

Adaptive Significance of Floral Movement

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Adaptive Significance of Floral Movement

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Since Darwin observed the reconfiguration of pollinia in orchards and referred to it as a function to reduce self-pollination, diverse floral movements have been investigated and various hypotheses have been proposed to explain their adaptive significance. However, adaptive significance of floral movement in some species has yet to be fully explained. Increasing evidence suggests that some floral movements, which have previously been considered as a mechanism to avoid self-pollination, may act as a mechanism to reduce intrafloral male-female interference. In this review, we first explore insect-induced floral movement—such as secondary pollen presentation—that enhances the efficiency and accuracy of pollination. Secondly, we outline the active movements of different floral structures of pistil (style), stamen (filament, anther, pollen), and corolla, such as flexistylis, pollen sliding and catapulting, and anther rotation. Thirdly, we introduce movement herkogamy, which makes herkogamy decrease or increase via the movements of floral structures, especially decreased approach herkogamy via style curvature in the Malvaceae with a monadelphous column. Fourthly, we highlight the different adaptive significances in floral movements for understanding their evolution, including reduction in intrafloral male-female interference, promotion of outcrossing and/or avoidance of self-pollination, delayed autonomous selfing, and tolerance to harsh environments. In particular, we explore the possibility of three functions of one floral movement in one species, which differs from the generally recognized and conventional notion of one floral movement in one species with only one or two functional mechanisms. Finally, we provide perspectives on the challenges and opportunities for using demographic and molecular genetic approaches to (i) study the relative importance and evolutionary mechanism of different adaptive significances in one floral movement; and (ii) simultaneously investigate the floral movement and correlative traits of broader species in related or unrelated families to test how they evolved and the evolutionary relationship between their functions.

Keywords insect-touched floral movement, active floral movement, delayed autonomous selfing, promotion of outcrossing, reduction in intrafloral male-female interference, multiple adaptive significances

I. INTRODUCTION

Unlike the sedentary nature of most plants, humans are usually more attracted to the movement of animals. However, some plants have faster and more conspicuous movement than animals. For example, the “touch me not” plant *Mimosa pudica* (Mimosaceae) exhibits rapid leaf folding (Raven *et al.*, 2005). Darwin (1880) studied the movements of the little leaflets of *Desmodium gyrans* (Fabaceae), which have a strategy to maximize sunlight by tracking the sun. After this, rapid movements of plant structures, which occur over a very short period of time (several hours, several minutes, and even under ms), have constantly intrigued biological scientists. Examples of this include the Venus flytrap (*Dionaea muscipula* (Droseraceae)), which closes its trap in about 100 ms (Forterre *et al.*, 2005); the flower of *Cornus canadensis* (Cornaceae), which opens its petals and fires pollen in less than 0.5 ms (Edwards *et al.*, 2005); and *Morus alba* (Moraceae), which moves petals to velocities in excess of one-half the speed of sound (Taylor *et al.*, 2006).

The diversity of flowering plants is tremendous and can be readily observed. The flower, which is the reproductive structure and is essential for the completion of a plant's life cycle, has received considerable attention. Much attention has been focused on the last stages of flower development, flower opening, and flower senescence. However, in many angiosperms, floral structures can undergo dramatic movements over relatively short periods. Lindley (1819; 1826) was one of the first scientists to describe the nature of floral parts, pollen transfer, and movement of the style. After this, different floral movements have been reported in different plant species, such as pollinia reconfiguration in the orchids (Darwin, 1862; Peter and Johnson, 2006), stigma lobe closure in *Campsis radicans* (Bignoniaceae) (Fetscher and Kohn, 1999), anther rotation in an orchid *Holcoglossum amesianum* (Orchidaceae) (Liu *et al.*, 2006), and corolla closure in *Fumana juniperina* (Cistaceae) (Carrió *et al.*, 2008).

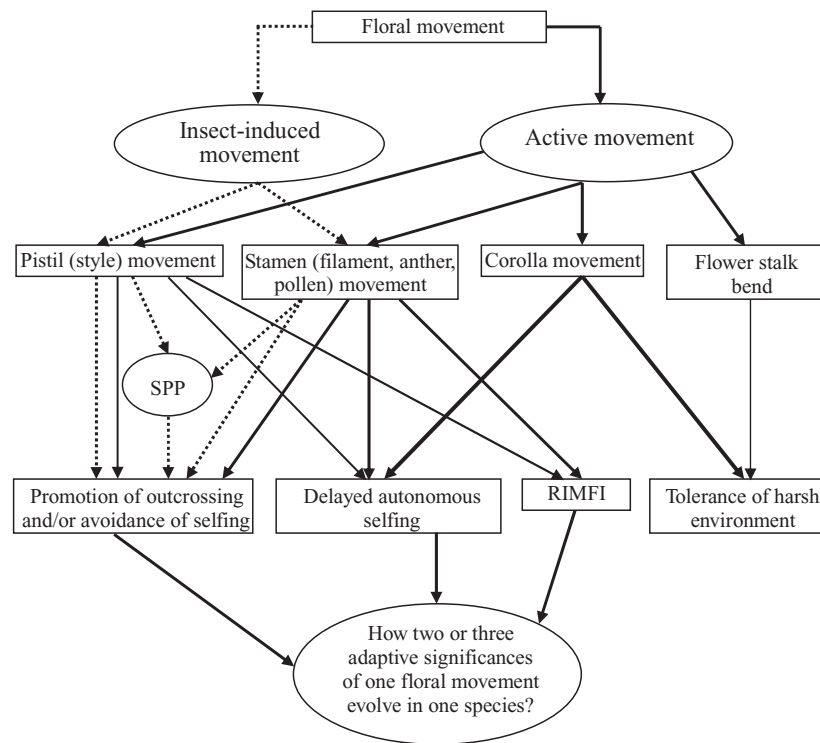


FIG. 1. Adaptive significance of insect-induced (dashed arrowheads) and active (solid arrowheads) floral movement. SPP: secondary pollen presentation; RIMFI: reduction in intrafloral male-female interference.

Accordingly, whether the floral movement is induced by a pollinator or not (Figure 1), it includes the following: (i) insect-touched floral movement, such as stamen movement in *Opuntia brunneogemma* (Cactaceae) touched by *Ptilothrix fructifera* (Anthophoridae), *Lithurgus rufiventris* (Megachilidae), and *Cephalocolletes rugata* (Colletidae) (Schlindwein and Wittmann, 1997a), anther release in *Kalmia latifolia* (Ericaceae) touched by *Bombus ternarius* (Apidae) (Rathcke and Real, 1993), and lip movement in *Bulbophyllum penicillium* (Orchidaceae) touched by a very small fruit fly (*Drosophila* sp.) (Liu *et al.*, 2010); and (ii) active floral movement, which is actively conducted by different floral structures (e.g., pistil (style), stamen (filament, anther, pollen) and corolla), but not touched by a pollinator.

Darwin (1862) proposed that physical reconfiguration of pollinia (comprising the pollen packets, the pollinia as well as associated accessory structures) serves as a mechanism for reducing the likelihood of self-pollination. Thereafter, various hypotheses have been proposed to explain the adaptive significance of different floral movements (Figure 1). These include reduction in intrafloral male-female interference (Fetscher, 2001; Sun *et al.*, 2007; Ruan *et al.*, 2010a), promotion of outcrossing and/or avoidance of self-pollination (Schlessman, 1986; Li *et al.*, 2001; Verma *et al.*, 2004; Edwards *et al.*, 2005; Peter and Johnson, 2006; Whitaker *et al.*, 2007), delayed autonomous selfing (Ruan *et al.*, 2004; Wang *et al.*, 2004; Liu *et al.*, 2006; Zhang and Li, 2008) and tolerance to harsh environments (Bynum and

Smith, 2001; Huang *et al.*, 2002). However, the adaptive significance of floral movement in some species has yet to be fully explained, presenting some challenging problems for evolutionary biologists. For example, Li *et al.* (2001) proposed that flexistylis in species of the genus *Alpinia* (Zingiberaceae) has evolved to encourage outcrossing (Li *et al.*, 2002), but flexistylis in *Alpinia blepharocalyx* (Zingiberaceae) most likely represents a means to reduce interference with pollen export (Sun *et al.*, 2007).

On the other hand, although some floral movements have previously been viewed as a mechanism to avoid self-pollination (Darwin, 1862), increasing evidence suggests that it may act as a mechanism to reduce intrafloral male-female interference (Barrett, 2003; Sun *et al.*, 2007); however, there are no examples on how to distinguish the reduction in intrafloral male-female interference from the avoidance of self-pollination. Additional studies also corroborate that a single floral movement could have more than one adaptive significance (Buttrose *et al.*, 1977; Schlessman, 1986; Freitas and Sazima, 2009), or as many as three (Ruan *et al.*, 2010a). For example, style movement in *Eremurus himalaicus* (Liliaceae) not only promotes outcross-pollination and/or avoids self-pollination (Verma *et al.*, 2004), but also ensures that the style is separated from the flight path of visitors. This separation may avoid the influence of the pistil on pollen export and improve male fitness.

In this review, we highlight the following: 1) insect-induced floral movement, such as secondary pollen presentation, which enhances the efficiency and accuracy of pollination; 2) the active

movements of different floral structures (pistil (style), stamen (filament, anther, pollen), and corolla), such as flexistylly, pollen sliding and catapulting, and anther rotation; 3) movement approach herkogamy making herkogamy decrease or increase via the movements of floral structures, especially decreased approach herkogamy via style curvature in the Malvaceae with a monadelphous column; 4) the different adaptive significance in different floral movements, including reduction in intrafloral male–female interference, promotion of outcrossing and/or avoidance of self-pollination, delayed autonomous selfing, and tolerance to harsh environments; and 5) especially the possibility of multiple functions of one floral movement in one species, since the presumption of three adaptive significances of one floral movement in one species presents a challenging notion for evolutionary biologists. In addition, we also present perspectives of the challenges and opportunities for studies on these adaptive significances, especially the relative importance and evolutionary mechanisms in one floral movement in one species.

II. INSECT-INDUCED FLORAL MOVEMENT

A. Insect-Touched Floral Movement

In the flowers of *Opuntia brunneogemma* and *Opuntia viridirubra* (Cactaceae), visiting bees touch the filaments and stimulate the movement of the stamens to the center of the flower (Schlindwein and Wittmann, 1997a). The anthers are densely packed around lower layers of the style. Through this stamen movement, the flowers hide most of their pollen from flower visitors but effectively favor pollination by effective oligolectic bees that specialize in collecting pollen from one genus or species (or from only a few genera or species) of flowering plants such as *Ptilothrix fructifera* (Anthophoridae), *Lithurgus rufiventris* (Megachilidae), and *Cephalocolletes rugata* (Colletidae). Except for secondary pollen presentation (see B. Secondary Pollen Presentation), the floral movement induced by pollinators has also been reported in some species of eight families (Lamiaceae, Asteraceae, Berberidaceae, Bignoniaceae, Cactaceae, Ericaceae, Loasaceae and Orchidaceae) (Table 1). These include (i) the oligolectic pollinator *Bicolletes pampeana* (Colletidae) elicit stamen movements in *Cajophora arechavaleatae* (Loasaceae) (Schlindwein and Wittmann, 1997b); (ii) a visiting insect, typically a bumblebee (*Bombus ternarius*), triggers the release of the anthers in *Kalmia latifolia* (Rathcke and Real, 1993; Nagy *et al.*, 1999), (iii) the pollinator of *Bombus sonorus* (bumblebees) causes closure of stigma lobes in *Chilopsis linearis* (Bignoniaceae) (Richardson, 2004); and (iv), a very small fruit fly (*Drosophila* sp.), which touches the lip in a continuous movement up and down or as a left swing in *Bulbophyllum penicillium* (Liu *et al.*, 2010). Most of these floral movements that are induced by a pollinator present effective cross-pollen transfer (Table 1).

The Brazilian species *Hyptis pauliana* (Lamiaceae) probably has an ornithophilous flower, in which explosive pollen presentation is effected by the sudden release of stamens from a petal

lobe, termed the carina (Brantjes and de Vos, 1981). Two hinges are situated in the suspensor of this carina. Shortly before anthesis, the filaments elongate so that the stamens enter deep into the carina. At anthesis, two hinges in the suspensor plate unfold and the stamens keep the carina in this excitable position. Disturbance by a pollinator causes the anthers to slip from the carina, which can then flip back, while the anthers swing up and eject the pollen on to the flower's visitor. In the receptive phase the stamens bend down and the style elongates. The floral movements in this species not only allow effective pollen export via pollen ejection, but are also useful for improving female-fitness via style elongation after pollen shed.

The movement of the lip (a modified petal, also called a *labellum*) has been reported in some orchid species: *Drakea* (Darwin, 1890), *Pterostylis* (Cady, 1965), *Paracaleana* (Firth, 1965) and *Caleana* (Dressler, 1993). *Bulbophyllum penicillium*, an orchid species, has a sensitive hairy lip, which shakes unceasingly if the flowers are unpollinated (Darwin, 1890) but loses its movable function once the flower is pollinated (Liu *et al.*, 2010). Once a fly lands on the lip, it begins to move up and down or swing left and right between two lateral sepals (Figure 2), pressing the foraging fly (*Drosophila* sp.) toward the column apex, touching the anther, and removing the pollinaria (Figure 2D); when entering another flower to search for food, the fly carrying the pollinaria is pressed to the column apex again by the moving lip (Liu *et al.*, 2010); thus, the pollinaria of the previous flower are left on the stigma of the latter flower, inducing cross-pollination.

B. Secondary Pollen Presentation

Secondary pollen presentation is pollen presentation conducted by the movements of flower structures (Table 2), other than the anthers, which are triggered by pollinators (Carolin, 1960; Lloyd and Yates, 1982; Yeo, 1993; Howell *et al.*, 1993; Kennedy, 1999; Erbar and Leins, 1995; Cerana, 2004). These include the stigmatic brush in *Crotalaria micans* (Leguminosae) (Etcheverry, 2001), the retraction of pollen-collecting hairs of the style in *Campanula rapunculus* (Campanulaceae) (Schlindwein *et al.*, 2005), the bending down of the staminal column and the shifting of the style within the staminal tube in Cuban bat-pollinated *Lobelia oxyphylla* (Lobeliaceae) (Koch and von Helversen, 2006), the downward movement of the keel in *Polygala vayredae* (Polygalaceae) (Castro *et al.*, 2008a), and the tense style-releasing staminode (Figure 3) in *Phrynium oliganthum* (Marantaceae) (Duan and Li, 2008).

The style of species in the Marantaceae is a curved elastic spring and the stigma is cup-shaped. The pollen is shed prior to anthesis while the flower is still in bud, and deposited in a shallow depression on the back of the style just behind the stigma (Kennedy, 1999). It is the upward growth of the style which forces the pollen grains from the anther, and onto the style depression ("stamp" of Andersson, 1981). At anthesis, the style is held in place under tension by the cucullate (hooded) staminode, which is also under tension pulling in the opposite direction, thus maintaining the style in static equilibrium. When

TABLE 1
Insect-touched floral movement

Species (Family)	Movement induced by a pollinator	Adaptive significance	References
<i>Hyptis pauliana</i> (Lamiaceae)	Before anthesis, the filaments elongate so that the stamens enter deep into the carina. At anthesis, two hinges in the suspensor plate unfold and the stamens keep the carina in the excitable position. A pollinator disturbance causes the anthers to slip from the carina, which then can flip back, while the anthers swing up and eject the pollen onto the flower visitor. In the receptive phase, the stamens bend down and the style elongates.	Pollen export.	Brantjes and de Vos, 1981
<i>Berberis vulgaris</i> (Berberidaceae)	Pollinators touch stamen movement towards the center of the flower.	Effective pollen transfer.	Lechowski and Białczyk, 1992
<i>Opuntia brunneogemma</i> , <i>O. viridirubra</i> and <i>O. spinosissima</i> (Cactaceae)	Pollinators touch the filaments and stimulate the movement of the stamens to the center of the flower.	Anthers are densely packed around lower layers of the style, which hide most of their pollen from the flower visitors but favor effectively pollination by effective oligolectic bees.	Schindwein and Wittmann, 1997a; Negrón-Ortiz, 1998
<i>Cajophora arechavaletae</i> (Loasaceae)	The oligolectic females of <i>Bicolletes pampeana</i> elicit stamen movements by pressing the scales of the nectaries outwards with their head while taking up nectar.	Pollen presentation.	Schindwein and Wittmann, 1997b
<i>Kalmia latifolia</i> (Ericaceae)	Pollinator triggers the release of the anthers.	Cross-pollination.	Rathcke and Real, 1993; Nagy <i>et al.</i> , 1999
<i>Chilopsis linearis</i> (Bignoniaceae)	Legitimate visitors sometimes cause stigma closure.	Cost plants by without depositing enough pollen to set a fruit.	Richardson, 2004
<i>Bulbophyllum penicillium</i> (Orchidaceae)	The lip is touched by a landing insect (a very small fruit fly (<i>Drosophila</i> sp.)); it will move up and down or swing left and right continuously. By suck lip movement, the pollinator will be pressed toward the column apex where anther and stigma are located.	Cross-pollination.	Liu <i>et al.</i> , 2010

the pollinator inserts its head into the flower in search of nectar, it depresses the appendage, or “trigger” (Kennedy, 1999), on the cucullate staminode, thus releasing the style that springs forward bringing the stigma into contact with the pollen (from a previously visited flower) on the pollinator’s body and in the same motion depositing its own pollen in the same spot. Due to their specialized floral morphology, the pollen and the stigma are spatially separated prior to pollination and, as the style movement is irreversible after tripping, its position prevents any pollen from subsequently entering the stigma (in nature) (Kennedy, 1999).

Flowers of *Campanula* (Campanulaceae) have a peculiar mechanism of secondary pollen presentation (Schindwein *et al.*, 2005): the anthers with introrse dehiscence open before anthesis and shed their pollen on the pollen-collecting hairs of the style (Kirchner, 1897; Jost, 1918; Shetler, 1979; Yeo, 1993). At the beginning of anthesis, all pollen grains adhere to these pollen-collecting hairs. During this functional male phase the hairs are retracted into the style (Leins and Erbar, 1990; Nyman, 1992, 1993a, b). Leins (2000) suggests that the retraction, which is stimulated by mechanical contact of the flower visitors, starts at the apex of the style and continues in

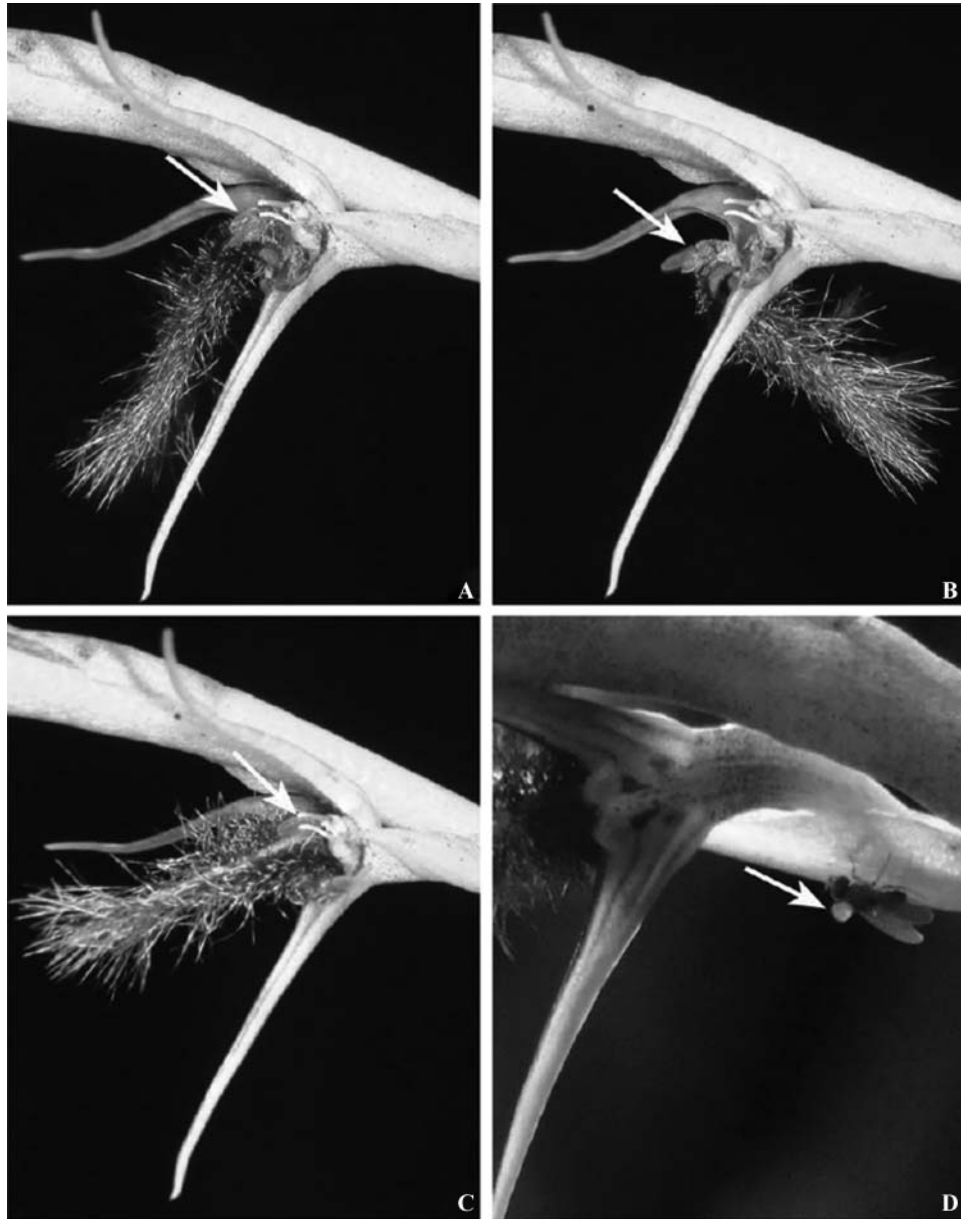


FIG. 2. Pollination mechanism of *Bulbophyllum penicillium* (Liu *et al.*, 2010). A: a fruit fly, *Drosophila* sp. (arrow), enters the base of the lip foraging for food and sets the lip in motion. B: the fruit fly (arrow) drops with the lip. C: the lip moves downwards and then upwards allowing the fruit fly (arrow) to touch the stigma and the anther. D: the fruit fly picks up two pollinia of *B. penicillium* on its thorax (arrow) after touching the anther.

the direction of the base, and functions by gradually liberating the pollen grains.

Secondary pollen presentation is the relocation and presentation of pollen in floral structures. The stigma of *Polygala vayredae* is divided into two regions, a sterile region in the shape of a basket (pollen presentation) where secondary pollination occurs, and a fertile region with the stigmatic papillae (Castro *et al.*, 2008a). The curved style runs along the corolla tube and fits inside the keel. The anthers open introrsely toward the pollen presentation, which is recharged in subsequent pollinator (such as the long-tongued bumblebee,

Bombus pascuorum) visits through the downward movement of the keel activated by pressure applied by the insect on the crest. Despite the deposition of pollen close to the stigma, no spontaneous self-pollination occurs. Significant pollen is lost (49% of total pollen) during secondary relocation in the pollen presenter (Castro *et al.*, 2008a). This secondary mechanism of pollen presentation may in fact be an accurate system for pollen transport, but it may also have its costs.

Thus, the various mechanisms of secondary pollen presentation (Table 2), which involve floral movement induced by pollinators, may act as mechanisms to enhance the efficiency

TABLE 2
Secondary pollen presentation

Species (Family)	Secondary pollen presentation	References
<i>Campanula rapunculus</i> (Campanulaceae)	The anthers with introrse dehiscence open before anthesis and shed their pollen on the pollen-collecting hairs of the style. At the beginning of anthesis, all pollen grains adhere to the pollen-collecting hairs that are retracted into the style, which is stimulated by mechanical contacts of the flower visitors starts at the apex of the style and continues in direction of the base. This is the function to gradually liberate the pollen grains.	Nyman, 1992; 1993 a, b; Schlindwein <i>et al.</i> , 2005
Species in the Marantaceae	At anthesis the style is under tension held in place by the cucullate (hooded) staminode which is also under tension pulling in the opposite direction, when the pollinator inserts its head into the flower in search of the nectar, it depresses the appendage, or “trigger,” on the cucullate staminode, thus releasing the style which springs forward bringing the stigma in contact with the pollen (from a previously visited flower) on the pollinator’s body and in the same motion depositing its own pollen in the same spot. These promote pollen export and stigma receiving pollen.	Kennedy, 1999
<i>Crotalaria micans</i> (Fabaceae: Papilionoideae)	Pollen was secondarily presented in a stigmatic brush, in response to the pressure applied by bees to wings and keel.	Etcheverry, 2001
<i>Mikania urticifolia</i> (Asteraceae)	Bushing type secondary pollen presentation favors cross-pollination.	Cerana, 2004
Species in the genus <i>Lobelia</i> (Lobeliaceae)	By the pressure exerted by the bat’s tongue, the staminal column is not only bent down, but also is the style shifted within the staminal tube, so that an exact dosage of pollen can be delivered onto the bat’s fur.	Koch and von Helversen, 2006
<i>Polygala vayredae</i> (Polygalaceae)	The anthers open introrsely toward the pollen presentation, which is recharged in subsequent pollinator visits through the downward movement of the keel activated by the pressure applied by the insect on the crest.	Castro <i>et al.</i> , 2008a
<i>Phrynium oliganthum</i> (Marantaceae)	In the bud stage, the pollen grains have already deposited into the dorsal part of the stigma. The style is stretched under tension by the hooded staminode which has a trigger-like appendage. When the pollinator touches the trigger, the style springs forward, scrapes off the pollen from the pollinator’s body and deposits its own pollen into the same site. These present the successful cross-pollination.	Duan and Li, 2008

and accuracy of pollen export and/or pollen reception, thus increasing male and/or female fitness. For example, in *Polygala vayredae*, pollen is presented to pollinators in the sterile branch (pollen presenter) rather than in the anthers, increasing male and female fitness (Ladd, 1994; Castro *et al.*, 2008b).

III. ACTIVE FLORAL MOVEMENT

Active floral movement is defined as the movement of floral structures with their own energy, and not including the induced or pressed movement by a pollinator. The time scale of such movements ranges from several ms to hours (Morillon *et al.*, 2001). For example, many evening primroses (*Oenothera* spp.) open their flowers at dusk to attract night-flying pollinators and close them again after sunrise (Lesica, 2003). The six tepals of *Rhododendrom pulchrum* (Ericaceae) are rolled back exposing the anthers on sunny days, but they remain extended over the

flower parts at night and on cloudy days (Shimizu *et al.*, 2005). The active movement of floral structures mainly includes the movement of the pistil (style), stamen (filament, anther, pollen) and corolla, as detailed next.

A. Pistil (Style) Movement

The pistil is in the center of the flower, consisting of a basal, swollen portion, the ovary, from which a long and slender style arises. The stigma at the tip of the style plays an important role in the reproductive success of flowering plants (Yang *et al.*, 2002). The pistil is the female reproductive organ, and movements of the stigma, style, and ovary, which influence pollination and mating systems, have been reported in some species of 13 families (Berberaceae, Bignoniaceae, Capparaceae, Gentianaceae, Liliaceae, Malvaceae, Passifloraceae, Polygalaceae, Ranunculaceae, Rubiaceae, Scrophulariaceae, Violaceae and

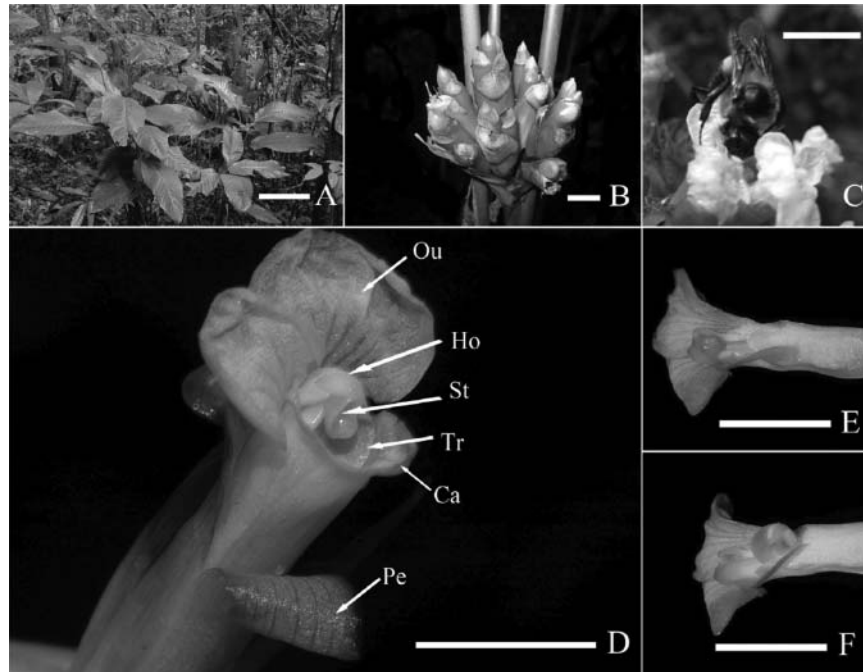


FIG. 3. Pollination biology of *Phrynium oliganthum* (Duan and Li, 2008). A: habitat. B: flower buds. C: an *Amegilla pseudobomboides* visiting the flowers of *P. oliganthum*. D: flower structure of *P. oliganthum*. E: before release of style. F: after release of style. Ca: callose staminode; Ho: hooded staminode; Ou: outer staminodes; Pe: petal; St: stigma; Tr: trigger. Scale bars: A = 50 cm; B–F = 1 cm.

Zingiberaceae) (Table 3). These include style elongation (Imbert and Richards, 1993), style curvature downward (Buttrose *et al.*, 1977; Klips and Snow, 1997; Culley, 2002; Ramsey *et al.*, 2003; Ruan *et al.*, 2004; Ruan *et al.*, 2010a) or upward (Schlessman, 1986) and their combination (Verma *et al.*, 2004), style bending (Bennington, 2003; Hong *et al.*, 2008), flexistily (Li *et al.*, 2001, 2002; Gao *et al.*, 2004; Ren *et al.*, 2007; Sun *et al.*, 2007), stigma movement (Yu and Huang, 2006; Zhang and Li, 2008; Freitas and Sazima, 2009), stigma lobe closure and re-opening (Nemcombe, 1922, 1924; Zomlefer, 1989; Fetscher and Kohn, 1999; Yang *et al.*, 2004; Weekley and Brothers, 2006; Sritongchuay *et al.*, 2010), and gynoecium bending (Xu *et al.*, 1997; Medan and Ponessa, 2003).

1. Style Curvature

Style curvature includes (i) single style bending downward in *Viola pubescens* (Violaceae) (Culley, 2002) or upward in *Ourisia macrocarpa* (Scrophulariaceae) (Schlessman, 1986), downward and back in *Eremurus himalaicus* (Verma *et al.*, 2004); and (ii) downward curvature of style branches in some species of the Malvaceae (Ruan *et al.*, 2010a) (see III. MOVEMENT HERKOGAMY).

In the flowers of *Eremurus himalaicus*, the stamens and pistil cluster together in flowers that have just opened (Figure 4A); after 2–4 h of anthesis, the style bends making an angle of 45° (Figures 4B and C) and within 6–8 h it makes a right angle with the ovary (Figures 4D and E); then, it continues to bend downward further for another 3–4 h (Figure 4F); after 12 h, it curves

back up, becomes upright and makes an angle of 180° with the ovary (Figure 4G) (Verma *et al.*, 2004). This style movement avoids self-pollination and promotes cross-pollination, because it is away from pollinators' flight path (i.e., it avoids receiving any leftover self-pollen) when pollen is shed, and then, back to the pollinators' flight path (i.e., it promotes cross-pollination).

2. Flexistily

Flowers of species in the genus *Alpinia* are hermaphroditic and last for only a day, with two different movements of the flower stigma (the phenotypes are termed cataflexistyled or hyperflexistyled flowers, depending on the direction of stigma movement during flowering) (Li *et al.*, 2001). When cataflexistyled flowers are fully open (06:00–06:30), the stigma is held above the open (dehiscence) anther from which pollen is released (Figure 5A). At the same time of day, the receptive stigma of hyperflexistyled flowers curves downwards, below the indehiscent anther from which pollen has not yet been shed (Figure 5B). Flowers of both types retain these respective stigma positions until about midday, when the stigma of the hyperflexistyle form elongates and becomes erect above the anther (male phase). This movement prevents contact with insect visitors and creates an angle larger than 170° between the stigma and the anther's ventral face (11:45–13:30); the anther then dehisces and pollen is released (14:30–15:00; Figure 5D) (Li *et al.*, 2001; 2002). The movement of the style of the cataflexistyle form is slower: here the stigma begins to move downwards and enter the receptive position (female phase; less than 170° from the dorsal

TABLE 3
Active floral movement and its adaptive significance

Floral organ	Movement	Adaptive significance	References
Pistil (style)	Style elongation in protandrous <i>Cephalanthus occidentalis</i> (Rubiaceae).	Display pollen shed onto the stigmatic surface in the bud.	Imbert and Richards, 1993
	Downward style curvature in <i>Viola pubescens</i> (Violaceae).	DS.	Culley, 2002
	Style branches curve downward in some species of the Malvaceae, such as <i>Hibiscus trionum</i> , <i>H. laevis</i> , and <i>Kosteletzkya virginica</i> .	DS, PO, or RIMFI.	Buttrose <i>et al.</i> , 1977; Klips and Snow, 1997; Ruan <i>et al.</i> , 2004
	Upward style curvature in <i>Ourisia macrocarpa</i> (Scrophulariaceae).	RIMFI.	Schlessman, 1986
	Style movement (downward and back) in <i>Erenurus himalaicus</i> (Liliaceae).	PO and avoidance of self-pollination.	Verna <i>et al.</i> , 2004
	Flexistylis in <i>Alpinia</i> , <i>Anomum maximum</i> and <i>Curcunomorpha longiflora</i> (Zingiberaceae).	PO or RIMFI.	Li <i>et al.</i> , 2001; 2002; Gao <i>et al.</i> , 2004; Ren <i>et al.</i> , 2007; Sun <i>et al.</i> , 2007
	Style bending in <i>Mikania micrantha</i> (Asteraceae) and in <i>Passiflora incarnata</i> (Passifloraceae).	PO.	Bennington, 2003; Hong <i>et al.</i> , 2008
	Flexible style movement in <i>Aquilegia yabeana</i> (Ranunculaceae).	Assistance of context dependent pollination.	Yu and Huang, 2006
	Hooked stigmas curl towards the anther in <i>Roscoeia schneideriana</i> (Zingiberaceae).	Promotion of autonomous selfing.	Zhang and Li, 2008
	Stigma movement towards the anthers in some species of the Gentianaceae (e.g., <i>Calolisianthus pedunculatus</i> , <i>Calolisianthus pendulus</i> , <i>Helia oblongifoli</i> and <i>Detanira nervosa</i>).	Promotion of spontaneous self-pollination.	Freitas and Sazima, 2009
	Two stigmatic lobes fold together in <i>Polygala lewtonii</i> (Polygalaceae).	Spontaneous self-pollination.	Zomlefer, 1989; Weekley and Brothers, 2006
	Stigma lobe closure in <i>Mimulus</i> (Scrophulariaceae) and <i>Campsis radicans</i> (Bignoniaceae).	RIMFI.	Fetscher and Kohn, 1999; Yang <i>et al.</i> , 2004
	Stigma lobe closure and re-opening in <i>Oroxylum indicum</i> (Bignoniaceae).	No effect on the number of conspecific pollen grains received.	Sritongchuay <i>et al.</i> , 2010
	Stigma lobe closure in <i>Spathodea campanulata</i> (Bignoniaceae).	Enclosing the pollen promotes, and in dry atmosphere is necessary for, pollen germination.	Nemcombe, 1922, 1924
Stamen (pollen)	Gynophore bending upwards in <i>Atamisquea emarginata</i> (Capparaceae) and downward and back in <i>Sinopodophyllum hexandrum</i> (Berberaceae).	DS.	Xu <i>et al.</i> , 1997; Medan and Ponessa, 2003
	Filament elongation in <i>Ourisia macrocarpa</i> (Scrophulariaceae).	Promotion of pollen export.	Schlessman, 1986
	Filament elongation in <i>Collinsia verna</i> (Scrophulariaceae).	DS.	Kalisz <i>et al.</i> , 1999; Armbruster <i>et al.</i> , 2002;

(Continued on next page)

TABLE 3
Active floral movement and its adaptive significance (Continued)

Floral organ	Movement	Adaptive significance	References
	Filament elongation in <i>Aquilegia canadensis</i> (Ranunculaceae), <i>Fuchsia magellanica</i> (Onagraceae), <i>Collinsia verna</i> and <i>Collinsia sparsiflora</i> (Scrophulariaceae), the genus of <i>Collinsia</i> and <i>Tonella</i> (Collinseae), <i>Crotalaria micans</i> (Leguminosae), <i>Jaltomata repandidentata</i> (Solanaceae) and <i>Gentianopsis paludosa</i> (Gentianaceae).	DS.	Eckhart and Schaeffer, 1998; Traveset <i>et al.</i> , 1998; Kalisz <i>et al.</i> , 1999; Armbruster <i>et al.</i> , 2002; Etcheverry <i>et al.</i> , 2003; Powell, 2007; Duan <i>et al.</i> , 2010
	Stamen elongation in <i>Gesneria citrina</i> (Gesneriaceae).	DS or favors pollen removal and siring success after pollination.	Chen <i>et al.</i> , 2009
	Stamen curvature upwards in <i>Kalmia latifolia</i> (Ericaceae).	DS.	Rathcke and Real, 1993
	Lately stamens bend down in <i>Sanguinaria canadensis</i> (Papaveraceae).	—	Lyon, 1992
	Stamens bend inwards to the style located in the center of the flower in <i>Opuntia brunneogemma</i> and <i>Opuntia viriditubra</i> (Cactaceae) and <i>Cajophora arechavaletae</i> (Loasaceae).	Promotion of pollen export.	Schindwein and Wittmann, 1997a, b
	Stamen movement towards the centre of the flower in <i>Cajophora arechavaletae</i> (Loasaceae) and in <i>Chimonanthus praecox</i> (Calycanthaceae).	Auto-pollination when pollinators are absent.	Wu and Hu, 1995; Schindwein and Wittmann, 1997b
	In the female phase of <i>Chimonanthus praecox</i> (Calycanthaceae), the stamens bent toward the tepals away from the pistils at a right angle. After approximately two days the stamens commence to move to enclose the pistils.	—	Azuma <i>et al.</i> , 2005
	Stamen movement downwards and upwards in <i>Cratogeomys formosum</i> (Guttiferae).	PO.	Lewis, 1982
	Stamen movement in <i>Lupinus sericeus</i> (Fabaceae).	Pollen dispensing.	Harder and Wilson, 1994
	Stamen cascade movement in <i>Cajophora coronata</i> (Loasaceae), <i>Tropaeolum majus</i> (Tropaeolaceae), <i>Ruta graveolens</i> (Rutaceae) and <i>Parnassia palustris</i> (Saxifragaceae).	Pollen export.	Cocucci and Sersic, 1998; Ma <i>et al.</i> , 2004; Ren, 2010
	Pollen sliding in <i>Caulokaempferia coenobialis</i> (Zingiberaceae).	DS.	Wang <i>et al.</i> , 2004
	Pollen catapulting in <i>Cornus canadensis</i> (Cornaceae).	PS.	Edwards <i>et al.</i> , 2005; Whitaker <i>et al.</i> , 2007
	High-speed pollen emission in <i>Morus alba</i> (Moraceae).	Enhanced pollen export.	Taylor <i>et al.</i> , 2006
	Anther rotation in <i>Holcoglossum amesianum</i> (Orchidaceae).	DS.	Liu <i>et al.</i> , 2006
	Pollinia reconfiguration in <i>Eulophia parviflora</i> (Orchidaceae).	PO.	Darwin, 1862; Peter and Johnson, 2006
Corolla	Dehiscence of corollas in <i>Verbascum blattaria</i> (Scrophulariaceae).	DS.	Kerner von Marilann, 1895; Gross and Werner, 1978; Donnelly <i>et al.</i> , 1998;
	Wind-dragged corolla movement in <i>Incarvillea sinensis</i> var. <i>sinensis</i> (Bignoniaceae).	Enhanced self-pollination.	Qu <i>et al.</i> , 2007

Corolla closure in <i>Gentiana algida</i> (Gentianaceae).	Tolerance to harsh environments.	Bynum and Smith, 2001
Corolla closure in <i>Kosteletzkya virginica</i> (Malvaceae) and <i>Fumana juniperina</i> (Cistaceae).	DS.	Ruan <i>et al.</i> , 2005a; Carrió <i>et al.</i> , 2008b
Corolla closure in <i>Zygostigma australe</i> (Gentianaceae).	Promotion of spontaneous self-pollination.	Freitas and Sazima, 2009
Corolla wilting in <i>Pedicularis dunniana</i> (Orobanchaceae).	DS.	Sun <i>et al.</i> , 2005
Corolla dragging (abscission) in <i>Lupinus nanus</i> (Leguminosae), <i>Mimulus guttatus</i> (Scrophulariaceae) and <i>Ruellia succulenta</i> (Acanthaceae).	DS.	Juncosa and Webster, 1989; Dole, 1990; Dieringer, 1999
Flower stalk bending in <i>Pulsatilla cernua</i> (Ranunculaceae).	Tolerance to harsh environments.	Huang <i>et al.</i> , 2002

DS: delayed selfing; PO: promotion of outcrossing; RIMFI: reduction in intrafloral male-female interference; Dash (—) : no report.

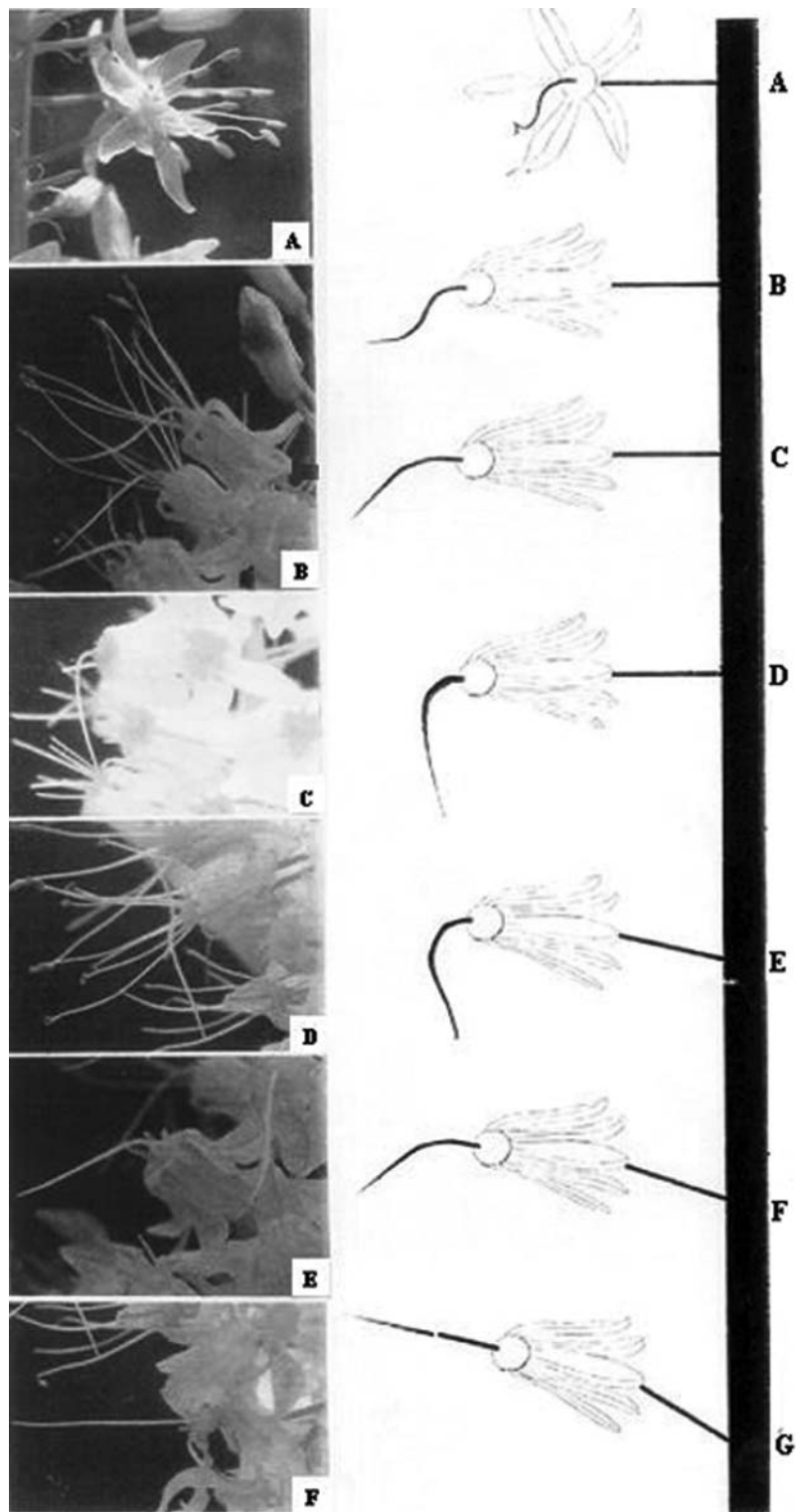


FIG. 4. Flowers of *Eremurus himalaicus* showing different style curvature (Verma *et al.*, 2004). Just opened flower with stamens and pistil clustered together (A); curvatures of style after 2, 4 (B, C), 6 (D), 8 (E), 12 (F) and 24 h of anthesis (G) and diagrammatic representations thereof (right A-G).

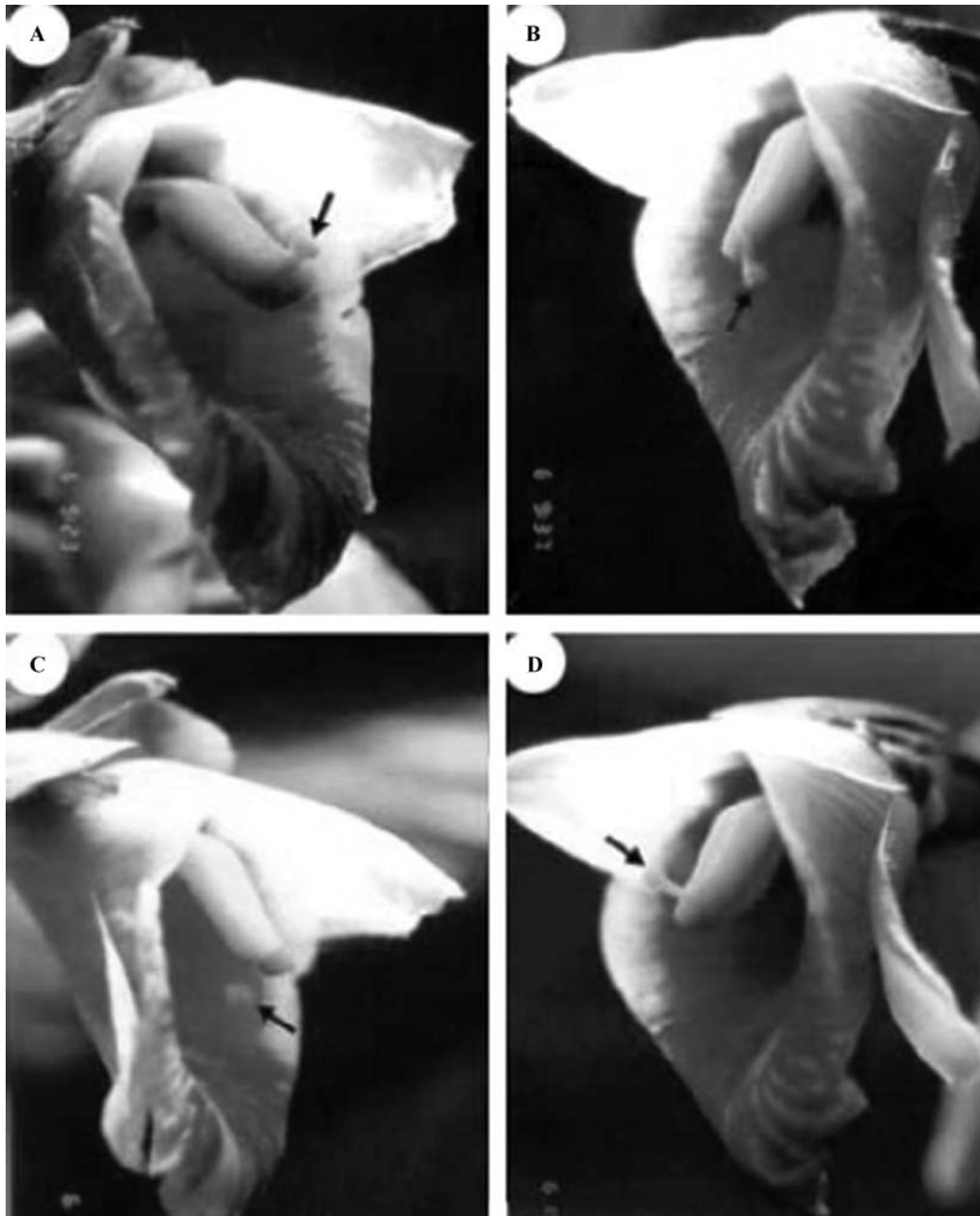


FIG. 5. Positions of the stigma of the two flower forms in *Alpinia kwangsiensis* at different stages of flowering (Li *et al.*, 2001). A: cataflexistyle flower in its male phase (before noon), in which the stigma is reflexed above the dehiscient anther. B: hyperflexistyle flower in its female phase (before noon), in which the stigma is deflexed below the indehiscent anther. C: the same flower as in A during its female phase (afternoon), with the stigma below the anther; note that pollen has been removed from the anther by insect visitors. D: the same flower as in B, but in its male phase (afternoon), with the stigma now erect above the anther, which then sheds its pollen. Arrows: stigma position.

face of the anther) between 14:40 and 15:00 (several minutes after anther dehiscence in hyperflexistyle flowers; Figure 5C). This floral strategy not only prevents self-pollination in a flower and within the same individual, but also among individuals of the same phenotype. It decreases inbreeding and promotes outcrossing by temporally and spatially separating the presentation of pollen and receptive stigmas through active floral movement. This floral movement mechanism was termed “flexistylly” by Li

et al. (2001), differing from other passive outbreeding devices such as dichogamy, herkogamy, enantiostyly and heterostyly (Richards, 1997).

3. Stigma Movement

Roscoeia schneideriana (Zingiberaceae) is a small perennial herb that inhabits shady habitats of mixed forests, or open stony slopes and ledges of mountain cliffs (Cowley, 1982; Wu and

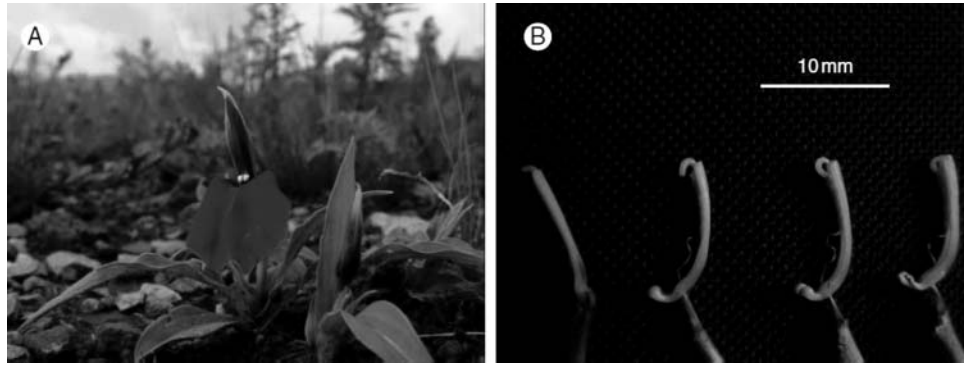


FIG. 6. The plants (about 60 mm in height) and flower of *Roscoeae schneideriana* in a natural population (A) and variations of sigma morphology of *R. schneideriana*: from left to right, before anthesis, then 12, 24, and 48 h after anthesis (B) (Zhang and Li *et al.*, 2008). Petals were removed to reveal the anthers and styles.

Larsen, 2000). It usually flowers from July to August (Zhang and Li, 2008) and produces one inflorescence per plant with 1–4 flowers per inflorescence. Inflorescences generally flower for 4–15 d and produce one flower after another at intervals of 2–6 d. Flowers usually begin anthesis in the early morning and last for 4 d. The slender-tubed flowers are purple or white, comprising an erect hooded dorsal petal, a large labellum which has two erect petal-like staminodes near its base, and two narrow lateral petals; the dorsal petal and two erect leaf-like staminodes form a floral chamber, where anther and style stand (Figure 6A). The anthers usually dehisce and stigmas produce stigmatic fluid at the beginning of anthesis. The distance between anthers and hooked stigmas is about 2 mm at that time. The funnel-like stigma progressively elongates and curls towards the erect anther during flowering (Figure 6B). Zhang and Li (2008) showed that stigmas of 66.7% of flowers of *R. schneideriana* could touch the dehiscent anther about 24 h after anthesis and continue curling; 80% of them could be self-pollinated in this way within 2 d of flowering.

Calolisianthus pendulus (Gentianaceae) is a small, sun-loving, short-lived annual herb (Figure 7A). Its flowers are horizontal (Figure 7D), with corolla tube of *c.* 25 × 9 mm. The stamens are aligned in two or three parallel lines in the lower portion of the corolla tube. The anthers are clumped together and face the corolla tube lumen or apex. The flowers are herkogamous because the style is longer than the anthers (Figure 7E). In late flowering, spontaneous self-pollination of *C. pendulus* may occur after stigmatic movements towards the anthers (Figure 7F) (Freitas and Sazima, 2009).

4. Stigma Lobe Closure

Oroxylum indicum (Bignoniaceae) is a small, self-incompatible tree. The flowers are nocturnal, hermaphroditic, and bell-shaped (Corner, 1988), with a cream-colored corolla tube and light-purple petal lobes (Figure 8). The fruit bat, *Eonycteris spelaea*, is a frequent visitor and pollinator of this species (Sritongchuay *et al.*, 2008). In an unpollinated flower, stigma

lobes are spread apart (Figure 8A). After pollination, the stigma lobes close such that their inner surfaces are pressed together (Sritongchuay *et al.*, 2010).

In addition, stigma lobe closure has also been reported in *Mimulus aurantiacus* (Scrophulariaceae), in which the bi-lobed stigma closes after receiving pollen, causing increased spatial separation of the anthers and stigma (movement herkogamy) (Fetscher, 2001). In *Campsis radicans* (Yang *et al.*, 2004), adequate pollen (> 350) deposition causes permanent closure of the stigma while in *Chilopsis linearis* (Richardson, 2004) stigmas remain permanently closed or reopened, depending on the number of pollen grains deposited, although this also tends to be affected by the source of pollination, i.e., either outcross or self.

5. Gynoecium Bending

Sinopodophyllum hexandrum (Berberaceae) is a perennial herb. When the flower is in bud or after it has just opened, the gynoecium is upright. However, when the flower is in full blossom, the gynoecium makes a turn of about 30° and places the whole gynoecium close to the anthers (Xu *et al.*, 1997). The stigma thus enters into contact with the anther and pollination occurs. After pollination, the gynoecium recovers, becoming upright (Figure 9). The whole pollination process lasts about 4–6 hours, and it represents successful self-pollination.

B. Stamen (Filament, Anther, and Pollen) Movement

1. Filament Elongation

In the flowers of *Collinsia verna* (Scrophulariaceae), the four anthers move towards the front of the flower and dehisce sequentially (Kalisz *et al.*, 1999). This includes the following six relatively discrete morphological stages (Figure 10) (Kalisz *et al.*, 1999): stage 0: the flower is a bud. There are no anthers shedding pollen, the style and anther filaments are not elongated (Figure 10A); stage 1: as the flower opens fully (Figure 10B), the front pair of anthers elongates toward the front of the flower and one anther sheds pollen; stage 2: the second anther dehisces while the stigma and the second pair of anthers remain in the

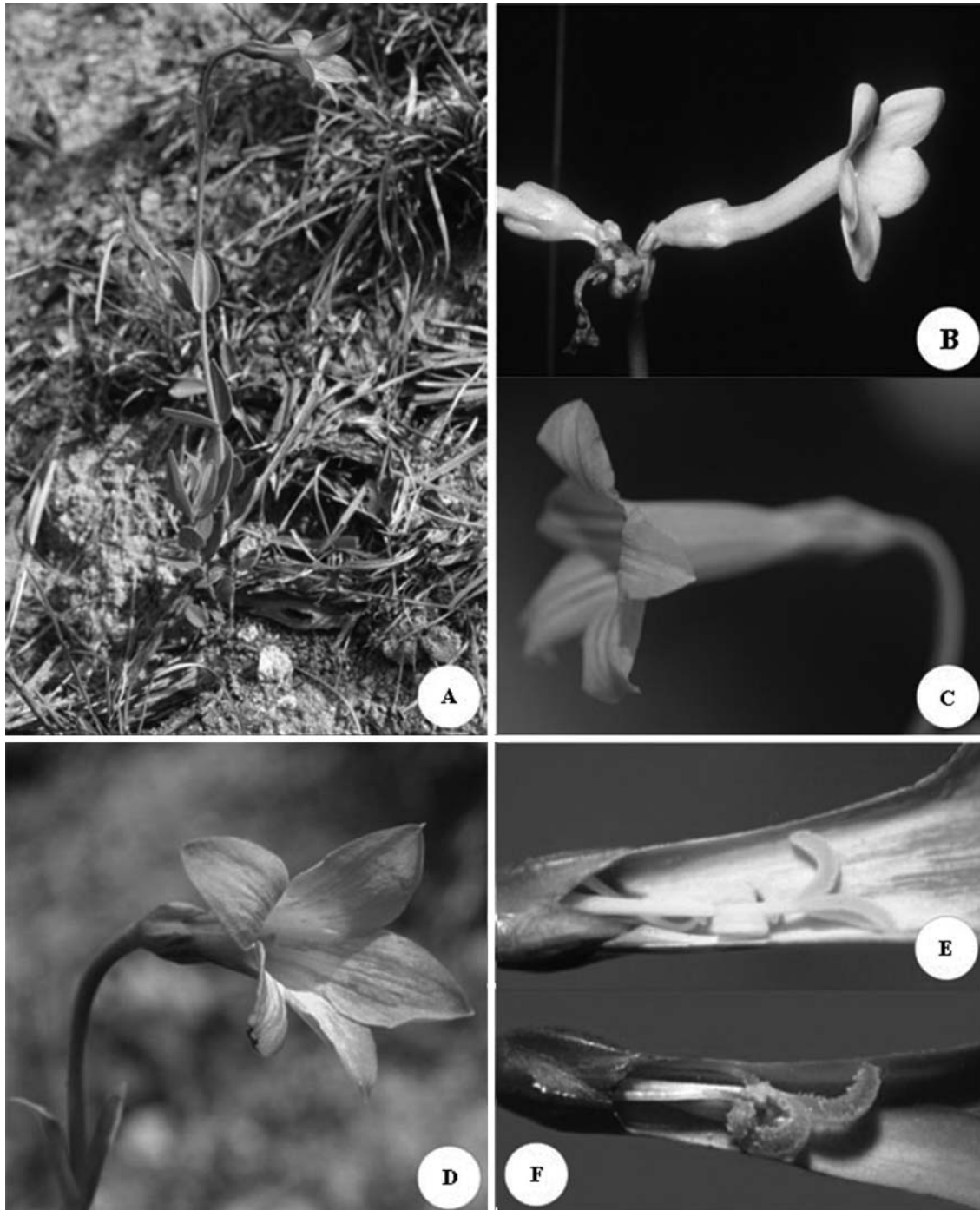


FIG. 7. Species of *Helieae* (Freitas and Sazima, 2009). A: habit and habitat of *Calolisianthus pendulus*. B: nocturnal phalaenophilous flower of *Helia oblongifolia*. C: nectarless ornithophilous-like flower of *C. pedunculatus*. D: melittophilous-like flower of *C. pendulus*. E: flower of *C. pendulus* at the onset of anthesis, the closed anthers and the anther–stigma separation (protandry associated with herkogamy). F: spontaneous self-pollination of *C. pendulus* after stigma movements towards the anthers.

rear (Figure 10C); stage 3: the two rear anthers move to the front, and one sheds its pollen (Figure 10D), thus three out of the four anthers have dehisced. In this stage, half of the stigmas have elongated to the same position as the anthers, thus flowers lack a stigma–anther separation; stage 4: the last anther sheds

its pollen. At this stage, most of the stigmas have elongated past the previously dehisced anthers, placing the stigma at the front of the flower (Figure 10E); and stage 5: the corolla abscises (Figure 10F). Reduction in the stigma–anther separation distances late in floral development implies that delayed selfing

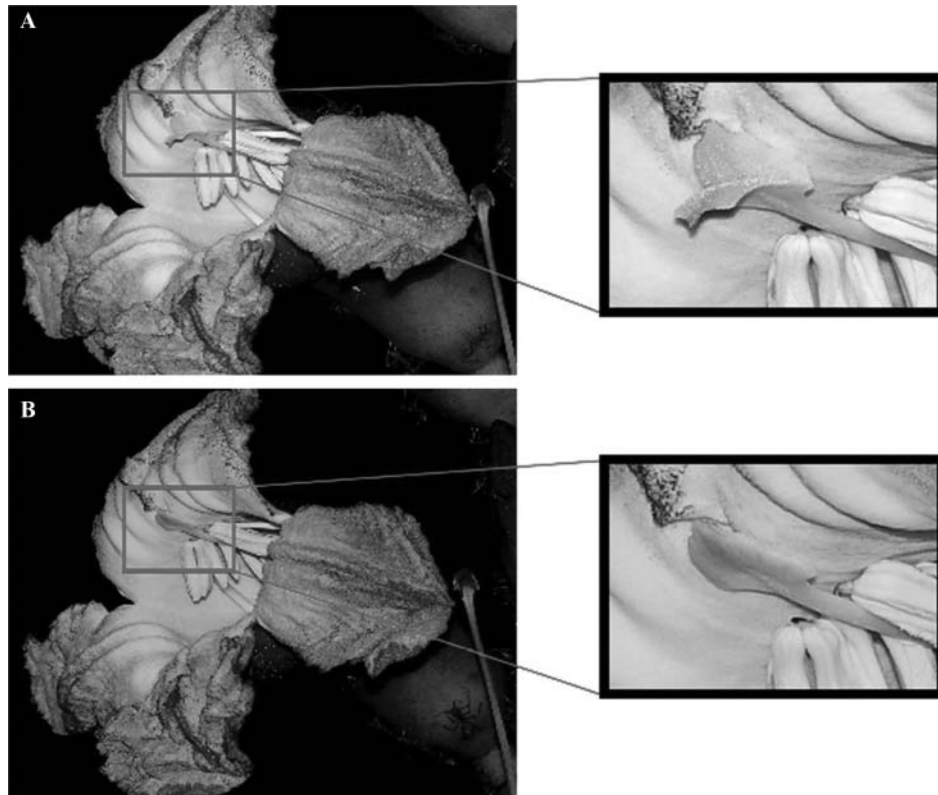


FIG. 8. Stigma lobe closure in *Oroxyllum indicum* (Sritongchuay *et al.*, 2010). A: in an unpollinated flower, stigma lobes are spread apart. B: after pollination, the stigma lobes close such that their inner surfaces are pressed together.

is possible due to the temporal and spatial overlap of receptive stigmas with the late maturing anthers.

This filament elongation has also been reported in some other species (Table 3). For example, in *Aquilegia canadensis*

(Ranunculaceae), the stamens elongate and anthers dehiscence close to a receptive stigma 3 d after the flower opens, and by that time the first group of 5–10 stamens have completely shed their pollen (Eckhart and Schaeffer, 1998). In *Crotalaria micans*, the filaments of the inner stamens grow linearly from 3~3.5 mm in the bud to 12 mm 38 h after flower opening (Etcheverry *et al.*, 2003). Similarly, in *Gentianopsis paludosa* (Gentianaceae), the anthers contact the central stigma due to the elongation of all filaments during late anthesis, resulting in autonomous selfing (Duan *et al.*, 2010).

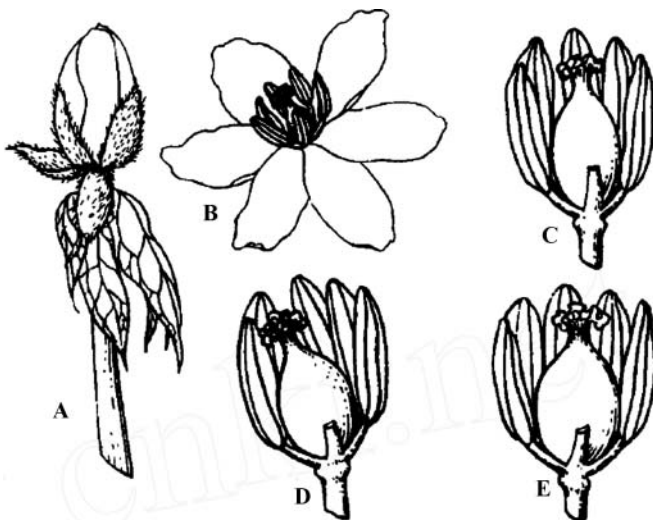


FIG. 9. Self-pollination in *Sinopodophyllum hexandrum* (Xu *et al.*, 1997). A: a flower shoot. B: a flower. C: the androecium and gynoecium. D: a turn of about 30° occurred in the gynoecium. E: the gynoecium recovered to upright and enlarged.

2. Stamen Cascade Movement

Continued stamen movement, in which pollen dispersal of each stamen takes place one by one, has been reported in all species of the Parnassiaceae family (Watson and Dallwitz, 1992), *Tropaeolum majus* (Tropaeolaceae) (Watson and Dallwitz, 1992; Ma *et al.*, 2004), most species of *Loasa* and *Nasa* (Loasaceae) (Cocucci and Sersic, 1998; Weigend and Gottschling, 2006) and *Ruta graveolens* (Rutaceae) (Ren, 2010). When flowers of *R. graveolens* open, stamens adhere to the indented and curled petals (Figure 11A1). With anthesis lasts, the petals spread and the filaments become straight and upright; then one stamen gradually stands up, separates from the petal and moves to the center of the flower, leading the anther to locate to the top of the stigma; after this, the anthers dehiscence

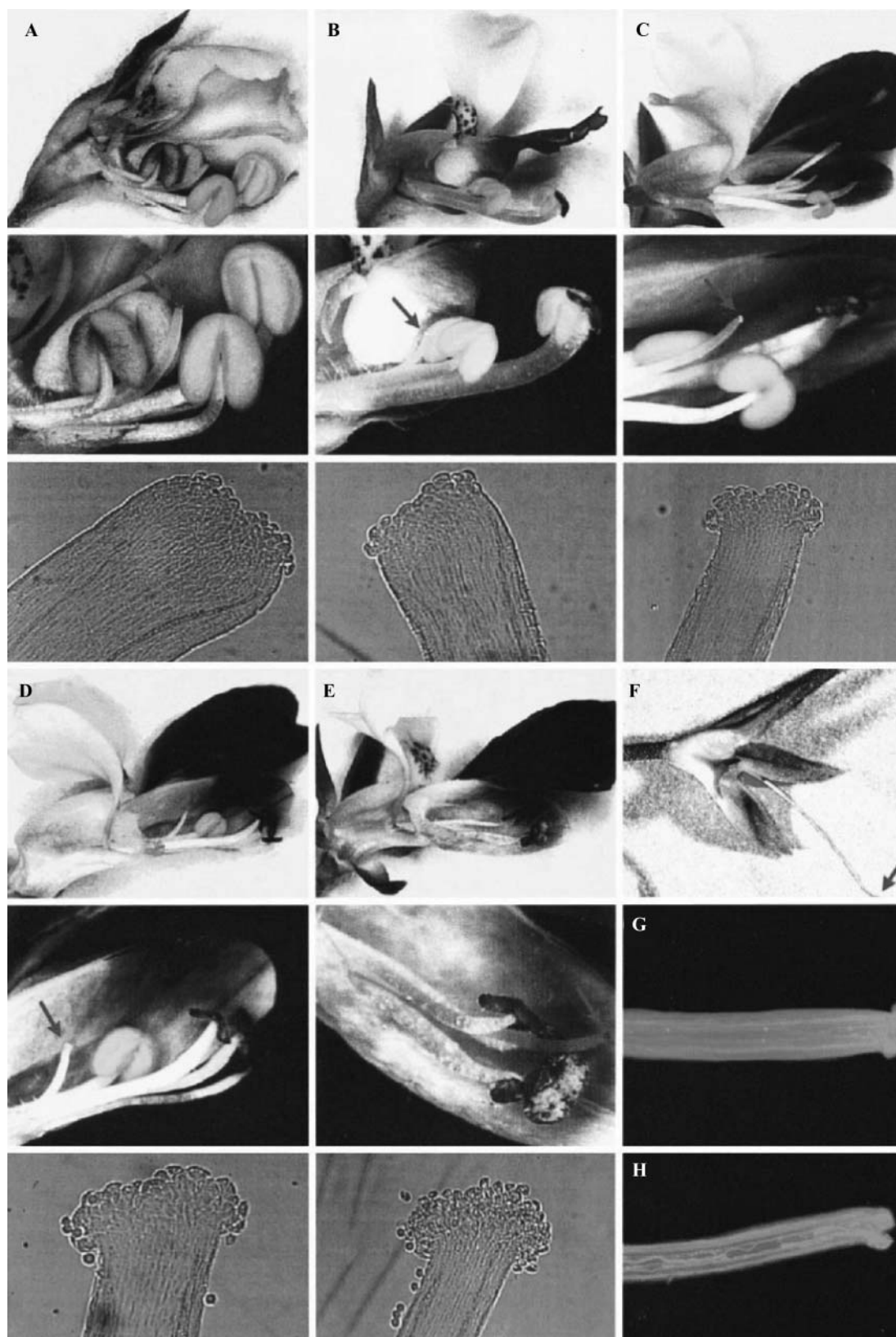


FIG. 10. Six stages of floral development in *Collinsia verna* (Kalisz *et al.*, 1999). A–E: whole flower (top panel), anthers and style (middle panel) and stigma (lower panel) for stages 0–4, respectively. Refer to the description of stages in the text. The keel petal has been partially removed, and the stigma position is indicated by a red arrow. F: whole flower at corolla drop, stage 5. G: pollen tubes in a stage 4 style. H: pollen tubes in a stage 5 style.

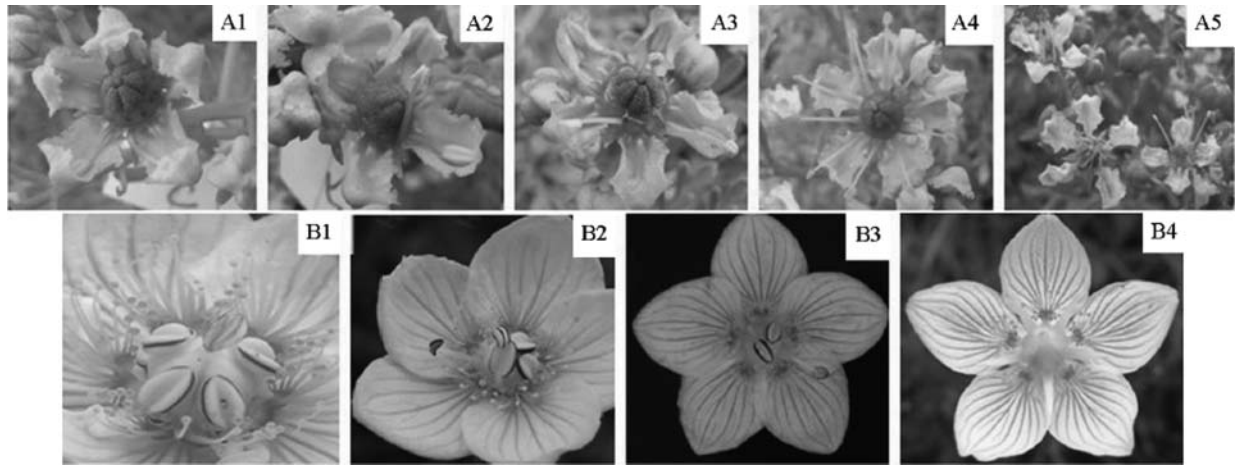


FIG. 11. Stamen cascade movement in *Ruta graveolens* (A) and *Parnassia palustris* (B) (Ren, 2010). A1: flower just opened. A2: one stamen moved to the center and dehiscent. A3: the dehiscent stamen moved to the outside and the next one moved to the center. A4: all the stamens moved to the outside after their cascade movements. A5: the stamens moved together to the center at the final phase of blooming. B1: flower just opened (all the anthers are positioned at the center of flower). B2: one stamen moved to the outside after dehiscing at the center. B3: one stamen dehiscent and moved to the outside after the former one finished moving. B4: all the stamens moved to the outside and the anthers dehiscent.

(Figure 11A2). When this stamen has completely shed its pollen, it continues to move to the outside of the flower and eventually becomes parallel with the petal; then, another stamen begins this inward and outward movement (Figure 11A3). Finally, all stamens move to the outside after this cascade movement and become parallel with the petal (Figure 11A4). Interestingly, at the end of flowering, all the stamens will have moved together to the center of the flower (Figure 11A5) (Ren, 2010).

For *Parnassia palustris* (Parnassiaceae), when the flower just opens, all the anthers are located in the center of the flower (Figure 11B1). With the continuation of anthesis, one stamen moves to the outside of the flower after dehiscing at the center (Figure 11B2); after this, one stamen dehisces and moves to the outside of the flower after the former movement is over (Figure 11B3). Finally, all the stamens move to the outside of the flower and the anthers dehisce (Figure 11B4) (Ren, 2010).

3. Pollen Sliding

Caulokaempferia coenobialis (Zingiberaceae) is a deciduous perennial herb of up to 50 cm in height. It is endemic to the Guangdong and Guangxi provinces of southern China, where it hangs on rock walls in humid monsoon forests (Larsen, 2002). It flowers from May to August, and generally produces three buds that open consecutively. Flowers open in the morning, last for two days, and fade during the afternoon of the second day. *C. coenobialis* flowers have yellow corollas with two short lateral lobes and one large central lobe up to 3 cm long (Figure 12A) and with two elongated, lengthwise-dehiscing pollen sacs that enclose the style (Wang *et al.*, 2004). The concave stigma lies almost exactly at the end of the pollen sacs (Figure 12B). The pollen grains in *C. coenobialis* are held together by pollen-connecting threads and have an abundance of oily pollen kits on their surface. The pollen kits in *C. coenobialis* are clear and

rich in unsaturated lipids. They form an oily film in which the pollen grains are suspended (Figures 12C and D). Soon after anthers dehiscence in the morning, a drop of pollen spills from each pollen sac. The two drops merge to form a film that quickly spreads across the style surface and slides towards the stigma (Figures 12C and D). A fringe of hairs around the style may prevent the pollen from spilling off the style.

4. Pollen Catapulting

As early as the eighteenth century, James Smith wrote that the stamens of *Parietaria* “fly up and throw their pollen about with great force” (Smith, 1788). Recent descriptions of this process in the Moreae include: “filaments are held under tension until they spring out violently” (Bawa and Crisp, 1980) and “pollen is forcibly ejected from the anthers . . . like puffs of smoke” (Simons, 1992). More recently, rapid pollen catapulting has been observed in *Cornus canadensis* (Edwards *et al.*, 2005); even the fastest motion yet observed in biology, which approaches the theoretical physical limits for movements in plants, was investigated in *Morus alba* (Taylor *et al.*, 2006).

Cornus canadensis grows in dense carpets in the vast spruce-fir forests of the North American taiga. Edwards *et al.* (2005) described how its flower stamens catapult pollen into the air as the flower opens explosively (1.0 ms). As *C. canadensis* flowers burst open, their petals separate rapidly and flip back to release the stamens (Figure 13). During the first 0.3 ms, the stamens accelerate at up to 24000 m s^{-2} , reaching a high speed (3.1 m s^{-1}) necessary to propel pollen, which is light and rapidly decelerated by air resistance (terminal velocity, 0.12 m s^{-1}). The pollen granules are launched to an impressive height of 2.5 cm, which is more than ten times the height of the flower, and from this height, they can be carried away by wind. Petals open independently of stamen activity, moving out of their way within the first

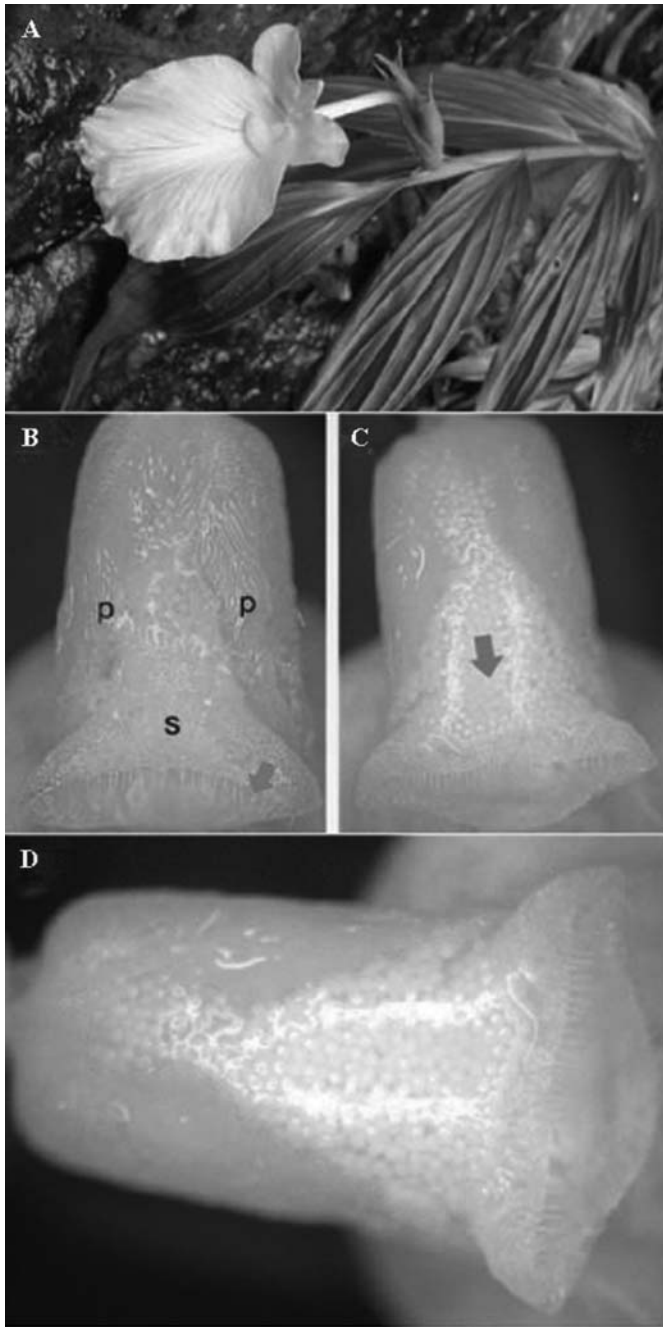


FIG. 12. Pollen sliding in *Caulokaempferia coenobialis* (Wang *et al.*, 2004). A: the flower in its natural position. B: the stigma (s) and the anther, consisting of two pollen sacs (p), which have pollen streams coming from them; arrow indicates stigma hairs. The stigma is about 3 mm in diameter. C: pollen film sliding (arrowhead) towards the stigma. D: pollen film stained red with Sudan III: the pollen film is on the style surface, about 0.2 mm from the stigma's margin; the pollen grains are visible in the oily film.

0.2 ms, and attain a maximum speed of 6.7 m s^{-1} , accelerating at up to $22,000 \text{ m s}^{-2}$ (Figure 13). The process of petal opening and pollen launch in *C. canadensis* plants occurs faster than the leap of froghoppers (*Philaeus spumarius* (Cercopidae):

0.5–1.0 ms) (Burrows, 2003), the strike of the mantis shrimp (*Odontodactylus scyllarus* (Odontodactylidae): 2.7 ms) (Patek *et al.*, 2004), and the snap of the Venus flytrap (100 ms) (Forterre *et al.*, 2005).

Recently, anemophilous plants described as catapulting pollen explosively into the air have been detailed in *Morus alba* (Taylor *et al.*, 2006). The stamen is inflexed within the floral bud. Exposure to dry air initially results in gradual movement of the stamen. This causes fine threads to tear at the stomium, ensuring dehiscence of the anther, and subsequently enables the anther to slip off a restraining pistillode. The sudden release of stored elastic energy in the spring-like filament drives the stamen to straighten in less than $25 \mu\text{s}$, and reflexes the petals to velocities in excess of half the speed of sound. The stamen movement less than $25 \mu\text{s}$ in *M. alba* is more than a factor of 20 faster than that of *Cornus canadensis* (Edwards *et al.*, 2005), the most rapid reported to date, and the initial velocity of the pollen grains was nearly two orders of magnitude greater.

Rapid motions, driven by slippage past a mechanical restraint and the sudden release of stored elastic energy, have evolved sporadically across a diversity of plant species, but are commonly found within the Moreae, and all species within the Urticaceae are also likely to utilize this mechanism to disperse pollen (Taylor *et al.*, 2006). In nature, pollen grains emitted beyond the boundary layer of the plant may be entrained by air currents and transported farther from the flower. High-speed pollen emission would be advantageous for anemophilous members of the Urticales in their native environments of sheltered valleys and flood plains (Taylor *et al.*, 2006). Thus, the ability to disperse pollen grains at very high velocities is an ancient evolutionary adaptation that enhances anemophily, especially under quiescent environmental conditions.

5. Anther Rotation

Holcoglossum amesianum grows on tree trunks at altitudes of 1200–2000 m. Liu *et al.* (2006) described a new type of self-pollination mechanism in this species, in which the bisexual flower turns its anther against gravity through 360° in order to insert pollen into its own stigma cavity without the aid of any pollinating agent or medium. An extended rostellum separates the pollen-producing anther and the receptive stigma in the flower (Figures 14A and B). When the flower is fully open, the anther cap opens and falls off the column (Figure 14C), uncovering two pollinia attached to a flexible stipe on the clinandrium. The stipe then rises (Figure 14D) and curves forwards and downwards, taking the pollinia across the edge of the rostellum (Figure 14E); it then curves back and upwards, pushing the pollinia towards the stigma cavity whose receptive surface faces downwards above the rostellum (Figure 14F), and finally inserts the pollinia into the stigma cavity (Figure 14G). The stipe's ring structure helps to secure the pollinia in the stigma cavity to ensure fertilization. Self-pollination may be unsuccessful if the anther cap sticks to the pollinia or if the stipe folds over and prevents the pollinia from reaching the stigma.

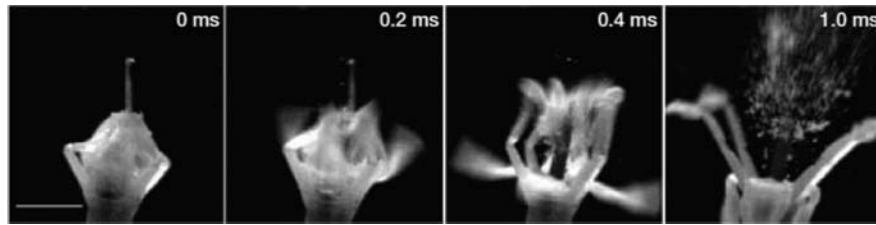


FIG. 13. *Cornus canadensis* flower opening, recorded on video at 10,000 frames per second (Edwards *et al.*, 2005). Time elapsed is indicated. First frame shows a closed flower with four petals fused at the tip, restraining the stamens. Blur represents the distance moved in 0.1 ms. Scale bar, 1 mm.

6. Pollinia Reconfiguration

Species in the orchids and asclepiads package their pollen into pollinia (Darwin, 1862; Johnson and Edwards, 2000;

Barrett, 2002a; Tremblay *et al.*, 2005), which often reorient gradually after withdrawal from the anther. This is typically due to bending or twisting of an accessory structure (such as a stipe or caudicle) that connects the pollinium to a sticky pad (the viscidium) in orchids (Johnson and Edwards, 2000) or mechanical clamp (corpusculum) in asclepiads (Bookman, 1981). These structures, in turn, attach the pollinium to the body of the pollinator. In orchids, the pollinium is rotated through an arc of 30–120° depending on the particular species. This movement is necessary for the pollinium to become correctly oriented for insertion into a stigma (Figure 15) (Peter and Johnson, 2006). In asclepiads the paired pollinia are initially flared at right angles, but reconfigure to be closely appressed to one another in the correct position to be inserted into the stigmatic chamber (Bookman, 1981).

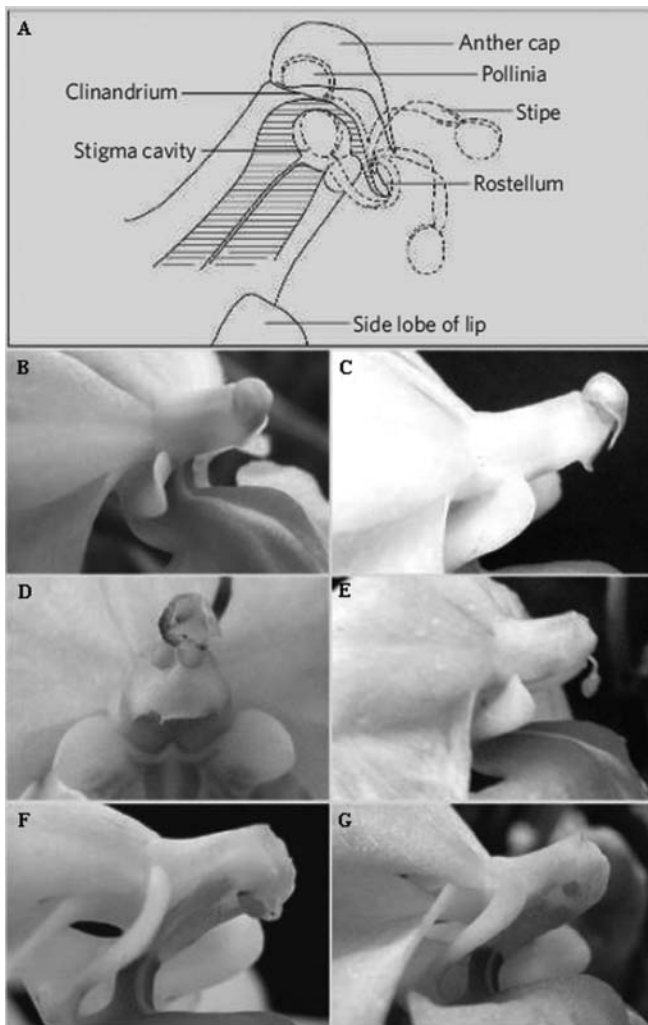


FIG. 14. Self-pollination in *Holcoglossum amesianum* (Liu *et al.*, 2006). A: arrangement of floral components and their movements (dashed lines) during the transport of pollen from the anther to the stigma (described in C–G). B: open flower before pollination starts; C: the anther cap opens and falls off its column. D: the stipe carries two pollinia on its tip and rises up from the clinandrium. E: curves downwards to cross the rostellum. F: the stipe next curves up towards the stigma and inserts the pollinia into the stigma cavity (G).

C. Corolla Movement

Daily floral movement is common in plants, and this movement includes (i) the orientation of the sunflower (*Helianthus annuus* (Asteraceae/Compositae)) to the sun (Salisbury and Ross, 1992); (ii) the flowers in bloodroot (*Sanguinaria canadensis* (Papaveraceae)), which open during the day and close each night (Lyon, 1992); and (iii) the flower stalks of *Pulsatilla cernua* (Ranunculaceae), which change position from erect to pendulous and back to erect during 6–10 d anthesis (Huang *et al.*, 2002). However, in this review, we present corolla movement that occurs during several hours, even within one hour or several seconds. For example, the corolla closes and reopens in *Gentianopsis paludosa* during frequent afternoon thunderstorms (Bynum and Smith, 2001); and flowers close within minutes of an approaching thunderstorm and reopen after direct sunlight returns.

In *Agalinis skinneriana* (Scrophulariaceae) flowers, timing of pollen tube growth indicates that selfed pollen is deposited on stigmas only late in anthesis excluded from pollinators, an example of delayed selfing (Dieringer, 1999). This late pollen deposition supports the idea that the anthers come into contact with stigmas as corollas fall from flowers, which is termed corolla dragging, which occurs in *Lupinus nanus* (Leguminosae) (Juncosa and Webster, 1989) and *Mimulus guttatus* (Scrophulariaceae) (Dole, 1990, 1992). Furthermore, corolla movement has also been observed to contribute to delayed selfing in some species (Table 2), such as corolla closure in

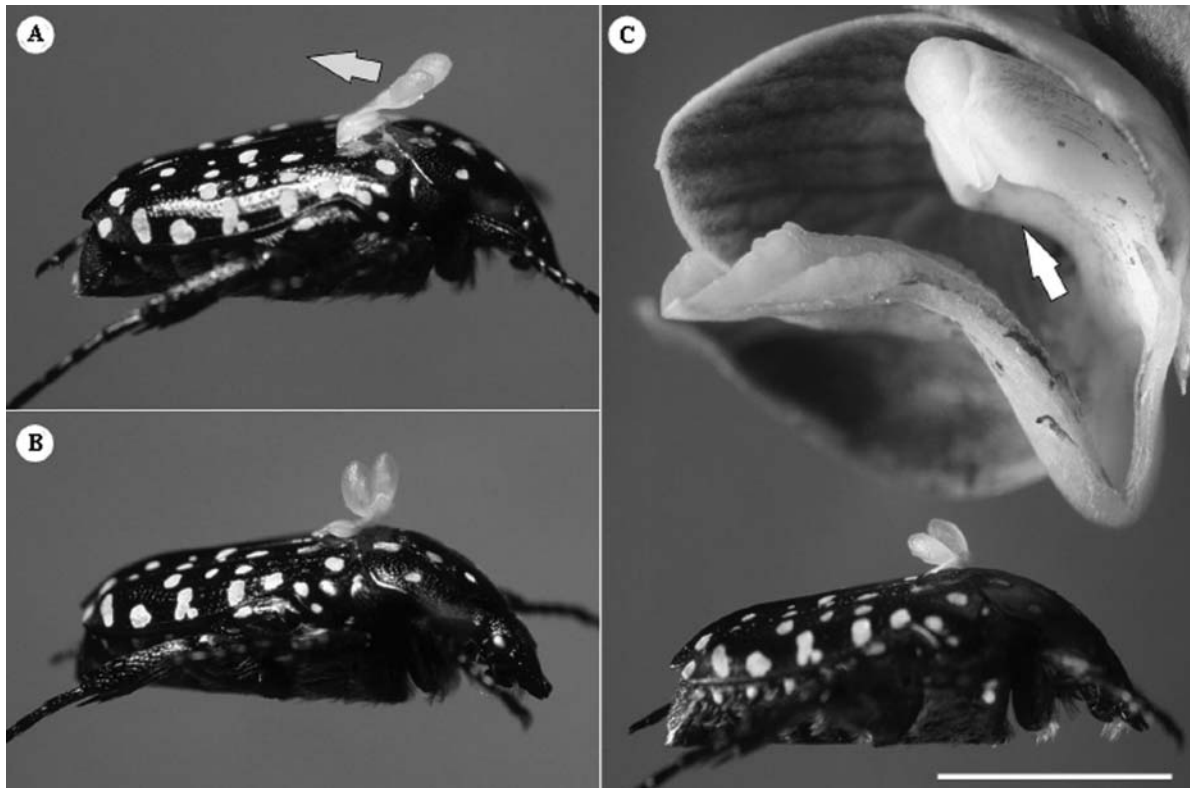


FIG. 15. Pollinia reconfiguration in *Eulophia parviflora* (Peter and Johnson, 2006). A: a pollinia of *E. parviflora* freshly affixed to a cetoniid beetle will bend in the direction of the yellow arrow as indicated in (B) with the pollinia half bent. C: after *ca.* 100 s the pollinia has reconfigured and the paired pollinia can be inserted into the stigma (white arrow) as the beetle backs out of a flower in the direction of the white arrow (shown in cross-section). Scale bar, 5 mm.

Kosteletzkya virginica (Malvaceae) (Ruan *et al.*, 2005a), corolla wilting in *Pedicularis dunniana* (Orobanchaceae) (Sun *et al.*, 2005), and wind-dragged corolla movement in *Incarvillea sinensis* var. *sinensis* (Bignoniaceae) (Qu *et al.*, 2007).

Incarvillea sinensis var. *sinensis*, an annual herb, grows mainly on open hillsides and fields (Zhang and Santisuk, 2003). It has a sparse raceme that produces 4–60 purple to red, campanulate/funnel-form bisexual flowers. The androecium is didynamous and inserted at the base of the corolla tube. The stigma is composed of two round lobes covered with dense short hairs. Each anther is composed of two separate anther sacs, connected by a globosely connective terminating each staminal filament (Figure 16C). A flat, oblong projection is attached at the front of the connective (distal from the rachis) (Figures 16A and B). A large papilla is joined to the back of the connective (near the rachis; Figures 16B and E). The style is appressed to the upper side of the corolla tube (Figures 16D and K). Qu *et al.* (2007) described wind-dragged corolla movement in this species, as follows: in the process of flower bud growth, two parallel sacs of the anther splay out at the connective (Figure 16B), and one of them then lifts upward and aligns with the other before initiation of anthesis (Figures 16C–E); at the same time, the straight staminal filament spontaneously bends slightly towards the style (Figures 16B and C), and the

two anthers of long and short stamens, respectively, adhere together in the front of the style through their flat, oblong projections on the connective (Figures 16C and D). Finally, two pairs of adherent anthers become parallel adnate to the style below the stigma lobes (Figures 16D and E), and their large papillae joined to the back of the connectives are positioned at the sides of the style (Figure 16E). The adherent flat, oblong projections and two papillae form a clip-like structure enclosing the style. This clip-like structure ensures that the anthers can slip along the style. The anthers dehisce longitudinally about 2–4 h before initiation of anthesis. Two stigma lobes open and curl downwards but make no contact with the anthers of the long stamens before initiation of anthesis (Figures 16D and E). During late anthesis corollas begin to abscise when the wind speed is over 2 m s^{-1} , the opened and unwilted corollas slipping forward and falling off (Figures 16F and G). When the wind speed is low ($<2 \text{ m s}^{-1}$), the corollas do not move and abscise, and wilt on the floral receptacle (Figure 16H). When the corolla moves forwards, driven by wind, the anthers that are inserted at the base of the corolla are dragged by the corolla and slip along the style under the limits imposed by the clip-like structure of the anthers (Figure 16I). When the anthers reach the stigma they turn upward, being blocked by the opening stigma lobes, and the filaments bend severely under the pressure of the moving

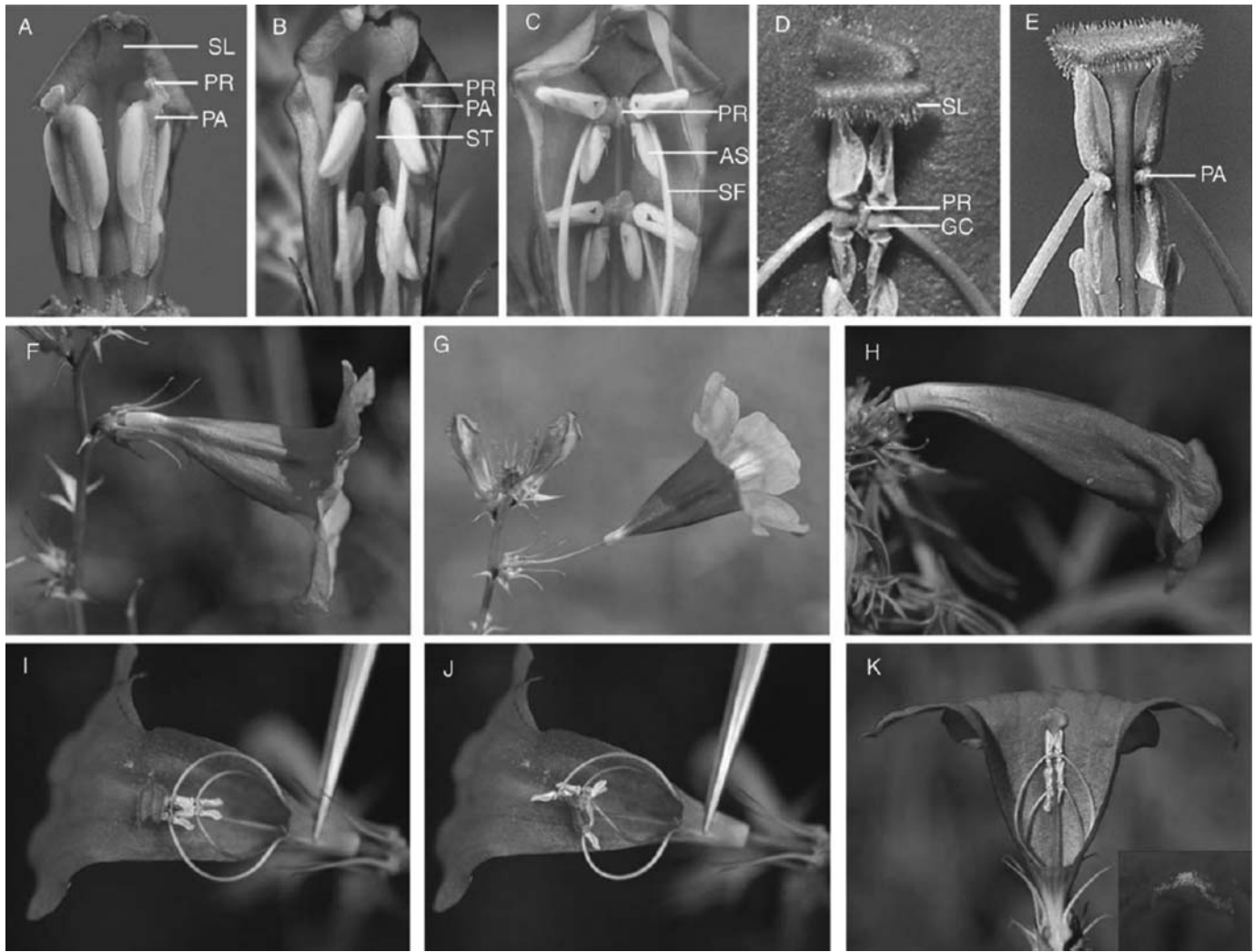


FIG. 16. The process of floral development and delayed self-pollination in *Incarvillea sinensis* var. *sinensis* (Qu *et al.*, 2007). A–E: the growth dynamics of stamens and pistil in the process of flower development, showing the process of lift of anther sacs, anther adherence and the formation of a clip-like structure. In which, A–C: the early stage to middle stage of flower bud growth (the view distal to rachis); D and E: the abdominal (distal to the rachis) and dorsal (near the rachis) view of the clip-like structure comprising stamens and pistil in the opening flower. F and G: corolla detachment from its floral receptacle and corolla slipping forward along the style during corolla abscission driven by wind. H: the wilted corolla on the flower in wind-excluding tents. I and J: stamen movement and self-pollination process when the corolla is abscised, showing the upward turning of anthers due to the blockage of the lower stigmatic lobe, and self-pollen deposition on stigma. K: The closed stigmatic lobes after being pollinated by bees. SL: stigmatic lobes; PR: flat oblong projection on the front connective; PA: large papillae at the back of connective; ST: style; AS: anther sac; SF: staminal filament; GC: globose connective.

corolla. Finally, the anthers are forcibly dragged to pass the stigma by the continually moving corolla. After the anthers pass the stigma, their dehiscent faces touch the inner surfaces of two stigma lobes, and brush pollen onto them (Figure 16J). Meanwhile, with the help of the force released from the severely bent filaments after the anthers have passed the stigma, the dehiscent sacs are able to shed pollen grains onto the inner surface of the stigma lobe. However, if the flower has been visited and pollinated by bees, the two open stigma lobes close upon contact with each other (Figure 16K). The closed stigma lobes fail to block the anthers and the pollen can not be deposited onto the surface of the stigma. Therefore, self-pollination can

not be achieved. If they are not touched, the stigma lobes remain open until corolla abscission. After pollinator visitation, the two open stigma lobes always close tightly.

D. Movements of Two Floral Organs within a Flower

In many floral movements, there is the combined movement of two floral organs such as filament elongation and style curvature in *Ourisia macrocarpa* (Schlessman, 1986), pollen sac separation and stigma curvature in *Curcumerphora longiflora* (Zingiberaceae) (Gao *et al.*, 2004), and style curvature and corolla closure in some *Kosteletzkya virginica* flowers (Ruan *et al.*, 2004; 2005a).



FIG. 17. Habitat, flowers in different sexual phases and visitors of *Curcumorpha longiflora* (Gao *et al.*, 2004). A: bagged flower in its male stage during the first day of flowering. B: bagged flower in its female stage during the second day of flowering. C: a butterfly visiting a flower. D: *C. longiflora* growing in the crevice of rocks. E: *Apis florea* visiting a first-day flower.

Each flower of *Curcumorpha longiflora* contains one stigma and one anther consisting of two adjacent anther sacs, and lasts about 36 h. On the first day, soon after flowers fully open, the anther dehisces and begins to release the pollen grains (Figure 17A). At the same time, the stigma is concealed between the two anther sacs, making it inaccessible to any visitors. This state lasts around 15 h. In the evening, the two pollen sacs begin to separate from the ventral face of the anther and curl up, exposing the stigma. The stigma then begins to curve downward and reaches the receptive position at midnight (Figure 17B). Afterwards, the flowers are in the female stage and wither in the evening of the second day. Thus, pollen transfer is only possible between different flowers (Figure 17F), and self-pollination is prevented (Gao *et al.*, 2004).

The flowers of *Ourisia macrocarpa* are zygomorphic, with a floral tube formed by partial fusion of the petals. The capitate stigma is exserted from the corolla tubes when the flower opens. The two pairs of four stamens, or parts of the stamens, are

referred to here as long and short. The corolla lobes are weakly bilabiate, with the middle posterior (“lower”) lobe slightly larger than the rest. The length of the corolla from the tips of the two anterior (“upper”) lobes to the tip of the middle posterior lobe is only slightly greater than the width between tips of the side posterior lobes. The orientation of open flowers is much nearer to the horizontal than to the vertical. The mean difference in orientation of a plane defined by the petal lobes (essentially perpendicular to the corolla tube) and the horizontal is only 13.1° . For a vertically oriented flower the difference would be 90° . Although the corolla lobes expand, the length of the tube does not change over the life of a flower (about 10 days). When the flowers open, the anthers are within the tube and only the stigma is exserted. About five days after opening the long anthers dehisce. During this time the long stamens grow so that their anthers emerge from the tube to occupy approximately the same position that the stigma had when flowers opened. At the same time the style curves upward, moving the stigma away from

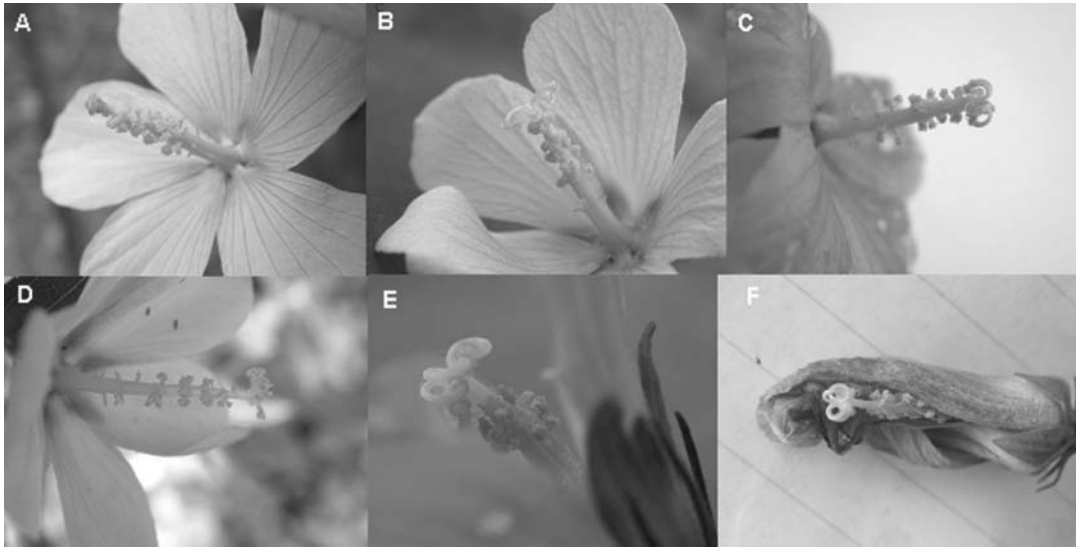


FIG. 18. Style and corolla movements of *Kosteletzkya virginica*. A: fully opened flower, stigmas are located on the top of the monadelphous column. If pollination fails, styles curve (B) and eventually bring stigmas into contact with the anthers (C); otherwise, styles cease curving (D) after pollination. E: in some flowers, corolla imminent closure about 16:00 intraday post-anthesis, in that time, style movement stopped and stigmas do not contact with its own anthers. F: corolla closure, self-pollination occurring as the gradually close corollas promoting the contact between stigmas and anthers.

the emerging long anthers. The short stamens also grow so that their anthers move towards the opening of the tube. Usually, the short anthers are not exerted. The short anthers dehiscence approximately one day after the long ones (Schlessman, 1986).

In the flowers of *Kosteletzkya virginica*, if stigmas are pollinated, styles remain erect (Figure 18A) or cease to curve (Figure 18D) when pollination occurs in the process of style curvature. However, if pollination fails, style branches curve downwards towards the anther (Figure 18B), eventually bringing stigmas into contact with the anthers (Figure 18C) and potentially resulting in self-pollination (Ruan *et al.*, 2004). About 5–9 h are needed for style curvature from the beginning (about 06:00–07:00) to cessation (about 11:00–16:00) (Ruan *et al.*, 2005b). However, in some *K. virginica* flowers, approach herkogamy of over 6.2 mm is too great to allow autonomous selfing only by style curvature (Ruan *et al.*, 2005c). In these flowers, comparative experiments between eliminated and un-eliminated corollas indicated that corolla closure (Figures 18E and F), in the absence of pollinators, is a mechanism of delayed self-pollination in this species (Ruan *et al.*, 2005a).

IV. MOVEMENT HERKOGAMY

Herkogamy, the spatial separation of pollen presentation and pollen receipt within a flower, occurs in many animal-pollinated plants (Webb and Lloyd, 1986; Barrett, 2002a, b). For example, the stigma of *Mimulus aurantiacus* is exerted beyond the anthers, presenting approach herkogamy (Fetscher and Kohn, 1999); and the bi-lobed stigma closes after receiving pollen, causing increased spatial separation of the anthers and stigma (movement herkogamy) (Webb and Lloyd, 1986;

Fetscher, 2001). However, in herkogamous flowers, too great a distance between stigmas and anthers reduces the probability that pollinators will be in contact with both sexual organs when visiting, and may decrease the veracity of cross-pollen transfer and male-female fitness. For example, the curvature of unpollinated stigma lobes results in autogamous selfing in *Hibiscus laevis* plants from northern populations more than in those from southern populations; this is because the distance between herkogamy before the curvature of unpollinated lobes for south populations is too great to allow selfing in plants (Klips and Snow, 1997). Additionally, too great herkogamy often leads pollinators with a small body to only contact pollen when the pollinators visit flowers (Spira, 1989; Spira *et al.*, 1992; Ruan *et al.*, 2010a).

Thus, to reduce intrafloral male-female interference from too great herkogamy, some species present decreased herkogamy via the movement of floral structures. The monadelphous column (filaments are united to form one set or tube, high or low anthers forming part of the tube are placed below the stigmas) in the Malvaceae segregates male and female reproductive organs, forming approach herkogamy. Thus, the curvature of un-pollinated styles towards the anthers presents movement approach herkogamy, which occurs in 23 species distributed in eight genera of four tribes among observed and investigated 52 species of the Malvaceae (Ruan *et al.*, 2010a). According to whether pollen is shed when the style begins to curve, movement approach herkogamy in the Malvaceae includes two types: Type I, styles curve before pollen shedding, and flowers have highly receptive stigmas and viable pollen when curvature brings stigmas into contact with anthers (Ruan *et al.*, 2010a). For example, the style branches are erect when the

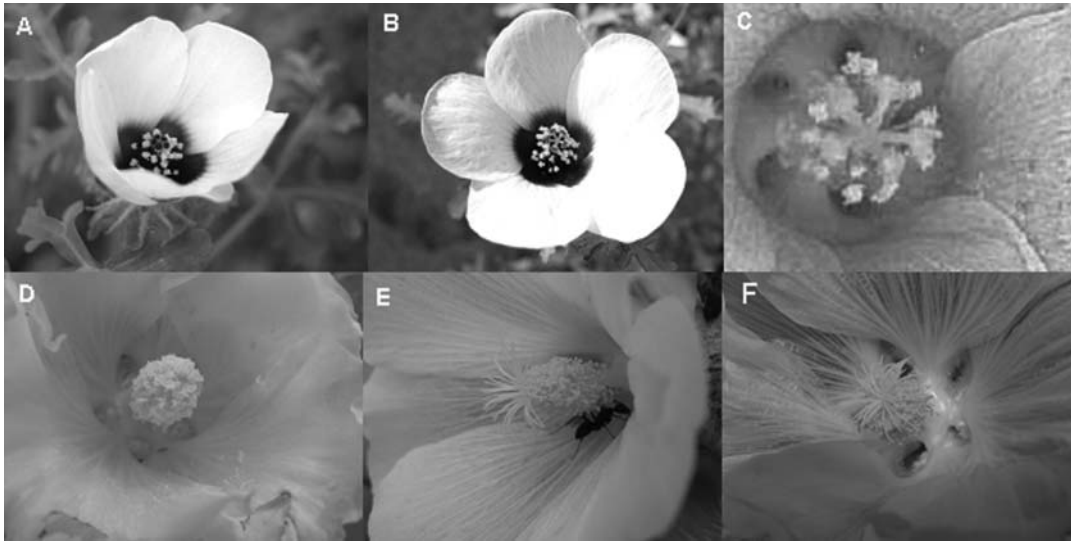


FIG. 19. Style movements in *Hibiscus trionum* and *Althaea rosea*. A: *H. trionum* has erect stigmas when flowers just and fully open, styles curve and bring stigmas into contact with the anthers (B and C (photo courtesy of Colleen Keena)) if the pollination fails. A. *rosea* has protandrous flowers (D), stigmas hide within the monadelphous column after flowers fully open; pollen shed after 1–2 days, then stigmas exsert from the column and begin to curve (E), and eventually some stigmas make contact with the anthers (F).

flowers of *Hibiscus trionum* just open (Figure 19A); however, if the flower is not pollinated, the style branches begin to curve and eventually make stigmas contact their own anthers at the end of flowering (Figures 19B and C). This type I curvature occurs in 20 species that belong to three tribes (Malvaceae, Urenaee and Hibisceae) of this family, including *Kosteletzkya virginica* (Figure 18C), *H. trionum* (Figure 19B and C), *Pavonia hastata* (Figure 20C) and *P. multiflora* (Figure 20D), *Urena lobata* (Figure 20E), *Abelmoschus sagittifolius* (Figure 20F), *A. manihot* (Figure 20G), *H. coatesii* (Figure 20H), *H. coccineus* (Figure 20I), *H. dasycalyx* (Figure 20J), *H. laevis* (Figure 20K), *H. moscheutos* ssp. *moscheutos* (Figure 20L), *H. moscheutos* subsp. *incanus* (Figure 20M), *H. moscheutos* subsp. *lasiocarpus* (Figure 20N), *H. moscheutos* subsp. *palustris* (Figure 20O), *H. normanii* (Figure 20P), *H. pedunculatus* (Figure 20Q), *H. sabdariffa* (Figure 20R), *H. surattensis* (Figure 20S), and *K. pentacarpus* (Figure 20T). Type II: styles curve after most pollen is shed, and this curvature often appears in the protandrous species of the Malveae tribe, such as *Althaea rosea* (Figure 19D), *Malope trifida* (Figure 20A) and *Malva neglecta* (Figure 20B). In type II flowers of *A. rosea* (Figure 19D), after having flowered for 2–3 days, style branches grow out of the monadelphous column (Figure 19E) and begin to curve, eventually bringing some stigmas down or in contact with the unshed anthers (Figure 19F).

V. ADAPTIVE SIGNIFICANCE OF FLORAL MOVEMENT

Various hypotheses have been proposed to explain the adaptive significances of the above mentioned floral movements (Table 3). The four major hypotheses are highlighted next.

A. Promotion of Outcrossing and/or Avoidance of Self-Pollination

Under the influence of Darwin's (1862) notion, there is increasing attention to the fact that floral movement may act as a mechanism to promote outcrossing and/or avoid self-pollination, by (i) positioning reproductive organs (e.g., style or pollen) in the flight path of visitors, (ii) separating reproductive organs (e.g., style or pollen) from the pollinators' flight path, and (iii) movement-assisted dichogamy, as detailed next.

1. Position of Reproductive Organs in the Pollinators' Flight Path

Some floral movements (e.g., pollinia reconfiguration and style curvature) position reproductive organs (e.g., stigma, pollinia, and pollen) in the flight path of visitors, and this may promote cross-pollination and/or avoid self-pollination (Kindy, 1999; Bennington, 2003; Hong *et al.*, 2008; Ren, 2010). Self-pollination in the European orchid *Anacamptis morio* (Orchidaceae) does not take place unless a pollinator's visits exceed the time (18s) taken for pollinia to undergo the flowers' bending movement (Johnson *et al.*, 2004). The rapid (1 ms) pollen catapult of self-incompatible *Cornus canadensis* may enhance cross-pollination: when insects trigger the opening flower, the pollen that is released sticks to their body hairs until it is transferred to an adhesive stigma (Edwards *et al.*, 2005).

Darwin was intrigued by the pollinia reconfiguration in orchards and referred to it as a 'beautiful contrivance' that would function to reduce self-pollination if the time taken for its completion exceeds the duration of a pollinator's visit to a plant (Darwin, 1862). To test Darwin's hypothesis, Peter and Johnson (2006) investigated pollinia reconfiguration (including pollinia



FIG. 20. Style movement in the Malvaceae. A: *Malope trifida* (http://www.em.ca/garden/ann_malope1.html). B: *Malva neglecta* (<http://www.msuturfweeds.net/images/galleries/mallow/6.jpg>). C: *Pavonia hastata* (photo courtesy of Geoff Keena). D: *Pavonia multiflora* (http://upload.wikimedia.org/wikipedia/commons/5/5b/Pavonia_multiflora0.jpg). E: *Urena lobata* (http://www.alabamaplants.com/Pinkalt/Urena_lobata_page.html). F: *Abelmoschus sagittifolius* (photo courtesy of Bill Hagblom). G: *Abelmoschus manihot* (<http://www.malvaceae.info/Genera/Abelmoschus/gallery.html>). H: *Hibiscus coatesii* (photo courtesy of E. McCrum). I: *Hibiscus coccineus* (<http://www.nature-by-design.com/Hibiscus%20coccineus%20small.jpg>). J: *Hibiscus dasycalyx* (<http://www.griffithpropagationnursery.com/Hibiscus%20dasycalyx%20flower.jpg>). K: *Hibiscus laevis* (photo courtesy of Jennifer Anderson). L: *Hibiscus moscheutos* ssp. *moscheutos* (http://www.remarc.com/craig/images/hib_mos.pinkx1200.jpg). M: *Hibiscus moscheutos* subsp. *incanus* (http://fr1.wikipedia.org/wiki/Hibiscus_moscheutos). N: *Hibiscus moscheutos* subsp. *lasiocarpus* (<http://botany.cs.tamu.edu/FLORA/hdwimages1/hibis1b.jpg>). O: *Hibiscus moscheutos* subsp. *palustris* (<http://www.fortunecity.com/business/koch/3/images/hibpalus.jpg>). P: *Hibiscus normanii* (photo courtesy of Geoff Keena and Colleen Keena). Q: *Hibiscus pedunculatus* (photo courtesy of R. Saunders). R: *Hibiscus sabdariffa* (photo courtesy of W.-Y. Zhao). S: *Hibiscus surattensis* (http://farm1.static.flickr.com/33/91104274_511b2dc907.jpg). T: *Kosteletzkya pentacarpos* (photograph by C.-J. Ruan).

bend, pollinia shrinking and anther cap retention) in 19 species of orchid and asclepiad families. They found that (i) there is a strong positive relationship ($r^2 = 0.79$) between reconfiguration time and the duration of pollinator visits. For example, one subspecies of *Eulophia parviflora* pollinated by slow-moving beetles has pollinaria that take an average of 100 s to reconfigure, while the other subspecies pollinated by rapidly moving bees has pollinaria that reconfigure in just 28 s; (ii) reconfiguration times from 22 to 8100 s (mean = 952 s) were also consistently longer than pollinator visit times (about 634 s); and (iii) reconfiguration mechanisms have evolved at least four times (pollinia bending in orchids and asclepiads, anther cap retention and pollinia shrinking in orchids) and perhaps many more times in these families. Their results provide strong support for Darwin's idea that this mechanism promotes cross-pollination. The mechanisms that reduce the likelihood of self-pollination appear to be particularly prevalent in plant families in which pollen is aggregated as pollinia (Catling and Catling, 1991; Borba and Semir, 1999; Johnson and Nilsson, 1999; Harder and Johnson, 2005). The remarkable evolutionary fine-tuning of pollinia reconfiguration in the orchids and asclepiads in response to pollinator visit times conveys a message about the central role that pollinator behaviour plays in the evolution of plant traits that promote cross-pollination (Peter and Johnson, 2006).

Bulbophyllum penicillium, an orchid species, has a sensitive lip, and there is a distance of 2–3 mm between the lip and column apex. Once the lip is touched by a landing insect, it will move up and down or swing left and right continuously, just like a moving caterpillar (Liu *et al.*, 2010). By suck lip movement, the pollinator, a very small fruit fly (*Drosophila* sp.), will be pressed toward the column apex where anther and stigma are located, and then cross-pollination takes place.

In the Malvaceae, type II style curvature positions stigmas in the path of the visiting pollinator and takes a very long time (5–10 h for *Kosteletzkya virginica*) before bringing stigmas into contact with their own anthers, which offers more opportunity to receive outcrossing pollen. Similarly, the adaptive mechanism of promoting outcrossing is also evidenced by Type I curvature in *Althaea rosea*, *Malope trifida* and *Malva neglecta*. In these three species, when style branches exert from the monadelphous column and begin to curve, most pollen is shed and pollen viability is lower when the curvature brings stigmas near to or in contact with the anthers.

2. Separation of Reproductive Organs from the Pollinators' Flight Path

Some species displays floral movements that separate reproductive organs from the pollinators' flight path to avoid self-pollination and/or promote outcrossing. For example, flexistylis, deployed by the species in the genus *Alpinia* (Zingiberaceae) may avoid self-pollination (Li *et al.*, 2001; 2002), in which the flower moves its stigma (style), which normally acts as the pollen receptor, out of the pollinators' way while its anther is releasing pollen.

3. Movement-Assisted Dichogamy

Atamisquea emarginata (Capparaceae) is a 2–4-m-high shrub growing in southern North America, north-central Argentina and adjacent parts of Bolivia and Chile (Wiggins, 1980; Zuloaga and Morrone, 1999). The creamy white, entomophilous flowers are protandrous and last 3.5–4.5 days. Pollen and stigmas are presented in the same place within the flower, but interference is prevented by a movement-assisted, complete dichogamy mechanism in which the bending ability of the gynophore plays a fundamental role (Medan and Ponessa, 2003). In flowering, the ensuing 1–1.5-day-long male phase begins with anther opening, while the stamens (at first concentrated in a bundle) spread away from the center of the flower and the petals become increasingly reflexed. At the same time, the gynophore tilts down and becomes straight, so removing the ovary from the anthers' position, and the stigma is not receptive. Visitors landing or hovering at the flowers easily contact the pollen presented on the anthers, while the ovary tip remains out of the visitors' approach route. By the end of the male phase, most pollen has been removed. The usually 1-day-long female phase starts with the shrivelling of the already empty anthers, which become C-shaped while the filaments wilt. Insect visits, nectar secretion and scent emission continue. The gynophore bends upwards, thus placing the ovary where the anthers stood before. The receptive stigma can be contacted by approaching visitors. By 3.5–4.5 days (or sooner if the weather is hot and dry) all perianth parts and stamens start to drop, nectar and scent disappear and the gynophore tilts down again, while the ovary (if ovules are fertilized) starts to enlarge.

B. Reduction in Intrafloral Male–Female Interference

Intrafloral sexual interference often contains physical interference and pollen clogging (Barrett, 2002a). Physical interference involves stamens obstructing the deposition of outcrossing pollen on stigmas (Parra-Tabla and Bullock, 2005) and pistil interfering with pollen export (Kohn and Barrett, 1992). Recently, increasing evidence supports that some floral movement, which was first considered as a mechanism to promote outcrossing and/or avoid self-pollination, may act as a mechanism to reduce intrafloral male–female interference (Fetscher, 2001; Yang *et al.*, 2004; Edwards *et al.*, 2005; Sun *et al.*, 2007; Ruan *et al.*, 2010a). Flexistylis is a sexual dimorphism where there are two morphs that differ in the temporal expression of sexual function and also involve reciprocal movement of the stigmatic surface through a vertical axis during the flowering period. The adaptive significance of flexistylis has been interpreted as a floral mechanism for outcrossing (Li *et al.*, 2001, 2002); however, differential maturing of male and female organs in *Alpinia blepharocalyx* is sufficient for avoiding selfing, obviating the need for style movements. Hence, the upward style curvature of the cataflexistylous morph in the morning and the anaflexistylous morph in the afternoon most likely represents a means of reducing interference with pollen export (Sun *et al.*, 2007).

1. Reduction in Intrafloral Male-Female Interference via Movement Herkogamy

More attention has been paid to the hypothesis (Darwin, 1876) that herkogamy has evolved as a mechanism to reduce the frequency of intrafloral self-pollination (Holtsford and Ellstrand, 1992; Brunet and Eckert, 1998). This is because (i) there exists a positive correlation between herkogamy and outcrossing rates in some species with mixed-mating systems (Belaoussoff and Shore, 1995; Karron *et al.*, 1997; Motten and Stone, 2000); and (ii) herkogamy influences self-pollination (Miyajima, 2001; Elle and Hare, 2002) and inbreeding depression (Stone and Motten, 2002). In contrast, increasing evidence suggests that herkogamy may act as a mechanism to reduce intrafloral male-female interference (Webb and Lloyd, 1986; Bertin and Newman, 1993; Barrett, 2003; Routley *et al.*, 2004). Studies of heterostylous species indicate that sex-organ reciprocity is a mechanical device increasing the proficiency of cross-pollination as a result of segregated pollen deposition on different parts of the bodies of pollinators, and that enantiostyly and stigma-height dimorphism also function in a similar manner (Jesson and Barrett, 2002; Thompson *et al.*, 2003). The stigma behavior (approach herkogamy) in *Campsis radicans* is not an outcrossing mechanism, but strongly indicates that it acts as a mechanism to facilitate pollination, and then enhance reproductive success (Yang *et al.*, 2004), this is because stigma lobe closure reduces the intrafloral interference of stigma to the pollinators.

Fetscher's study (2001) provides the first experimental evidence that selection to reduce intrafloral male-female interference can be a strong selective force and can drive the evolution of floral characters, usually interpreted as mechanisms to reduce self-fertilization. In hummingbird (such as *Calypte anna* (Anna's) (Trochilidae), *Selasphorus sasin* (Allen's) (Trochilidae), *Calypte costae* (Costa's), *Archilochus alexandri* (Black-chinned) (Trochilidae), *Selasphorus rufus* (rufous) or *Stellula calliope* (Calliope))-pollinated *Mimulus aurantiacus* with approach herkogamy, upon receipt of pollen, most stigmas remain closed for the remaining lifetime of the flower, even if less pollen is received than is needed for full seed set. Those stigmas that do reopen after pollination generally require between 20 and 28 h to do so, much longer than for unpollinated stigmas (2.5–4.5 h). Reopening after pollination appears to be a response to low seed set rather than to low pollen load. This stigma closure could represent increased "movement herkogamy" in which female organs, after pollen receipt, move to reduce interference with pollen dissemination.

However, extra-separated approach herkogamy (over a certain separated distance between stigmas and anthers) might decrease the veracity of cross-pollen transfer and male-female fitness (Zhang, 2004), because it decreases the probability that pollinators simultaneously contact both sexual organs when visiting. For example, approach herkogamy of 6.2 mm is too long to allow autonomous selfing only by style curvature in *Kosteletzkya virginica* (Ruan *et al.*, 2005c). The *K. virginica* flower with a large corolla (diameter = 53.11 ± 0.83 mm) and approach

herkogamy of 3.64 ± 0.08 mm, the length of the body of most pollinators is less than that of the monadelphous column (19.77 ± 0.38 mm) and that of the style (23.40 ± 0.37 mm). For example, the body length of *Bombus speciosus* (about 22.7 mm), one of 12 categories of pollinators visiting *K. virginica* flowers in the Jiansu populations of China, is more than that of the monadelphous column. Most floral visitors collecting pollen or nectar directly visit the flower through the flank of its corolla, thus missing stigmas and only having contact with the stamens when styles do not curve. This distance interference between male-female functions may pertain to stamens that prevent stigmas from just contacting potential pollinators (Bertin and Newman, 1993; Barrett, 2002a), resulting in the decrease of male-female fitness.

Hence, the decrease of too great approach herkogamy via style curvature in the Malvaceae may (i) reduce intrafloral male-female interference from extra-separated approach herkogamy; and (ii) maximize the mating opportunity offered by also improving male-female fitness through style curvature, because it positions the stigmas in the flight path of visiting pollinators, which favors receiving self- and crossing-pollen. In *Hibiscus trionum* var. *trionum*, curvature is reversible, with partially curved styles regaining an erect position after receiving pollen (Buttrose *et al.*, 1977). This reversible curvature, which separates pollinated stigmas from pollinators, may be beneficial for pollen export. On the other hand, in the flowers of some *Kosteletzkya virginica* individuals with approach herkogamy of 6.23 ± 0.053 mm (Ruan *et al.*, 2005c), the decreased approach herkogamy after style curvature ceases is still about 1.3 mm (Ruan *et al.*, 2005b). In this case, though the decreased distance does not directly result in self-pollination, it is a precondition for self-pollination combining style curvature with corolla closure (Ruan *et al.*, 2005a). If otherwise, the occurrence of self-pollination is not possible even though corolla closure may push pollen upwards, because approach herkogamy (3.6 mm) before styles curve is about 2.8 times the decreased distance (1.3 mm). This fact may provide additional evidence for style curvature, which decreases too great approach herkogamy to a certain degree, and reduces intrafloral male-female interference (Ruan *et al.*, 2010a).

In addition, reduction of herkogamy after pollination in *Gesneria citrina* (Gesneriaceae) may favor increased pollen removal and setting success, while the reduction in stigma-anther distance no longer imposes the risk of interference between male and female functions (Chen *et al.*, 2009). Pollen export may be higher if the anthers are at the same level as the stigma, but having both anthers and stigma at similar positions in the floral tube may result in interference with pollen deposition on the stigmas, in addition to contributing to increased selfing. However, if the stamen filaments reach stigma height only after pollen has been deposited on the stigmas, then the opportunity for both interference and selfing is reduced. This pollination-induced reduced herkogamy is the opposite of increased movement herkogamy, where separation of male and female function occurs with the

displacement of anthers from the stigma as often occurs with protandry, or where the stigma closes after pollination, for example, in *Mimulus* (Barrett, 2002a).

2. Reduction in Intrafloral Male-Female Interference via Position Variability of Reproductive Organs

Avoidance of interference between the reception and donation of pollen may also be an important factor in the evolution of style movement (Schlessman, 1986). In *Ourisia macrocarpa*, after five days' flowering, the pollinated stigmas curve upwards to empty their position to the elongation of filaments that brings the anthers just near the position in the path of the visiting pollinator, which is helpful for pollen dispersal (Schlessman, 1986). This position variability via style movement may reduce the interference of the pistil to pollen export. Similarly, this mechanism reducing male-female interference also occurs in *Eremurus himalaicus*, which presents a downward and recovered style movement (Verm et al., 2004).

In addition, stamen cascade movements present pollen to pollinator group by group, which not only enhances pollen export by different pollinators (Cocucci and Sersic, 1998; Ma et al., 2004; Ren, 2010), but also avoids the interference of pollen-shed stamens to stamens that will disperse their pollen.

C. Delayed Autonomous Selfing

Lloyd (1979) proposed three modes of selfing: "prior," "competing," and "delayed," depending on the relative timing of selfing and outcrossing. Prior selfing occurs before the receipt of outcross pollen. In competing selfing, self- and outcross pollen simultaneously compete for ovules. Both "prior" and "competing" selfing provide reproductive assurance; however, they also lower the potential for outcrossing and are subject to pollen and seed discounting (Lloyd and Schoen, 1992). Delayed selfing occurs after the opportunity for outcross pollen receipt has passed. The movements of stamen, style and corolla during anthesis seem to be the most common method of spontaneous self-pollination in angiosperms, which has been reported in many species of 22 families (Acanthaceae, Berberaceae, Bignoniaceae, Calycanthaceae, Capparaceae, Cistaceae, Collinsieae, Ericaceae, Gentianaceae, Gesneriaceae, Leguminosae, Loasaceae, Malvaceae, Onagraceae, Orchidaceae, Orobanchaceae, Polygalaceae, Ranunculaceae, Scrophulariaceae, Solanaceae, Violaceae and Zingiberaceae) (Table 3). Delayed selfing is always advantageous because it assures seed production when pollinators are scarce (reproductive assurance) while allowing outcrossing to dominate when they are abundant (Klips and Snow, 1997; Kalisz et al., 2004). However, there are only a few cases in which the impact of delayed selfing on reproductive assurance has been tested quantitatively (Eckert and Schaefer, 1998; Donnelly et al., 1998; Nagy et al., 1999; Herlihy and Eckert, 2002; Kalisz and Vogler, 2003; Kalisz et al., 2004; Ruan et al., 2008a; Ruan et al., 2009a, 2009b). Next, we highlight delayed selfing via different floral movements and its contribution to reproductive assurance.

1. Delayed Autonomous Selfing

Different floral movements may result in delayed autonomous selfing, as follows:

- (1) pistil (style) movement, such as style curvature in *Viola pubescens* (Culley, 2002) and some species in the Malvaceae (Buttrose et al., 1977; Klips and Snow 1997; Ramsey et al., 2003, Ruan et al., 2004; Ruan et al., 2010a), stigma movement in *Roscoea schneideriana* (Zhang and Li, 2008) and some species in the Gentianaceae (Freitas and Sazima, 2009), stigma lobe overlap in *Polygala lewtonii* (Polygalaceae) (Weekley and Brothers, 2006), and gynophore bending in *Atamisquea emarginata* (Medan and Ponessa, 2003) and *Sinopodophyllum hexandrum* (Xu et al., 1997).
- (2) Stamen (filament, anther, pollen) movement, such as filament elongation in *Collinsia verna* (Kalisz et al., 1999), *Aquilegia canadensis* (Eckert and Schaefer, 1998), *Fuchsia magellanica* (Traveset et al., 1998), the genera *Collinsia* and *Tonella* (Armbruster et al., 2002), *Crotalaria micans* (Etcheverry et al., 2003), *Jaltomata repandidentata* (Powell, 2007), *Gesneria citrine* (Chen et al., 2009) and *Gentianopsis paludosa* (Duan et al., 2010); stamen curvature in *Kalmia latifolia* (Rathcke and Real, 1993) and *Sanguinaria canadensis* (Lyon, 1992); stamen movement in *Cajophora arechavaletae* (Schlindwein and Wittmann, 1997b) and *Chimonanthus praecox* (Calycanthaceae) (Wu and Hu, 1995); pollen sliding in *Caulokaempferia coenobialis* (Wang et al., 2004); and anther rotation in *Holcoglossum amesianum* (Liu et al., 2006).
- (3) corolla movement, such as wind-driven corolla abscission in *Incarvillea sinensis* var. *sinensis* (Qu et al., 2007), corolla closure in *Kosteletzkya virginica* (Ruan et al., 2005a) and *Zygostigma australe* (Gentianaceae) (Freitas and Sazima, 2009), corolla wilting in *Pedicularis dunniana* (Sun et al., 2005), and corolla dragging (abscission) in *Lupinus nanus* (Juncosa and Webster, 1989), *Mimulus guttatus* (Dole, 1990) and *Ruellia succulenta* (Dieringer, 1999).

2. Contribution of Delayed Autonomous Selfing to Reproductive Assurance

Delayed selfing is always advantageous because it is due to delayed autonomous self-pollination. However, the results of testing the contribution of delayed autonomous selfing to reproductive assurance have been modest. In some cases, delayed autonomous selfing has been reported to increase reproductive success. Delayed selfing in *C. verna* provides reproductive assurance (Kalisz et al., 2004) because the amount of autonomous selfing in *Collinsia verna* varies depending on pollinator conditions (Kalisz and Vogler, 2003), with the amount of selfing increasing when decreasing pollinator abundance. Small, emasculated flowers produce very few seeds, relative to small, intact flowers in *Collinsia parviflora* (Scrophulariaceae) (Elle and Carney, 2003). Under natural pollination, emasculated flowers of *Verbascum thapsus* (Scrophulariaceae) without delayed

selfing present a reduction in seed set, compared to intact flowers with delayed selfing (Donnelly *et al.*, 1998). In contrast, other available studies indicate that autonomous selfing does not substantially increase seed set. By comparing intact with emasculated open-pollinated flowers, Nagy *et al.* (1999) found that autonomous self-pollination in *Kalmia latifolia* does not increase fruit production. In *Aquilegia canadensis*, Herlihy and Eckert (2002) found that autonomous selfing increases seed production, but this benefit is outweighed by the loss of high-quality seed as a result of seed discounting and inbreeding depression.

In species of the Malvaceae with delayed selfing, *Kosteletzkya virginica* has a well-developed capacity for delayed autonomous selfing, which provides reproductive assurance. This is because (i) the mean number of seeds per capsule from intact open-pollinated flowers is higher than that of emasculated open-pollinated flowers (Ruan *et al.*, 2008a), and (ii) adverse weather conditions significantly increase the incidence of delayed selfing, whereas elimination of delayed selfing by experimental manipulation reduced fruit and seed set compared to non-emasculated flowers, even under adverse weather conditions (Ruan *et al.*, 2009a). In contrast, Klips and Snow (1997) observed that autonomous self-pollination in *Hibiscus laevis* did not contribute significantly to fruit production of open-pollinated flowers.

D. Tolerance to Harsh Environments

Floral movements in response to environmental changes have been reported in *Gentiana algida* (Bynum and Smith, 2001) and *Pulsatilla cernua* (Huang *et al.*, 2002). *Gentiana algida* flowers close within minutes of an approaching thunderstorm and reopen after direct sunlight returned. Corolla opening widths decrease $\sim 10\%/min$ prior to rainfall, in close correspondence to declines in air and corolla temperatures. Furthermore, individual *G. algida* plants forced experimentally to remain open during rain showed substantial losses of pollen after single rain events (up to 34%) and if forced to remain open for the entire flowering period (59%). Subsequent seasonal reductions in female fitness (up to 73%) also occurred, including seed size and mass, number of ovules produced, number of viable seeds produced per ovule, and seed germination. Thus, corolla closing and opening in *G. algida* associated with frequent summer thunderstorms may be a behavioral adaptation that improves both paternal and maternal reproductive effort (Bynum and Smith, 2001).

Flower stalk bending in *Pulsatilla cernua*, an early spring herb in north temperate Asia, seems to be important to maintain pollen viability in a rainy habitat with a scarcity of pollinators, because (i) pollen damage by water is serious in this species; and (ii) the bending of the flower stalk during anthesis avoids rain damage to pollen grains in this species (Huang *et al.*, 2002). During the 3–6 d period of pollen presentation, the petals elongate and are covered with unwettable hairs. Together with movement of flower stalks, this is enough to protect the organs inside the flower from rain.

VI. POSSIBILITY OF MULTIPLE SIGNIFICANCE OF ONE FLORAL MOVEMENT IN ONE SPECIES

In general, it has been recognized that one floral movement in one species has a single functional mechanism. However, more and more studies corroborate that a single floral movement in one species could have (at least) two adaptive mechanisms (Buttrose *et al.*, 1977; Schlessman, 1986; Edwards *et al.*, 2005). Next, we first present cases of two adaptive mechanisms from one floral movement and then conclude with the possibility of three adaptive significances in one floral movement in one species, which presents a challenging notion for evolutionary biologists.

A. Two Adaptive Significances from One Floral Movement in One Species

Unpollinated style curvature in *Hibiscus trionum* has been viewed as a potential mechanism to give outcrossing the highest priority, while retaining the ability to self if outcrossing fails (Buttrose *et al.*, 1977). Similarly, one floral movement reflecting dual functional significances has also been reported in some species, such as *Scrophularia nodosa* (Scrophulariaceae) (Faegri and van der Pijl, 1979), *Ourisia macrocarpa* (Schlessman, 1986), and *Eremurus himalaicus* (Verma *et al.*, 2004). In *Ourisia macrocarpa*, in the prime of flowering, stigmas exert from the corolla tube and stamens stay hidden within it, which favors outcrossing (Schlessman, 1986). Then, after five days of flowering, pollinated stigmas curve upwards, the elongation of filaments brings the anthers just near the position in the path of the visiting pollinator, which is helpful for pollen dispersal.

Individual flowers of *Verbascum thapsus* are ephemeral, opening before dawn and closing before mid-afternoon of the same day (Gross and Werner, 1978). They are protogynous, the style maturing first and then bending downward once the anthers appear (Kerner von Marilann, 1895). The two anterior stamens are naked, and provide most of the fertilizing pollen. The hairs of the posterior three probably provide a foothold for visitors, for example, hover-flies (*Eupeodes latifasciatus* (Syrphidae), *Syrphus ribesii* (Syrphidae), and *Sericomyia silentis* (Syrphidae)) which gather nectar and pollen from the posterior anthers while their abdomens are dusted with pollen from the anterior pair. Although visited by a wide variety of insects, only short- and long-tongued bees are effective vectors of cross-pollination (Gross and Werner, 1982). Flowers are also autogamous, self-pollination occurring at the end of the day if cross-pollination has not occurred. The style returns to its original position, and the corolla closes, pushing the still receptive stigma against the anthers (Gross and Werner, 1978). This process involves two adaptive significances: (i) style curvature may decrease its interference to pollen export; and (ii) lately returned curvature is useful to delayed selfing.

B. Three Adaptive Significances from One Floral Movement in One Species

Style curvature in one species of the Malvaceae has one (Klips and Snow, 1997; Ramsey *et al.*, 2003) or two (Buttrose

et al., 1977) functional significances. Ruan *et al.* (2010) concluded that the adaptive significance of style curvature occurring in one species of the Malvaceae may involve delayed selfing, promotion of outcrossing, and reduction in intrafloral male-female interference. We now discuss this possibility by explaining the three adaptive significances of style curvature in *Kosteletzkya virginica*.

The curvature of unpollinated styles in *Kosteletzkya virginica* is simultaneously involved in three functions, including the reduction in intrafloral male-female interference from too great approach herkogamy, the promotion of outcrossing and the achievement of delayed selfing. In *K. virginica*, the curvature of

unpollinated styles positions the stigmas in the flight path of visiting pollinators or provides the precondition for self-pollination combining style curvature and corolla closure if pollination fails (Ruan *et al.*, 2005a, 2005c), which favors the receipt of self- and outcrossing pollen, to a certain degree reducing the above interference between intrafloral male-female functions from extra-separated approach herkogamy (first adaptive significance). In the first half of the process of style curvature, the upper surface of stigmas, which are very receptive, is located in the path of pollinators visiting the flower (the styles indicated by dashed arrowheads in Figures 21A and B), which will increase the veracity of cross-pollen transfer (Stephens, 1948) (second

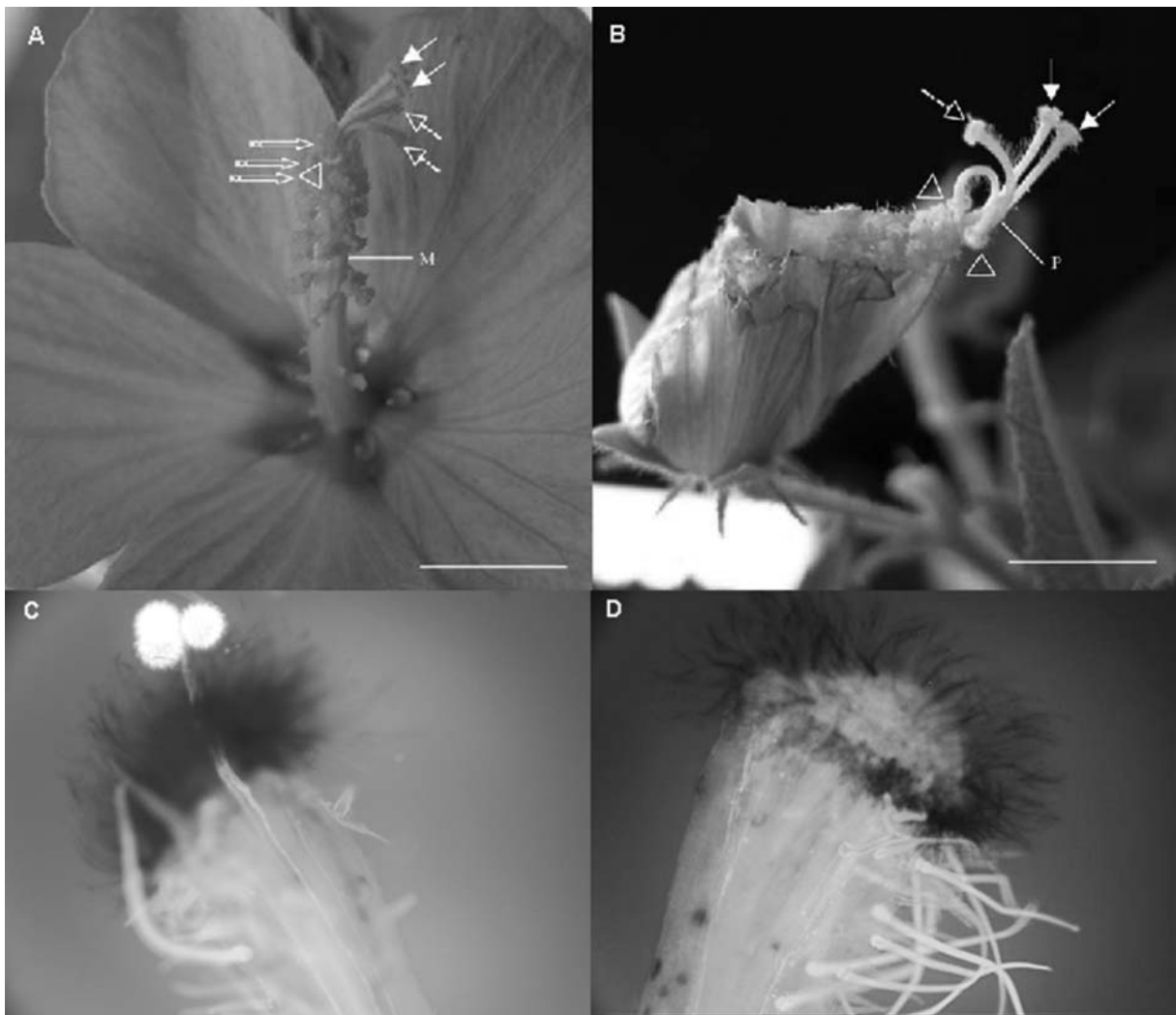


FIG. 21. Each of the styles within *Kosteletzkya virginica* flowers curve independently. A: two styles (solid arrowheads) ceased curving after early hand-pollination; two styles that were pollinated later (dashed arrowheads) immediately ceased curving after pollination; while the last style (triangle) which was not hand-pollinated, continued to curve until it contacted the upper anthers and self-pollinated. Three open arrowheads indicate the upper most stamen; M: monadelphous column. B: two styles (solid arrowheads) remained erect after hand-pollination; the remaining three unpollinated styles curved until one of them was hand-pollinated (dashed arrowhead) and immediately ceased curving; the last two styles (triangles) were not hand-pollinated, and continued to curve until contacting the anthers to self-pollinate. P: pistil; scale bar (A and B): 1 cm. C: after pollination, the stigma lobe ceases to curve downward. Pollen deposited on the stigmatic surface germinated, and the pollen tube (arrowhead) grew beyond the lobe. D: after pollination, the stigma lobe continued to curve because the pollen tube did not germinate and grow beyond the lobe. Ungerminated pollen is easy to remove by washing the stigma lobe during preparation.

adaptive significance). When pollinators retreat from the flowers, the lower surface of stigmas has no receptive contact with pollinators, which avoids self-pollination. However, if pollination always fails, curvature will continue to bring stigmas into contact with their own anthers (the styles indicated by triangle in Figures 21A and B), potentially resulting in delayed selfing (Ruan *et al.*, 2004) because the style stops curvature only when the pollen tube grows beyond the stigma lobe (Ruan *et al.*, 2008b) (third adaptive significance).

Variation in approach herkogamy is nearly ubiquitous in all species of the Malvaceae (Akpan, 2000). In particular, it is obvious for species displaying style curvature, such as approach herkogamy ranging from 0.12 to 4.83 mm in *Hibiscus trionum*, from 0.12 to 6.84 mm in *Kosteletzkya virginica*, from 0.08 to 3.78 mm in *Malva neglecta*, and from 0.31 to 9.76 mm in *Pavonia hastata*. In addition, in the Malvaceae, herkogamy could have evolved before style curvature, and style curvature may have evolved as a mechanism to reduce the deficiency from too great herkogamy and improve the male-female fitness (Ruan *et al.*, accepted). Thus, these provide indirect evidence for the possibility of style curvature in the Malvaceae that has three adaptive significances.

VII. FLORAL MOVEMENT: A BROADER PROSPECTIVE

Since Darwin (1862) observed pollinia reconfiguration, dramatic movements of different floral structures (e.g., pistil (style), stamen (filament, anther, pollen), and corolla) have intrigued plant evolutionary biologists. Interestingly, high-speed pollen release ($<25 \mu\text{s}$) in *Morus alba* was investigated using high-speed video (Taylor *et al.*, 2006). For these exciting floral movements, various adaptive significances have been proposed and studied, such as reduction in intrafloral male-female interference, promotion of outcrossing and/or avoidance of self-pollination, delayed autonomous selfing, and tolerance to harsh environments. Although it is possible that one floral movement in one species may involve two or three adaptive significances, there is no example to simultaneously test the evolution of different adaptive significances from one floral movement, the relative importance and their mechanism of coevolution.

It is important for understanding diverse floral movements and their adaptive significances to investigate the evolution of floral movement at the level of family and its evolutionary relationships with other plant traits, mating system and ecological habitat shifts (especially pollinator environments) (Herlihy and Eckert, 2002; Kalisz *et al.*, 2004; Goodwillie *et al.*, 2005; Barrett, 2008). Mapping trait state transition and characters that are relative to this transition on a phylogenetic tree may provide new insights for estimating the number of trait transitions and provide insights into the ecological basis of its selection (Weller and Sakai, 1999; Crisp *et al.*, 2009). Based on the molecular phylogenetic tree for *Alpinia* and the distribution of flexistylis in this family, Kress *et al.* (2005) showed that flexistylis may have evolved in the common ancestor of the tribe Alpinieae or

independently at least 3–5 times in the tribe. Based on molecular phylogenetic trees constructed using chloroplast DNA sequences of *ndhF* and the *rpl16* intron and their combination of 52 species of 13 genera in the Malvaceae (in which 23 species of eight genera display style curvature), style curvature evolved at least five times in species with herkogamous flowers; the occurrence of style curvature was associated with a shift to annual or perennial herbs with herkogamous flowers, and an unpredictable pollinator environment is likely an important trigger for this evolution (Ruan, 2010b; Ruan *et al.*, accepted).

Briefly, diverse and skillful floral movements present different adaptive significances (promotion of outcrossing, achievement of delayed selfing, reduction in intrafloral male-female interference); however, how evolutionary relationships between floral movement and other relative traits, mating systems and pollinator environments evolved is still a challenging problem for evolutionary scientists. In the face of this interesting challenge, in future research a synthesis of demographic and genetics approaches (Cheptou and Schoen, 2007) should be used to (i) study the relative importance and harmonious mechanism of different adaptive significance of dramatic floral movements, such as dissecting patterns of selfing into individual components (Goodwillie *et al.*, 2005), testing fitness of different adaptive significance combining a cost-benefit approach (Eckert and Herlihy, 2004); and (ii) simultaneously documenting broader species in a certain or relative families to determine in which floral movement is or not and the plant traits (e.g., reproductive character, nutritive character, micromorphological and embryonic character, breeding system, pollination biology and breeding system) to test the evolution and evolutionary relationship between floral movement and plant traits, by the mapping of these traits on a complete phylogenetic tree constructed by molecular, morphological and fossil data.

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