prychid. 2004. Comparative floral anatomy of Pontederiaceae. Botanical Journal of the Linnean Society 144: 395–408.

Struwe, L. & V. A. Albert. 2002. Tribe Helieae. *In:* L. Struwe & V. A. Albert (eds). Gentianaceae: Systematics and natural history, 137–170. Cambridge University Press, Cambridge.

Stützel, T. 1984. Blüten- und infloreszenzmorphologische Untersuchungen zur Systematik der Eriocaulaceen. Dissertationes Botanicae 71: 1–108.

Takeuchi, W. 2001. An unusual new species of *Steganthera* (Monimiaceae) from Papua New Guinea. Kew Bulletin 56: 995–998.

Tamura, M. N. 1998a. Liliaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 343–353. Springer, Berlin.

——— 1998b. Melanthiaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 369–380. Springer, Berlin.

——— 1998c. Trilliaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 444–452. Springer, Berlin.

Tanaka, N. 2003. New status and combinations for Japanese taxa of *Chionographis* (Melanthiaceae). Novon 13: 212–215.

Tank, D. C., P. M. Beardsley, S. A. Kelchner & R. G. Olmstead. 2006. Review of the systematics of Scrophulariaceae s.l. and their current disposition. Australian Systematic Botany 19: 289–307.

Taroda, N. & P. E. Gibbs. 1986. A revision of the Brazilian species of *Cordia* subgenus *Varronia* (Boraginaceae). Notes Royal Botanic Garden Edinburgh 44: 105–140.

Tebbitt, M. C., L. Lowe-Forrest, A. Santoriello, W. L. Clement & S. M. Swenson. 2006. Phylogenetic relationships of Asian *Begonia*, with an emphasis on the evolution of rain-ballist animal dispersal mechanisms in sections *Platycentrum*, *Sphenanthera* and *Leprosae*. Systematic Botany 31: 327–336.

Teeri, T. H., M. Kotilainen, A. Uimari, S. Ruokolainen, Y. P. Ng, U. Malm, E. Pöllänen, S. Broholm, R. Laitinen, P. Elomaa & V. A. Albert. 2006. Floral developmental genetics of *Gerbera* (Asteraceae). Advances in Botanical Research 44: 324–351.

Teppner, H. 1988. *Lathyrus grandiflorus* (Fabaceae-Vicieae): Blüten-Bau, -Funktion und *Xylocopa violacea*. Phyton (Austria) 28: 321–336.

Thiv, M. & J. W. Kadereit. 2002a. A morphological cladistic analysis of Gentianaceae-Canscorinae and the evolution of anisomorphic androecia in the subtribe. Systematic Botany 27: 780–788.

——— & ———. 2002b. Tribe Chironieae. Pp 108–128. *In:* L. Struwe & V. A. Albert (eds). Gentianaceae: Systematics and natural history. Cambridge University Press, Cambridge.

Tiagi, Y. D. 1969. Vascular anatomy of the flower of certain species of the Combretaceae. Botanical Gazette (Crawfordsville) 130: 150–157.

Tilak, V. D. & P. M. Nene. 1978. Floral anatomy of the Rutaceae. Indian Journal of Botany 1: 83–90.

Tobe, H. 2012. Floral structure of *Cardiopteris* (Cardiopteridaceae) with special emphasis of the gynoecium: Systematic and evolutionary implications. Journal of Plant Research 125: 361–369.

Torgard, S. S. 1924. Studien über die Morphologie und Baumechanik der Oleaceen-Blüte. Appeltofft, Kalmar.

Troll, W. 1929. *Roscoea purpurea* Sm., eine Zingiberacee mit Hebelmechanismus in den Blüten. Mit Bemerkungen über die Entfaltungsbewegungen der fertilen Staubblätter von *Salvia*. Planta 7: 1–28.

——— 1951. Botanische Notizen II. Abhandlungen der Akademie der Wissenschaften und der Literatur, Mainz, Mathematisch-Naturwissenschaftliche Klasse 1951: 25–80.

——— 1961. *Cochliostema odoratissimum* Lem. Organisation und Lebensweise. Nebst vergleichenden Ausblicken auf andere Commelinaceen. Beiträge zur Biologie der Pflanzen 36: 325–389.

Tsai, W.-C., Y.-Y. Hsiao, Z.-J. Pan, C.-C. Hsu, Y.-P. Yang, W.-H. Chen & H.-H. Chen. 2008. Molecular biology of orchid flowers: with emphasis on *Phalaenopsis*. Advances in Botanical Research 47: 99–145.

Tsou, C.-H. & S. A. Mori. 2007. Floral organogenesis and floral evolution of the Lecythidoideae (Lecythidaceae). American Journal of Botany 94: 716–736.

Tucker, S. C. 1984. Origin of symmetry in flowers. Pp 351–396. *In:* R. A. White & W. C. Dickison (eds). Contemporary problems in plant anatomy. Academic, Orlando.

——— 1991. Helical floral organogenesis in *Gleditsia*, a primitive caesalpinioid legume. American Journal of Botany 78: 1130–1149.

——— 1996. Trends in evolution of floral ontogeny in *Cassia* sensu stricto, *Senna*, and *Chamaecrista* (Leguminosae: Caesalpinioideae: Cassieae: Cassiinae); a study in convergence. American Journal of Botany 83: 687–711.

——— 1999. Evolutionary lability of symmetry in early floral development. International Journal of Plant Sciences 160(Suppl): S25–S39.

——— 2002. Comparative floral ontogeny in Detarieae (Leguminosae: Caesalpinioideae). 2. Zygomorphic taxa with with petal and stamen suppression. American Journal of Botany 89: 888–907.

——— **& P. Bernhardt.** 2000. Floral ontogeny, pattern formation, and evolution in *Hibbertia* and *Adrastea* (Dilleniaceae). American Journal of Botany 87: 1915–1936.

———**, A. W. Douglas & H.-X. Liang.** 1993. Utility of ontogenetic and conventional characters in determining phylogenetic relationships of Saururaceae and Piperaceae (Piperales). Systematic Botany 18: 614–641.

Uhl, N. W. & J. Dransfield. 1987. Genera Palmarum. Allen Press, Lawrence, Kansas.

Ushimaru, A. & F. Hyodo. 2005. Why do bilaterally symmetrical flowers orient vertically? Flower orientation influences pollinator landing behaviour. Evolutionary Ecology Research 7: 151–160.

van Bruggen, H. W. E. 1998. Aponogetonaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 4: 21–25. Springer, Berlin.

van Jaarsveld, E. 2003. *Tylecodon*. Pp 354–364. *In:* U. Eggli (ed). Illustrated handbook of succulent plants: Crassulaceae. Springer, Berlin.

Verhoek, S. 1998. Agavaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 3: 60–70. Springer, Berlin.

Vincent, C. A. & E. S. Coen. 2004. A temporal and morphological framework for flower development in *Antirrhinum majus*. Canadian Journal of Botany 82: 681–690.

Vöchting, H. 1886. Über Zygomorphie und deren Ursachen. Jahrbücher für Wissenschaftliche Botanik 17: 297–346.

Vogel, S. 1954. Blütenbiologische Typen als Elemente der Sippengliederung, dargestellt anhand der Flora Südafrikas. Fischer, Jena.

——— 1974. Ölblumen und ölsammelnde Bienen. Tropische und Subtropische Pflanzenwelt 7: 1–267.

——— 1978. Evolutionary shifts from reward to deception in pollen flowers. Pp 89–96. *In:* A. J. Richards (ed). The pollination of flowers by insects. Academic, London.

——— 1990. Ölblumen und ölsammelnde Bienen. Dritte Folge. *Momordica*, *Thladiantha* und die Ctenoplectridae. Tropische und Subtropische Pflanzenwelt 73: 1–186.

——— 1998. Remarkable nectaries: structure, ecology, organophyletic perspectives IV. Miscellaneous cases. Flora 193: 225–248.

von Balthazar, M., G. E. Schatz & P. K. Endress. 2003. Female flowers and inflorescences of Didymelaceae. Plant Systematics and Evolution 237: 199–208.

Wagner, A. 2008. Gene duplications, robustness, and evolutionary innovations. Bioessays 30: 367–373.

Wagner, G. P. 1986. The systems approach: an interface between development and population genetic aspects of evolution. Pp 149–165. *In:* D. M. Raup & D. Jablonski (eds). Paterns and processes in the history of life. Springer, Berlin.

——— 1989. The origin of morphological characters and the biological basis of homology. Evolution 43: 1157–1171.

——— 2007. The developmental genetics of homology. Nature Review Genetics 8: 473–479.

Wagner, W. L., P. C. Hoch & P. H. Raven. 2007. Revised classification of the Onagraceae. Systematic Botany Monographs 83: 1–240.

Wang, L., Q. Gao, Y. Z. Wang & Q.-B. Lin. 2006. Isolation and sequence analysis of two *CYC*-like genes, *SiCYC1A* and *SiCAC1B*, from zygomorphic and actinomorphic cultivars of *Saintpaulia ionantha* (Gesneriaceae). Acta Phytotaxonomica Sinica 44: 353–361.

Wang, Z., Y. Luo, X. Li, L. Wang, S. Xu, J. Yang, L. Wenig, S. Sato, S. Tabata, M. Ambrose, C. Rameau, X. Feng, X. Hu & D. Luo. 2008. Genetic control of floral zygomorphy in pea (*Pisum sativum* L.). Proceedings of the National Academy of Sciences of the United States of America 105: 10414–10419.

Webb, C. J. & D. G. Lloyd. 1986. The avoidance of interference between the presentation of pollen and stigmas in angiosperms. II. Herkogamy. New Zealand Journal of Botany 34: 164–178.

Weber, H. 1955. Über die Blütenkelche tropischer Rubiaceen. Abhandlungen der Akademie der Wissenschaften und der Literatur in Mainz, Mathematisch-Naturwissenschaftliche Klasse 1955: 449–466.

Weckerle, C. & R. Rutishauser. 2003. Comparative morphology and systematic position of *Averrhoidium* within Sapindaceae. International Journal of Plant Sciences 164: 775–792.

Weibel, R. 1941. Fleurs cléistogames particulières chez certaines Violettes chiliennes. Compte Rendu de la Société de Physique et d'Histoire Naturelle de Genève 58: 146–148.

Weigend, M. 2004. Loasaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 6: 239–254. Springer, Berlin.

Werth, E. 1956. Bau und Leben der Blumen. Die blütenbiologischen Bautypen in Entwicklung und Anpassung, Enke, Stuttgart.

Westerkamp, C. 1993. The co-operation between the asymmetric flower of *Lathyrus latifolius* (Fabaceae–Vicieae) and its visitors. Phyton 33: 127–137.

——— 1997. Keel blossoms: bee flowers with adaptations against bees. Flora 192: 125–132.

——— 1999. Keel flowers of the Polygalaceae and Fabaceae: a functional comparison. Botanical Journal of the Linnean Society 129: 207–221.

——— **& R. Classen-Bockhoff.** 2007. Bilabiate flowers: The ultimate response to bees? Annals of Botany 100: 361–374.

——— **& A. Weber.** 1997. Secondary and tertiary pollen presentation in *Polygala myrtifolia* and allies (Polygalaceae, South Africa). South African Journal of Botany 63: 254–258.

Weston, P. H. 2007. Proteaceae. *In:* K. Kubitzki (ed). Families and genera of vascular plants, 9: 364–404. Springer, Berlin.

Whalen, M. D. 1978. Reproductive character displacement and floral diversity in *Solanum* sect. *Androceras*. Systematic Botany 3: 77–86.

——— 1979. Taxonomy of *Solanum* section *Androceras*. Gentes Herbarum 11: 359–426.

Whipple, C. J. & R. J. Schmidt. 2006. Genetics of grass flower development. Advances in Botanical Research 44: 385–424.

Wilken, D. H. 2004. Polemoniaceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 6: 300–312. Springer, Berlin.

Wilkinson, H. P. & L. Wanntorp. 2007. Gunneraceae. *In:* K. Kubitzki (ed). The families and genera of vascular plants, 9: 177–183. Springer, Berlin.

Wilson, C. A. & C. L. Calvin. 2006. Character divergences and convergences in canopy-dwelling Loranthaceae. Botanical Journal of the Linnean Society 150: 101–113.

Woodward, G. L. & T. M. Laverty. 1992. Recall of flower handling skills by bumblebees—a test of Darwin interference hypothesis. Animal Behaviour 44: 1045–1051.

Worberg, A., M. H. Alford, D. Quandt & T. Borsch. 2009. Huertales sister to Brassicales plus Malvales, and newly circumscribed to include *Dipentodon*, *Gerrardina*, *Huertea*, *Perrottetia*, and *Tapiscia*. Taxon 58: 468–478.

Wurdack, K. J. & C. C. Davis. 2009. Malpighiales phylogenetics: gaining ground on one of the most recalcitrant clades in the angiosperm tree of life. American Journal of Botany 96: 1551–1570.

Wydler, H. 1844. Einige Bemerkungen über Symmetrie der Blumenkrone. Botanische Zeitung 2(609–611): 706–707.

Xiao, L. H. & Y. Z. Wang. 2007. Single nucleotide polymorphisms of *Gcyc1* (*Cycloidea*) in *Conandron ramondioides* (Gesneriaceae) from Southeast China. Plant Systematics and Evolution 269: 145–157.

Zhang, W., E. M. Kramer & C. C. Davis. 2010. Floral symmetry genes and the origin and maintenance of zygomorphy in a plant-pollinator mutualism. Proceedings of the National Academy of Sciences of the USA 107: 6388–6393.

———, ——— & ———. 2012. Similar genetic mechanisms underlie the parallel evolution of floral phenotypes. PLoS ONE 7: e36033.

Zhou, X.-R., Y.-Z. Wang, J. F. Smith & R. Chen. 2008. Altered expression patterns of TCP and MYB genes relating to the floral developmental transition from initial zygomorphy to actinomorphy in *Bournea* (Gesneriaceae). New Phytologist 178: 532–543.

Zhu, X. Y., M. W. Chase, Y.-L. Qiu, H.-Z. Kong, D. L. Dilcher, J.-H. Li & Z.-D. Chen. 2007. Mitochondrial *matR* sequences help to resolve deep phylogenetic relationships in rosids. BMC Evolutionary Biology 2007, 7: no. 217.

Zimmermann, W. 1933. Beiträge zur Kenntnis der Georeactionen. IV. Blütenbewegungen und andere Umstimmungsbewegungen. Jahrbücher für Wissenschaftliche Botanik 77: 393–506.

——— 1975. Ranunculaceae. *In*: J. Damboldt (ed.), Gustav Hegi's Illustrierte Flora von Mitteleuropa (edn. 2), III, 3, 1: 53–341. Parey, Berlin.