FLORAL SYMMETRY AND ITS ROLE IN PLANT-POLLINATOR SYSTEMS: Terminology, Distribution, and Hypotheses

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ABSTRACT
Floral symmetry has figured prominently in the study of both pollination biology and animal behavior. However, a confusion of terminology and the diffuse nature of the literature has limited our understanding of the role that this basic characteristic of flower form has played in plant-pollinator interactions. Here, we first contribute a classification scheme for floral symmetry that we hope will resolve some of the confusion resulting from the inconsistent application of terms. Next, we present a short review of the distribution of floral forms in angiosperm families. Finally, we provide a list of hypotheses and, when available, supporting evidence for the causes of the evolution of floral symmetry.
INTRODUCTION

Floral symmetry played an important role in Sprengel’s (110) pioneering attempt to relate form to function in the pollination of flowering plants. He recognized two types of floral symmetry, regular and irregular. Regular flowers were those in which the pistil(s), stamens, and segments of the perianth radiated out uniformly from the central axis. Furthermore, all segments of each organ type were equal in size and form. Irregular flowers were those in which any parts of the perianth or sexual organs did not meet these criteria. Sprengel suggested that regularity should be the rule unless circumstances resulted in an advantage to irregularity. He went on to propose several hypotheses concerning circumstances that would result in such an advantage.

Several forms of irregular flowers [i.e. nonradially symmetric or nonactinomorphic in modern terminology (see below and Table 1)] have been recognized. The modern phylogenetic approach, although philosophically far from Sprengel’s teleological and creationistic outlook (121), suggests that most of the species with irregular flowers were derived from species with regular flowers (i.e. radially symmetric or actinomorphic) (16, 112, 114). We are still looking for the circumstances that give the advantage to irregularity.

Study of pollination ecology has played an important role in investigations of floral symmetry. In particular, honeybees have been the subject of many studies related to symmetry preferences (69) and perception (39, 59). Honeybees can be trained to respond to various visual stimuli, allowing investigation of the perceptual and processing mechanisms associated with the responses to these stimuli.

As a result of a long history and interest by biologists in a variety of fields, the literature regarding floral symmetry is widely scattered in publications about botany, ecology, animal physiology, and behavior. Unfortunately, the diffuse nature of the literature and diversity of interests of the investigators have prevented an integrated understanding of floral symmetry. The problem is further exacerbated by inconsistent use of terminology regarding symmetry. We point out and reconcile some of the problems relating to the description and classification of floral symmetry. We summarize the hypotheses that have been used to explain evolutionary changes in symmetry and suggest some directions for new research in floral symmetry.

PLANES OF SYMMETRY AND FLORAL PHYLOGENY

Floral symmetry is the repeated pattern in structural units as assessed in relation to the principal axis of the flower (i.e. the line or vector emanating from the center of the receptacle) (129). Accordingly, we address symmetry of the flower
**Table 1** Classification of floral symmetry types

<table>
<thead>
<tr>
<th>Planes of symmetry</th>
<th>Symmetry type&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Symmetrical images (principal axis of flower relative to subtending leaf)</th>
<th>Synonyms&lt;sup&gt;c&lt;/sup&gt;</th>
<th>Examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Usually more than two (polysymmetric)</td>
<td>Actinomorphy or radial symmetry</td>
<td>Rotational</td>
<td>Regular, pleomorphy, multisymmetry, stereomorphy</td>
<td>Primula (Primulaceae), Narcissus (Amaryllidaceae), Pyrosia (Ericaceae)</td>
</tr>
<tr>
<td>Two (disymmetric)</td>
<td>Disymmetry</td>
<td>Reflectional in two perpendicular orientations</td>
<td>Bisymmetry, bilateral</td>
<td>Dicentra (Parnassiaceae)</td>
</tr>
<tr>
<td>One (monosymmetric)</td>
<td>Zygomorphy</td>
<td>Reflectional</td>
<td>Bilabiate, bilateral, irregular, ligulate, medial zygomorphy</td>
<td>Salvia (Lamiaceae), Orchis (Orchidaceae), Scrophularia (Scrophulariaceae) Fumaria and Corydalis (Parnassiaceae)</td>
</tr>
<tr>
<td>Medial zygomorphy or bilateral symmetry</td>
<td>Right-left reflectional</td>
<td>Bilabiate, equilateral, medial zygomorphy</td>
<td>Aesculus (Hippocastanaceae), found in Malpighiaceae, Sapindaceae, Trigonaeaceae, Vochysiaeaceae</td>
<td></td>
</tr>
<tr>
<td>Transverse zygomorphy</td>
<td>Upper-lower reflectional (see text on morphogenesis vs functional position)</td>
<td>Oblique zygomorphy</td>
<td>Salvia (Lamiaceae), Orchis (Orchidaceae), Scrophularia (Scrophulariaceae) Fumaria and Corydalis (Parnassiaceae)</td>
<td></td>
</tr>
<tr>
<td>Diagonal zygomorphy</td>
<td>Right-left reflectional slightly off vertical</td>
<td></td>
<td>Aesculus (Hippocastanaceae), found in Malpighiaceae, Sapindaceae, Trigonaeaceae, Vochysiaeaceae</td>
<td></td>
</tr>
<tr>
<td>None (asymmetric)</td>
<td>Ancestral asymmetry or haplomorphy&lt;sup&gt;d&lt;/sup&gt;</td>
<td>Translational; floral organs arranged in spirals rather than whorls</td>
<td>Actinomorphy, radial, regular</td>
<td>Magnolia (Magnoliaceae), Nymphaea (Nymphaeaceae)</td>
</tr>
<tr>
<td>Derived asymmetry</td>
<td>None</td>
<td>Irregular, asymmetry</td>
<td>Centranthus (Valerianaceae), found in Cannaceae, Fabaceae, Marantaceae, Zingiberaceae</td>
<td></td>
</tr>
<tr>
<td>enantiomorphy</td>
<td>Right-left reflectional perianth but with right- and left-styled morphs (stamens taking position opposite the style)</td>
<td>Enantiostyly, inequilateral</td>
<td>Cassia (Caesalpinaceae), Cynella (Tecophilaceae), Monochoria (Pontederiaceae), Solanum (Solanaceae), Barbevita and Wuchendorfia (Haemodoraceae)</td>
<td></td>
</tr>
<tr>
<td>mono-enantiomorphy</td>
<td>Both style-stamen morphs on one plant</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>di-enantiomorphy</td>
<td>Style-stamen morphs on separate plants</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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<sup>a</sup>Modified from References 32, 73, 102, 123, and 129.

<sup>b</sup>Symmetry based on overall pattern of flower, not solely on perianth; see text for discussion.

<sup>c</sup>Terms listed may be full or partial synonyms; many have been ambiguously applied.

<sup>d</sup>Although organs radiate from the principal axis, the spiral arrangement of organs results in no repetition of pattern for the flower as a whole.
only en face, with a two-dimensional perspective; the third dimension of depth (as in the tubular portion of the perianth of some flowers) is not considered. Repetition of pattern of floral structural units can be obtained through three symmetry operations: rotation, reflection, and translation (129). Symmetry arising by a translational operation, which is the repetition along a straight line (e.g. successive whorls of floral organs) along the principal axis of the flower (i.e. depth), has received little or no attention in regard to pollination biology and is not considered here. Symmetry arising by a rotational operation occurs when a pattern is repeated as a plane turns about the principal axis and results in two or more repetitions of the pattern over 360°. Symmetry arising by a reflectional operation occurs when a plane of symmetry through the principal axis produces a pattern of two mirror images.

In general, the primitive state of floral organs (e.g. petals or stamens) is (a) a spiral (helical) arrangement of organ members, (b) an indefinite number of each floral organ (e.g. many petals or stamens), and (c) similar morphology of all members of each organ type (30, 31, 114, 117). The derived state is (a) a whorled arrangement of floral organs, (b) a definite number of each floral organ (often multiples of three or five), and (c) dissimilar morphology among the members of an organ type (e.g. banner, keel, and wings of papilionaceous flowers). As a result of a spiral arrangement of floral organs (but often also of the overlapping arrangement of an indefinite number of members) many primitive flowers (e.g. many Magnoliaceae and Nymphaceae) are asymmetrical (i.e. there is no repetition of pattern for the flower as a whole; see Table 1). The whorled arrangement of floral organ members and the reduction in organ members creates rotationally arising symmetry (e.g. many Ranunculaceae, Liliaceae) with polysymmetry (i.e. two to many planes of symmetry). Monosymmetry results when the organs on the two sides of one plane develop differentially through reflectional operation (e.g. Scrophulariaceae, Lamiaceae). The term disymmetry is reserved for the case of two planes of reflectionally derived symmetry (e.g. Dicentra: Fumariaceae). Asymmetry has also been secondarily derived (e.g. Centranthus: Valerianaceae) (32, 49).

PROBLEMS IN THE TERMINOLOGY OF FLORAL SYMMETRY

Synonyms

Some confusion has been caused by the use of synonyms for symmetry types and, in some cases, the application of the same name to more than one form of floral symmetry (Table 1). Perhaps the biggest source of confusion has resulted from Leppik’s (72–75) use of the terms actinomorphy and zygomorphy to
describe overall floral form (i.e. three-dimensional shape) but radial and bilateral to describe floral symmetry. Most researchers have used the term radial symmetry as a synonym of actinomorphy, and the term bilateral symmetry as a synonym of zygomorphy. However, according to Leppik’s classification scheme, not all radially symmetric flowers are actinomorphic, and bilateral flowers may or may not be zygomorphic. Leppik (72–75) also used similar terms to describe structures other than flowers (for example, paleomorphy for primitive nonangiosperm fossil forms and amorphy for flowers arranged in clusters (e.g. catkins in *Salix* and capitula in Asteraceae). In Table 1, we present a classification of floral symmetry aimed to remove much of the present ambiguity. In accordance with common usage in the literature, we equate radial symmetry with actinomorphy. Similarly, we equate bilateral symmetry with the most common type of zygomorphy (i.e. medial zygomorphy). We favor the term medial zygomorphy over dorsiventral zygomorphy because the latter implies a vertical en face orientation of the flower; the term is thus inappropriate for species that are oriented horizontally (e.g. most Apiceae, Asteraceae, Dipsacaceae).

**Orientation of Symmetry Planes**

A second problem of terminology is establishing a point of reference for orienting symmetry planes in flowers with different types of symmetry. Ideally, the method of orientation should meet three criteria. First, the same method should be used for describing the symmetry planes for all flower types. Second, the description should not depend on the orientation of the flower in space, yet, third, it should be possible to relate the orientation of the planes of symmetry to the orientation of the flower. These criteria would allow the developmental or morphological aspects of symmetry (i.e. orientation in relation to growth of the plant) to be evaluated separately from the ecological or functional aspects of symmetry (i.e. orientation in the pollination process). In practice, none of these three criteria is met.

In an attempt to give orientation to floral diagrams, some authors (81, 129) define the median (or central) plane of the flower as the plane that passes through the principal axis (i.e. the line or vector emanating from the center of the receptacle) and the subtending leaf. Actinomorphic and disymmetric forms are characterized by most authors in relation to the principal axis of the flower. Symmetry is thus independent of flower orientation but could be related to it by indicating whether the flower is erect, pendulous, or obliquely or upwardly inclined. However, orientations of planes of symmetry are not discussed in relation to the median plane. This omission is not generally a problem in actinomorphic flowers because the orientation of the planes may have neither developmental nor ecological significance because of the large number of planes.
In most zygomorphic and most enantiomorphic forms, developmental and ecological planes of symmetry are coincident. This coincidence occurs because the en face surface of most zygomorphic flowers is oriented vertically or obliquely (inclining or declining). The plane of symmetry is, therefore, often designated as vertical (resulting in right and left mirror images). However, there are some exceptions. For example, in most, if not all, transversely zygomorphic species, the symmetry is vertically oriented at anthesis, even though the developmental plane of symmetry is transverse to the median axis. The vertical orientation of the plane of symmetry—the ecologically important plane—is obtained in these species by rotation of the pedicel shortly before the flower opens. Thus, in transverse zygomorphy the plane of symmetry in the mature flower is vertical as in medially zygomorphic flowers, not horizontal as might be expected from the name.

Whole Versus Parts of Flowers

A third problem of terminology arises when not all organs of the flower exhibit the same pattern of symmetry. When symmetry differs among organs, designation of symmetry is usually based on the form of the corolla (112). Differences may be trivial from the ecological perspective or, at least, in terms of pollination. For example, in many species of Verbascum the corolla is zygomorphic (although often weakly so), but the calyx is actinomorphic. It seems unlikely that the form of calyx would affect the pollination process in these species (114). Some flowers that appear to be actinomorphic may not actually be so in the strict sense. For example, each whorl of floral organs (petals, stamens, ovary locules) may be radially arranged but contains different numbers of member components (e.g. five petals and three stigmas in the Polemoniaceae). This inequality might have ecological consequences if pollinators align themselves according to the petals and contact with the stigmas is asymmetrical on the body of the pollinator. In other cases, the inequality obviously has important effects on the pollination process. For example, in many species of Hibiscus the corolla is radially symmetrical, but the style and anthers are upwardly curved, which results in the sternotribic deposition of pollen (i.e. on the ventral surface of the vector). Most authorities classify such flowers as radially symmetrical (i.e. actinomorphic) based on the form of the corolla. A similar situation arises in most enantiomorphic species (see Table 1), which are generally classified as bilaterally symmetrical (i.e. medially zygomorphic) based on the form of their corollas despite the asymmetric nature of the pistil and stamens.

Individual organs may be asymmetric but be arranged symmetrically. For example, in a condition that has been called pseudo-actinomorphy (116), individual petals of many Apocynaceae are asymmetrical but the flower as a whole...
appears to be actinomorphic. Similarly, some radially symmetrical flowers consist of units that function like bilaterally symmetrical flowers (e.g. *Iris*, *Moraee*). Focus on the symmetry of the corolla ignores other aspects of floral symmetry with important ecological consequences. Terminology must clearly indicate the organs to which the description of symmetry is applied. Published reports characterize symmetry by the corolla only, by the perianth (corolla and calyx taken together), or by the flower as a whole. Terminology is applied inconsistently even within some publications. We suggest that symmetry designations be applied to the pattern of the flower as a whole unless otherwise indicated. This usage would be consistent with Sprengel’s usage in which he considered all forms of irregularity within a flower. We distinguish two types of regular forms based on the repetition of rotational patterns over all floral organs of the flower (i.e. planes of symmetry through sepals, petals, stamens, and carpels). Actinomorphic forms exhibit repeating patterns as a plane rotates the principal axis of the flower, while haplomorphic forms do not.

**FREQUENCY OF FLORAL SYMMETRY TYPES**

To assess the frequency of floral symmetry types, we consulted several taxonomic and morphological references (55, 56, 68, 98, 104, 105). Where symmetry designations differed within a family, the differences could usually be resolved by taking into account usage of terminology and taxonomic classification. We excluded from the survey those families with minute flowers that lacked a perianth because most references do not give a symmetry designation for these families, and most of the excluded families are thought to be wind pollinated. A well-developed perianth, or at least one that has not been extremely reduced, is generally thought to be an adaptation to anthophily (33, 100, 110). We consider symmetry at the level of the entire flower, not just the corolla or perianth, so we consider a flower with an actinomorphic corolla but medi ally zygomorphic pistil and stamens (e.g. *Hibiscus schizopetalus*: Malvaceae, *Adansonia digitata*: Bombacaceae, *Gloriosa superba*: Liliaceae) to be medi ally zygomorphic.

The survey resulted in symmetry designations for a total of 241 families (212 dicot, 29 monocot). Actinomorphy and medial zygomorphy were the most common symmetry types (Table 2). Actinomorphy was found in 83% of dicot and 72.4% of monocot families, while medial zygomorphy was found in 33% of dicot and 44.8% of monocot families. The more highly derived forms of symmetry (i.e. disymmetry, transverse and diagonal zygomorphy, and derived asymmetry) were found in only 7.1% of dicot and 13.8% of monocot families. Similarly, ancestral asymmetry is uncommon—4.7% of dicots and
Table 2  Frequency of symmetry types across angiosperm families

<table>
<thead>
<tr>
<th>Symmetry type</th>
<th>All families</th>
<th>Dicots</th>
<th>Monocots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Actinomorphy</td>
<td>197</td>
<td>176</td>
<td>21</td>
</tr>
<tr>
<td>Disymmetry</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Zygomorphy</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Medial</td>
<td>83</td>
<td>70</td>
<td>13</td>
</tr>
<tr>
<td>Transverse</td>
<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Diagonal</td>
<td>5</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Asymmetry</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ancestral</td>
<td>11</td>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td>neo-asymmetry</td>
<td>4</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>mono-enantiomorphy</td>
<td>7</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>di-enantiomorphy</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Totalb</td>
<td>309</td>
<td>271</td>
<td>39</td>
</tr>
</tbody>
</table>

*a Compiled from References 3, 55, 56, 68, 98, 104, and 105.
b 212 dicots and 29 monocots were examined for symmetry type. Totals exceed these values because many families possess more than one symmetry type.

3.4% of monocots. Of families with actinomorphy, 54.7% of dicots and 44% of monocots were exclusively actinomorphic, while only 5.7% of dicots and 3.4% of monocots were exclusively medially zygomorphic (Table 3).

MOLECULAR GENETICS AND THE DEVELOPMENT OF FLORAL SYMMETRY

The development of zygomorphy occurs during different phases of floral ontogeny in various species (12, 117). This supports the suggestion of multiple, independent origins of monosymmetry (114). Species with late development of zygomorphy are usually found in taxonomic groups that are otherwise predominantly actinomorphic (32). In some flowers with late-developing zygomorphy, gravity appears to facilitate, directly or indirectly, the ontogeny of bilateral symmetry (32, 119, 129). Coen (12) suggested that a gravimetrically controlled system may have become coupled to internal cues then eventually evolved into the more typical, genetically controlled system with an early development of zygomorphy.

Most research on the ontogeny of non-actinomorphic floral symmetry has focused on *Antirrhinum majus* (Scrophulariaceae) and is based on the ABC model of organ identity. The ABC model postulates three overlapping regions of gene function, with each region affecting two adjacent whorls of floral organs...
Table 3  Consistency of symmetry types across families

<table>
<thead>
<tr>
<th>Symmetry type</th>
<th>Number of families</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>All families</td>
</tr>
<tr>
<td>Ancestrally asymmetric</td>
<td></td>
</tr>
<tr>
<td>Exclusively</td>
<td>10</td>
</tr>
<tr>
<td>Primarily</td>
<td>1</td>
</tr>
<tr>
<td>Actinomorphic</td>
<td></td>
</tr>
<tr>
<td>Exclusively</td>
<td>129</td>
</tr>
<tr>
<td>Primarily</td>
<td>46</td>
</tr>
<tr>
<td>Equally actinomorphic and medially zygomorphic</td>
<td>14</td>
</tr>
<tr>
<td>Medially zygomorphic</td>
<td></td>
</tr>
<tr>
<td>Exclusively</td>
<td>13</td>
</tr>
<tr>
<td>Primarily</td>
<td>28</td>
</tr>
<tr>
<td>Total</td>
<td>241</td>
</tr>
</tbody>
</table>

*a Compiled from References 3, 55, 56, 68, 98, 104, and 105.

(e.g. petals and stamens, or stamens and pistil) (13, 133). The polar coordinate model for zygomorphy builds on the ABC model to hypothesize that another gene(s) varies in function in the upper and lower halves of the flower, generally with a gradient of increasing functional effect through the vertical axis of the flower (7, 12, 79). There is, thus, a unique polar coordinate specified for each floral organ and the result is reflectional symmetry. This model explains several phenomena of floral morphology and/or function observed in *A. majus* and other species. For example, the vestigial uppermost stamen in *A. majus* and other species in the Scrophulariaceae may result because it lies further up along the vertical axis than do the other stamens.

Position of flowers in the inflorescence also appears to play an important role in floral symmetry (12). The inflorescence of *A. majus* has indeterminant growth; however, there is a recessive allele that results in mutants with terminal flowers (62). These flowers have radial symmetry and all organs resemble those in the lower half of the typical zygomorphic flower, so they are peloric mutants. There are, however, other mutants with peloric flowers in axillary positions (12). The asymmetric environment of the axillary floral meristem of the inflorescence may be necessary for action of genes controlling zygomorphic floral symmetry (14, 79). That zygomorphy is a derived condition is suggested by the fact that there are many mutations producing actinomorphic flowers in normally zygomorphic species, but few mutations in the reverse direction (21, 136). Certainly, the evolution of zygomorphy and the evolution of the inflorescence may be intimately related (11).
SYMMETRY, ADAPTIVE SUITES, AND THE SYNDROME CONCEPT

The pollination syndrome concept holds that suites of floral characteristics such as corolla morphology and color, and reward quantity and quality cluster in phenotypic space and are associated with broad taxonomic groups of pollinators (33, 112). Pollination syndromes are generally designated by pollinator type. Monosymmetrical floral symmetry, particularly medial zygomorphy, has been associated with melittophily (pollination by bees) and ornithophily (pollination by birds) (33, 100, 103, 112).

However, neither melittophily nor ornithophily is a single phenomenon. For example, different suites of floral characteristics have been assigned to different groups of bees (17, 33, 120). Not all of these suites include zygomorphic floral symmetry. Moreover, many pollinators are often seen to visit many types of flowers, and flowers are often visited by many types of pollinators (108). Stebbins (113) suggested that the characteristics of flowers might be molded by the most common and most effective pollinators. More recently, Herrera (54) suggested that ecological factors may constrain both the occurrence of and the response to selection by pollinators on floral characteristics. Thus, the syndrome concept has received much criticism (54, 127).

It may be premature, however, to discard all aspects of the pollination syndrome. For example, monosymmetrical floral symmetry, particularly medial zygomorphy, has originated multiple times from actinomorphy (113). Furthermore, monosymmetry is often associated with particular states of other characteristics (e.g. herbaceous habit, increases in the number of ovules, reduction in the number of stamens, and sympetal) (33, 100, 103, 112). Thus, floral characteristics may in fact cluster in phenotypic space. If so, we should not rule out the possibility that there are adaptive benefits to suites of floral characteristics that are independent of phylogeny. For example, Chittka (10, 127) found that the 154 plant species found in a nature reserve near Berlin can be grouped into distinguishable color clusters or color categories. Moreover, each of these categories seems to have a distinctive level of nectar reward (41). However, clustering of floral character states using a range of characters that are commonly employed to typify syndromes has not been studied. Whether suites cluster in phenotype space needs to be tested using modern phylogenetic approaches (1, 48).

HYPOTHESES OF FLORAL SYMMETRY

The hypotheses presented below vary in their approach to evolutionary trajectories, with some implying coevolution in the narrow sense [i.e. a series of
reciprocal evolutionary changes with each change in one species caused by a change in the other (36)] and others suggesting that one member of the pollination system (i.e. flower or pollinator) adapts to the other. The plant may be seen to manipulate pollinators, or the plants may adapt to pollinator behavior or morphology. However, recent phylogenetically based studies of insect mouth parts (63) and photoreceptor types (8) suggest that plants have adapted to insect pollinators. Large changes in insect morphology as adaptations or compensations to floral morphology might be prohibited because they would interfere with flight efficiency, whereas flowers are not constrained in this way.

Most hypotheses relating to floral symmetry address only the evolution of bilateral (i.e. medial zygomorphy) from radial (i.e. actinomorphic) forms. The citations given here are not necessarily the first expression of the hypothesis but were chosen for their clear presentation, frequent citation, or supporting data. Some hypotheses were intended by their authors to explain the evolution of medial zygomorphy under specific conditions, while others were intended to be all-inclusive. There is much overlap among hypotheses; some are mutually exclusive, but others are not. The same or similar evidence has been used in support of opposing hypotheses. Some hypotheses are based on proximate factors (e.g. behavior patterns of pollen vectors) that may ultimately affect reproductive success (e.g. increased efficiency). Other hypotheses begin with the ultimate advantages (e.g. increased outcrossing is advantageous) and work toward proximate factors (e.g. pollen placement on the vector). Despite this, hypotheses can be placed into four operational groups (with significant overlap) based on the stage of the pollination process at which selection acts on floral symmetry: (a) environmental conditions, (b) perception by the pollinators, (c) information processing (i.e. learning abilities and innate preferences) by the pollinators, and (d) activity patterns (i.e. behavior and movement) of the pollinators.

Environmental Conditions

PROTECTION FROM RAIN HYPOTHESIS As originally proposed by Sprengel (110), the upper lip of horizontally positioned flowers functions as a “nectar cover,” protecting the nectar from rain. The lower lip, which does not serve this function, differs in shape. Sprengel suggested that the upper lip would be similar in form to the corolla of a pendulous flower, while the lower lip would resemble that of an erect flower. It has also been proposed that protection of the pollen from rain may be the driving force in the evolution of medial zygomorphic symmetry (118). We know of no systematic research on the relationships among symmetry, covers over nectar and/or pollen, dilution of nectar by rain, and effects of rain (water) on pollen viability and presentation.
Perception by the Pollinators

OPTICAL INFORMATION HYPOTHESIS This hypothesis suggests that, according to information theory, bilateral symmetry should “give much greater possibilities for the transmission of visually mediated information than radial symmetry” (23, p. 241). This is based on the fact that fewer signals are required to transmit the information pertaining to an actinomorphic shape than to a zygomorphic one. For instance, in the former, information about only one petal would be information about the radial image, while for the latter at least half the pattern would be necessary. Furthermore, “the difference [italics in the original] between the two floral symmetries in ability to transmit information becomes even greater when they are in real or apparent motion” because motion increases the information in proportion to the original information content (23, p. 250). Davenport & Kohanzadeh (23) suspected that with more investigation, some correlation will be found between image complexity and pollinator specificity. However, such an analysis was discredited (24) because the nature of the processing of visual information in the pollinators was not taken into account.

Davenport & Lee (25) also proposed that increased complexity of the floral image in zygomorphic flowers has resulted in a greater opportunity for floral diversity (i.e. the more elements in an image, the more that image can vary). They argued that a greater diversity would allow recognition to be more specific: Zygomorphic flowers would increase discrimination possibilities of pollinators, resulting in greater foraging success. This in turn would favor increased information complexity of zygomorphy. However, this approach ignores that pollinators, including honeybees (111, 122, 130) as well as generalize features among patterns (127). Nevertheless, Davenport & Lee (25) were the first to use two-dimensional fast Fourier transform and convolution procedures of images to quantify flower patterns. This approach allows precise quantification of parameters that pollinators may use in evaluating a pattern [e.g. the total energy change across the different orientations of a pattern (39)] and provides an accurate tool for classifying flowers in different pattern dimensions.

UNEQUAL IMAGE PROJECTION HYPOTHESIS Insects may memorize and recognize the shape of a flower by matching the actual image perceived by the eye with a memorized template (15, 38, 44–46, 131). According to this idea, choice is determined by degree of overlap between memorized image and observed flower shape (38, 46, 131). It has even been proposed that retinotopic matching is the visual strategy by which the memorized and the actual images are compared (26).

The algorithm used by insects in calculation of such overlap is unknown and seems to vary with the training schedule used (107). However, matching in the lower part of the visual field is critical for the recognition of a shape upon
which an insect has been trained (9, 38, 131). For colored patterns, however, this applies only to long-wavelength colors; in ultraviolet light, the upper part of the visual field seems to have a more important role (83).

Flies remember the position of stimuli in the visual field and are able to distinguish two identical patterns displaced by 9° in space (26). Such displacement experiments reveal that position information is a prerequisite for recognition of a learned pattern. Thus, stimuli learned at one height relative to the én face axis of the flower would not be distinguished at a new height. Clearly, the restriction of the approach direction resulting from vertically presented bilateral symmetry contributes to position invariance and, thus, to efficient recognition of flower patterns. Visual fixation and scanning behavior would also greatly contribute to recognition. Indeed, before landing on a vertically presented pattern, honeybees fix it visually by adjusting all six degrees of locomotor freedom (roll, pitch, and yaw as well as forward-backward, sideways, and upward-downward movements) relative to the landing point (132) and scan it on suspended flight (70).

Thus, we postulate that manipulation of the landing of hymenopteran pollinators (and possibly other groups) will be enhanced in flowers with vertical advertising surfaces if the more complicated color pattern (e.g. nectar guides) as well as the dissected parts of the flower corolla (e.g. labellum or lobes) are concentrated at the lower part of the flower. Different patterns in the upper and lower halves of the flower will result in medial zygomorphic symmetry patterns. The position of the flower relative to an approaching visitor is critical in this hypothesis. It seems significant that, in contrast to radially symmetrical flowers, zygomorphic flowers are primarily vertical in én face orientation and tend to have less variable orientation both within and between plants (84, 97, 99, 112). Such a spatial orientation results in a restriction of the approach flight of the bee and thus facilitates the matching strategy.

It would be interesting to compare the visual complexity of the upper and lower halves of zygomorphic flowers pollinated by bees and by birds, which presumably do not have this visual field bias. However, ornithophilous flowers with hovering and nonhovering pollinators should be considered separately because flowers pollinated by hovering birds may have a reduced lower margin for other reasons (see the dangerous lower margin hypothesis below).

FLOWER DISTINCTIVENESS HYPOTHESIS This hypothesis is based on reasoning similar to the optical information hypothesis. Zygomorphy provides more variation by which pollinators can distinguish and establish fidelity to plant species (94). An increase in fidelity would be especially important for plants in more diverse floras and for rare species.

Zygomorphy is positively correlated with plant diversity (number of zoophilous species/m²) across 25 communities of the Wasatch Mountains of Utah and
Idaho (94). Harper (47) suggested that zygomorphy is more common among rare species (but see comments under the pollen position hypothesis below).

**MARGINAL FLOWER–ATTRACTION AND MARGINAL FLOWER–LANDING PLATFORM HYPOTHESES** The marginal flowers of compact inflorescences of several families (e.g. Dipsacaceae, Apiaceae, Verbenaceae, Caprifoliaceae, Asteraceae) are bilaterally symmetrical, while the rest of the flowers are radially symmetrical. Although marginal flowers may have full or partial sexual function (e.g. male in Apiaceae, female in Asteraceae), commonly they are sterile and nectarless (74).

Two hypotheses have been proposed in which selection would favor the evolution of zygomorphic marginal flowers, but few, if any, critical studies have attempted to test or differentiate these hypotheses. In the marginal flower–attraction hypothesis, conspicuousness of the inflorescence as a whole would be heightened (43, 74, 134). Leppik (74) suggested that marginal flowers produce an overall form of the inflorescence that mimics the shape of solitary flowers. Good (43) suggested that marginal flowers enhance the “target-like effect” or result in a “more solid centre surrounded by a periphery of petaline rays” (43, p. 277).

The marginal flower–landing platform hypothesis postulates that in species with flat-topped, rounded cyme or corymb inflorescences (e.g. Asteraceae or some species of *Gentiana*), the zygomorphic, horizontally spreading petals or rays provide the platform for pollinators’ landing (112, 113). In this case, the expanded marginal petals serve in the same capacity as the petals of a horizontal bowl-shaped flower.

**Information Processing by the Pollinators**

**INNATE SYMMETRY PREFERENCE HYPOTHESIS** Although pollinators may not have as strong a fidelity to suites of characteristics as previously believed [see criticisms of the syndrome concept (54)], different taxonomic groups of pollinators might preferentially visit flowers of one symmetry type. For example, Leppik (71) found that beetles, honeybees, moths, and butterflies visited primarily actinomorphic forms, while bumblebees visited primarily zygomorphic forms. However, a close examination shows that Leppik’s results were from casual (although systematic) observations and cannot be reliably subjected to statistical tests. Free (35) found that when given a choice between radially and bilaterally symmetrical models, honeybees trained on radial models preferred the radial models. Free also stated that training on oblong (i.e. bilateral) models “did not reverse the usual preference for radially symmetrical models” (35, p. 272). However, this conclusion cannot be unambiguously drawn from the data he presented. Moreover, since the previous experience of the honeybees...
in Free’s experiments was not controlled, their choices may have reflected the information they learned in their encounters with flowers in the field and not an innate preference.

Nevertheless, it has been repeatedly suggested that pollinators “spontaneously” prefer symmetrical flowers and/or models (35, 69, 86, 88). The critical problem in testing these so-called spontaneous preferences is control of the previous experience of the animals. Most researchers tested these preferences without attention to this aspect. Insects, particularly honeybees, were usually trained to collect sucrose solution at a site that was not associated with any particular stimulus and then, at the same site, were presented with various stimuli that were, in principle, novel to them. The choices made may have reflected their previous experience with flower stimuli in the field rather than true spontaneous preferences. Only tests with naive pollinators [e.g. bumblebees (78), honeybees (41), butterflies (109), hawkmoths (61)] can provide evidence on innate preferences for particular stimuli.

Bees trained to discriminate bilaterally symmetric from nonsymmetric patterns learn the task and transfer it appropriately to novel stimuli, thus demonstrating a capacity to detect and generalize symmetry versus asymmetry (39), showing that bees use symmetry as an independent feature in pattern perception. Horridge (59) confirmed that bees can be trained to distinguish the axis of bilateral symmetry of a set of different patterns. Bees trained to select symmetrical patterns performed better than bees trained to select asymmetrical patterns (39). This result may reflect an innate predisposition to respond to stimuli that are biologically relevant (41, 82) and has important consequences in the field of pollination: If potential pollinators particularly beneficial to the plant (e.g. having high levels of constancy, pollen transfer efficiency, outcross pollen deposition) have an innate preference for zygomorphic forms, there should be strong selection for this morphology (but see 54).

Møller (86) suggested that impairing symmetry of a bilaterally symmetric flower (e.g. by cutting parts of flower petals) reduces the visitation rate of pollinators such as bumblebees and, thus, that bumblebees perform assortative pollination on the basis of symmetry as a flower feature. However, care must be exercised in interpreting experiments that damage a flower because the visitors may be responding to confounding factors such as changes in flower size, chemical signature, or optical properties that result from damaging the flower. Much more needs to be learned about the innate preferences of all pollinator groups as well as their relative qualities as pollinators.

FLUCTUATING ASYMMETRY HYPOTHESIS As originally applied to animal mate choice (86), fluctuating asymmetry (i.e. small random deviations from symmetry, especially from bilateral symmetry) is thought to be the result of genetic
or environmental stress (89, 96). Whether caused by genetic or environmental factors, individuals with higher levels of fluctuating asymmetry have been shown, in many cases, to be less fit and, therefore, tend to be discriminated against as potential mates (85, 95). With regard to pollination, the hypothesis suggests that the dependence of plants on pollinators allows the discriminatory properties of the pollen vectors to be interjected into the pollination process (87, 88). The suggested benefits of lower levels of fluctuating asymmetry to the plant are (a) higher visitation rates, which result in greater pollen removal and deposition and (b) receipt of pollen of superior quality.

Three modes of action are suggested (87). First, asymmetry, as in animals, may be an indication of genetic or environmental stress, and symmetry may be correlated with the amount of the reward (e.g. pollen or nectar) available (86). Second, in plant species with pollination involving sexual deception (e.g. *Ophrys* spp.), an innate preference for bilateral symmetry in mates by the pollinators will select for greater symmetry in the flowers. Third, pre-existing bias for bilateral symmetry may result from a selective advantage for pollinators to recognize predators, parasites, and/or competitors. The first of these modes applies to selection for symmetry in general, while the second and third apply to bilateral symmetry in particular.

Møller & Eriksson (88) found, after controlling for petal size, that bees preferentially visited flowers that were more symmetrical than their nearest neighbors in 7 of 10 species of plants studied (6 with radially symmetrical flowers, 4 with bilaterally symmetrical flowers). They also found significant assortative pollination with respect to fluctuating asymmetry in three species of plants in which it was tested. There was a tendency for the standing crop of nectar and rate of nectar production to decrease with fluctuating asymmetry, but there was no significant relationship with sugar content of the nectar. Although in this type of study it is difficult or impossible to control for correlated character states (e.g. intensity of floral odor correlated with the amount of nectar), the data do suggest that fluctuating asymmetry may play an important role in floral symmetry.

In animals, sexual characters usually exhibit greater levels of fluctuating asymmetry than nonsexual characters (89, 96). To test this in plants, Møller & Eriksson (87) compared levels of asymmetry in flowers and leaves of 19 species from Spain, Sweden, and Denmark. They found no significant difference in fluctuating asymmetry between floral and vegetative characters, suggesting that selection does not act differentially with regard to flowers and vegetative structures.

Comparing values given by Møller & Eriksson (87) for relative asymmetry in radial and bilateral flowers, we found that bilateral species have significantly lower levels of petal asymmetry (one-tailed t-test: \( t = 2.34 \), d.f. = 17, \( p = 0.016 \)). The relative leaf asymmetry for the bilateral group also appears to be
lower than for the radial group (one-tailed t-test: $t = 1.73$, d.f. = 17, $p = 0.051$). These results, limited as they are, suggest that the level of fluctuating asymmetry may be lower, in general, for species with bilaterally symmetrical flowers than for species with radially symmetrical flowers. The data are somewhat preliminary, but they do suggest that further investigation is warranted.

COMPLEXITY–NEURONAL/BEHAVIORAL SOPHISTICATION HYPOTHESIS According to this hypothesis, complex flowers (bilateral symmetry being one type of floral complexity) require more sophisticated neuronal processing or behavioral versatility on the part of pollinators to attain floral rewards (51, 64, 67, 71, 74, 77). The notion of floral (usually morphological) complexity is a topic that can be interpreted in many ways. In general, a more complex flower is one likely to have bilateral symmetry and a narrow and/or long floral tube. There is a specific entrance indicated by (nectar) guides leading to an inaccessible reward. The entrance is likely to be closed, with a forced entry required. The complexity of a flower thus results from a combination of character states that may differentially affect pollinator taxa. Complexity is usually assessed in terms of the probability of or time required for successfully obtaining or learning to obtain the floral reward. Using these criteria, it is relatively straightforward to judge the relative complexity of different flowers for one pollinator. However, these criteria may not be good indicators when rates of energy needs differ among pollinators. Finally, the interaction of various floral characters with different pollinator taxa make it difficult to make unambiguous assessments of absolute levels (i.e. using a common unit of measurement) of floral complexity.

The use of the term “intelligence” to describe the sophistication level of pollinators (33, 51) is problematic because it is not unambiguously definable, quantifiable, or comparable across species. As such, this vague term should be discarded with regard to the abilities of pollinators to gain access to floral rewards.

The complexity–neuronal/behavioral sophistication hypothesis can be subdivided into three components: manipulation skills, learning ability, and sensory perception. Interaction among these components is certainly possible. For example, manipulation skills may be improved with learned experience, but the skill required for some flowers may be beyond the level of some pollinators regardless of learning ability.

Regarding manipulation skills, Heinrich (51) noted that zygomorphic flowers (e.g. many species in the Fabaceae and Scrophulariaceae) may require forced entry to gain access to the nectar reward. He concluded that only pollinators “such as higher or social bees can get entry, and many of the behaviorally less versatile foragers are excluded” (51, p. 172). Furthermore, Heinrich (51) noted
that not all individuals of a species may acquire the ability to extract rewards from some complex flowers (e.g. bumblebees on *Aconitum napellus*).

Although this hypothesis applies generally to all taxonomic groups (71, 74), most research has focused on the learning ability of the bees (e.g. 27, 64, 67). Within the superfamily Apoidae, bees are often classified into two groups based on their behavioral sophistication or learning ability. Several different sets of contrasting terms have been used to distinguish between the groups (e.g. sophisticated, advanced, higher, specialist, social, and literate contrasted with less advanced, primitive, lower, generalist, unskilled, solitary, and illiterate). In addition, the terms generalist and specialist are sometimes used to describe diet breadth rather than neuronal properties of the bees (67). More sophisticated bees are said to be found on more complex flowers. The argument sometimes becomes circular because the bees are often classified by the flowers they visit, rather than by experimental tests of learning ability. Within the “higher” Apoidae (i.e. the Family Apidae and possibly Anthophoridae), Dukas & Real (27) claimed that social *Bombus* (Family Apidae) have better learning capacities than solitary *Xylocopa* (Family Anthophoridae) concerning flower reward, but we are not aware of any experimental evidence showing that “higher” Apoidae have better learning ability and/or better memory capabilities than “lower” Apoidae. Their study also raises the problem of the control of the rewarded trials for studies of learning abilities. If learning rates are to be characterized, a complete record of the rewarded and nonrewarded trials must be kept. The latter are critical for learning because they constitute extinction trials in which a bee learns that a given signal is not associated with reward. Usually, they are ignored, as in the study of Dukas & Real (27), but revisiting a just-depleted flower is as important as getting a reward from it.

Few data exist regarding other pollinator groups and their ability to obtain rewards from flowers of different “complexity.” Lewis (77) determined discovery time (i.e. time from landing on a flower to finding nectar) in successive visits for the cabbage butterfly, *Pieris rapae*, on a variety of flowers varying in “complexity” as assessed by the human eye. Lewis concluded that it is difficult to determine “precisely how flower features influence learning time. The results do, however, suggest that flower morphology does influence learning time, with human judgements of morphological complexity having some predictive value” (77, p. 232). Despite this, it is clear that an face knowledge of floral morphology will not permit specific prediction about the relative difficulty that different pollinators will have in obtaining access to various flowers (65, 77). More data of this type need to be collected across a wide range of pollinators and flower types, quantifying complexity rigorously.

The complexity–neuronal/behavioral sophistication hypothesis also suggests that bilaterally symmetrical flowers require higher sensory perception in
pollinators than radially symmetrical flowers and “other less complicated flowers,” which would be expected to be associated with pollinators having less sensory development. Much of the evidence for this part of the hypothesis has been indirect or speculative.

A mechanism based on matching with neuronal filters has been proposed for the perception of symmetry (58, 69). Neuronal detectors that are specialized in detection of radial, circular (i.e. patterns of concentric rings), or spiral motion have been shown in humans (90), and it was proposed that bees (and other pollinators) use similar detectors to categorize radial and circular patterns on the basis of symmetry, without attention to other local cues. In the same way, similar neuronal detectors for bilaterally symmetric patterns have been proposed to exist in bees and other pollinators (39). Alternatively, it has been postulated that symmetry might be detected by the interactive combination of a radial filter (58, 69) and an average-orientation filter (59) such as those found in dragonflies (92) and in honeybees (137). After being passed through a radial filter, many bilaterally symmetrical patterns are left with some preferred orientation, which would reveal the axis of symmetry. There is no evidence for deciding between the two possibilities. Regarding radial versus bilateral symmetry detection, there is no evidence to suggest that one class of detector should be considered perceptually more sophisticated than another. Moreover, that classes of detectors operate with different types of symmetry is not necessarily correlated with differences in learning ability.

**COMPLEXITY-CONSTANCY HYPOTHESIS** According to this hypothesis, complex (e.g. zygomorphic) flowers promote floral constancy as a result of more efficient foraging by pollinators (64, 77) and, hence, greater outcrossing (22). Constancy in complex flowers (as compared to simple flowers in which access is easy or easily learned) can be promoted by two mechanisms. First, morphological complexity (e.g. long floral tubes) may require morphological adaptations of pollinators that limit them to flowers with similar morphology (77). However, as pointed out above, there is no evidence that zygomorphic flowers and bilateral symmetry are better learned than actinomorphic flowers and radial symmetry. This aspect of the hypothesis seems to be the inverse of the reward wastage hypothesis (see below) in that pollinators are limited to, rather than excluded by, a particular morphology. Moreover, the observation that many, if not most, pollinators visit a wide range of flowers (108, 127) tends to discount this hypothesis. Waser (126) has termed this type of floral specialization “fixed preference” rather than “floral constancy.”

The second mechanism hypothesized to promote constancy is that the cost of learning to extract the reward from complex new flowers may outweigh the benefits of obtaining additional sources of reward (22, 64, 77). There may be
an energetic cost whereby time spent learning to handle the complex new form reduces the rate of reward intake compared to flowers with which the pollinator has experience (52, 66). The argument has also been made that cost of constancy and fully learning to handle a complex flower ultimately results in a higher return (22) as well as reduces competition from less constant pollinators or individuals (64). However, Laverty (66) found for bumblebees that the cost in time of switching was small and not likely to account for constancy. Another possible cost of learning to handle additional flowers might be interference with the efficiency on, or even elimination of, the ability to handle flowers already learned (76, 125, 126). There is some support for interference in several pollinator taxa (76, 77, 91), but interpretation of these results is difficult because many of the early studies lack appropriate controls for the motivation and experience of the animals tested. However, in a series of studies on bumblebees Laverty and his group have found no evidence of a complete elimination of an already learned skill, even as long as 24 h after learning to handle a new flower (37, 66, 67, 135).

Activity Patterns of the Pollinators

**Natural Position Hypothesis** Sprengel (110) observed that the natural position of insects in flight is upright. Similarly, although an inverted position is possible when walking or standing, it is usually avoided because it requires more effort. As a result of this “natural position,” all horizontal or downward inclining flowers would be approached from only one direction. Sprengel suggested that, therefore, the anthers and stigma would be placed in the position most “suitable” for the natural position of the pollinators (i.e. irregular anthers and stigma(s) would result in better contact with the pollinator). Under the influence of gravity, changes in the orientation of a flower sometimes result in irregularity of stamens and style (e.g. *Epilobium angustifolium*) (129).

**Inflorescence Type–Flower Orientation Hypothesis** According to this hypothesis, actinomorphic flowers arranged in vertical racemes or spikes, especially those with tightly clustered flowers, would provide poor landing platforms (110, 112, 113). Therefore, in species visited by pollinators that land on the flower (as opposed to those that only hover, e.g. hummingbirds and hawkmoths), the lower lip of the flower is expanded to provide a platform. Sprengel (110) also suggested that, because pollinators will approach and contact the flower from one direction, the lower lip may be enlarged for attraction, in addition to its function as a landing platform.

**Pollen Position Hypothesis** This hypothesis suggests that in bilaterally symmetrical flowers, the visitor is restricted to certain directions in its approach to and its movement on and/or within the flower. This is in contrast to radially symmetric flowers in which the visitor may approach the flower from
any direction (33, 47, 74). The restricted approach results in increased precision of pollen placement on, and stigma contact with, the pollinator’s body (2, 51, 64, 80). The increased precision thus results in a higher proportion of pollen reaching the stigma. Bowers (4) proposed a similar process for evolution of enantiomorphy.

In an unusual application of this hypothesis, Harper (47) suggested that “floral zygomorphy confers a reproductive advantage to rare plants” as a result of the enhanced pollination efficiency (47, p. 135). He found over-representation of bilaterally symmetry in the rare flowers of five floras (one each in California and Colorado, and three in Utah), but only in one of these was the association significant. Therefore, his statement that there is a “universal over-representation of bilaterally symmetrical flowers among the rare taxa of all floras” needs further validation, especially in light of modern concepts concerning the definition of “rarity” in plants (101, p. 134).

Leppik (74) hypothesized that bilateral symmetry (i.e. medial zygomorphy) would make pollination be more efficient and also speculated (without giving a reason) that cross-pollination would thereby be more effective. Increased outcrossing has also been proposed as the driving force behind enantiomorphy (28, 29, 93), However, Fenster (34) suggested that enantiomorphy might actually increase selfing through geitonogamous visits to both morphs on the same plant. Fenster (34) found a small increase in the outcrossing rate of artificially non-enantiomorphous compared to enantiomorphous plants, and concluded that enantiomorphy is not a mechanism to promote outcrossing. Robertson (106, p. 344) hypothesized that “flower features that promote approach from all directions will lead to higher (pollen) carryover.” Thus, in direct contrast to various versions of the pollen position hypothesis, actinomorphy should be the symmetry type that promotes outcrossing.

REWARD WASTAGE HYPOTHESIS This hypothesis also relies on the restriction of approach by flower visitors (51, 74, 97, 115). However, in this case, morphology prevents (or at least limits) inefficient pollinating species or thieves (sensu 60) from obtaining and, thus, wasting the reward (usually nectar), which, in zygomorphic flowers, is often hidden and requires complicated behaviors and/or specialized morphology for access. Furthermore, in many zygomorphic flowers, the reward can be legitimately obtained only by a mechanical deformation of the flower requiring a minimum weight or strength of the visitor. Access is thus limited to “specialized” pollinators capable of more complicated behavior patterns and/or larger pollinators capable of mechanically forcing the flower (84). Such specialized and larger pollinators are thought to be more likely to transfer pollen between conspecific flowers because they tend to fly faster, farther, and more efficiently under adverse conditions (51, 115).
The pollen position and reward wastage hypotheses are difficult to separate. Both are thought to promote more efficient pollination (i.e. greater reproductive return from investment in pollen and reward). Although these arguments sound logical, experimental evidence is scarce and most of the aspects need validation, especially in comparison to actinomorphic flowers. Does bilateral symmetry result in more efficient pollination? For example, what proportion of pollen is actually deposited on stigmas in actinomorphic versus medial zygomorphic flowers? Does the proportion differ for generalist and specialist pollinators?

**PRECISE STEERING—INDIVIDUAL FLOWER HYPOTHESIS** This hypothesis might be considered a variant of the pollen position hypothesis. For bird-pollinated species in western Australia, Holm (57) suggested that zygomorphic symmetry allows “precise steering” of the bird as it forages on single flowers. In contrast, in radially symmetric brush-type flowers, found in inflorescences where the birds do not discriminate individual flowers, the anthers brush the bird more or less at random (57). However, Holm also described a typical brush-type inflorescence with zygomorphic flowers. He noted that several species of *Banksia* have stiff, curved stigmas (and a reduced but zygomorphic perianth) that serve as perches for birds foraging on the inflorescence.

**DANGEROUS LOWER MARGIN HYPOTHESIS** Zygomorphy is often associated with ornithophily (32, 33, 99, 115). In some bird-pollinated species, zygomorphy is thought to result from the elimination of the lower margin of the corolla (i.e. lower petals or lip of flowers with a horizontal or oblique en face orientation) (33). Faegri & van der Pijl (33) called the lower margin “dangerous” from the perspective of the plant and gave two reasons for its reduction: removal of a landing place for insects and elimination of an “obstacle” for the avian pollinators that are too large to alight on the flower itself. The benefits of these two effects to the plant were not stated explicitly. However, the benefits of excluding insects might be functionally identical to those proposed in the reward wastage hypothesis. Furthermore, in species visited primarily or exclusively by nonhovering birds, flowers (e.g. *Protea, Aloe*) often have an associated perch and are oriented toward this perch, while in species visited by hovering birds (hummingbirds or possibly sunbirds) the flowers (e.g. *Pedilanthus, Quassia*) are held away from potential perches (33). The absence of the lower margin but the presence of an associated perch provides easy visitor access in the nonhovering bird-pollinated species, while the absence of the perch requires hovering in the hovering bird-pollinated species. In both groups of plants, the direction of approach to the flower would be channeled, giving this hypothesis some aspects of the natural position, pollen position, and/or precise steering hypotheses. Finally, in some flowers enforcement of hovering may be the critical function leading to the loss of the dangerous lower margin. To
meet the energetically higher costs of hovering, birds would have to visit more flowers (53). Hovering would also accelerate the rate at which flowers could be visited (50). Both of these effects would tend to increase outcrossing rates.

FEEDING ANther–POLLEN COLLECTION HYPOTHESIS Faegri & van der Pijl (33) mentioned in passing that zygomorphy may be induced in families dominated by radially symmetrical flowers. This is thought to result from the tendency for feeding anthers to cluster in one part of the flower. Faegri & van der Pijl (33) implied that the manipulations required to remove pollen from feeding anthers (e.g. squeezing or vibrating anthers) may be the ultimate cause of the zygomorphy, but gave no specific selective forces. Dulberger (28) suggested that enantiomorphy may reduce the possibility of damage to the stigma during the vigorous manipulation required during buzz-pollination. Furthermore, separation of stigma and anthers in enantiomorphy may reduce the possibility of self-pollination resulting from the cloud of dry pollen released as the vector [usually a bee (6)] vibrates the anthers. Fenster (34) compared enantiomorphy to heterostyly and suggested that both may function to facilitate pollen collection and dispersal by reducing interference between male and female organs (128).

DISCUSSION AND CONCLUSIONS

What have we learned about floral symmetry since Sprengel? Several relatively uncommon types of symmetry have been described. The predominant type of irregular floral form, namely medial zygomorphy, has independently arisen many times (113). Multiple origins and the variety of hypotheses for these origins suggest that the evolution of non-actinomorphic floral symmetry is not a singular process. Apparently, reversion to actinomorphy is relatively uncommon. It would be instructive to compare pollination parameters (e.g. efficiency of pollination, constancy of pollinators) of pairs of closely related species differing in symmetry. Pairs should be chosen such that symmetry types could be represented in both the ancestral and the derived conditions.

A major trend in the evolution of floral symmetry has been the derivation of actinomorphic floral symmetry from ancestral forms with asymmetric flowers (namely haplomorphy). Given the rarity of ancestral haplomorphy, there must be advantages to actinomorphy over this primitive type of asymmetry. Floral organs radiate out from the central principal axis in both ancestrally asymmetric and actinomorphic flowers. Did selection for symmetry of pattern play a role in the transition from a spiral arrangement to a whorled arrangement of floral organs? We were unable to find hypotheses regarding the role that pollination might have played in this transition. Although of lesser importance in terms of the numbers of species, we were also unable to find hypotheses regarding the evolution of transverse and diagonal zygomorphy, disymmetry, and derived asymmetry.
With so many advantages to bilateral symmetry, the question then arises, why are not all flowers medially zygomorphic? There have been no good comparative studies showing the magnitude of the proposed advantages for most hypotheses. It may be difficult or impossible to quantify the importance of symmetry as proposed by some of the hypotheses. The hypotheses emphasize the advantages of zygomorphy, but little is said about the disadvantages. One disadvantage of zygomorphic flowers requiring specialized pollinators may be a risk of no pollination in years when the populations of pollinators are depressed (TM Laverty, personal communication). Laverty, therefore, suggested (personal communication) that the hypothesis of a greater tendency for zygomorphy in perennial species should be tested.

Is symmetry an absolute phenomenon? From most directions or orientations, flowers are perceived as asymmetrical no matter what type of symmetry they possess (19). It is only when pollinators are oriented along the principal axis of the flower that the “true” symmetry becomes apparent. What aspects of floral symmetry are important to the pollinators? In general, there is an accordance between the symmetry of external contour (of the flower outlines) and the “internal” one (of the “nectar guides”) (18). When, if at all, does the symmetry of a flower become important to a pollinator (5)? For example, how close must a pollinator be to a flower before it perceives symmetry? To answer these questions, other flower parameters must also be taken into account—for example, size of the corolla and the visual angle that such a flower subtends at the pollinator eye (42). In the case of the honeybee, for instance, stimulus detection is organized in a sequential way, each stage mediated by a different visual subsystem. First, a target is detected by its achromatic contrast against the background, through the long-wave receptor system (40, 42). Then, chromatic information itself is perceived by the color vision system from a visual angle of approximately 15°, and finally, only very close to the target is the global form, and therefore the symmetry, perceived (124).

Similarly, is symmetry important only when the pollinator views the flower en face? If not, how far from the en face view is the pattern of symmetry recognized? Little or nothing is known about these aspects of flower and visitor interactions for most pollinator groups. Most of our knowledge about the role that symmetry plays in the behavior of pollinators (e.g. perception, recognition, innate preferences, learning) comes from the study of one species, the honeybee. While the honeybee is important in some pollination systems, its sensory capabilities and behavior may differ from those of some butterfly, fly, hummingbird, and even solitary bee species. Much more needs to be learned about the sensory capabilities and behavior patterns of other pollinator groups regarding all aspects of floral characters including symmetry.

Possibly the biggest gap in our understanding of the evolution of floral symmetry is the connection between the results of laboratory and field studies. In
an attempt to control extraneous or unintended cues for the pollinators, laboratory studies have used somewhat simplified systems. These studies often use artificial patterns that have little resemblance to natural flowers. Similarly, the focus has been on flowers or patterns in isolation. Little is known about the role of floral symmetry in the morphological hierarchy of architectural complexity (20), that is, how pollinators react to individual flowers versus inflorescences versus patches of plants. For example, the distance at which floral symmetry becomes important to a particular pollinator may depend on whether flowers are in compact versus diffuse inflorescences, or are solitary. The trainability and ease of manipulation of the honeybee has, as mentioned above, limited most studies laboratory studies to this species. Field studies, on the other hand, often suffer from a lack of control. It is difficult to determine which floral characteristics pollinators are using, and it is impossible to know whether the behavior of pollinators is the result of innate preferences or learning. Finally, laboratory and field studies have tended to focus on different aspects of floral symmetry. Many laboratory studies are concerned with the behavior of the pollinators, while many field studies center on the details of floral morphology and its relationship to pollinator morphology and movement patterns.

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