SYMMETRY IN FLOWERS: DIVERSITY AND EVOLUTION

Peter K. Endress[1]

Institute of Systematic Botany, University of Zurich, Zollikerstrasse 107, 8008 Zurich, Switzerland

This article traces research on floral symmetry back to its beginnings. It brings together recent advances from different fields that converge in floral symmetry and new unpublished material on diversity and development of floral symmetry. During floral development, symmetry may change: monosymmetric flowers may have a polysymmetric early phase; polysymmetric flowers may have a monosymmetric or even asymmetric early phase; more than one symmetry change is also possible. In Lamiales s.l. (comprising the model plant *Antirrhinum*, where the *cycloidea* gene produces monosymmetric flowers with the adaxial side of the androecium reduced), taxa also occur in which the androecium is reduced on both sides, adaxial and abaxial. As a trend in asymmetric flowers, enantiomorphy (with two mirror-image morphs) at the level of individuals seems to occur only in groups in which the flowers are predominantly of a relatively simple construction. In contrast, one morph is fixed at the level of species or higher taxa in groups with more complicated flowers. This is indicated by the apparent lack of enantiomorphy in corolla contortion in asterids but its predominance in rosids with contort flowers, or by the apparent lack of enantiomorphy in the pollination organs of asymmetric flowers in Faboideae but its presence in asymmetric flowers in Caesalpinioideae. To study the evolution of the diverse symmetry patterns, a concerted approach from different fields including molecular developmental genetics, pollination biology, and comparative diversity research is necessary.

Keywords: contort aestivation, enantiomorphy, flower development, flower evolution, flower symmetry, Lamiales.

Introduction

Symmetry has always fascinated humans in nature and art (e.g., Weyl 1952; Shubnikov and Koptsik 1974; Stork 1985; Sitte 1986; Bock and Marsh 1991; Heilbronner and Dunitz 1993; Enquist and Arak 1994; Henley 1996). And today, more than ever before, symmetry is the focus of scientific research in biology. There are two very different fields of current activity: an intrinsic (proximate), the study of development of symmetry in molecular developmental genetics, and an extrinsic (ultimate), the study of visual perception of symmetry by animals. Plants and their flowers (and pollinating animals) are at a meeting point of both these fields. Both fields have their own very different questions and methodologies. However, an area where they converge is the question of the evolution of floral symmetry. My own research is in neither of these two fields but in a third, diversity and evolution of flowers. And this focal point, the approach from the diversity of forms and their evolution, may be expected to be a source of catalyzing questions for both fields. Although this is a review article, it also contains original material, especially in the two case studies on Lamiales and on contort flowers. Most of the illustrations are original as well.

The Rise of Floral Symmetry Research

The interest in patterns of floral symmetry may have started with the pioneer in floral biology, Christian Sprengel (1793),

[1] Fax 41-1-63484-03; e-mail pendress@systbot.unizh.ch.

who, as a result of his meticulous studies on diversity of flowers, wondered about the significance of "regular" (with more than one symmetry plane) and "irregular" (with one symmetry plane) flowers in pollination.

In the first half of the nineteenth century, interest turned to the "cause" (i.e., the developmental mechanism) of irregular flowers, which was seen in mechanical pressure on one side of the floral bud (De Candolle 1813, 1827; Moquin-Tandon 1832; Dutrochet 1837). German-speaking botanists elaborated on the terminology of symmetry patterns. Braun (1835, 1843) introduced "zygomorph" for Sprengel's "irregular" flowers, whereas Schneckenburger (in Mohl 1837) and Wydler (1844) used "symmetrisch" for the same; Schneckenburger (in Mohl 1837) and Wydler (1844) emphasized the presence of two symmetrical halves in such flowers.

A short but innovative period of experimental research on floral symmetry appeared between 1885 and 1892. It was a boom time for plant physiology in Germany, led by persons like Sachs, Pfeffer, and Vöchting. With the invention of the clinostat, experiments on the influence of gravity on plant structure became possible, and lively discussion followed the new discoveries (Dufour 1885; Noll 1885, 1887; Vöchting 1885, 1886; Hildebrand 1886; Delpino 1887; Robertson 1888; Chodat 1889; Bateson and Bateson 1891; Schwendener and Krabbe 1892). Vöchting (1886) showed that in some plants gravity induced monosymmetric flowers, whereas in others it had no effect at all, and in still others it had only partial effect. Vöchting called the first positional monosymmetry and the second constitutional monosymmetry. This was the first experimental approach to the development of mono-

Fig. 1 Different symmetry patterns and change of symmetry during development. *A–C*, Monosymmetric flowers. *A*, Constitutional monosymmetry: *Kohleria eriantha* (Gesneriaceae). *B, C,* Positional monosymmetry. *B, Passiflora lobata* (Passifloraceae). *C, Chiranthodendron pentadactylon* (Malvaceae s.l.). *D–F,* Monosymmetric flowers; simple or reduced monosymmetry: all flowers with a single abaxial stamen. *D, Sarcandra glabra* (Botanic Garden Hamburg, HBG 439-80; Chloranthaceae, archaic angiosperms). *E, Lacistema aggregatum* (E 97-121; Flacourtiaceae, rosids). *F, Hippuris vulgaris* (E 98-5; Antirrhinaceae, asterids). *G–I,* Asymmetric flowers. *G,* Elaborate asymmetry: *Vigna cf. speciosa* (Faboideae, Leguminosae). *H,* Unordered asymmetry: *Zygogynum tieghemii* (Winteraceae), stamen arrangement irregular. *I,* Asymmetry by reduction: *Centranthus ruber* (Valerianaceae), open flower seen from abaxial side: the spur is abaxial, the only stamen is lateral, the style is curved away from the stamen. *J–L,* Symmetry in flowers with spiral phyllotaxis (the numbers designate subsequent organs of the ontogenetic

symmetry, although Hofmeister (1868) had mentioned before that in some flowers monosymmetry was produced by gravity. However, Vöchting's publication provoked discussions by floral biologists who used a different approach. Whereas Vöchting (1886) and Robertson (1888) took extreme positions at both ends of the biological spectrum of floral symmetry, the proximate and the ultimate, both in their own right, Delpino (1887) was perhaps the first to express the value of different biological aspects of floral symmetry.

After this first experimental period, there were few innovative studies on floral symmetry in the first half of this century. However, noteworthy are comparative studies on the diversity of symmetry phenomena in flowers by Goebel (1908, 1924a, 1928); his approach was whole-plant physiological with emphasis on nutritional factors.

It is only in recent decades that there has been a great upswing in symmetry research with regard to flowers, especially as a result of the advent of developmental biology, biology of visual perception, and increased activity in evolutionary biology in general. This new development can be grouped around four different themes: (1) perception of floral symmetry by pollinating insects and function of symmetry in pollination (Leppik 1972; Giurfa et al. 1995, 1996; Lehrer et al. 1995; Dafni and Kevan 1996; Dafni 1997; Møller and Sorci 1998; Neal et al. 1998); (2) comparative developmental morphology, diversity, and evolution of floral symmetry (Tucker 1984a, 1989a, 1991, 1998; Erbar and Leins 1985, 1997; Endress 1987, 1992, 1994, 1998; Baum 1998; Donoghue et al. 1998; Reeves and Olmstead 1998); (3) molecular developmental genetics of floral symmetry (Coen and Nugent 1994; Coen et al. 1995; Coen 1996; Luo et al. 1996; Almeida et al. 1997); and (4) fluctuating asymmetry in floral traits (Møller 1995; Evans and Marshall 1996; Fenster 1997; Møller and Swaddle 1997; Møller and Sorci 1998).

Diversity of Symmetry

Basic Categories

What symmetry patterns occur in flowers? The simplest kind of distinction is that between polysymmetric and monosymmetric flowers, for which the terms "symmetrical" (or "regular") versus "asymmetrical" (or "irregular") have generally been used. These terms have been used since the time of Linnaeus (1751), and they are used today by molecular developmental geneticists who work on *Antirrhinum* flowers (Luo et al. 1996).

When the entire diversity of floral forms is considered, however, these two terms are not sufficient. The terms "asymmetric" or "irregular" are especially confusing for monosym-

metric flowers because monosymmetric flowers may have a high degree of order and because the terms have different connotations in the extended terminology of floral symmetry patterns. The conventional terms of floral symmetry according to number of symmetry planes are "asymmetric" (without any symmetry plane); "monosymmetric," "zygomorphic" (with one symmetry plane); "disymmetric" (with two symmetry planes); and "polysymmetric," "actinomorphic" (with several symmetry planes).

Frey-Wyssling (1925) expanded on the aspects of symmetry by introducing additional terms that are used in crystallography: (1) translational symmetry, (2) rotational symmetry, and (3) mirror symmetry. These can also be combined, as in (1,2) spiral symmetry, (1,3) translational mirror symmetry, and (2,3) rotational mirror symmetry. In flowers, not all these types and combinations are present; patterns 2, 3, and 1,2 are especially important. Patterns 1 and 1,3 occur in vegetative shoots and inflorescences. Leppik (1955, 1957, 1972) added three-dimensional aspects in his terminology of floral shape and symmetry relevant with respect to pollination biology, with emphasis on visual perception. Neal et al. (1998) critically discussed the floral symmetry terminology and proposed an elaborate modified classification of forms, also primarily from the point of view of pollination, i.e., visual perception of mature flowers.

Despite the elaboration of the terminology of symmetry patterns, the current formal categories of symmetry apply to very biologically disparate flower forms, especially in monosymmetry and asymmetry. However, this is not a flaw of the terminology. The terms apply to the architecture of mature flowers (Endress 1994) and do not take into consideration floral organization and changes in symmetry during development and phylogeny. The same architecture forms occur convergently in many different clades with different organizations.

Kinds of Monosymmetry

1. The Lamiales are a group par excellence with elaborate monosymmetric flowers (see below). Almost all representatives have monosymmetric flowers. They are characterized by Vöchting's (1886) constitutional monosymmetry, and they include *Antirrhinum majus*, which served as model plant for the initiation of molecular developmental genetics of monosymmetry by Coen and collaborators (Coen 1996). Other groups of this category are large parts of Leguminosae and Asterales (fig. 1A).

2. Taxa with monosymmetric flowers also occur in groups with predominantly polysymmetric flowers. Monosymmetry here arises by a late ontogenetic modification and probably corresponds largely to Vöchting's positional monosymmetry.

spiral). *J*, Approximately polysymmetric flower: *Nigella damascena* (Ranunculaceae). *K*, Approximately monosymmetric flower: *Consolida ajacis* (Ranunculaceae). *L*, Asymmetric flower: *Hypserpa decumbens* (E 9270; Menispermaceae). *M–O*, Symmetry change of style head in Apocynaceae s.l. during development from disymmetric to polysymmetric: *Asclepias physocarpa* (E 6406). *M*, The two carpels beginning to unite postgenitally. *N*, The two carpels are completely united and have attained the pentagonal outline of the adjacent androecium. *O*, Transverse section of style head and adjacent anthers in *Vincetoxicum nigrum* (E 4690; Apocynaceae s.l.); the two vascular bundles of the two original carpels still present in the style head; the five edges of the style head are secretory (dark purple) and have secreted five clips and arms (dark red) that connect with the pollinia of the adjacent pollen sacs. Magnification bars: $L = 1$ mm; $D, E, N = 0.5$ mm; $O = 0.4$ mm; $F = 0.1$ mm; $M = 0.05$ mm. In all legends, "E" with voucher number is for "Endress."
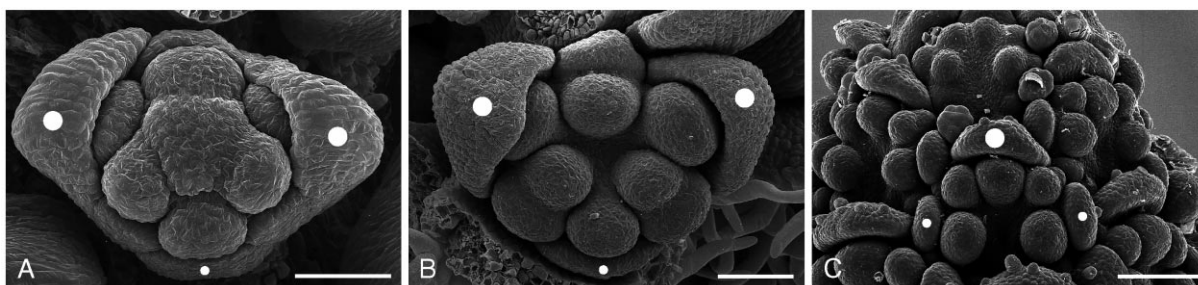
Fig. 2 Early monosymmetry in polysymmetric flower development, with tepals (sepals) on abaxial side (small dots) delayed as compared with those on adaxial side (large dots). *A*, *Bulbine frutescens* (E 9785; Asphodelaceae), young flower with tepals and stamens. *B*, *Veratrum album* (E 7465; Melanthiaceae), young flower with tepals and stamens. *C*, *Tiarella cordifolia* (E 7583; Saxifragaceae), upper part of young inflorescence, in one flower sepals marked with dots. Magnification bars = 0.1 mm.

In some cases, only the gynoecium is affected by curvature of the style and stigma; in other cases, both androecium and gynoecium are affected, e.g., *Geranium* (Geraniaceae), *Epilobium* (Onagraceae), *Pyrola* (Ericaceae), *Exacum* (Gentianaceae), *Solanum* (Solanaceae), *Gladiolus* (Iridaceae) (Hildebrand 1886; Vöchting 1886; Haeckel 1931; Nelson 1954). Often, such flowers are large and are pollinated by large animals, such as birds or bats, which approach the flowers from the side, e.g., *Adansonia*, *Chiranthodendron*, *Hibiscus*, and *Hibiscadelphus* (all Malvales); *Passiflora lobata* and *Passiflora mucronata* (Passifloraceae); and *Gloriosa* (Colchicaceae) (M. and I. Sazima 1978; Endress 1994) (fig. 1*B*, 1*C*).

3. A number of taxa show simple or simplified floral monosymmetry. Each flower consists only of a stamen and a carpel. There is no way to arrange those in a polysymmetric pattern. Such a simple pattern may occur as a potentially archaic condition (*Sarcandra*, Chloranthaceae); it may have evolved by reduction from moderately elaborate flowers in rosids (*Lacistema*, Flacourtiaceae) or from highly elaborate flowers in asterids (*Hippuris*, Antirrhinaceae; cf. Reveal et al. 1999) (fig. 1*D*–1*F*).

Kinds of Asymmetry

1. Most asymmetric flowers are highly complicated and highly ordered. They are in no way irregular, as the term "asymmetry" may imply. Here, asymmetry has evolved from monosymmetry. There are many examples within larger groups with predominantly monosymmetric flowers (e.g., Leguminosae, Lamiales, Orchidaceae, Zingiberales). In some taxa, two asymmetric morphs that are mirror images of each other are present (enantiomorphic flowers). There are three possible variants: (*a*) both morphs occur on the same individual (e.g., *Cyanella*, Tecophilaeaceae; Dulberger and Ornduff 1980; *Senna*, Leguminosae; Dulberger 1981; *Dialium*, Leguminosae; Tucker 1998), (*b*) the two morphs occur on different individuals of a species (*Wachendorfia*, Haemodoraceae; Ornduff and Dulberger 1978), or (*c*) cases where only one morph seems to occur in a species or larger group (e.g., *Lathyrus*, Leguminosae; Teppner 1988; Westerkamp 1993; *Vigna*, Leguminosae; Hoc et al. 1993; P. Endress, personal observation) (fig. 1*G*).

2. In a few basal angiosperms, there are unordered simple asymmetric flowers. In some *Zygogynum* species (Winteraceae), the innermost perianth parts and the stamens are all irregularly arranged (fig. 1*H*).

3. Asymmetric flowers may also evolve by reduction, simplification. The flowers of *Centranthus* (Valerianaceae) have a single stamen, which is not in the median plane, whereas the conspicuous spur is in the median plane; these flowers are also enantiomorphic (fig. 1*I*).

Development and Symmetry

Phyllotaxis and Symmetry

Floral phyllotaxis is a component of symmetry (Barabé and Jean 1998). However, floral symmetry, as it is perceived in mature flowers, is largely independent of phyllotaxis.

In phyllotaxis spiral, whorled, and irregular patterns can be distinguished. The examples discussed in this article have whorled floral phyllotaxis (except for Winteraceae with irregular phyllotaxis and simple forms with just one stamen, where these categories are not directly applicable).

Flowers with a spiral phyllotaxis may attain approximately the same three symmetry patterns as whorled flowers: (1) almost polysymmetric, if the flowers have a larger number of organs—this is the predominant case in spiral flowers (e.g., *Adonis*, *Nigella*, Ranunculaceae; Hirmer 1931; Schöffel 1932) (fig. 1*J*); (2) almost monosymmetric, if the flowers become dorsiventrally differentiated (e.g., *Aconitum*, *Consolida*, *Delphinium*, Ranunculaceae; Braun 1858; Mair 1977) (fig. 1*K*); and (3) asymmetric, if there are only few organs (e.g., *Hypserpa decumbens*, Menispermaceae; Endress 1995*a*) (fig. 1*L*).

Flowers with an irregular phyllotaxis tend to be asymmetric if they have a low number of organs (e.g., some species of *Zygogynum*, Winteraceae). They may also approach polysymmetry if they have many organs (e.g., some Annonaceae, Monimiaceae).

It has to be considered that during the long process of floral development from initiation to anthesis several levels of form are superimposed on each other. Floral phyllotaxis is established at the time the floral organs are initiated. In contrast, changes in symmetry may occur throughout development. They may lay in special developmental processes of the flower itself, or they may be influenced (especially in early phases) by the symmetry of the entire inflorescence. The mechanisms of
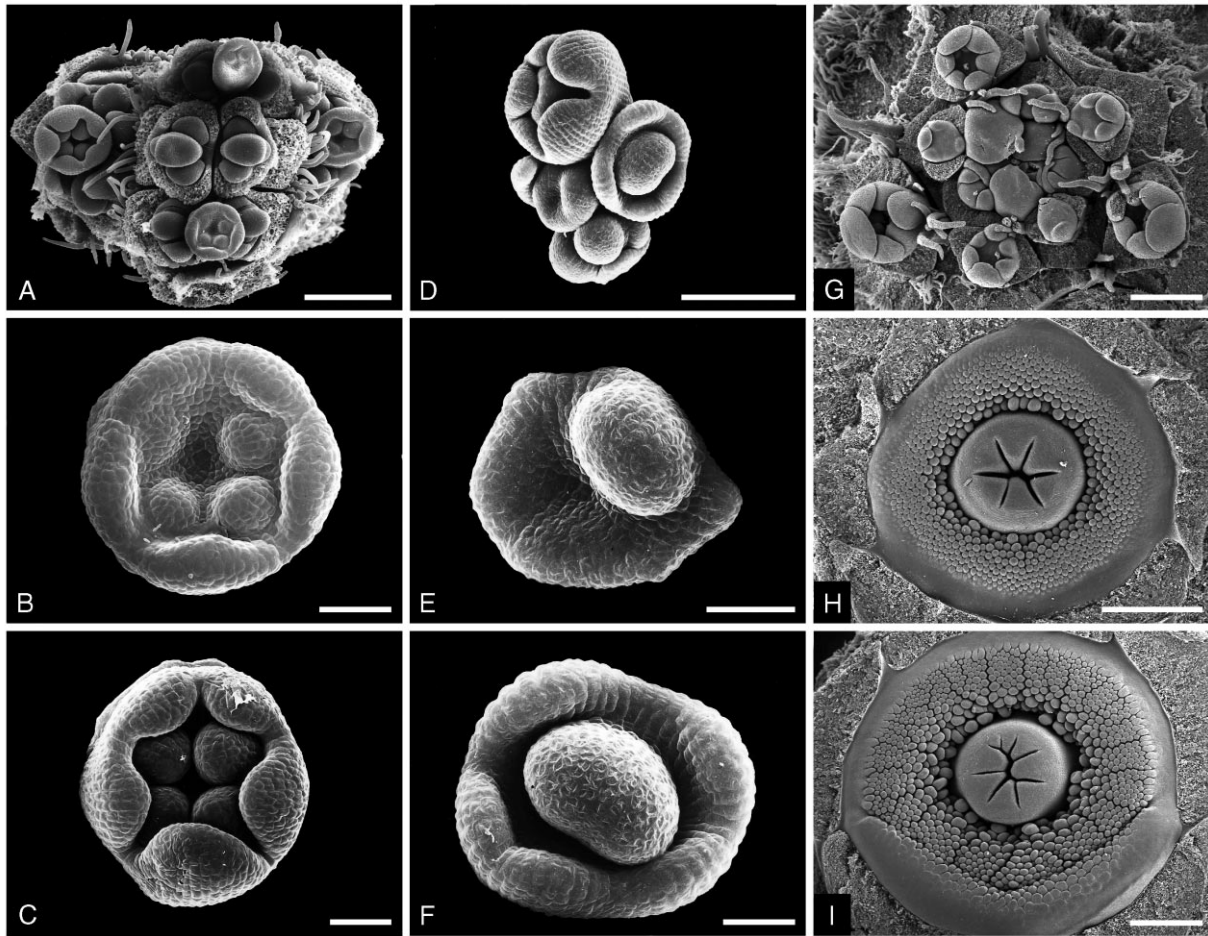
Fig. 3 *A–C*, Early asymmetry in monosymmetric flowers: *Patrinia gibbosa* (E 98-44; Valerianaceae). *A*, Upper part of young inflorescence. *B*, Flower with petals and stamens formed, left side delayed. *C*, Slightly older flower with asymmetry partly equalized. *D–F*, Asymmetry of flowers with a single stamen: *Centranthus ruber* (E 98-11; Valerianaceae). *D*, Monochasial partial inflorescence showing pendulum symmetry of subsequent flowers. *E*, Young flower with primordial petals and single stamen. *F*, Slightly older flower. *G–I*, Double change in floral symmetry during development: *Couroupita guianensis* (E 9393; Lecythidaceae). *G*, Inflorescence apex with young flowers: flowers monosymmetric by adaxial delay in development. *H*, Flower bud with young androecium and gynoecium: polysymmetric. *I*, Slightly older flower bud with incipient monosymmetry of androecium. Magnification bars: *G, H* = 0.5 mm; *A* = 0.25 mm; *D* = 0.2 mm; *B, C, E, F* = 0.05 mm.

these changes, genetic and epigenetic, are largely unknown. However, comparative studies over a large range of plants may help in finding hypotheses about such underlying mechanisms.

Changes of Symmetry Patterns in Development

Early monosymmetry in polysymmetric flowers. Changes of floral symmetry during development have long been known. It seems that symmetry of flowers in early development is influenced by the entire system of which the flowers are a part, i.e., the inflorescence. Only later do the flowers become more independent and their own symmetry more prominent (see also Goebel 1908, 1928). In many plants with polysymmetric flowers, floral development begins pronouncedly monosymmetric, especially in spikes or racemes.

For example, in many plants the abaxial half of the flower is delayed in early development. It may be speculated that this is caused by the floral subtending bract. When this bract is formed, it uses up part of the meristem that gives rise to the

floral meristem, and therefore the floral meristem is initially weakened on the side adjacent to the bract. Another explanation would be pressure by the subtending bract as a cause of a delay in development of the abaxial half of the young flower. Examples are present in all larger clades of the angiosperms (e.g., *Euptelea* [Eupteleaceae; Endress 1986], *Adoxa* [Adoxaceae; Erbar 1994], *Chrysosplenium* [Saxifragaceae; Ronse Decraene et al. 1998], *Bulbine* [Asphodelaceae], and *Veratrum* [Melanthiaceae; both Endress 1995*b*]) (see also fig. 2*A*–2*C*).

In flowers where a subtending bract is highly reduced or lacking, such a gradient may be lacking, e.g., in *Achlys* (Berberidaceae; Endress 1989), Araceae (Buzgo 1999), and *Potamogeton* (Potamogetonaceae; Posluszny and Sattler 1974). The gradient may also be reversed so that the adaxial half of the flower is delayed in early development, such as in *Acorus* (Acoraceae; Buzgo 1999) or *Nymphaea* (Nymphaeaceae; Cutter 1957). This reversed gradient may even be present in flow-

ers with a subtending bract, e.g., in *Trochodendron* (Trochodendraceae; Endress 1986). In Saururaceae, where the flowers have a subtending bract, both gradients were found (Tucker et al. 1993). A possible explanation for an adaxial delay despite the presence of a subtending bract is that the bract is precocious to such an extent that the young floral meristem is no longer abaxially weakened when the first floral organs appear on the flower primordium. In contrast, the floral gradient here may reflect the developmental gradient of the main shoot, the shoot being less developed on the adaxial side than on the abaxial side of the flower.

As a working hypothesis, we may assume the presence of two developmental gradients: (1) main shoot (acropetal gradient) and (2) subtending bract (basipetal gradient). The flower primordium is under the influence of these two gradients of opposite directions. The gradient of flower development will be different depending on the strength of the two superimposed gradients. The stronger the main shoot gradient and the weaker the bract gradient, the more the young flower will be adaxially delayed, and vice versa; i.e., the weaker the main shoot gradient and the stronger the bract gradient, the more the young flower will be abaxially delayed. If the strength of the main shoot gradient and the bract gradient are approximately equal, the young flower will be evenly developed.

Early asymmetry in monosymmetric or polysymmetric flowers. The influence of the entire inflorescence on floral symmetry is even more striking in cymose, especially monochasial, inflorescences. Here, early floral stages are often asymmetric. In some cases, even the mature flowers are prominently asymmetric (*Centranthus*, Valerianaceae, see below; *Qualea*, Vochysiaceae; Eichler 1878). It should be added that there are also asymmetric flowers in racemose inflorescences, where asymmetry is superimposed on a monosymmetric pattern during development (many Leguminosae; *Pedicularis*, Orobanchaceae; see below).

In *Patrinia* (Valerianaceae), the flowers have four stamens and are monosymmetric (with the adaxial stamen lacking) at anthesis. However, early development is asymmetric (fig. 3*B*, 3*C*) (and the internal structure of the gynoecium remains asymmetric in having only one fertile carpel in lateral position). The flowers are in dichasia; the peripheral branches of the system are often monochasial. Floral asymmetry in *Patrinia* follows two rules, as shown by Hofmann and Göttmann (1990): (1) in early floral development the two stamens on the side toward the weaker subsequent ramification of the dichasium appear earlier than their counterparts, and the abaxial stamen of these two appears earlier than the adaxial (fig. 3*A*); and (2) the fruit wing develops on the side of the fertile ovary locule, which is always turned away from the second-preceding flower of the branching system and at the same time adjacent to the subsequent flower. This is also the case in *Morina* (Morinaceae; Hofmann and Göttmann 1990).

In *Centranthus* (Valerianaceae), floral asymmetry is still more pronounced because the androecium is more reduced and only one lateral stamen is left. Thus, the flowers appear asymmetric (fig. 3*E*, 3*F*) also at anthesis (fig. 1*I*). The stamen and the fertile ovary locule of each flower are turned toward the symmetry plane of the system, or, more precisely, the stamen is adjacent to the preceding flower of the monochasium and the fertile locule of the gynoecium is adjacent to the subsequent

flower (Goebel 1908). Thus, in *Centranthus* the sequence of flowers along a monochasium shows a regular change of chirality (enantiomorphy). Seen as an entity, this regular pattern of asymmetric flowers forms a kind of a monosymmetric superstructure (see also Wichura 1846; Goebel 1908) (fig. 3*D*). This kind of symmetry is known as pendulum symmetry; it is still more common in vegetative shoots than in inflorescences (Goebel 1928; Charlton 1998). A similar condition is present in Marantaceae with asymmetric flowers, where flower pairs (but here not monochasia) are regularly enantiomorphic (Eichler 1875; Kirchoff 1983; Kunze 1985), whereas, in the related Cannaceae, subsequent flowers (although in monochasia) are not enantiomorphic (Eichler 1875; Kirchoff 1983).

More than one change in symmetry. There are also more complicated flowers with more than one change in symmetry during development. In floral development of *Couroupita* (Lecythidaceae), at first the upper half of the young flower is retarded (fig. 3*G*). It later becomes polysymmetric when the inner organs, stamens, and carpels are initiated (fig. 3*H*). The stamens are numerous, and they develop from a large ring meristem in centrifugal direction. However, later there is another change back to monosymmetry (fig. 3*I*). The lower sector of the androecium conspicuously proliferates and forms a tonguelike part with sterile stamens, which have a particular function in pollination biology (Prance 1976). Thus, in *Couroupita* there are two changes of symmetry during floral development, from monosymmetric to polysymmetric and back to monosymmetric (Endress 1994).

Symmetry in individual organisms is never perfect in a mathematical sense. There are always small deviations (fluctuating asymmetry). Symmetry with only a minimal amount of deviation is maintained in flowers with a high degree of synorganization of organs. Peaks of synorganization are present in Orchidaceae and in Apocynaceae (including asclepiads) (see also Endress 1990, 1994; Endress and Bruyns 1999). Asclepiads have extremely complicated flowers. The most peculiar feature is an apparatus for pollen transfer, a so-called pollinarium. This is formed by close synorganization between androecium and gynoecium. The style head of the gynoecium secretes a clip and two arms, which connect with the pollen masses of the two adjoining anther thecae (Demeter 1922; Schnepf et al. 1979). Five such pollinaria are formed in each flower. In the mature flower, they are presented exactly between five guide rails, each differentiated by two adjoining anther flanks. They guide legs or other insect parts directly into the clip, which attaches to the insect.

This synorganization requires a highly exact symmetry, which is obvious in transverse sections. The style head in the center has five edges, which form the five clips, and they are exactly between the adjacent locules of two anthers (fig. 1*O*). It is interesting that this precisely pentasymmetric style head is disymmetric in the beginning because the gynoecium is dimerous. It starts development with two free carpels (fig. 1*M*). Later the carpels unite postgenitally and the outline of the gynoecium becomes pentasymmetric, caused by the five stamens that act like a mold for the apical part of the gynoecium (fig. 1*N*). Furthermore, it was shown for *Catharanthus roseus* that the two carpels are different in size in earliest development (Verbeke in Mlot 1998).

Thus, in the gynoecium of *Catharanthus* (and probably in

other Apocynaceae as well) there is a developmental change from monosymmetry to disymmetry and from disymmetry to polysymmetry (at least in the apical part). Furthermore, the example shows that the individual form of an organ may later be modified by neighboring parts. Although it has not been experimentally shown that the style head is actively molded by the adjoining anthers, this may be expected from the requirement of a high degree of precision for the functioning of the entire apparatus. This interplay of individual shape (*Eigenform*) and imprinted shape (*Anpassungsform*) is an interesting problem in the study of symmetry in plants and animals (e.g., Endress 1975, 1994; Grasshoff 1996).

Irregularities in early development do not impede later symmetry. In phyllotaxis hypotheses in which inhibition fields govern pattern formation, the regular sequence of organ initiation is important. Each newly formed organ determines (together with the pattern established by earlier organs) the position of the subsequent organ. This is obvious in vegetative apices with relatively long plastochrons and continuity of formation of the same organ type. In flowers the situation is often different. Plastochrons are shorter, and there is a regular change of organ categories. It is intriguing that the appearance of floral organs of a whorl is sometimes not simultaneous (or in a very rapid spiral sequence), as one would expect, but irregular and unpredictable or in adaxial or abaxial direction, and this without having an effect on the position of the subsequent organs and the symmetry of the flower (Erbar and Leins 1985, 1997; Tucker 1989*a*; Endress 1992; Douglas and Tucker 1996*b*; Lyndon 1998). Flowers are more complicated, more integrated systems than vegetative shoots, especially flowers with fixed number and position of organs, and it may be expected that the genetic/epigenetic mechanisms are also more integrated, so that the position of the inner organs is determined not successively by the position of the next outer organs during development but simultaneously with the outer organs.

Appearance times of organ primordia of different organ categories may overlap (Tucker 1984*b*, 1989*b*; Erbar and Leins 1997). The question is whether the organs are really initiated at different times. Initiation precedes appearance, and it should be investigated whether the time discordance develops in this interval or whether it is present from the beginning (see also Endress 1992). The result of organ initiation is first seen histologically by meristem activation of the floral apex before a bulge appears at the surface. It is curious that Alexander Braun also noted (Goebel 1924*b*) that organ primordia may be present without being visible from the outside and that this was later claimed to be a shortcoming of idealistic morphology by Goebel (1924*b*, p. 86). For example, Goebel (1924*b*) mentioned the "missing" subtending bracts of Brassicaceae, which, indeed, were later found to be initiated but no longer visible in older stages (Hagemann 1963).

However, Goebel (1924*a*) also mentioned that the position of the organs is already defined before primordia are visible. This is what was later expressed with the cascade model of gene action in flower development, in which a sequence of activity of cadastral genes and organ identity (homeotic genes) was postulated (Coen and Meyerowitz 1991).

Function and Evolution of Symmetry

Evolution of Elaborate Monosymmetry from Polysymmetry

The evolutionary transition from polysymmetry to elaborate monosymmetry as it appears in so many large plant groups is especially prominent in flower evolution. However, the question of how this transformation was attained has rarely been addressed. What were the steps from polysymmetric to monosymmetric flowers?

Robertson (1888) was perhaps the first to attempt an explanation from the point of view of selection by the action of pollinators, especially bees (see below). As a rule, monosymmetric flowers are borne in lateral, rather than terminal, position (in spikes, racemes, or thyrses). They are commonly directed more or less sideways, so that their lower and upper halves have different shapes (Schneckenburger in Mohl 1837; Dafni 1994). In a number of groups with polysymmetric flowers, the flowers, if directed sideways, may also attain a slightly monosymmetric shape by the bending of stamens and style, which may be induced by gravity (positional monosymmetry; see Vöchting 1886, and examples cited above). This common phenomenon may have been a predisposition for the convergent evolution of more elaborate constitutional monosymmetry in a number of angiosperm groups.

Large successful groups with monosymmetric flowers, such as Lamiales s.l., Orchidaceae, Zingiberales, and Leguminosae must have attained monosymmetry in the beginning of their phylogeny. There was time for the genetic/epigenetic mechanism of monosymmetry development to become elaborate and autonomous (constitutive), largely independent of the influence of gravity (see also Coen 1991). Monosymmetry is here expressed early in floral development, in many groups by complete loss of particular organs. Thus, in these clades the advent of monosymmetry could have been a key innovation, which was accompanied by an explosive radiation (Coen and Nugent 1994; Endress 1998, 1999). In other families or orders with only exceptional monosymmetric species among predominantly polysymmetric taxa, these species show only superficial monosymmetry, not autonomous but induced by gravity, depending on the position of the flower.

Studies on the visual pattern attractiveness to bees by Lehrer et al. (1995) show that bees prefer symmetrical radiating shapes and monosymmetric shapes with a perpendicular symmetry plane over all other patterns. These two patterns are precisely what occur most frequently in flowers. In addition, the nectar guides also have this pattern (Dafni and Kevan 1996). If this preference of monosymmetric shapes by bees was present since the time monosymmetric flowers originated, it may have been an extrinsic motor for the radiation of plants with monosymmetric flowers.

It may be speculated that the evolutionary start for monosymmetry was flowers on racemes, spikes, or thyrses that were horizontally directed and that had some capability of gravitropic structural modification from original polysymmetry, as it is present also in the vegetative region of many plants. Such slightly superficially monosymmetric flowers were selectively furthered by bee pollination. As a landing place, either stamen and style or the lower petals were used. Accordingly, the flow-

ers became sternotribic or nototribic, which led to greater pollen economy. In addition, in some taxa, the pollination organs became included in the lower petals (keel flowers) or upper petals (lip flowers), which further enhanced pollen economy (e.g., Westerkamp 1997). Similar arguments were discussed by Robertson (1888) and Stebbins (1974), and more aspects were added by Neal et al. (1998). Another advantage of monosymmetry may be the enhanced diversity of possible visual patterns (Davenport and Kohanzadeh 1982). Coen et al. (1995) and Bradley et al. (1996) point out that the correlation between racemose (indeterminate) inflorescences and monosymmetric flowers may also result from a developmental constraint. This is indicated by the *centroradialis* (*cen*) mutant in *Antirrhinum*, which effects determinate inflorescences with polysymmetric terminal flowers.

In the taxa with elaborate monosymmetric flowers, sympetaly and other kinds of fusions or mechanical connections of unfused floral parts for stabilization are predominant. A monosymmetric flower of this type is a highly integrated apparatus that needs mechanical robustness to ensure mechanical function of the parts that are worked by sometimes heavy and forceful bees or other animals.

A special kind of monosymmetric flowers, the evolution of which from polysymmetric ones can relatively easily be traced, are heterantherous pollen flowers in some groups of otherwise mainly polysymmetric flowers. In pollen flowers there is a trend to evolve stamen heteromorphy with some feeding stamens and only a small number of large pollinating stamens in a monosymmetric arrangement (Vogel 1978). This trend culminates in the presence of a single fertile stamen on the abaxial side of the flower. This has evolved in several families: *Testulea* (Ochnaceae; Pellegrin 1924), *Solanum* sect. *Androceras* (Solanaceae; Bowers 1975; Whalen 1978), *Rhynchanthera* species (Melastomataceae; Renner 1990), *Pyrrorhiza neblinae* (Haemodoraceae; Simpson 1990), and Philydraceae (Hamann 1966).

Another special case is Fumarioideae (Papaveraceae). The floral ground plan is with dimerous whorls. The basic pattern is therefore disymmetric. This is present in the basal genus *Hypecoum* and still more pronounced in *Dicentra* and related genera (Lidén et al. 1997) because it has two spurs in one symmetry plane. From here, there is an evolutionary trend to monosymmetry by reduction of one of the two spurs (as in *Corydalis*). The symmetry plane here is transverse and not median; however, the open flowers are turned in such a way that the symmetry plane is secondarily vertical. Flowers can revert to disymmetry in two ways. They can regain two spurs, as exceptionally observed in *Corydalis solida* (Goebel 1928) or *Corydalis sempervirens* (Ryberg 1955), or they can lose both spurs, as in *Corydalis cheilanthifolia*. In this species the flowers are dimorphic: in addition to normal monosymmetric flowers, there are reduced disymmetric flowers, which do not produce any nectar and are cleistogamous (Ryberg 1955; P. Endress, personal observation). Thus, they represent a peculiar evolutionary transition from monosymmetry to disymmetry by reduction.

Among the basal angiosperms (magnoliids), there are no monosymmetric flowers (except for simplified patterns, see paragraph 3 in "Kinds of Monosymmetry"). Among basal eudicots, monosymmetric flowers are rare (Proteaceae, Doug-

las and Tucker 1996a; Douglas 1997; Delphinieae of Ranunculaceae, Mair 1977; some Fumarioideae of Papaveraceae, see above). Among rosids and especially asterids, they are much more common and constitute some very large groups. In the fossil record, the first monosymmetric flowers appear in the Upper Cretaceous (Turonian) and are tentatively associated with Capparales (Crepet 1996). In terms of angiosperm evolution, this is relatively late but is not surprising in view of the systematic distribution of monosymmetric flowers among the extant angiosperms.

### Evolution of Elaborate Asymmetry from Monosymmetry

The human body is perfectly monosymmetric at the surface. However, it is considerably asymmetric as seen from the inside. The heart is on the left side; the lung has three lobes on the right side but only two on the left, and so on. It is remarkable that this asymmetry is always in the same direction. However, one in 20,000 human individuals has a mirror-image inversion of organ placement. This usually does not cause any adverse effects (see Levin and Mercola 1998). The presence of asymmetric traits superimposed on a monosymmetric ground pattern seems to be predominant in animals (Palmer 1996a, 1996b). This is also true for many seemingly monosymmetric flowers. As a more complicated variant, in echinoderms body shape changes from monosymmetric to asymmetric to polysymmetric (e.g., Lowe and Wray 1997), which is reminiscent of the floral examples with more than one symmetry change that were discussed above.

It was proposed that the cause of the constant one-sided internal asymmetry in many animals was chiral molecules at a certain point in early development, which always bring the body to the same one-sidedness (Brown and Wolpert 1990). Molecular developmental genetic studies attempt to find key genes that determine asymmetry development in the entire vertebrates (e.g., Harvey 1998; Hyatt and Yost 1998; Levin and Mercola 1998; Ryan et al. 1998). A recent discovery is directed motion of cilia in mouse embryos that may concentrate left-right determinants on one side of the embryo (Nonaka et al. 1998; Vogan and Tabin 1999). In plants, enantiomorphic mutants were described for *Arabidopsis*: *tortifolia* (*tor 1* and *2* cause dextrorse twist, *tor 3* causes sinistrorse twist of petioles in *Arabidopsis* [by chiral cell expansion] [Fabri et al. 1996]). However, their developmental mechanisms are unknown. Asymmetry in flowers has not yet been studied by molecular developmental genetics.

Leguminosae are well known for their monosymmetric flowers. On a closer look, a surprising number of them have a twist into asymmetry (Goebel 1924a). In Faboideae the subtribe of the beans, Phaseolinae, is asymmetric. Their keel is curved or even coiled to one side (fig. 1G). The same is true for *Lathyrus* of Vicieae and for some other Faboideae (see above). In Caesalpinioideae flowers, there is no keel, but in species of *Chamaecrista* and *Senna* the gynoecium and stamens are curved to one side.

What is the significance of this asymmetry? Older morphologists, such as Goebel (1924a) and Troll (1928), were too presumptuous in saying that asymmetry in legume flowers was without any functional significance. This was contradicted in the 1980s by several authors who conducted pollination ex-
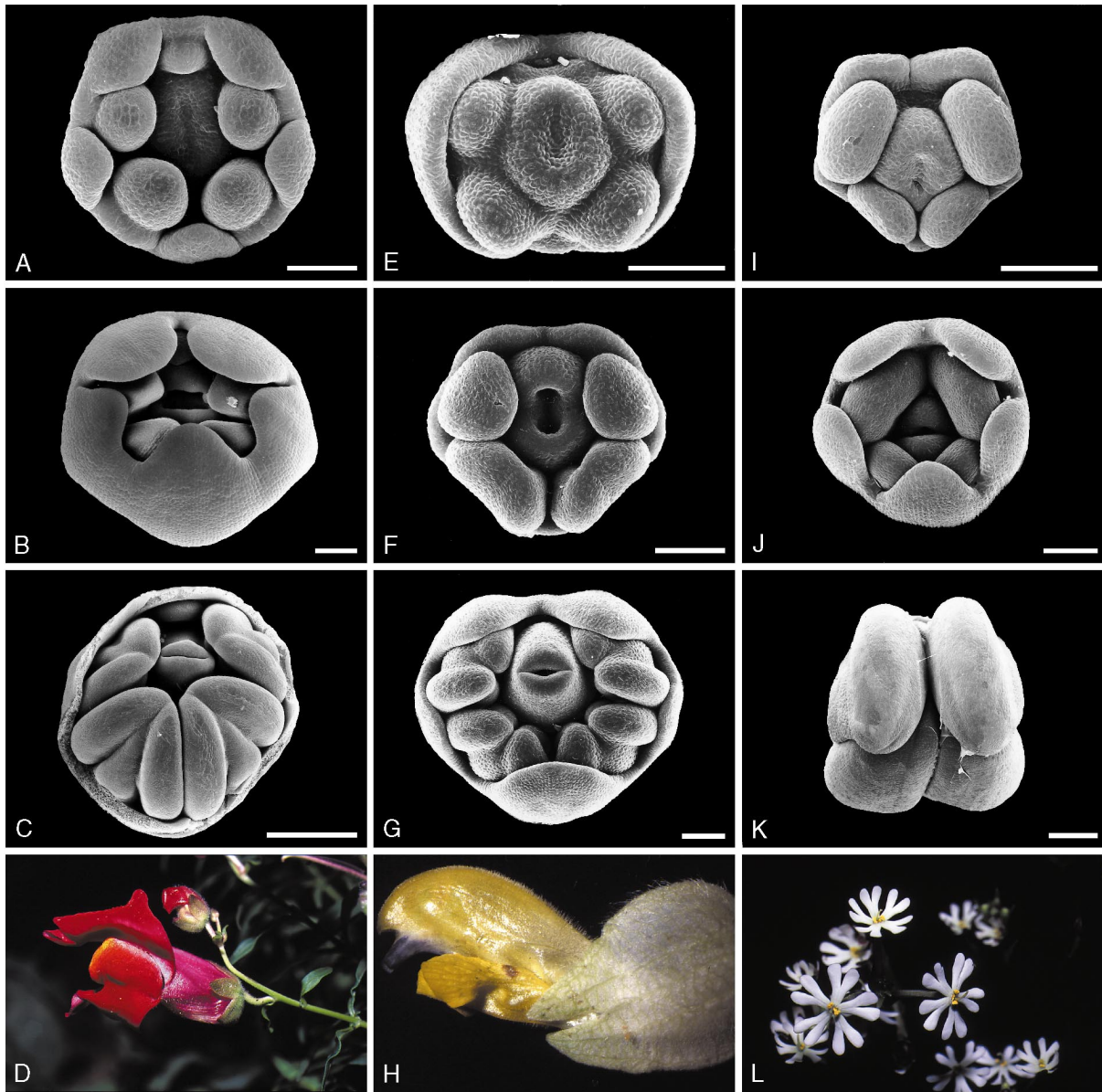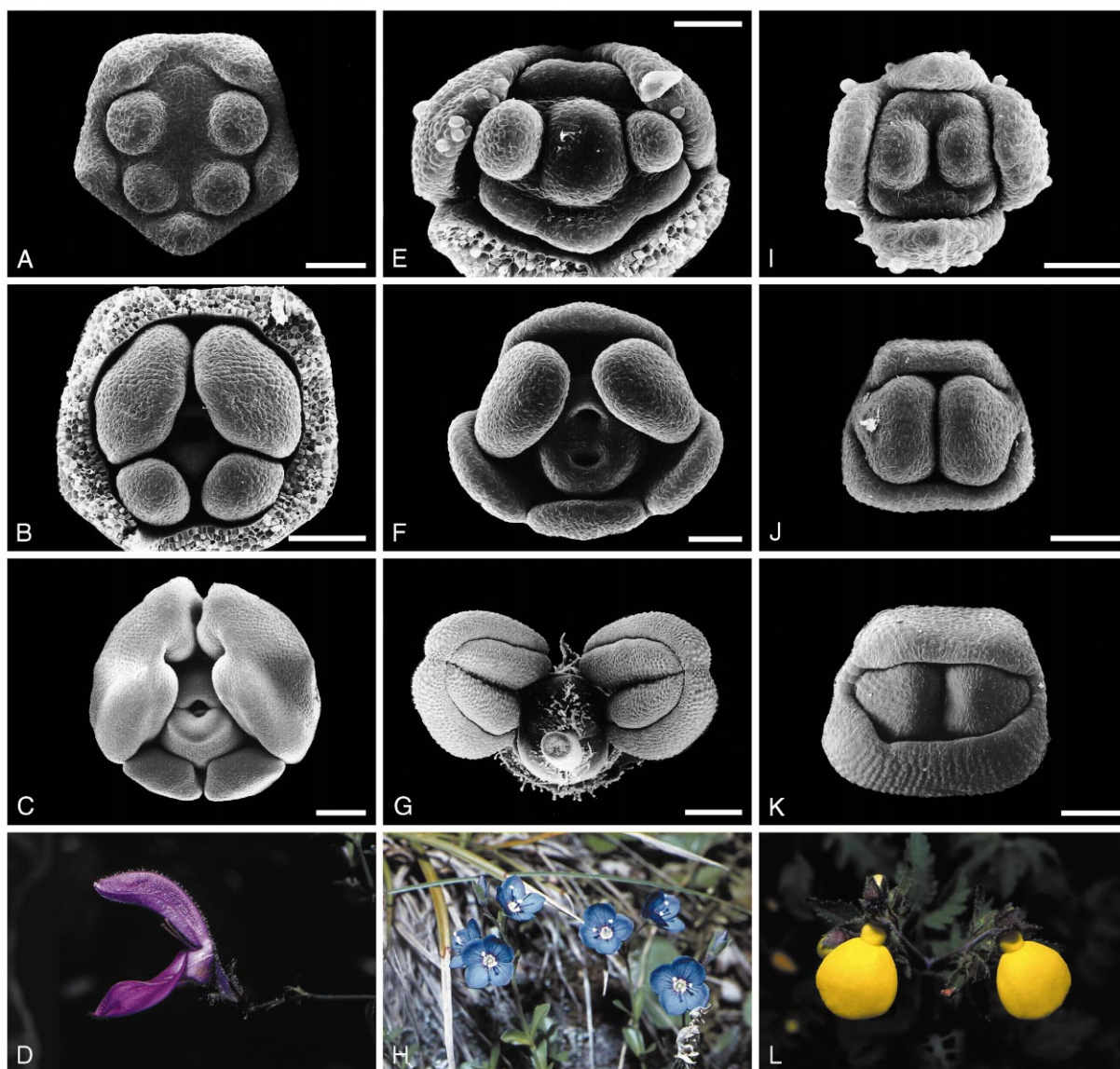
Fig. 4 Floral development in Lamiales; flowers with four fertile stamens. *A–D*, *Antirrhinum majus* (E 9984; Antirrhinaceae). *E–H*, *Rhinanthus alectorolophus* (E 98-13; Orobanchaceae). *I–L*, *Zaluzianskya capensis* (E 9860; Scrophulariaceae s.str.). Magnification bars: *C* = 0.5 mm; *L* = 0.2 mm; *A*, *B*, *E–G*, *I*, *J* = 0.1 mm.

periments on various taxa. They found in species of *Macroptilium* (Brizuela et al. 1993), *Vigna* (Hoc et al. 1993), *Lathyrus* sect. *Lathyrus* (Teppner 1988; Westerkamp 1993), and *Lotus* sect. *Simpeteria* (Cooper 1985) that pollen deposition on large bees (such as *Xylocopa*, *Centris*, and *Megachile*) was at a relatively small spot laterally (pleurotribic) on the head, thorax, leg, or wing, a spot that was not contaminated by pollen of other plants with another floral symmetry or size and that would ensure pollen deposition on a stigma of the same species. Darwin (1857) observed pleurotribic pollination in beans (*Phaseolus*). From the fragmentary knowledge of these asymmetric Faboideae, it seems that a single morph is present in a species or larger group (see also Schmucker 1924 and

above). The significance would be in economic pollination and (interspecific) genetic isolation, which would be enhanced with the step from monosymmetry to asymmetry still more than with the earlier step from polysymmetry to monosymmetry. It may also be speculated that it is more economical for bees to work a relatively complicated asymmetric flower form that needs some force always from the same side. Learning to handle complicated flowers takes time and may also be seen in light of the evolution of flower constancy in bees (Darwin 1876; Laverty 1980, 1994; Waser 1983; Lewis 1993).

In contrast to Faboideae, among Caesalpinioideae in *Cassia* s.l. (*Chamaecrista, Senna*) species, the style may be curved to the left or to the right (both morphs in the same inflorescence),

Fig. 5 Floral development in Lamiales; flowers with two fertile stamens. *A–D, Brillantaisia lamium* (E 98-10; Acanthaceae). *E–G, Veronica spicata* (E 10030; Antirrhinaceae). *H, Veronica fruticans* (Antirrhinaceae). *I–L, Calceolaria tripartita* (E 9972; Scrophulariaceae s.l.). Magnification bars: *G* = 0.5 mm; *B, C, I–K* = 0.1 mm; *A, E, F* = 0.05 mm.

which may or may not be part of an outbreeding mechanism, depending on the flowering strategy of the plant (e.g., Dulberger 1981; Bahadur et al. 1991; Fenster 1995). In *Delonix regia*, the nectar gate is asymmetric, between the median adaxial stamen and one of the two adjacent stamens (Lindman 1902); both morphs are present in the same individual (Endress 1994).

In other families with elaborate keel or lip flowers, asymmetry with only one floral morph also occurs. It was found in keel flowers of *Polygala* (Polygalaceae; Westerkamp and Weber 1997) with probably lateral pollen deposition on the pollinators. Among lip flowers, asymmetry occurs in part of *Pedicularis* (Orobanchaceae, see below) by rotation of the corolla to the left side (Wichura 1852; Müller 1881). Müller

(1881) mentioned that this asymmetry makes it easier for the pollinating bumblebees to exploit these flowers. In orchids, asymmetric flowers are known from a number of genera. However, their significance in pollination biology has only rarely been studied (e.g., *Tipularia*; Stoutamire 1978).

Case Studies

Monosymmetry in Antirrhinum *and Lamiales s.l.*

Antirrhinum.   The snapdragon (*Antirrhinum majus*) has become the model plant for studies of monosymmetric flowers. Enrico Coen and his collaborators were instrumental in these studies (Carpenter and Coen 1990; Coen 1991, 1996; Coen
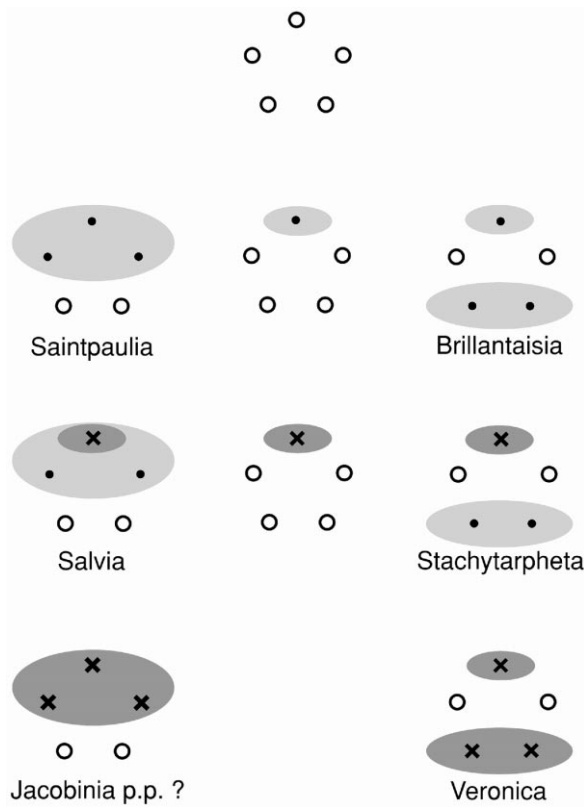
Fig. 6 Monosymmetric flowers in Lamiales s.l.; patterns of androecium reduction. Middle column, reduction of adaxial stamen. Left column, reduction of adaxial stamen and upper stamen pair. Right column, reduction of adaxial stamen and lower stamen pair (circles: fertile stamens; dots: sterile stamens; crosses: stamens completely lost; light shading: area of stamen reduction; dark shading: area of stamen loss).

and Meyerowitz 1991; Coen and Nugent 1994; Coen et al. 1995; Luo et al. 1996).

The flowers have a stable organization with 17 organs. Calyx, corolla, and androecium have five organs each in alternating whorls. The gynoecium has two carpels. Monosymmetry is expressed especially in corolla and androecium. The two upper petals form the upper lip; the three lower petals, the lower lip (fig. 4D). The adaxial (uppermost) odd stamen,

which is the one in the symmetry plane, is reduced. It remains as a tiny staminode in the mature flower (fig. 4C). This configuration is also representative of the majority of the relatives of *Antirrhinum*.

Initially, the flower is almost polysymmetric. But from the beginning, the adaxial stamen is slightly smaller and retarded (fig. 4A). This becomes more pronounced during development. Slightly later, the monosymmetry of the corolla becomes apparent (fig. 4B).

An ecological (architectural) reason for the reduction of the adaxial stamen is that the flowers of *Antirrhinum* and of most of its relatives have their pollination organs curved into the upper part of the flower, and pollination mostly happens via the head of the pollinators (Robertson 1888; review by Kampny 1995). With this architecture, the style and stigma occupy the upper median position, so that the presence of the adaxial stamen would be disadvantageous for the functioning of the flower. The remaining four stamens often are synorganized in pairs.

With the help of polysymmetric *Antirrhinum* mutants, so-called pelorias, Coen and coworkers found the gene *cycloidea* to be important in establishing floral monosymmetry. *Cycloidea* is expressed specifically in the uppermost (adaxial) region of the young flower in a very early stage of development, when the flower is still polysymmetric (Luo et al. 1996). It is the region where the upper lip will be formed and where the adaxial stamen will be reduced. In mutants with abnormal polysymmetric flowers, the pelorias, this gene is not present. Other genes that also play a part in the development of monosymmetry in *Antirrhinum* flowers are *divaricata* and *dichotoma* (Almeida et al. 1997).

Lamiales s.l. Similar flower symmetry patterns are common in the relatives of *Antirrhinum*. This is a large group, Lamiales s.l., with some 17,000 species. Fortunately, this clade is now under intensive phylogenetic study, especially by R. Olmstead and his collaborators (Olmstead et al. 1993). This is an important basis for evolutionary interpretations of changes in floral characteristics, including floral symmetry.

I am interested in the diversity in development of the corolla and especially the androecium in Lamiales s.l. I screened the literature and I studied the floral development of species of ca. 50 genera of different families of the Lamiales in an ongoing long-term project (see also Endress 1998 for an earlier stage of the project).

For the corolla, the presence of two lips is characteristic for
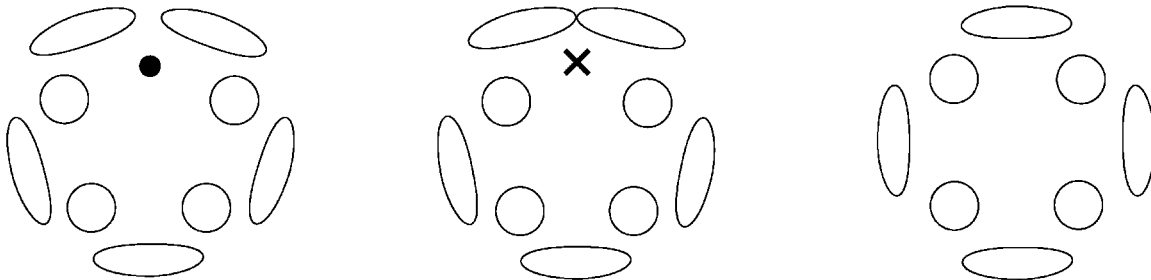
Fig. 7 Potential evolutionary transition from a pentamerous monosymmetric flower to a tetramerous polysymmetric flower by progressive reduction of the uppermost floral sector.
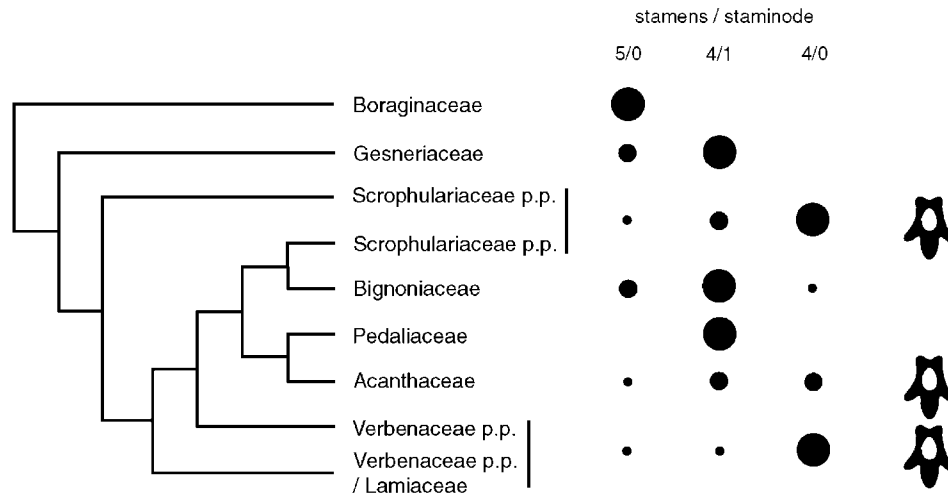
Fig. 8 Simplified cladogram of the Lamiales s.l. based on *rbc*L and *ndh*F sequences after Olmstead and Reeves (1995; redrawn after Endress 1998). The size of the dots indicates the predominance of the respective pattern (five stamens/four stamens and an odd staminode/four stamens and no staminode); the families with predominant highly monosymmetric lip flowers are marked with a lip flower sign. Boraginaceae are assumed to be the sister group of the Lamiales s.l.

the majority of Lamiales s.l. Most representatives show the same configuration as that mentioned for *Antirrhinum*: two petals form the upper lip and three petals form the lower lip. This configuration is termed the 2 : 3 pattern (Donoghue et al. 1998), but other patterns also occur: the 4 : 1 pattern, e.g., in *Hebenstretia* (Scrophulariaceae) and in *Perovskia* (Lamiaceae), and the 0 : 5 pattern, e.g., in *Crossandra* (Acanthaceae) and in *Teucrium* (Lamiaceae) (see also Donoghue et al. 1998). In the corolla there are also different aestivation patterns that are characteristic for larger groups and that are produced by different developmental modes of the corolla after initiation of the petals (e.g., Armstrong and Douglas 1989).

The family Scrophulariaceae seems to exhibit the greatest diversity of floral forms of all families of the Lamiales *sensu lato*. This may be less surprising in the light of recent molecular systematic results. The Scrophulariaceae in the traditional circumscription turned out to be highly polyphyletic. At least three major clades that are separated from each other by other families can be distinguished: Scrophulariaceae s.str., Antirrhinaceae (including *Antirrhinum* and the bulk of the former Scrophulariaceae), and Orobanchaceae (including the hemiparasitic genera of the former Scrophulariaceae plus the former

Orobanchaceae); in addition, there are several smaller clades that include segregates of the former Scrophulariaceae (Olmstead and Reeves 1995; Young et al. 1997; Nickrent et al. 1998; Olmstead et al. 1998; Reeves and Olmstead 1998; Reveal et al. 1999).

The degree of reduction of the odd stamen in the Scrophulariaceae in the traditional sense is diverse. There are two major groups that consistently seem to lack an odd staminode from the beginning of development. The first is the Orobanchaceae. Developmental similarity of the former Pedicularieae and Orobanchaceae fits with the results of molecular studies by De-Pamphilis et al. (1997), Young et al. (1997), and Nickrent et al. (1998), who include Pedicularieae in Orobanchaceae (fig. 4E–4H).

The second group with a missing odd stamen is the South African tribe Manuleae of the Scrophulariaceae s.str. (fig. 4 I–4K). This is surprising, since the floral architecture is relatively polysymmetric (fig. 4L). There is a contrast between polysymmetry of the corolla and pronounced monosymmetry of the androecium (see Hilliard 1994). Still more surprising is that in this group not only the odd staminode is missing but, in addition, the two remaining stamen pairs have very different lengths, so that monosymmetry of the androecium is still more pronounced (fig. 4I–4K). It may be a sign that this clade went through a phase of stronger floral monosymmetry in its phylogeny.

In another clade of Scrophulariaceae s.str., containing *Verbascum* and *Scrophularia*, the flowers are also only weakly monosymmetric, but the odd stamen is relatively large and in *Verbascum* even fertile. Thus, in Scrophulariaceae s.str., the odd stamen runs the entire gamut, from fertile to lacking.

The molecular systematic studies by Olmstead and Reeves (1995) have revealed that two genera, *Hippuris* and *Callitriche*, both water plants with extremely reduced flowers, evolved within Antirrhinaceae. In *Hippuris*, each flower has a single stamen and carpel and a tiny collar-like perianth (fig. 1F). The
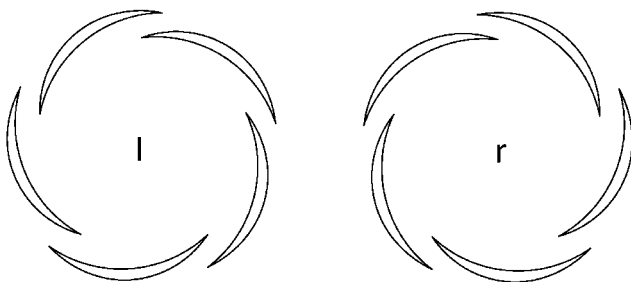
Fig. 9 Diagrams of left-contort (sinistrorse) and right-contort (dextrorse) corollas.
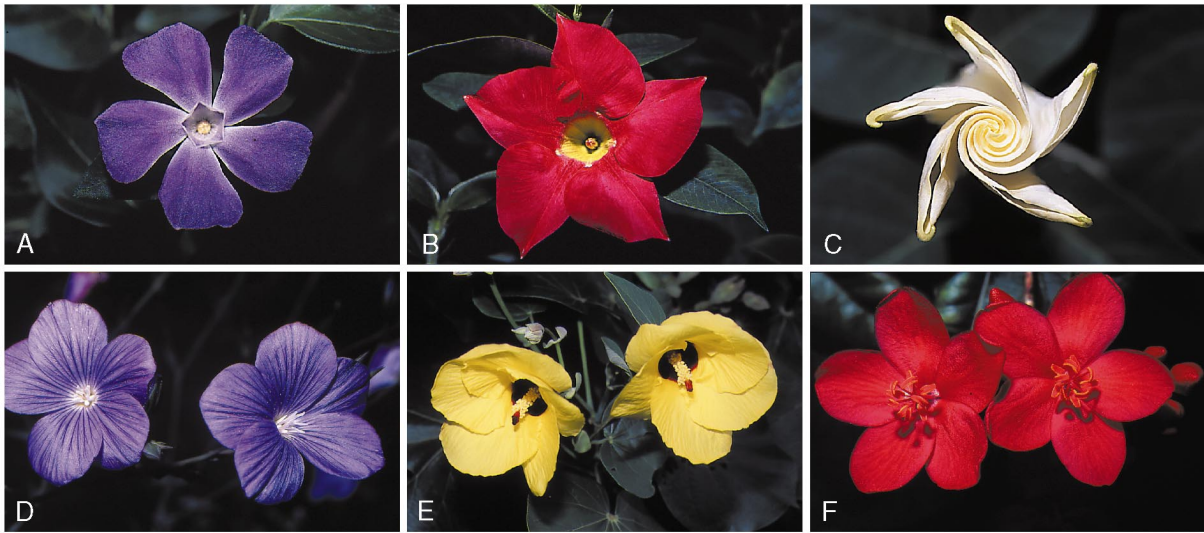
Fig. 10 *A–C*, Plants with fixed corolla contortion. *A, Vinca major* (Apocynaceae), sinistrorse. *B, Mandevilla laxa* (Apocynaceae), dextrorse. *C, Datura metel* (Solanaceae), dextrorse. *D–F*, Plants with enantiomorphic corolla contortion. In each figure the flower on the left is sinistrorse; the flower on the right, dextrorse. *D, Linum narbonense* (Linaceae). *E, Hibiscus tiliaceus* (Malvaceae). *F, Jatropha integerrima* (Euphorbiaceae).

position of the stamen is unusual for Lamiales s.l. because it is abaxially median. This may result from the complete loss of the petals. The stamen may have the position of the lower lost petal. The development shows that from the beginning there is just one stamen. The perianth is delayed in development. In some flowers, two perianth parts can be recognized flanking the stamen, which may correspond to the lower sepal pair in other Scrophulariaceae. In *Callitriche*, the perianth has completely disappeared (Leins and Erbar 1988).

All examples of Lamiales s.l. shown above have the upper sector of the flower more or less reduced, which could correspond to the action of a *cycloidea* gene, as in *Antirrhinum*.

However, there are also flowers with a more complicated reduction pattern in Lamiales s.l. In *Brillantaisia* (Acanthaceae), not only the upper odd stamen but also the lower stamen pair is reduced; only the upper pair is well developed. The lower stamen pair is retarded in an early stage and at maturity forms only small staminodes. The same is true for the odd stamen, where this retardation and reduction is still more pronounced (fig. 5A–5D). In *Veronica* and allied genera (Antirrhinaceae) only the two stamens of the upper pair are initiated; the upper petals are completely united and appear as one organ. Only rarely are two tips still present (Noll 1883; Wunderlin 1992; Kampny et al. 1993, 1994; Hufford 1995) (fig. 5E–5H).

In *Calceolaria* (former Scrophulariaceae s.l.) this tendency is still more pronounced. As in *Veronica*, only the upper stamen pair is left. In addition, the three petals of the lower lip and the two of the upper lip are completely united and the individual organs can no longer be distinguished (fig. 5I–5L). According to Olmstead and collaborators (personal communication), *Calceolaria*, surprisingly, forms a small separate clade at the base of the Lamiales s.l. In light of this fact, another interpretation of this peculiar floral structure may be tempting. Oleaceae have disymmetric flowers with only two (often lat-

eral) stamens. The two lateral stamens in *Calceolaria* could then be directly derived from this condition and its bilabiate corolla, from a tetramerous (or dimerous?) corolla. This is an open question.

In conclusion, in Lamiales s.l. there are various androecial patterns, with progressive reduction of parts and progressive expression of monosymmetry (fig. 6). The most common trend is progressive reduction of the adaxial (upper) floral sector. Genetically, this may be related to the action of the *cycloidea* gene (see above). However, in addition to the adaxial floral sector, reduction may also occur in the abaxial (lower) sector. Here, a more complicated developmental mechanism may be expected.

Another possible evolutionary step is from monosymmetry to secondary polysymmetry by further reduction (fig. 7). Here the upper floral sector completely disappears so that the pentamerous flower is changed into a tetramerous one, which, again, is more or less polysymmetric. *Plantago* is an example. According to Olmstead and Reeves (1995), it is nested in the Scrophulariaceae s.l. Its flowers may be interpreted as the outcome of loss of the upper floral sector, although indications of a former pentamery are lacking (see also Schwarzbach 1991). For *Torenia* the same fluctuation between five- and four-parted corolla and presence or absence of an odd staminode was described (Armstrong 1988). *Veronica* still has five tepals but in most cases only four petals (although there is some lability in this feature) and two stamens (the upper pair, appearing more or less transverse in the mature flower). These three genera are in the Antirrhinaceae. However, similar trends are also present in other families.

These trends of progressive reduction of stamen number and petal individuality are polyphyletic in Lamiales s.l. because they occur in more than one family, although they may be dependent on the same genes. However, each family has its own idiosyncratic pattern of expression of the diversity

Table 1

Direction of Contortion in Contort Flowers in Rosids and Asterids

	Both directions (right and left) in the same individual[a]	Direction fixed in a species or larger taxon[b]
Rosids	Bombacaceae	Combretaceae
	Burseraceae (*Canarium*)	Crassulaceae
	Caricaceae	Haloragaceae (*Haloragodendron*)?
	Cistaceae	Limnanthaceae
	Clusiaceae	Melastomataceae
	Cochlospermaceae	Onagraceae
	Dipterocarpaceae	Turneraceae
	Euphorbiaceae	
	Geraniaceae	
	Linaceae	
	Malvaceae	
	Ochnaceae	
	Oxalidaceae	
	Rosaceae (*Gillenia*)	
	Sterculiaceae	
	Tiliaceae	
	Trigoniaceae	
	Zygophyllaceae	
Asterids	Ericaceae (*Lysinema*)?	Acanthaceae
		Apocynaceae
		Boraginaceae
		Convolvulaceae
		Ebenaceae
		Ericaceae
		Geniostomataceae
		Gentianaceae
		Hydrangeaceae
		Hydrophyllaceae
		Myrsinaceae
		Oleaceae
		Polemoniaceae
		Primulaceae
		Rubiaceae
		Sapotaceae
		Solanaceae

[a] Wichura 1852; Eichler 1878; Lam 1932; Schoute 1935; Davis 1964, 1966, 1974; Davis and Selvaraj 1964; Davis and Ghoshal 1966; Davis and Ramanujacharyulu 1971; Davis and Bhattacharya 1974; Bahadur and Venkatesvarlu 1976a, 1976b; Davis and Ghosh 1976; Kanai and Sohma 1980; Bahadur et al. 1984; Nandi 1998; V. Grob and P. Rusert, personal communication.

[b] Wydler 1851a; Wichura 1852; Eichler 1875, 1878; Schoute 1935; Allard 1947; Orchard 1975; Bremer 1987; Robbrecht 1988; Renner 1993; Scotland et al. 1994; Endress and Albert 1995; Endress et al. 1996.

of these organs. It is broad in some, such as Scrophulariaceae in the traditional sense (which are polyphyletic), or narrow in others, such as Lamiaceae. Probably, the basal Lamiales already had monosymmetric flowers and all polysymmetric cases in Lamiales are derived from monosymmetric ones (Olmstead and Reeves 1995; Donoghue et al. 1998). If floral features are mapped on the cladogram by Olmstead and Reeves (1995) (fig. 8), it seems that reversals were easiest in the basalmost family, Gesneriaceae, with the weakest overall expression of monosymmetry and, in general, the least reduction of the odd stamen (Endress 1998). However, in groups with extremely monosymmetric elaborated lip flowers, such as in parts of the traditional Scrophulariaceae, Acanthaceae, and Lamiaceae, the odd stamen is so much reduced that it is no longer even initiated, and reversion to polysymmetric flowers seems to be less common (Endress 1998). Is monosymmetry in the latter groups genetically more deeply rooted than in Gesneriaceae? However, if it becomes established that Oleaceae and the *Calceolaria* group are sisters of the rest of the Lamiales s.l. (R. Olmstead, personal communication), other interpretations will have to be explored as well (see above).

Patterns of Direction of Contortion in Flowers with Contort Petals

A peculiar kind of symmetry in flowers is contort aestivation of the corolla, which is often pinwheel shaped, as in the per-
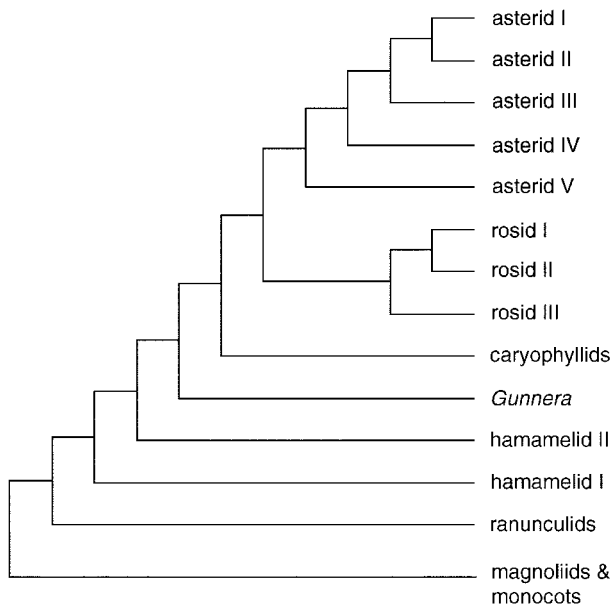
Fig. 11 Simplified cladogram of the angiosperms based on *rbc*L sequences after Chase et al. (1993), showing distribution of plants with fixed corolla contortion (dark shading) and of those with enantiomorphic corolla contortion (light shading). In the unshaded groups, corolla contortion is largely lacking.

iwinkle (*Vinca major*, Apocynaceae) (fig. 10*A*). Each petal is asymmetric, but the entire corolla has a rotational symmetry. It seems perhaps paradoxical that contort aestivation is the most symmetrical of all imbricate patterns in pentamerous flowers. Contort petal aestivation occurs predominantly in polysymmetric flowers and rarely in monosymmetric ones (which was already noticed by Brongniart [1831]). Notable exceptions of monosymmetric flowers with contort aestivation are in Trigoniaceae and Acanthaceae (Eichler 1875, 1878; Scotland et al. 1994; Schönenberger and Endress 1998).

Petal asymmetry and contort aestivation are in some way correlated, although petal asymmetry is not evident in all taxa with contort corolla. Asymmetry may originate very early, before the petals overlap, e.g., in *Asclepias* (Apocynaceae s.l.) (Endress 1994).

There are two forms of contortion: direction to the left (sinistrorse) and direction to the right (dextrorse) (in the sinistrorse pattern, the left side of each organ overlaps its neighbor if a floral bud is viewed from the side; in the dextrorse pattern, vice versa) (fig. 9). It is especially interesting that the distribution of the two morphs is different from taxon to taxon. Although only a few examples have been critically studied, a systematic pattern seems to emerge among angiosperms.

In many plant taxa, both morphs, left and right, occur equally in each individual (figs. 10*D*–10*F*). But this is not so in others (fig. 10*A*–10*C*). There are two intriguing facts: (1) In some plant groups, only one morph is realized in a genus or even in a family (Braun [1831, 1839] mentioned some examples). The most detailed study so far is that by Schoute (1935), based on literature and his own observations. Schoute also emphasized that in taxa with fixed direction of petal con-

tortion the direction of the spiral of the sepals can still be in either direction. Thus, the behavior of the petals is independent from that of the sepals of the same flower (autotropic corolla, according to Schoute 1935). In contrast, in taxa where both corolla morphs occur in the same individual, the direction of corolla contortion follows that of the calyx spiral (heterotropic corolla). (2) A closer look at the large-scale distribution reveals that these two behaviors—occurrence of both morphs in an individual (nonfixed pattern, enantiomorphy), or occurrence of only one morph (fixed pattern)—are not randomly distributed among the flowering plants. Among the eudicots the fixed pattern seems to be almost restricted to the asterids, whereas the first case occurs only outside the asterids (except, perhaps, for *Lysinema* of Ericaceae, according to Schoute 1935). To my knowledge, this second finding has not been reported before (table 1; fig. 11). For Haloragaceae, Schoute (1935) mentions the occurrence of the fixed pattern. However, figures of *Haloragodendron* flowers in Orchard (1975) show both morphs. Among rosids, contort flowers occur especially in rosids I and II, while they are rare in rosids III (*sensu* Chase et al. 1993).

Outside of rosids and asterids, contort petals occur only sporadically. This may reflect the fact either that, in basal angiosperms, petals are often not in perfect whorls or that flowers, in general, are less elaborate and regular. In addition, in monocots with trimerous whorls, the tendency for the petals (tepals) of a whorl to overlap is less pronounced than in eudicots with predominantly pentamerous whorls. Among caryophyllids, both patterns, fixed and nonfixed, seem to occur in Caryophyllaceae (Braun 1839) and Plumbaginaceae (Schoute 1935; Bahadur et al. 1984); Myricariaceae have a nonfixed pattern (Schoute 1935) and Droseraceae, a fixed (?) pattern (Eichler 1878). Among ranunculids, two genera of Papaveraceae are mentioned as having a fixed pattern (Schoute 1935). Among monocots, Arecaceae and a few Amaryllidaceae have a nonfixed pattern (Eichler 1875; Davis and Selvaraj 1964), whereas Trilliaceae and Bromeliaceae have a fixed pattern (Eichler 1875). In magnoliids, well-differentiated petals and contort aestivation are lacking altogether.

In *Oxalis* (Oxalidaceae) and in Malvaceae, which have both floral morphs on the same individual, the two morphs are arranged in a regular pendulum symmetry in the monochasial partial inflorescences (Wydler 1851*b*, 1859). For *Oxalis*, this was confirmed (V. Grob and P. Rusert, personal communication).

In Apocynaceae, the direction is fixed in larger groups, but it changes at least once within the family, as shown by Endress and Albert (1995). It appears that the basal Apocynaceae are left contort but that one large clade within the family is right contort (fig. 12).

Therefore, it seems that the fixed pattern is an innovation for the asterids. In rosids, it has a very sparse and erratic occurrence, with the notable exception of Myrtales (Combretaceae, Melastomataceae, Onagraceae), where it is also predominant. However, it should also be emphasized that most asterids do not have contort petals at all and, in addition, that the biological meaning of this feature is not clear. What is the genetic background of these forms? Is it just a stable genetic by-product of another change? Or is it a consequence of selection by pollinators, resulting from the more complicated (sympetalous) flowers in asterids than in rosids, in parallel to

Corolla lobe aestivation
- ▭ sinistrorse
- ▭ dextrorse
- ■ valvate
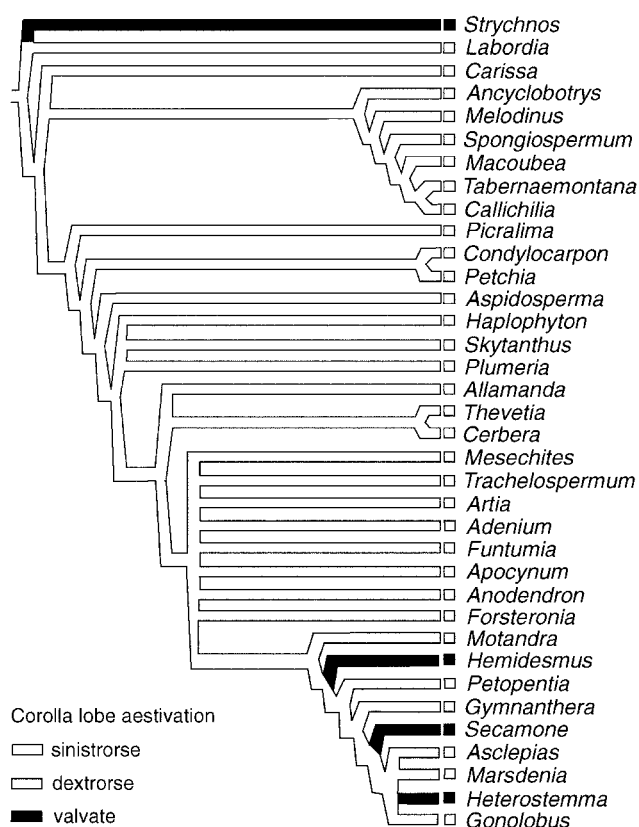
Fig. 12 Cladogram (unpublished) from the work of Endress and Albert (1995), showing the change from sinistrorse to dextrorse corolla aestivation in Apocynaceae.

the case of Faboideae versus Caesalpinioideae (see above)? In this respect, it is of interest that among Crassulaceae of rosids the fixed pattern occurs in the genus *Kalanchoe* (including *Bryophyllum*; Schoute 1935), which is exceptional for its sympetalous flowers among rosids.

Conclusions and Outlook

Symmetry of mature flowers may be different from the symmetry in early development. At the beginning of development, floral symmetry is established by the ordered initiation of floral organs, the floral phyllotaxis. Later, symmetry can be changed by differential growth of floral sectors. Then a superstructure, formed by several organs, may be effected (e.g., lip formation involving two or three petals). In the mature flower, symmetry is to a great extent independent of phyllotaxis, so that flowers with both whorled and spiral phyllotaxis can become polysymmetric, monosymmetric, or asymmetric. Thus, floral symmetry is partly independent of floral organization; it is an aspect of floral architecture.

Perhaps in the majority of angiosperm taxa, the symmetry pattern does not change during floral development. However, there are also many other cases. Monosymmetric flowers may have a polysymmetric phase in early development. The reverse

also often occurs: polysymmetric flowers have monosymmetric or even asymmetric phases in early development. This is probably a result of developmental gradients of the entire inflorescence or of the subtending bract/flower primordium complex (or results from pressures by adjacent parts of the inflorescence); these gradients influence the floral symmetry until the flower has established its own symmetry. It would be interesting to know how polysymmetry is then upregulated later in development. Asymmetry is not uncommon, especially in groups with highly elaborated and otherwise monosymmetric flowers.

As shown by Coen and collaborators, the monosymmetry of *Antirrhinum* flowers is largely established by the *cycloidea* gene. Its activity reduces the uppermost stamen. This may be valid for the entire Lamiales s.l. with monosymmetric flowers where the stamen is practically always reduced to a greater or lesser extent. However, there are also more complicated forms in some Lamiales s.l., where not only the upper but also the lower stamens are reduced. In these groups, action of an analogous counterpart of *cycloidea* may be expected.

In this article, it has been reported for the first time that, among eudicots, flowers with contorted petals that show both morphs—dextrorse and sinistrorse—on the same individual are largely restricted to rosids, whereas this condition is not known in asterids. In asterids, only one morph occurs in an individual, species, or even larger taxonomic group, whereas this condition is rare in rosids (except for Myrtales).

A comparison of the occurrence of enantiomorphic forms in both asymmetric flowers and flowers with contort petal aestivation shows that in both cases they are restricted to groups with, in general, less elaborated flowers. In these the enantiomorphic flowers are arranged in a regular pendulum symmetry if they occur in monochasial inflorescences. In groups with more elaborated flowers, all flowers of an individual or species are of the same morph. It will be fascinating to study this difference from developmental and from pollination biological aspects.

As the phylogeny of larger groups is revealed in more detail by molecular and nonmolecular analyses, it will become increasingly possible to map floral symmetry features on the cladograms and to reconstruct the evolutionary changes of symmetry.

Questions for molecular developmental geneticists: Is there one mode or are there different modes to change floral polysymmetry into monosymmetry (or vice versa) in Lamiales s.l. and in angiosperms in general? What is the genetic basis for monosymmetric flowers in those Lamiales s.l. where in the androecium not only an adaxial but also an abaxial sector is reduced? What is the genetic difference between constitutional and positional monosymmetry? What is the genetic distinction between plants with a single fixed asymmetric floral morph and those with floral enantiomorphy?

Questions for evolutionary biologists: How did monosymmetry become established in Lamiales s.l. (or in their ancestors)? How did fixed, monomorphic corolla contortion become established in asterids (or in their ancestors)? Was it in a phase where elaborate flowers constrained floral shape to a single morph? When did the preference of bees (or their ancestors) for radiating polysymmetric shapes and perpendicular monosymmetric shapes evolve?

In organic evolution, the degree of overall symmetry of organisms decreases while the degree of complexity increases. There is a repeated break of symmetry and emergence of new partial symmetries (e.g., Riedl 1978; Vogel 1991; García-Bellido 1996). This trend is also seen in flowers with the evolutionary sequence polysymmetry, disymmetry, asymmetry and in the evolution of new symmetries, e.g., by arrangement of asymmetric flowers into monosymmetric pairs (e.g., Marantaceae) or of monosymmetric flowers into polysymmetric heads (e.g., Asteraceae). Other evolutionary directions also occur but are less prominent. In flowers, as in organisms in general (Riedl 1978; Wuketits 1996), symmetry may be a factor that influences evolution.

Symmetry in flower evolution is a vast unexplored field (Cronk and Møller 1997; Baum 1998; Donoghue et al. 1998). Because floral symmetry is so aesthetically attractive, it is an especially inviting area for molecular developmental geneticists, pollination biologists, and plant evolutionists to meet for a more profound understanding of the diversity and evolution of plant form.

Acknowledgments

Literature Cited

Allard HA 1947 The direction of twist of the corolla in the bud and twining of the stems in Convolvulaceae and Dioscoreaceae. Castanea 12:88–94.

Almeida J, M Rocheta, L Galego 1997 Genetic control of flower shape in *Antirrhinum majus*. Development 124:1387–1392.

Armstrong J 1988 The suppression and loss of androecial primordia and their affect on corolla form in Scrophulariaceae. Am J Bot 75: 17–18.

Armstrong JE, AW Douglas 1989 The ontogenetic basis for corolla aestivation in Scrophulariaceae. Bull Torrey Bot Club 116:378–389.

Bahadur B, A Chaturvedi, N Rama Swamy 1991 SEM studies of pollen in relation to enantiostyly and heteranthery in *Cassia* (Caesalpiniaceae). J Palynol, Silver Jubilee Commemoration Volume, 7–22.

Bahadur B, NP Reddy, MM Rao, SM Farooqui 1984 Corolla handedness in Oxalidaceae, Linaceae and Plumbaginaceae. J Indian Bot Soc 63:408–411.

Bahadur B, T Venkateshwarlu 1976a Isomerism in flowers of *Carica papaya* L. J Indian Bot Soc 55:89–94.

—— 1976b Isomerism in flowers of four species of *Jatropha* L. J Indian Bot Soc 55:30–37.

Barabé D, RV Jean, eds 1998 Symmetry in plants. World Scientific, Singapore.

Bateson W, A Bateson 1891 On variations in the floral symmetry of certain plants having irregular corollas. J Linn Soc Lond Bot 28: 386–424.

Baum DA 1998 The evolution of plant development. Curr Opin Plant Biol 1:79–86.

Bock GR, J Marsh 1991 Biological asymmetry and handedness. Wiley, Chichester.

Bowers KAW 1975 The pollination ecology of *Solanum rostratum* (Solanaceae). Am J Bot 62:633–638.

Bradley D, R Carpenter, L Copsey, C Vincent, S Rothstein, E Coen 1996 Control of inflorescence architecture in *Antirrhinum*. Nature 379:791–797.

Braun A 1831 Vergleichende Untersuchung über die Ordnung der Schuppen an den Tannenzapfen als Einleitung zur Untersuchung der Blattstellung überhaupt. Nova Acta Acad Caes Leopold-Carol 15: 195–402.

—— 1835 Dr. Carl Schimper's Vorträge über die Möglichkeit eines wissenschaftlichen Verständnisses der Blattstellung, nebst Andeutung der hauptsächlichen Blattstellungsgesetze und insbesondere der neuentdeckten Gesetze der Aneinanderreihung von Cyclen verschiedener Maasse. Flora 18:145–192.

—— 1839 Über die gesetzlichen Drehungen im Pflanzenreiche. Flora 20:311–314.

—— 1843 Über Symmetrie in der Pflanzenbildung. Verh Ges Dtsch Naturforsch Arzte 1842:196–197.

—— 1858 Über den Blüthenbau der Gattung *Delphinium*. Jahrb Wiss Bot 1:307–370.

Bremer B 1987 The sister group of the paleotropical tribe Argostemmateae: a redefined neotropical tribe Hamelieae (Rubiaceae, Rubioideae). Cladistics 3:35–51.

Brizuela MM, PS Hoc, VS di Stilio, MA Agulló, RA Palacios, P Hazeldine, J Genise 1993 Biología floral de *Macroptilium bracteatum* (Leguminosae, Phaseoleae). Darwiniana 32:41–57.

Brongniart A 1831 Sur l'insertion relative des diverses pièces de chaque verticille floral, et sur son influence sur la régularité ou irrégularité des fleurs. Ann Sci Nat 23:225–244.

Brown NA, L Wolpert 1990 The development of handedness in left/right asymmetry. Development 109:1–9.

Buzgo M 1999 Flower structure and development of Acoraceae and basal Araceae and their systematic position among basal monocotyledons. PhD diss. University of Zurich.

Carpenter R, Coen E 1990 Floral homeotic mutants produced by transposon mutagenesis in *Antirrhinum majus*. Genes Dev 4: 1483–1493.

Charlton WA 1998 Pendulum symmetry. Pages 61–87 in RV Jean, D Barabé, eds. Symmetry in plants. World Scientific, Singapore.

Chase MW et al 1993 Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene rbcL. Ann Mo Bot Gard 80:528–580.

Chodat R 1889 Un cas intéressant d'irrégularité florale. Arch Sci Phys Nat Ser 3 22:272–275.

Coen ES 1991 The role of homeotic genes in flower development and evolution. Annu Rev Plant Physiol Plant Mol Biol 42:241–279.

—— 1996 Floral symmetry. EMBO J 15:6777–6788.

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

Coen ES, JM Nugent 1994 Evolution of flowers and inflorescences. Development, Suppl, 107–116.

Coen ES, JM Nugent, D Luo, D Bradley, P Cubas, M Chadwick, L Copsey, R Carpenter 1995 Evolution of floral symmetry. Philos Trans R Soc Lond B Biol Sci 350:35–38.

Cooper KW 1985 Asymmetrical marking of bees of the family Megachilidae by certain species of *Lotus*: complementation of flower asymmetry and bee behavior. Lotus Newsl 16:51–53.

Crepet WL 1996 Timing in the evolution of derived floral characters: Upper Cretaceous (Turonian) taxa with tricolpate and tricolpate-derived pollen. Rev Palaeobot Palynol 90:339–359.

Cronk Q, M Möller 1997 Genetics of floral symmetry revealed. Trends Ecol Evol 12:85–86.

Cutter EG 1957 Studies of morphogenesis in the Nymphaeaceae. I/II. Phytomorphology 7:45–56/57–73.

Dafni A 1994 Note on side advertisement in flowers. Funct Ecol 8:136–138.

——— 1997 The response of *Amphicoma* spp. (Coleoptera; Glaphyridae) beetles to red models differing in area, shape, and symmetry. Isr J Plant Sci 45:247–254.

Dafni A, PG Kevan 1996 Floral symmetry and nectar guides: ontogenetic constraints from floral development, colour pattern rules and functional significance. Bot J Linn Soc 120:371–377.

Darwin C 1857 Bees and fertilisation of kidney beans. Gard Chron 1857(43):725.

——— 1876 On the effects of cross and self fertilisation in the vegetable kingdom. J Murray, London.

Davenport D, Y Kohanzadeh 1982 Orchids, bilateral symmetry and insect perception. J Theor Biol 94:241–252.

Davis TA 1964 Aestivation in Malvaceae. Nature 201:515–516.

——— 1966 Floral structure and stamens in *Bombax ceiba* L. J Genet 59:294–328.

——— 1974 Enantiomorphic structures in plants. Proc Indian Nat Sci Acad 40B:424–429.

Davis TA, C Bhattacharya 1974 Some morphological observations in *Durio zibethinus* Murr. (Bombacaceae). J Indian Bot Soc 53:48–58.

Davis TA, SS Ghosh 1976 Morphology of *Adansonia digitata*. Adansonia 15:471–479.

Davis TA, KK Ghoshal 1966 Variation in the floral organs of *Hibiscus rosa-sinensis*. J Indian Bot Soc 45:30–43.

Davis TA, C Ramanujacharyulu 1971 Statistical analysis of bilateral symmetry in plant organs. Sankhya Ser B 33:259–290.

Davis TA, C Selvaraj 1964 Floral asymmetry in Malvaceae. J Bombay Nat Hist Soc 61:402–407.

De Candolle AP 1813 Théorie élémentaire de la Botanique. 1st ed. Deterville, Paris.

——— 1827 Organographie végétale. I. Deterville, Paris.

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

Demeter K 1922 Vergleichende Asclepiadeenstudien. Flora 15:130–176.

DePamphilis CW, ND Young, AD Wolfe 1997 Evolution of plastid gene *rps2* in a lineage of hemiparasitic and holoparasitic plants: many losses of photosynthesis and complex patterns of rate variation. Proc Natl Acad Sci USA 94:7367–7372.

Donoghue MJ, RH Ree, DA Baum 1998 Phylogeny and evolution of flower symmetry in the Asteridae. Trends Plant Sci 3:311–317.

Douglas AW 1997 The developmental basis of morphological diversification and synorganisation in flowers of Conospermeae (*Stirlingia* and Conosperminae: Proteaceae). Int J Plant Sci 158(suppl):S13–S48.

Douglas AW, SC Tucker 1996a Comparative floral ontogenies among Persoonioideae including *Bellendena* (Proteaceae). Am J Bot 83:1528–1555.

——— 1996b Inflorescence ontogeny and floral organogenesis in Grevilleoideae (Proteaceae), with emphasis on the nature of the flower pairs. Int J Plant Sci 157:341–372.

Dufour J 1885 De l'influence de la gravitation sur les mouvements de quelques organes floraux. Arch Sci Phys Nat Ser 3 14:413–424.

Dulberger R 1981 The floral biology of *Cassia didymobotrya* and *C. auriculata* (Caesalpiniaceae). Am J Bot 68:1350–1360.

Dulberger R, R Ornduff 1980 Floral morphology and reproductive biology in four species of *Cyanella* (Tecophilaeaceae). New Phytol 86:45–56.

Dutrochet H 1837 Mémoires pour servir à l'histoire anatomique et physiologique des végétaux et des animaux. II. Baillière, Paris.

Eichler AW 1875 Blüthendiagramme. I. Engelmann, Leipzig.

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

Endress ME, VA Albert 1995 A morphological cladistic study of Apocynaceae: trends in character evolution within a broadened familial circumscription. Am J Bot 82(suppl):127.

Endress ME, PV Bruyns 1999 A revised classification of Apocynaceae s. l. Bot Rev (in press).

Endress ME, B Sennblad, S Nilsson, L Civeyrel, MW Chase, S Huysmans, E Grafström, B Bremer 1996 A phylogenetic analysis of Apocynaceae s.str. and some related taxa in Gentianales: a multidisciplinary approach. Opera Bot Belg 7:59–102.

Endress PK 1975 Nachbarliche Formbeziehungen mit Hüllfunktion im Infloreszenz- und Blütenbereich. Bot Jahrb Syst 96:1–44.

——— 1986 Floral structure, systematics, and phylogeny in Trochodendrales. Ann Mo Bot Gard 73:297–324.

——— 1987 Floral phyllotaxis and floral evolution. Bot Jahrb Syst 108:417–438.

——— 1989 Chaotic floral phyllotaxis and reduced perianth in *Achlys* (Berberidaceae). Bot Acta 102:159–164.

——— 1990 Patterns of floral construction in ontogeny and phylogeny. Biol J Linn Soc 39:153–175.

——— 1992 Evolution and floral diversity: the phylogenetic surroundings of *Arabidopsis* and *Antirrhinum*. Int J Plant Sci 153(suppl):S106–S122.

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

——— 1995a Floral structure and evolution in Ranunculanae. Plant Syst Evol, Suppl 9, 49–61.

——— 1995b Major evolutionary traits of monocot flowers. Pages 43–79 in PJ Rudall, P Cribb, DF Cutler, CJ Humphries, eds. Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew.

——— 1998 *Antirrhinum* and Asteridae—evolutionary changes of floral symmetry. Symp Ser Soc Exp Biol 53:133–140.

——— 1999 The origins of flower morphology. *In* G Wagner, ed. Character concept in evolutionary biology. Academic Press, San Diego, Calif. (in press).

Enquist M, A Arak 1994 Symmetry, beauty and evolution. Nature 372:169–172.

Erbar C 1994 Contributions to the affinities of *Adoxa* from the viewpoint of floral development. Bot Jahrb Syst 116:259–282.

Erbar C, P Leins 1985 Studien zur Organsequenz in Apiaceen- Blüten. Bot Jahrb Syst 105:379–400.

——— 1997 Different patterns of floral development in whorled flowers, exemplified by Apiaceae and Brassicaceae. Int J Plant Sci 158(suppl):S49–S64.

Evans AS, M Marshall 1996 Developmental instability in *Brassica campestris* (Cruciferae): fluctuating asymmetry of foliar and floral traits. J Evol Biol 9:717–736.

Fabri C, T Laux, M Hauptmann, A Schäffner 1996 *TORTIFOLIA* genes are involved in chiral cell expansion of plant petioles. Page 102 in AW Alfermann et al., eds. Botanikertagung 1996, Düsseldorf, Abstracts. University of Düsseldorf, Düsseldorf.

Fenster CB 1995 Mirror image flowers and their effect on outcrossing rate in *Chamaecrista fasciculata* (Leguminosae). Am J Bot 82:46–50.

——— 1997 Developmental homeostasis and floral form: evolutionary consequences and genetic basis. Int J Plant Sci 158(suppl):S121–S130.

Frey-Wyssling A 1925 Geometrische Symmetriebetrachtung. Flora 120:87–98.

García-Bellido A 1996 Symmetries throughout organic evolution. Proc Natl Acad Sci USA 93:14229–14232.

Giurfa M, W Backhaus, R Menzel 1995 Color and angular orientation in the discrimination of bilateral symmetric patterns in the honeybee. Naturwissenschaften 82:198–201.

Giurfa M, B Eichmann, R Menzel 1996 Symmetry perception in an insect. Nature 382:458–461.

Goebel K 1908 Über Symmetrieverhältnisse in Blüten. Pages 151–166 in K Linsbauer, ed. Wiesner-Festschrift. Konegen, Wien.

——— 1924a Die Entfaltungsbewegungen der Pflanzen und deren teleologische Deutung. 2d ed. Fischer, Jena.

——— 1924b Wilhelm Hofmeister: Arbeit und Leben eines Botanikers. Akademische Verlagsgesellschaft, Leipzig.

——— 1928 Organographie der Pflanzen. 1. 3d ed. Fischer, Jena.

Grasshoff M 1996 Strahlige Symmetrie bei Tieren. Pages 63–75 in W Hahn, P Weibel, eds. Evolutionäre Symmetrietheorie: Selbstorganisation und dynamische Systeme. Hirzel, Stuttgart.

Haeckel I 1931 Über Iridaceen. Flora 125:1–82.

Hagemann W 1963 Weitere Untersuchungen zur Organisation des Sprossscheitelmeristems; der Vegetationspunkt traubiger Floreszenzen. Bot Jahrb Syst 82:273–315.

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

Harvey RP 1998 Links in the left/right axial pathway. Cell 94: 273–276.

Heilbronner E, JD Dunitz 1993 Reflections on symmetry. Helvetica Chimica Acta, Basel.

Henley EM, ed 1996 Symmetries throughout the sciences. Proc Natl Acad Sci USA 93:14215–14301.

Hildebrand F 1886 Die Beeinflussung durch die Lage zum Horizont bei den Blüthentheilen einiger Cleome-Arten. Ber Dtsch Bot Ges 4: 329–337.

Hilliard OM 1994 The Manuleae, a tribe of Scrophulariaceae. Edinburgh University Press, Edinburgh.

Hirmer M 1931 Zur Kenntnis der Schraubenstellungen im Pflanzenreich. Planta 14:132–206.

Hoc PS, VS di Stilio, MA Agulló, MM Brizuela, RA Palacios, P Hazeldine, J Genise 1993 Biología floral de Vigna longifolia (Leguminosae, Phaseoleae). Darwiniana 32:27–39.

Hofmann U, J Göttmann 1990 Morina L. und Triplostegia Wall. ex DC. im Vergleich mit Valerianaceae und Dipsacaceae. Bot Jahrb Syst 111:499–553.

Hofmeister W 1868 Allgemeine Morphologie der Gewächse. Engelmann, Leipzig.

Hufford L 1995 Patterns of ontogenetic evolution in perianth diversification of Besseya (Scrophulariaceae). Am J Bot 82:655–680.

Hyatt BA, HJ Yost 1998 The left-right coordinator: the role of Vg1 in organizing left-right axis formation. Cell 93:37–46.

Kampny CM 1995 Pollination and flower diversity in Scrophulariaceae. Bot Rev 61:350–366.

Kampny CM, TA Dickinson, NG Dengler 1993 Quantitative comparison of floral development in Veronica chamaedrys and Veronicastrum virginicum (Scrophulariaceae). Am J Bot 80:449–460.

——— 1994 Quantitative floral development in Pseudolysimachion (Scrophulariaceae): intraspecific variation and comparison with Veronica and Veronicastrum. Am J Bot 81:1343–1353.

Kanai H, R Sohma 1980 A preliminary study of petal disposition types in five-petaled flowers. I. Bull Nat Sci Mus Tokyo B 6:101–113.

Kirchoff BK 1983 Floral organogenesis in five genera of the Marantaceae and in Canna (Cannaceae). Am J Bot 70:508–523.

Kunze H 1985 Die Infloreszenzen der Marantaceen und ihr Zusammenhang mit dem Typus der Zingiberales-Synfloreszenz. Beitr Biol Pflanz 60:93–140.

Lam HJ 1932 Beiträge zur Morphologie der dreizähligen Burseraceae-Canarieae. Ann Jard Bot Buitenzorg 42:25–55.

Laverty TM 1980 The flower visiting behaviour of the bumble bees: floral complexity and learning. Can J Zool 58:1324–1335.

——— 1994 Bumble bee learning and floral morphology. Anim Behav 47:531–545.

Lehrer M, GA Horridge, SW Zhang, R Gadagkar 1995 Shape vision in bees: innate preference for flower-like patterns. Philos Trans R Soc Lond B 347:123–137.

Leins P, C Erbar 1988 Einige Bemerkungen zur Blütenentwicklung und systematischen Stellung der Wasserpflanzen Callitriche, Hippuris und Hydrostachys. Beitr Biol Pflanz 63:157–178.

Leppik EE 1955 Some viewpoints on the origin and evolution of flowering plants. Acta Biotheor 9:45–56.

——— 1957 Evolutionary relationships between entomophilous plants and anthophilous insects. Evolution 11:466–481.

——— 1972 Origin and evolution of bilateral symmetry in flowers. Evol Biol 5:49–85.

Levin M, M Mercola 1998 The compulsion of chirality: toward an understanding of left-right asymmetry. Genes Dev 12:763–769.

Lewis AC 1993 Learning and the evolution of resources: pollinators and flower morphology. Pages 219–242 in DR Papaj, AC Lewis, eds. Insect learning: ecology and evolutionary perspectives. Chapman & Hall, New York.

Lidén M, T Fukuhara, J Rylander, B Oxelman 1997 Phylogeny and classification of Fumariaceae, with emphasis on Dicentra s.l., based on the plastid gene rps16 intron. Plant Syst Evol 206:411–420.

Lindman CAM 1902 Die Blüteneinrichtungen einiger südamerikanischer Pflanzen. I. Leguminosae. Bihang Sven Vet-Akad Handl 27 III, 14:1–63.

Linnaeus C 1751 Philosophia botanica. Kiesewetter, Stockholm.

Lowe CJ, GA Wray 1997 Radical alterations in the roles of homeobox genes during echinoderm evolution. Nature 389:718–721.

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

Lyndon RF 1998 Phyllotaxis in flowers and in flower reversion. Pages 109–124 in RV Jean, D Barabé, eds. Symmetry in plants. World Scientific, Singapore.

Mair O 1977 Zur Entwicklungsgeschichte monosymmetrischer Dicotylen-Blüten. Diss Bot 38:1–90.

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

Møller AP 1995 Bumblebee preference for symmetrical flowers. Proc Natl Acad Sci USA 92:2288–2292.

Møller AP, G Sorci 1998 Insect preferences for symmetrical artificial flowers. Oecologia 114:37–42.

Møller AP, JP Swaddle 1997 Asymmetry, developmental stability, and evolution. Oxford University Press, Oxford.

Mohl H 1837 Über die Symmetrie der Pflanzen. Flora 20:385–431.

Moquin-Tandon A 1832 Considérations sur les irrégularités de la corolle dans les Dicotylédones. Ann Sci Nat 17:225–290.

Müller H 1881 Alpenblumen, ihre Befruchtung durch Insekten und ihre Anpassungen an dieselben. Engelmann, Leipzig.

Nandi OI 1998 Floral development and systematics of Cistaceae. Plant Syst Evol 212:107–134.

Neal PR, A Dafni, M Giurfa 1998 Floral symmetry and its role in plant-pollinator systems: terminology, distribution, and hypotheses. Annu Rev Ecol Syst 29:345–373.

Nelson E 1954 Gesetzmässigkeiten der Gestaltwandlung im Blütenbereich, ihre Bedeutung für das Problem der Evolution. Nelson, Chernex-Montreux.

Nickrent DL, RJ Duff, AE Colwell, AD Wolfe, ND Young, KE Steiner, CW DePamphilis 1998 Molecular phylogenetic and evolutionary studies of parasitic plants. Pages 211–241 in PS Soltis, DE Soltis, J Doyle, eds. Molecular systematics of plants. II. Kluwer Academic, Boston.

Noll F 1883 Zur Entwicklungsgeschichte der Veronica-Blüte. PhD diss. University of Marburg.

——— 1885 Über die normale Stellung zygomorpher Blüthen und ihre Orientirungsbewegungen zur Erreichung derselben. I. Pages

189–252 *in* J Sachs, ed. Arbeiten des Botanischen Instituts in Würzburg. Engelmann, Leipzig.

——— 1887 Über die normale Stellung zygomorpher Blüthen und ihre Orientirungsbewegungen zur Erreichung derselben. II. Pages 315–371 *in* J Sachs, ed. Arbeiten des Botanischen Instituts in Würzburg. Engelmann, Leipzig.

Nonaka S, Y Tanaka, Y Okada, S Takeda, A Harada, Y Kanai, M Kido, N Hirokawa 1998 Randomization of left-right asymmetry due to loss of nodal cilia generating leftward flow of extraembryonic fluid in mice lacking KIF3B motor protein. Cell 95:829–837.

Olmstead RG, B Bremer, KM Scott, JD Palmer 1993 A parsimony analysis of the Asteridae sensu lato based on rbcL sequences. Ann Mo Bot Gard 80:700–722.

Olmstead RG, CW DePamphilis, AD Wolfe, ND Young, PA Reeves 1998 Disintegration of the Scrophulariaceae: from the ashes. Am J Bot 85(suppl):148–149.

Olmstead RG, PA Reeves 1995 Evidence for the polyphyly of the Scrophulariaceae based on chloroplast rbcL and ndhF sequences. Ann Mo Bot Gard 82:176–193.

Orchard AE 1975 Taxonomic revisions in the family Haloragaceae. I. Bull Auckl Inst Mus 10:1–299.

Ornduff R, R Dulberger 1978 Floral enantiomorphy and the reproductive system of *Wachendorfia paniculata* (Haemodoraceae). New Phytol 80:427–434.

Palmer AR 1996*a* From symmetry to asymmetry: phylogenetic patterns of asymmetry variation in animals and their evolutionary significance. Proc Natl Acad Sci USA 93:14279–14286.

——— 1996*b* Waltzing with asymmetry. BioSci 46:518–532.

Pellegrin F 1924 La flore du Mayombe d'après les récoltes de M. Georges Le Testu. Mem Soc Linn Normand 26:1–126.

Posluszny U, R Sattler 1974 Floral development of *Potamogeton richardsonii*. Am J Bot 61:209–216.

Prance GT 1976 The pollination and androphore structure of some Amazonian Lecythidaceae. Biotropica 8:235–241.

Reeves PA, RG Olmstead 1998 Evolution of novel morphological and reproductive traits in a clade containing *Antirrhinum majus* (Scrophulariaceae). Am J Bot 85:1047–1056.

Renner SS 1990 Reproduction and evolution in some genera of neotropical Melastomataceae. Mem N Y Bot Gard 55:143–152.

——— 1993 Phylogeny and classification of the Melastomataceae and Memecylaceae. Nord J Bot 13:519–540.

Reveal JL, WS Judd, R Olmstead 1999 Proposal to conserve the name Antirrhinaceae against Plantaginaceae (Magnoliophyta). Taxon 48:182.

Riedl R 1978 Order in living organisms. Wiley, Chichester.

Robbrecht E 1988 Tropical woody Rubiaceae. Opera Bot Belg 1:1–271.

Robertson C 1888 Zygomorphy and its causes. I–III. Bot Gaz 13:146–151, 203–208, 224–230.

Ronse Decraene LP, P Roels, EF Smets, A Backlund 1998 The floral development and floral anatomy of *Chrysosplenium alternifolium*, an unusual member of the Saxifragaceae. J Plant Res 111:573–580.

Ryan AK, B Blumberg, C Rodriguez-Esteban, S Yonei-Tamura, K Tamura, T Tsukui, J de la Peña et al. 1998 Pitx2 determines left-right asymmetry of internal organs in vertebrates. Nature 394:545–551.

Ryberg M 1955 A taxonomical survey of the genus *Corydalis* Ventenat with reference to cultivated species. Acta Horti Bergiani 17:115–175.

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

Schmucker T 1924 Rechts- und Linkstendenz bei Pflanzen. Beih Bot Centralbl, Abt I, 41:51–81.

Schnepf E, F Witzig, R Schill 1979 Über Bildung und Feinstruktur des Translators der Pollinarien von *Asclepias curassavica* und *Gom-*

phocarpus fruticosus (Asclepiadaceae). Trop Subtrop Pflanz 25:1–39.

Schöffel K 1932 Untersuchungen über den Blütenbau der Ranunculaceen. Planta 17:315–371.

Schönenberger J, PK Endress 1998 Structure and development of the flowers in *Mendoncia, Pseudocalyx,* and *Thunbergia* (Acanthaceae) and their systematic implications. Int J Plant Sci 159:446–465.

Schoute JC 1935 On corolla aestivation and phyllotaxis of floral phyllomes. Verh K Akad Wet Amsterdam, Afd Natuurkunde, Sec 2, 34 (4):1–77.

Schwarzbach A 1991 Zur Blütenentwicklung von *Plantago coronopus* L. Diplomarbeit. University of Heidelberg.

Schwendener S, G Krabbe 1892 Untersuchungen über die Orientirungstorsionen der Blätter und Blüthen. Abh K Akad Wiss Berl, Physikal-Math Cl 1:1–115.

Scotland RW, PK Endress, TJ Lawrence 1994 Corolla ontogeny and aestivation in the Acanthaceae. Bot J Linn Soc 114:49–65.

Shubnikov AV, VA Koptsik 1974 Symmetry in science and art. Plenum, New York.

Simpson MG 1990 Phylogeny and classification of the Haemodoraceae. Ann Mo Bot Gard 77:722–784.

Sitte P 1986 Bio-Symmetrie. Pages 47–58 *in* B Krimmel, ed. Symmetrie in Kunst, Natur und Wissenschaft. 1. Stadt Darmstadt, Darmstadt.

Sprengel CK 1793 Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen. Vieweg d. Ae., Berlin.

Stebbins GL 1974 Flowering plants: evolution above the species level. Harvard University Press, Cambridge, Mass.

Stork H, ed 1985 Symmetrie. Aulis, Köln.

Stoutamire W 1978 Pollination of *Tipularia discolor*, an orchid with modified symmetry. Am Orchid Soc Bull 47:413–415.

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

Troll W 1928 Organisation und Gestalt im Bereich der Blüte. Springer, Berlin.

Tucker SC 1984*a* Origin of symmetry in flowers. Pages 351–395 *in* RA White, WC Dickison, eds. Contemporary problems in plant anatomy. Academic Press, Orlando, Fla.

——— 1984*b* Unidirectional organ initiation in leguminous flowers. Am J Bot 71:1139–1148.

——— 1989*a* Evolutionary implications of floral ontogeny in legumes. Monogr Syst Bot Mo Bot Gard 29:59–75.

——— 1989*b* Overlapping organ initiation and common primordia in flowers of *Pisum sativum* (Leguminosae: Papilionoideae). Am J Bot 76:714–729.

——— 1991 Helical floral organogenesis in *Gleditsia*, a primitive caesalpinioid legume. Am J Bot 78:1130–1149.

——— 1998 Floral ontogeny in legume genera *Petalostylis, Labichea,* and *Dialium* (Caesalpinioideae: Cassieae), a series in floral reduction. Am J Bot 85:184–208.

Tucker SC, AW Douglas, H-X Liang 1993 Utility of ontogenetic and conventional characters in determining phylogenetic relationships of Saururaceae. Syst Bot 18:614–641.

Vöchting H 1885 Über die Ursachen der Zygomorphie der Blüthen. Berl Dtsch Bot Ges 3:341–345.

——— 1886 Über Zygomorphie und deren Ursachen. Jahrb Wiss Bot 17:297–346.

Vogan KJ, CJ Tabin 1999 A new spin on handed asymmetry. Nature 397:295–298.

Vogel S 1978 Evolutionary shifts from reward to deception in pollen flowers. Pages 89–96 *in* AJ Richards, ed. The pollination of flowers by insects. Academic Press, London.

——— 1991 Struktur lebender Systeme: Grundzüge und Problematik. Pages 27–50 *in* W Marx, ed. Die Struktur lebendiger Systeme: Zu ihrer wissenschaftlichen und philosophischen Bestimmung. Klostermann, Frankfurt a.M.

Waser NM 1983 The adaptive nature of floral traits: ideas and evidence. Pages 241–285 *in* L Real, ed. Pollination biology. Academic Press, Orlando, Fla.

Westerkamp C 1993 The co-operation between the asymmetric flower of *Lathyrus latifolius* (Fabaceae-Vicieae) and its visitors. Phyton 33:121–137.

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

Westerkamp C, A Weber 1997 Secondary and tertiary pollen presentation in *Polygala myrtifolia* and allies (Polygalaceae, South Africa). S Afr J Bot 63:254–258.

Weyl H 1952 Symmetry. Princeton University Press, Princeton, N.J.

Whalen MD 1978 Reproductive character displacement and floral diversity in *Solanum* section *Androceras*. Syst Bot 3:77–86.

Wichura M 1846 Beiträge zur Lehre von der Blatt- und Knospenstellung. III. Flora 29:240–247.

——— 1852 Über das Winden der Blätter. Flora 35:35–108.

Wuketits FM 1996 Evolution und Symmetrie. Symmetrie als Evolutionsfaktor? Pages 13–23 *in* W Hahn, P Weibel, eds. Evolutionäre Symmetrietheorie. Selbstorganisation und dynamische Systeme. Hirzel, Stuttgart.

Wunderlin U 1992 Untersuchungen zur vergleichenden Entwicklungsgeschichte von Scrophulariaceen-Blüten. Diss Bot 188:1–313.

Wydler H 1844 Einige Bemerkungen über die Symmetrie der Blumenkrone. Bot Zeitg 2:609–611.

——— 1851a Die Knospenlage der Blätter in übersichtlicher Zusammenstellung. Flora 34:113–128.

——— 1851b Über die symmetrische Verzweigungsweise dichotomer Inflorescenzen. Flora 34:289–301, 305–312, 321–330, 337–348, 353–365, 369–378, 385–398, 401–412, 417–426, 433–448.

——— 1859 Kleinere Beiträge zur Kenntniss einheimischer Gewächse. Flora 42:257–268, 274–287, 289–304, 305–318, 321–332, 337–345, 353–368, 369–383, 449–457, 554–560.

Young ND, KE Steiner, CW DePamphilis 1997 A revolutionary view of the parasitic Scrophulariaceae/Orobanchaceae. Am J Bot 84(suppl):247.