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The Pollination Biology of North American Orchids: Volume 1

North of Florida and Mexico

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Charles L. Argue, Ph.D.
University of Minnesota
College of Biological Sciences
Saint Paul, MN, USA
argue001@umn.edu

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Preface

Orchids employ an amazing array of impressive strategies to achieve sexual reproduction. These strategies have intrigued biologists and amateur naturalists at least since Christian Konrad Sprengel (1750–1816) first associated the variation in orchid flowers with the attraction of pollinators. Since Darwin's 1862 book, *The Various Contrivances by Which Orchids are Fertilized by Insects*, and especially in the past 50 years, a very large number of studies have revealed remarkable complexity and diversity in orchid–pollinator relationships. These studies comprise a vast literature currently scattered in numerous, often obscure, journals and books. *The Pollination Biology of North American Orchids* brings together, for the first time, a comprehensive treatment of this information for all native and introduced American orchids found north of Mexico and Florida. The book offers detailed descriptions and information on genetic compatibility, breeding systems, pollinators, pollination mechanisms, fruiting success, and limiting factors for each species. Distribution, habitat, and floral morphologies are also summarized. In addition, detailed line drawings emphasize orchids' reproductive organs and their adaptation to known pollinators. All drawings are by the author, sometimes based on the published work of others, as indicated. Areas where information is limited are noted, thus spotlighting topics in particular need of further research.

The Pollination Biology of North American Orchids will be of interest to both regional and international audiences including the following:

- Researchers and students in this field of study who are currently required to search through the scattered literature to obtain the information gathered here.
- Researchers and students in related fields with an interest in the coevolution of plants and insects.
- Conservation specialists who need to understand both the details of orchid reproduction and the identity of primary pollinators to properly manage the land for both.

- Orchid breeders who require accurate and current information on orchid breeding systems. The artificial cultivation and breeding of native orchids is an important conservation measure aimed at reducing and, hopefully, eliminating the collection and sale of wild orchids.
- General readers with an interest in orchid biology. Technical terminology is kept to a minimum, and the text includes an introduction to concepts and terminology (Chap. 1) supplemented by brief parenthetical explanations of terms where they first appear in later chapters. An extensive glossary is also provided for the non-specialist reader.

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Part I Subfamily Cypripedioideae (The Slipper Orchids)

Part II Subfamily Orchidoideae (Part One)

Chapter 1
Introduction

Abstract The morphology of the orchid flower and the strategies orchids employ to attract pollinators are described. The types of breeding systems found in North American orchids are introduced along with the concept of pollinator syndromes and functional groups.

Keywords Breeding system • Pollinator syndrome • Functional group • Deceit • Mimicry • Magnet species • Competition • Pollinator attraction • Floral morphology

Orchid flowers and their pollinators provide many examples of highly specialized relationships. The plants are often fertile across species and even generic boundaries, and selection for reproductive isolation has led to the evolution of novel floral morphologies and pollinator behaviors. Biologists have devoted much effort to untangling the interactions between these flowers and their pollen vectors. Field and laboratory studies have now disclosed much about the pollination process, the breeding system, and the factors that limit or otherwise influence fruiting success in many species. Before discussing these findings, however, it is necessary to provide a very brief introduction to the general morphology of the orchid flower and the terminology used to describe orchid breeding systems and reproductive strategies. The ideas introduced here will be considered more fully below as they relate to specific orchid taxa. Readers interested in a more detailed introductory treatment should consult Arditti (1992), Dressler (1993), and Pridgeon et al. (1999). Those seeking a critical assessment of current concepts and techniques should begin with Glover (2007).

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The Orchid Flower

Orchids are members of a large group of flowering plants known as monocotyledons. A basic feature of this group is the arrangement of flower parts in whorls of three. Although fundamentally true to this design, orchid flowers have diverged significantly from the basic monocot pattern. The extent and direction of this divergence can best be appreciated through a comparison of homologous floral parts in orchids and less specialized monocots. The basic pattern is evident in *Hypoxis*, a distant relative of the orchids. Here, all members of the perianth (the outer whorl of three sepals and the inner whorl of three petals) are alike in size, shape, and color (Figs. 1.1a and 1.2a). In contrast, the orchid perianth usually shows a high degree of differentiation. The dorsal sepal frequently differs from the others in size and shape and sometimes converges with the lateral sepals or petals to form a tube or bonnet of varying length (e.g. Figs. 9.1b and 12.1b). In others, such as the lady's-slippers (*Cypripedium*), the lateral sepals may partially or completely fuse with one another to form a single structure, the synsepal (Fig. 1.2b).

The median orchid petal, the lip or labellum, also typically differs markedly in size, shape, and often color from the other petals (Figs. 1.1b and 1.2b, c). Moreover, its orientation is often distinctive. In the early stages of flower development, it lies uppermost in erect inflorescences with the dorsal sepal positioned below, the customary orientation in monocots (as represented in Fig. 1.2b, c). But in mature orchids, it is usually lowermost in the flower (Fig. 1.1b). This position is usually achieved in North American orchids by a twisting of the flower stalk or ovary through an angle of 180°. The process is termed resupination, and the flower is said to be resupinate. In some species, rotation does not occur or proceeds through an angle of 360°, and such flowers are said to be non-resupinate.

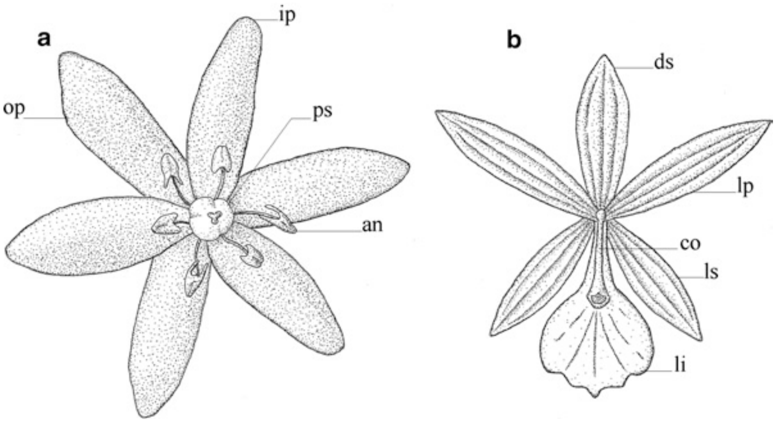

Fig. 1.1 (**a**) *Hypoxis* flower, (**b**) Generalized orchid flower. *an* anther, *co* column, *ds* dorsal sepal, *ip* inner perianth member (petal), *li* lip, *lp* lateral petal, *ls* lateral sepal. *op* outer perianth member (sepal), *ps* pistil

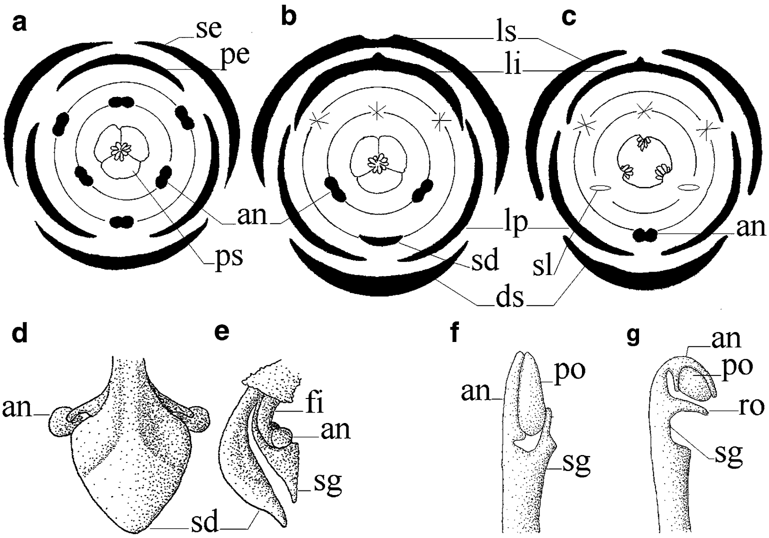

Fig. 1.2 (**a–c**) Floral diagrams. (**a**) *Hypoxis*; (**b**) Diandrous orchid; (**c**) Monandrous orchid; (**d**, **e**) Column of the diandrous orchid *Cypripedium fascicultum*. (**d**) Top view; (**e**) Side view. (**f**, **g**) Columns of monandrous orchids. (**f**) Erect anther, side view; (**g**) Incumbent anther, side view. *an* anther (spore producing part of stamen), *ds* dorsal sepal, *fi* filament (stalk of stamen), *li* lip, *lp* lateral petal, *ls* lateral sepal, *pe* perianth member, *ps* pistil, *po* pollinium, *ro* rostellum, *sd* staminodium, *se* sepal, *sg* stigmatic area, *sl* stelidia (small staminodia)

The most highly modified part of the orchid flower is a structure at its center called the column or gynostemium. The basic monocot pattern is represented as two whorls of three male organs, the stamens (bearing terminal sporangia or anthers). These surround a central female organ, the pistil (Figs. 1.1a and 1.2a). Alterations of this pattern in orchids include a reduction in the number of parts and a fusion of male and female components. In North American orchids, the column has either one or two functional anthers, and the orchids are accordingly said to be either monandrous or diandrous. The lady's-slippers (*Cypripedium*) are diandrous (Fig. 1.2b, d). The two lateral anthers of the inner whorl in the basic monocot pattern (Fig. 1.2a) are retained (Fig. 1.2b), and a median anther of the outer whorl is modified to form a prominent shield-like element called the staminodium (Fig. 1.2b, d, e). The remaining anthers may be fused with the column or may be lost (Darwin 1862). Other North American orchids are monandrous, retaining only a single fertile anther at the apex of the column (Fig. 1.2c, f, g). The retained anther is homologous with the median stamen of the outer whorl in *Hypoxis* (Fig. 1.2a) and the staminodium in *Cyripedium* (Fig. 1.2b). The two lateral stamens of the inner whorl are sometimes visible as small staminodes (horns, wings, stelidia, auricles) on the sides of the column (ellipses in Fig. 1.2c). As in diandrous orchids, rudiments of the remaining anthers may be variously incorporated into the structure of the column or lost altogether (see, e.g. Darwin 1862, Dressler 1993). The staminal or staminodial stalks, the filaments, are often united so completely with the pistil that the individual

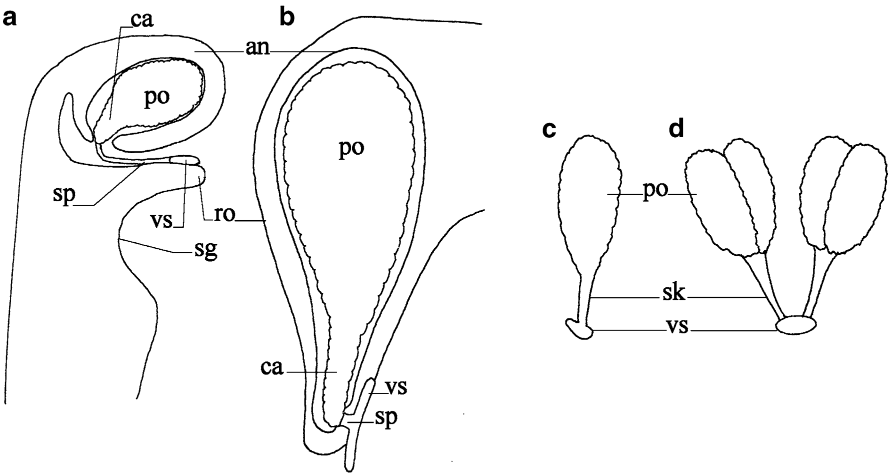

Fig. 1.3 (**a**, **b**) Columns, side view; (**c**, **d**) Pollinaria with one (**c**) and four (**d**) pollinia per viscidium. *an* anther, *ca* caudicle, *po* pollinium, *ro* rostellum, *sg* stigma, *sk* stalk, *sp* stipe, *vs* viscidium

components cannot be distinguished. However, in *Cypripedium* and some more advanced orchids such as *Spiranthes,* the union may be only partial (Fig. 1.2e) (Bonatti et al. 2006). The orchid stigma, a surface that receives the male gametophyte or pollen during pollination, is projected in *Cypripedium* (Fig. 1.2e) but is usually a shallow depression on the inner side of the column below and behind the anther in monandrous orchids (Fig. 1.2f, g). It is basically three-lobed although the lobes are fused and the median or dorsal lobe is often larger than the lateral lobes (Dressler 1993; Bonatti et al. 2006).

A morphologically variable structure that often forms a flap between the stigmatic surface and the anther is the rostellum (Fig. 1.2f, g). A number of functions have been attributed. Its positioning between the anther and stigma is thought to reduce or prevent accidental self-pollination. It may also display an adhesive surface, the viscidium (Fig. 1.3), which functions in sticking the pollen to a pollinator's body. In some cases, wounding of the rostellum during removal of the pollen also triggers ethylene evolution, which leads to senescence of the emasculated flowers (Avadhani et al. 1994). A viscidium is often reduced or absent in self-pollinating or primitive species such as *Cypripedium* or *Cephalanthera.*

The anther is essentially an elongated sac comprised of two to four locules or sporangia. This morphology is retained in primitive orchids but may be modified in advanced groups as, for example, the Epidendroideae, where the locules are sometimes transversely divided to produce eight pollen chambers. In other cases, the locules can be united in various ways or their development may be checked, leading to a reduction in their numbers and a reorientation of their partitions.

Anthers can be erect or incumbent (Fig. 1.2f, g). An erect anther is oriented parallel to the axis of the column and has the filament at its base as in many other monocots (Fig. 1.2f). This condition is considered relatively primitive and is found, for example, in many Orchidoideae. An incumbent anther is bent downward (Fig. 1.2g) and is associated with a more specialized pollination strategy. In some less specialized members of the Epidendroideae, the transition can be observed during ontogeny (development of the organ during floral maturation), the anther being erect in the young bud but bending downward 90–120° as development proceeds to maturity (Dressler 1981). The incumbent condition is modified in various ways in advanced members of the Epidendroideae (Dressler 1981).

The anthers of most orchids do not produce particulate pollen grains as in most flowering plants but discrete pollen masses called pollinia (Fig. 1.3). Pollinia can bear an extension or stalk called a caudicle. This extension differentiates within the anther and is comprised of the remains of aborted pollen mother cells and possibly pollen grains and the tapetum (a layer of tissue lining the inside of the anther locule) (Rasmussen 1986). An extension of the caudicle that is derived from columnar tissue outside the anther in some specialized orchids is termed a stipe (Fig. 1.3a, b). There are two kinds of stipe (Rasmussen 1986). One, the tegula, is a plate developed from the dorsal epidermis of the rostellum; the other, the hamulus, is derived from an upwardly curved, distal extension of the rostellar apex. The caudicle or the stipe, if present, is usually attached to a sticky pad, the aforementioned viscidium, formed by the rostellum (Fig. 1.3). An easily ruptured, sac-like membrane, the busicle, which keeps the viscidium fresh and sticky, may cover it. The entire structure, comprising pollinia, stalk, and viscidium, is called a pollinarium (pl. pollinaria) (Fig. 1.3a–d). In animal-vectored species that lack a viscidium, the pollen may attach directly to a sticky, stigmatic, or rostellar secretion, smeared onto the pollinator immediately prior to contact with the pollen.

In many orchids the basic structure of the anther with its four cells gives rise to the formation of four pollinia. In other orchids, the cells fuse in pairs resulting in a two-celled anther with two pollinia. However, pollinaria may include as few as one or as many as eight separate pollinia attached to a single viscidium (Fig. 1.3c, d). The flowers in many Orchideae produce two separate viscidia, each with a separate stalk and one or more pollinia.

Pollinia may be relatively uniform in structure or sectile. Sectile pollinia are comprised of numerous, small, loosely associated sub-compartments or packets of pollen, the massulae, within which pollen grains are variously interconnected (Zee et al. 1987; Dressler 1993). During pollination, individual massulae detatch from the pollinium and a number may be deposited on each of a series of successively visited stigmas. In most orchids the pollen grains derived from a single pollen mother cell do not separate following meiosis but are structurally united by a partially shared pollen wall to form a group of four called a tetrad. However, the pollen grains are shed singly (as monads) rather than as tetrads in the subfamily Cypripedioideae and either as monads or tetrads in the subfamily Vanilloideae, in the tribe Cranichideae of subfamily Orchidoideae, and in the tribe Neottieae of subfamily Epidendroideae.

The texture of pollinia may be granular (soft) or hard and waxy. Granular pollinia are characterized by numerous intercellular spaces among the pollen grains, and individual grains may have well developed pollen walls. A relatively high ratio of air to pollen wall surface refracts the light, and the pollinia appear more or less opaque. “Hard” pollinia have relatively little air space within the pollinium, and pollen walls are present only on the peripheral tetrads. Refraction is thus reduced and the pollinia appear translucent (Zavada 1990).

Pollen loads on individual stigmas can vary with the pollinator species, the size of the stigma, and other factors (Neiland and Wilcock 1995). However, very high loads, such as pollination with an entire pollinium, would routinely lead to much wastage of pollen: many massulae would fail to contact the stigma and would not germinate. Intermediate size loads, involving the deposition of a number of massulae rather than an entire pollinium, avoid this wastage while still providing high levels of pollen germination, maximum seed set, and some pollen tube competition to promote fitness among the progeny (e.g. Ottaviano et al. 1980; Neiland and Wilcock 1995).

The number of pollen grains produced and ovules or potential seeds contained in the ovary, the pollen to ovule (P:O) ratio, for massulate orchids such as *Platanthera*, *Galearis*, *Amerorchis*, and *Goodyera* is relatively low compared to outcrossing plants which do not have large pollen dispersal units. However, it is about double that seen in the Asclepiadaceae, which also have pollen grouped in pollinaria (Cruden 1977; Neiland and Wilcock 1995). In the latter, however, massulae are absent, and the entire pollinium is deposited into the stigmatic chamber. A low P:O ratio is therefore energetically efficient since a single pollinium cannot fertilize the ovules of more than one flower (Neiland and Wilcock 1995). In massulate orchids, on the other hand, where only a few massulae are usually deposited on any one stigma (e.g. Kevan et al. 1989; Neiland and Wilcock 1995), a higher P:O ratio increases the probability that a number of plants can be pollinated by pollen from the same pollinium (Neiland and Wilcock 1995).

Breeding Systems

Several breeding systems are present in North American orchids. Different breeding systems result in different levels of genetic recombination, a process that leads to offspring having different combinations of genes than their parents. This shuffling of genes is thought to have many advantages including an increase in adaptive potential and a reduction in the accumulation of deleterious genes. Many orchids are facultative and combine several breeding systems resulting in an increase in their reproductive versatility.

Self-Compatible Orchids

Self-compatible orchids are able to produce seed when a flower receives its own pollen or pollen from another flower on the same plant. If the pollen is transferred from the anther to the stigma within a flower without the mediation of a pollinator and pollination is followed by fertilization of the ovules, the flower is said to be automatically self-pollinated and autogamous. If the process occurs while the buds are still closed, the flower is cleistogamous. If pollen transfer from the anther of one flower to the stigma of another results in fertilization, the process is called geitonogamy when the two flowers are on the same plant, cross-pollination (xenogamy, allogamy, or outcrossing) when on separate plants, and hybridization when on separate species. The potential levels of recombination and variation in the offspring range from low in autogamy and geitonogamy to high in cross-pollination.

Self-Incompatible Orchids

Self-incompatible orchids only produce seed if they receive pollen from a different plant, and fertilization in such a plant is therefore obligately xenogamous. Some species may just experience a reduction in seed number or viability when selfed and are therefore partially self-incompatible. Self-incompatible and partially self-incompatible plants may also suffer a reduction in capsule set or seed viability when restricted pollen and seed dispersal result in closely spaced plants receiving pollen from genetically related neighbors, an occurrence called biparental inbreeding. Various mechanisms tend to reduce the incidence of selfing in self-incompatible or partially self-incompatible plants. These will be discussed in connection with the breeding systems of individual orchid species.

Agamospermy (Apomixis)

Agamospermous orchids produce seed asexually. The embryos are derived wholly from maternal tissues, and no sexual recombination is involved. Like other breeding systems, agamospermy may be facultative and associated with varying levels of sexual reproduction.

General Attraction of Pollinators

Sexual reproduction in orchids is often limited by the availability or activity of pollinators. North American orchids employ a number of strategies to increase visitation. These will be elaborated in the sections dealing with individual orchid taxa, but in our flora usually involve general rewards, unique rewards, or deception (van der Pijl and Dodson 1966). Many offer nectar as a reward. Nectar usually contains a nutritious mixture of glucose, fructose, and sucrose along with some less common sugars and other substances. Composition of the mixture may be more or less constant for a given species, and may, to some extent, reflect pollinator preferences (Cingle van der 1995). In addition to composition, nectar may vary in total sugar concentration as well as volume and time of secretion. Concentration and volume in a given orchid may vary with atmospheric pressure, relative humidity, and time of day.

Color, including ultraviolet, distinguishes flowers from their background and advertises a potential reward. Because the color vision of pollinators varies, flower color can be somewhat discriminating. Flower shape and fragrance also attract the attention of vectors. Flower color and shape provide long distance signals that insects can recognize (Kevan 1972). Floral fragrance can act either as a long or short distance advertisement, and in the latter case may prompt the pollinator to land and probe for nectar. Orchids may produce varying combinations of fragrant compounds, and these and their time of production may reflect a specific relationship between the orchid and its pollinator(s).

Some orchids provide no reward and attract pollinators by deceit. The mechanisms of deception include simulation of a food reward, mimicry of rewarding flowers, imitation of shelter or brood sites, rendezvous attraction, pseudoantagonism, and sexual deception. Non-rewarding flowers experience lower pollinator visitation rates and thus, lower levels of fruit and seed set. The evolution of deception has therefore proved to be something of an evolutionary puzzle. Since non-rewarding orchids comprise about one-third of all orchid species, it may be assumed, however, that this condition confers fitness advantages in some situations.

Two principal hypotheses have been advanced in an attempt to explain how deception could increase fitness. The first is that resources required for the production of a reward are limited and better reallocated to flower and seed production (Snow and Whigham 1989, Ackerman and Montalvo 1990). The second is that pollinators visit fewer flowers and spend less time on the inflorescences of non-rewarding plants, resulting in a decrease in geitonogamy and an increase in cross-pollination (Hodges 1981; Harder and Barrett 1995; Johnson and Nilsson 1999; Johnson et al. 2004). Other ideas have been proposed. Smithson and Gigord (2001), for example, in the study of a Mediterranean orchid, found that pollinaria were removed more frequently from nectarless plants. They argued that systems of deception evolved in response to a male function advantage. These hypotheses are reviewed in Jersakova et al. (2006) (see also Kropf and Renner 2008) and will be revisited below with reference to particular orchid species.

Not all the mechanisms of deception are found among North American orchids. Simulation of a food source (usually nectar but sometimes pollen) is the most common form of deceit in our flora and employs floral attractants, including flower shape, color, and scent, that pollinators associate with food. These may fit floral syndromes that typically attract a particular class of pollinators and may rely on newly emerged, inexperienced agents. Some pollinators are able to recognize scent more quickly than color (Bogdany 1978). Others may be more attuned to visual stimuli. Variation in floral odor or color might therefore function adaptively in reducing the rate at which the pollinators learn to recognize and avoid non-rewarding flowers (Ackerman 1986; Ackerman et al. 1997; Ferdy et al. 1998; Roy and Widmar

1999; but see Smithson et al. 2007). Variable flower color, for example, is sometimes associated with a lack of scent production, forcing the pollinator to rely on visual stimuli. However, variation, particularly in scent, can also occur in rewarding species, and the effect on the behavior of pollinators needs further study (Patt et al. 1989, Tollsten and Bergstrom 1989, Kaiser 1993).

Some deceptive orchids produce features that suggest a specific food source such as nectar guides or yellow hairs that simulate anthers or pseudonectaries (e.g. spurs) that produce no nectar (Gumbert and Kunze 2001, Galizia et al. 2005). Still others produce pheremones that elicit specific responses in the vector or structures, textures, and/or odors that suggest the presence of the vector's larval hosts. Characters may be differentially associated as part of an adaptive array to deceive the pollinator.

The flowers of deceitful orchids may also mimic the appearance of specific, sympatric flowers that provide a reward, and pollinators may visit the mimics by mistake. The subject of mimicry, as it applies to plants, remains controversial, and according to some workers, what appears to be mimicry represents an exploitation of evolved perceptual biases such as a pollinator's generalized preference for flowers of a certain size, shape, or color (Vereecken and Schiestl 2008, Schaefer and Ruxton 2009, but see Gumbert 2000). It seems difficult, however, to explain some forms of mimicry in these terms, as, for example, the evolution of flowers that attract male insects by simulating the appearance and odor (pheromones) of conspecific females.

It has also been debated whether either non-rewarding or rewarding plants occurring in a mixed population with other plant species that produce a reward are likely to experience improved pollination success as a result of an increase in the local abundance of potential pollinators, the so-called "magnet species effect" (Thomson 1978, Feinsinger 1987), or suffer reduced success as a result of increased competition for their services.

Johnson et al. (2003), for example, found significantly greater pollination success in Swedish plants of the non-rewarding orchid *Anacamptis morio* Bateman, Pridgeon, and M. W. Chase that were placed within clusters of nectar-producing plants compared to those placed outside such clusters (ca. 20 m away). The insects most likely to visit the orchid were those foraging on magnet species resembling the orchid in flower color and shape. When, as in this case, the orchid is a non-rewarding species, success generally requires that the magnet species be relatively more abundant than the mimic (Smithson and Macnair 1997, Ferdy et al. 1998, Johnson et al. 2003, cf Lammi and Kuitunen 1995). Smithson and Macnair (1997) and Ferdy et al. (1998) found that queen bumblebees quickly learned to avoid non-rewarding orchid flowers where they occurred in dense aggregations.

Interspecific facilitation of pollinators is also documented in mixed arrays of exclusively rewarding species. Duffy and Stout (2008), for example, found a positive relationship between the number of pollinator visits to the rewarding orchid, *Spiranthes romanzoffiana* Chamisso, and total floral density in mixed patches of this and other rewarding plants.

Where competition is a dominant factor, it might be to the advantage of the plant to bloom at another time or to grow at a remote site (Heinrich 1975, Boyden 1980, Nilsson 1980, Dafni 1984, Firmage and Cole 1988). Mosquin (1971) suggested that natural selection would favor the evolution of earlier or later blooming dates in plants forced to compete for pollinators with other species producing plentiful resources. The frequently occurring pattern of early spring blooming in food-deceptive orchids, for example, has been considered an adaptive shift to secure pollination by newly emerged, naïve insects before the appearance of later blooming, rewarding species (Nilsson 1980; Internicola et al. 2008; but see Ruxton and Schaefer 2009 and Sietvold et al. 2010). Staggered flowering patterns can, however, reflect phylogenetic constraints or timing of resource acquisition or seed dispersal rather than competition among plants for pollinators (Johnson 1992, Johnson et al. 2003).

Lammi and Kuitunen (1995) obtained experimental evidence consistent with the so-called "remote habitat effect." They found that the experimental addition of nectar-producing violet flowers to patches of the non-rewarding marsh orchid *Dactylorhiza incarnata* (L.) Soo reduced pollination success in the orchid, especially if the flower colors of the orchid and violet were a close match. However, in a similar experiment, Pellegrino et al. (2008) reported just the opposite. They set up patches of the non-rewarding orchid *Dactylorhiza sambucina* (L.) Soo and *Viola aethnensis* Parl. and found that competition only occurred when different color morphs were paired. When the color morphs of the orchid and violet were matched, the orchid appeared to benefit from the co-occurrence of the violet through floral mimicry and/or the magnet species effect, just as in the *Anacamptis morio* study. Internicola et al. (2007) obtained similar results using artificial flowers.

Competition and facilitation probably represent opposite ends of a continuum. The magnet effect might facilitate pollination at one time in a particular habitat, while earlier or later in the flowering season or at other sites with variable population densities and/or different plant species competition may predominate. Facilitation might, of course, also give rise to increased competition among members of the same species, leading to maximum seed set by those plants with the most attractive flowers.

Foraging insects only visit nonrewarding orchids or orchids in mixed arrays intermittently (Rathcke 1983; Stout et al. 1998). Such behavior can lead to reproductive interference, where the stigma may become clogged with heterospecific pollen, and pollen may be wasted through export to heterospecific stigmas (Free 1968, Waser 1983). This can be significant, but with regard to pollen receipt, orchid stigmas are wide and except for the introduction of pollinia from other orchid species, may be less likely than many other plants to suffer a lowering of reproductive success based on stigma contamination (Harder and Thomson 1989, Johnson and Edwards 2000).

The size of the plant population, the density of plants within the population, and the size of the inflorescence may also influence the attraction of pollinators. Studies that have investigated the impact of these variables on visitation rates and sexual reproduction in orchids have produced varying results. Once again, these will be considered below for individual orchid species.

Pollinator Syndromes in North American Orchids

Orchid flowers exhibit a complex of characters that tend to reflect adaptation to the morphology and behavior of their primary pollinator(s). The assumption is that co-evolution has led to the development of particular floral features that enhance the probability of attracting and exchanging pollen with certain pollinators or groups of pollinators. Differential combinations of floral characters are sometimes used to establish pollination classes or syndromes (Delpino 1868–1874, Faegri and van der Pijl 1971). The borders of the syndromes are not clearly demarcated, and a number of orchids attract a variety of visitors. In fact, Waser et al. (1996) and Waser and Ollerton (2006) believe that pollinator generalization may be the rule in the majority of plant–pollinator systems because variation in pollinator visitation levels and efficiency restrict the degree to which plants are able to specialize on single pollinators. Rather than focusing on single pollinators, however, Fenster et al. (2009) examined the effect of what they called functional groups (e.g. long-tongued bees, nocturnal moths etc.) and reported that about 75% of the plants they considered were adapted to a single functional group, sometimes including over 25 different species. They considered that it is the general morphological and behavioral characters of the functional group, rather than a particular pollinator species or taxonomic group, that exert selective pressure on floral evolution. If most flowers are adapted to functional groups, pollination syndromes have the potential to reflect, in a general way, a suite of reciprocal adaptations between the flowers and their pollinators. In addition to characteristics that attract certain pollinators, syndromes may also include features that exclude non-pollinating visitors. The following summary of pollinator syndromes is based largely on the classic works of van der Pijl and Dodson (1966) and Faegri and van der Pijl (1971).

Bee-Pollinated Orchids

Flowers that are primarily adapted to bee- or wasp-pollination are said to be melittophilous. About 60% of orchids fall into this category. Bee flowers typically have a well-developed landing platform with nectar guides or marks of contrasting color pointing the way to the nectary. The latter may or may not contain nectar. When present, the nectar occurs in moderate amounts and is usually more or less concealed. In some cases, the nectar guides reflect only ultraviolet light and are invisible to the human eye. The bee's visual spectrum is shifted toward the shorter wavelengths. Thus, it perceives ultraviolet as well as violet, blue, green, and yellow, but not red or orange, and bee flowers, usually brightly colored, appear to us to be blue, green, yellow, or white. However, some red or pink flowers contain ultra-violet absorbing pigments, which make them more attractive to bees. Bee flowers are open during the day, emit fresh and sweet odors, are often funnel or gullet shaped, and tend to be oriented horizontally. Pseudo-pollen may be present. Bee pollinators include both long- and short-tongued species, and nectar may accordingly be present in shallow or deep receptacles.

Moth-Pollinated Orchids

Two moth pollination syndromes are recognized: phalaenophily or pollination by moths that often land on the flowers (Geometridae, Noctuidae and related families), and sphingophily or pollination by hawkmoths (Sphingidae) that hover in front of the flower. Flowers may be diurnal but are often crepuscular or nocturnal. Both moth groups are often attracted to horizontal or hanging, whitish to pale green, tubular flowers, with hawkmoths showing a preference for fringed perianth parts, and diurnal members, purple or purplish-pink colors (Hapeman and Inoue 1997). Landing platforms are absent in hawkmoth-pollinated orchids but may be present in some others. Ample supplies of nectar are produced and concealed in deep, narrow spurs in hawkmoth flowers or moderately deep spurs in flowers pollinated by shorter-tongued moths. Nectar guides are absent. Floral shape or sometimes grooves acting as mechanical tongue-guides may assist the pollinator's search for nectar. Both flower types usually produce a musky-sweet or vegetable-like odor, stronger in hawkmoth flowers.

Butterfly-Pollinated Orchids

This pollination syndrome is called psychophily. Butterfly- and skipper-pollinated flowers are usually erect and sometimes have a horizontal landing platform. Open during the day, they are often bright red, orange, yellow or blue, and nectar guides may be present. Fragrances are sweet, but generally not as strong as in moth-pollinated flowers. Nectar is often produced and is typically concealed in a deep, narrow spur.

Fly-Pollinated Orchids

Several types of fly pollination are known. Flowers adapted to most flies (e.g. the families Syrphidae (hover or flower flies), Bombylidae (bee flies), some Tachinidae (a large and diverse group of true flies) and Culicidae (mosquitoes)) are called myophilous. They vary in color from yellow or green to sometimes purple in keeping with the variable color vision of fly species. The perianth segments are often fringed, and horizontal landing platforms are present in some. Such flowers frequently attract bees, butterflies, and beetles as well as flies. When present, nectar is usually available in easily accessible or superficial nectaries, although some bee flies, for example, may have proboscises approaching 10 mm in length permitting them to reach more deeply hidden nectar. Nectar guides are present or absent. Flowers may be open day or night, and floral odors vary from sweet to unpleasant.

Flowers adapted to carrion flies (family Calliphoridae) and dung flies (family Scathophagidae) are called sapromyophilous. They imitate the odor and appearance of decaying substances, are purple–brown or greenish in color, and are open either day or night. Nectar guides and usually nectar are absent. Some authors distinguish a form of sapromyophily known as mycetomyophily where the flowers mimic fungi, the natural food or substrate for egg deposition of certain flies or their prey.

Bird-Pollinated Orchids

Bird pollination (ornithophily) has been reported in a few North American orchids. The vectors are hummingbirds, and the flowers are more or less tubular, horizontal or freely hanging, and often bright red or orange and odorless. Nectar guides are absent. Flowers are open during the day and produce abundant nectar in medium long, relatively wide spurs with damage-resistant walls. Since hummingbirds generally hover in front of flowers while feeding, a landing platform is not present.

Beetle-Pollinated Orchids

Some North American orchids are pollinated, in part, by beetles (cantharophily). In general, beetle flowers have readily accessible nectar and often produce a distinct, sometimes fruity odor. Flowers may open day or night. Although their color is often described as dull, some flowers copollinated by beetles are very showy.

Orchid Classification

Interested readers will find the history and theory of orchid classification and phylogeny well summarized in a number of sources including, for example, Arditti (1992), Dressler (1993), and Pridgeon et al. (1999). The present treatment generally follows the arrangement of orchid taxa published in *Genera Orchidacearum* (Pridgeon et al. 1999, 2001, 2003, 2005, 2009).

Orchid names follow the *Flora of North America* and/or *Kew's Checklist of Monocotyledons*. Where these differ, the choice made is clearly noted. Some insect names used by a cited author are no longer valid. In such cases, both the valid name and the outdated name are given.

Additional Topics

A number of additional topics including, for example, the evolution of autogamy and agamospermy, male and female fitness and function, the development or retention of deceptive pollination, evolutionary stable reproductive strategies, and factors influencing reproductive effort are briefly discussed in this work only as they may pertain to selected orchid taxa. An extensive literature is available on each of these subjects, and a full review lies beyond the scope of the present book.

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Part I

Subfamily Cypripedioideae (The Slipper Orchids)

The slipper orchids comprise a natural (monophyletic) group, sharing a shield-shaped staminode, two fertile anthers, and a sac-shaped lip (Figs. 1.2d, e and 2.1a). Their distinctness is evidenced by the fact that they are sometimes placed in a family of their own, the Cypripediaceae. Included are 5 monophyletic genera and about 180 species distributed from temperate Eurasia to the Asian tropics, Australia, and the Americas. One genus along with 12 of approximately 47 Eurasian and American species occurs in our flora.

Chapter 2
Cypripedium L. (The Lady's-Slippers), Introduction

Abstract Pollination mechanics, floral attraction, and pollinator behavior are described for the non-rewarding genus *Cypripedium*. The flowers are of a type known as trap blossoms. To obtain their release, traped insects are forced to follow a prescribed sequence of behaviors that lead to pollination of the flower. Insects, usually bees, are attracted by deception based on a false promise of reward, mimicry, or an instinctual response to pheromone-like secretions. Reproductive isolation is critically related to the size of the entrance and especially the diameter of the anther exit hole and the space between the labellar floor and the stigma.

Keywords *Cypripedium* • Trap blossom • Pollinator deceit • Naïve pollinators • Food deception • Pheromones • Reproductive isolation

Among the differences that distinguish the Cypripedioideae from other North American orchids, the most conspicuous is probably the deeply saccate lip of the flowers from which the plants take their common name. This lip or labellum plays a critical role in the pollination of *Cypripedium.* All species of this genus have resupinate flowers of a type known as trap or semi-trap blossoms (van der Pijl and Dodson 1966; Dressler 1981). The flowers temporarily imprison their insect pollinators and force them to follow a prescribed sequence of behaviors in order to obtain their release. An insect of the appropriate size, usually a bee, enters the lip through the obvious large opening or mouth at its top (Fig. 2.1). The lip's slippery inner surface and in-folded margins are often said to prevent it from leaving by the same route (e.g. Summerhayes 1951; Proctor and Yeo 1972). Knoll (1922) and Daumann (1968), however, have shown that bees are unable to exit the lip of the European *C. calceolus* L. even after the in-folded margins are cut away. Bees sometimes escape by chewing through the labellum (Guignard 1886; Stoutamire 1971), but most find a different way out. A foothold is provided by tightly packed hairs (trichomes) on the bottom of the lip (Ziegenspeck 1936; Summerhayes 1951; Stoutamire 1967; Proctor and Yeo 1972). These lead up a pathway ("haarstrassen")

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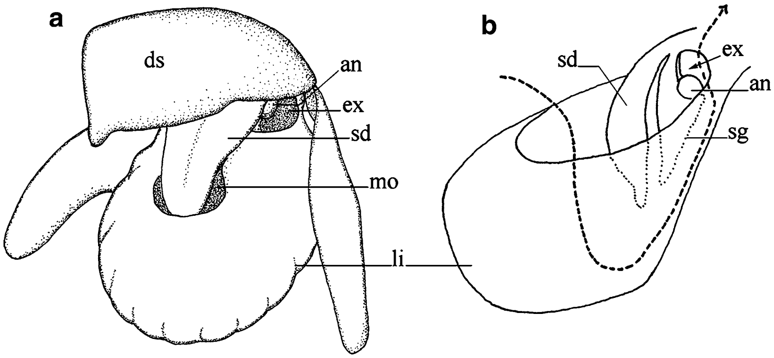

Fig. 2.1 *Cypripedium* flower. (**a**) Oblique view; (**b**) Partial section of lip and column showing route of pollinator through the flower. *an* anther, *ds* dorsal sepal, *ex* exit hole, *li* lip, *mo* mouth, *sd* staminodium, *sg* stigma

toward exit holes at the base or heel of the slipper (Fig. 2.1a, b). The escaping bee may also be attracted along this path by colored lines (false nectar guides) on the lip's inner surface (Arzt 1954) and by light coming from the exit holes or, in some species, from translucent areas ("light windows") in the side of the lip near its base (Webster 1886; Troll 1951; Faegri and van der Pijl 1971). Nilsson (1979) considered evidence for such phototactic behavior to be inconclusive, but Daumann (1968) reported that although bees were well able to find their way out when these "windows" were covered, light gradients were a definite orienting factor. It thus took a bee an average of 11 min to escape the labellum of *C. calceolus* under natural light conditions, but only 2 or 3 min when an external light source was focused on the base of the labellum. When the light was focused on the apex, the time was increased to 30 min.

Nilsson (1981) believes that the hairs inside the labellum may have an additional function. Droplets of oil that are present on their distal tips could absorb body odors (pheromones) from visiting bees and these odors could serve to attract additional pollinators (see below). Because the hairs are strongly light refractive, Ziegenspeck (1936) speculated that they might also stimulate a phototactic response complementing that of the light coming from the base of the labellum.

In its escape the bee must pass two points where the passageway is narrowed. At the first of these it is forced to squeeze under and rub its back against the surface of the stigma (Fig. 2.1b) (e.g. Stoutamire 1967). The stigma in most species is covered by minute, sharp-pointed papillae. These are directed forward and effectively brush the pollen off the insect's back as it passes. The stigma also provides leverage that allows the bee to push down on and slightly depress the labellum, which is elastically hinged to the ovary. The passageway is thus enlarged and can to some extent accommodate variation in the size of the pollinator. (e.g. Wright 1975; Nilsson 1979). Ziegenspeck (1936) considered that an additional function of the basal trichomes might be to reduce friction between the base of the labellum and the insect at this point.

The second narrow passage is the exit hole itself. One exit hole is located on either side of the base of the flower (Fig. 2.1a, b). An anther is so positioned beside each exit that a bee of the proper size cannot force its way out without contacting the anther and carrying away a mass of pollen on the dorsal surface of its thorax (van der Pijl and Dodson 1966; Stoutamire 1967). The pollen itself is sticky, and the non-sectile pollen mass lacks both a viscidium and a stalk. Since the bee contacts the stigma before the anther and usually does not reverse directions, it does not ordinarily transfer pollen to the stigma of the same flower. Rather, pollination is effected when and if the bee, upon escaping from the first flower, is subsequently trapped again, usually in a different flower, and the escape process repeated.

Individual bees do, in fact, frequently visit several flowers in succession (Kipping 1971; Nilsson 1979). Davis (1986), for example, observed five bumblebees follow the prescribed course of entry and exit from flowers of *C. acaule* Ait at a site in Massachusetts. Two were carrying pollen masses on their thoraxes when they entered the flower, and each deposited the pollen on the stigmas. In a study of this orchid in Nova Scotia, O'Connell and Johnston (1998) found a greater than 90% correlation in male and female reproductive success. In other words, over 90% of the flowers that had a pollen mass removed also received one. Visitation rates were low, but once removed, pollen had a 36–51% chance of being transferred to the stigma of another flower. These and similar observations in other lady's-slippers seem to refute the contention that once having endured the ordeals of entrapment and the subsequent lack of reward (see below), bees avoid repeating the experience (Webster 1886; Baxter 1889; cf Gill 1989). Gill (1989, 1996) reported that most pollinator visits occurred during the first few days of the flowering season, perhaps before the bees learned to reject *Cypripedium* flowers.

Although the pollination mechanism promotes cross-pollination, *Cypripedium* reproduces vegetatively, and some transfer of pollen among members of a single clone undoubtedly occurs (Proctor et al. 1996). In addition, a flowering period with two or more simultaneously open flowers on each plant in some cases provides ample opportunity for pollen transfer among flowers of the same inflorescence.

Biologists are uncertain just why bees enter the flowers in the first place. Sometimes the entry is inadvertent. The bees, exploring the outer surface of the lip, tumble into the trap. This has been associated with an inflected rim near the staminodium, the so-called sliding zone (Nilsson 1981). In other cases, entry appears quite deliberate (e.g. Nilsson 1981). Daumann (1968) believes that insects may collect oil from the hairs on the inside of the lip. This has yet to be confirmed. It has also been conjectured that small amounts of nectar are present or that the bees feed on the hairs in the labellum (Stoutamire 1967; Nilsson 1979 and references therein), but according to Ziegenspeck (1936) and Daumann (1968), the hairs are not eaten. It now appears likely that the flower provides no food, and the insects are simply deceived by false nectar guides and the color and odor of the blossoms, which promise nectar or other rewards where none is available (Nilsson 1979). In addition, the staminodium, which projects into the labellum (Figs. 2.1a and 4.1a), is often bright yellow in color with contrasting spots and may appear to be a source of pollen (Vogt 1990).

The possibility that the flowers of some North American species of *Cypripedium* mimic flowers of other, more abundant species that offer a reward must also be considered. Pollinators might then confuse the flowers of *Cypripedium* with those of the rewarding species and visit them by mistake. Sugiura et al. (2002), for example, provided evidence for such a case of floral mimicry involving the Japanese lady-slipper, *C. macranthus* Sw. (as *C. m.* var. *rebunense* (Kudo) Miyabe and Kudo) and a rewarding species, *Pedicularis schistostegia* Vved. (Orobanchaceae).

Fruiting success in *Cypripedium* and other orchids that offer no reward is consistently much lower than in orchids that provide nectar or which mimic plants that do (e.g. Gill 1989; Larson and Larson 1990). Stoutamire (1971) believes that bees learn by experience which flowers offer the best food source and will come to avoid those that offer no reward at all. According to this view, seed production in the lady's-slippers may be dependent upon naïve or possibly "forgetful" pollinators, insects that are newly hatched, new to the area, or shifting from a depleted to a new food source (Delpino 1874; van der Pijl 1966; Dressler 1981; Ackerman 1986). On the other hand, Johnson et al. (2003), in a study on the island of Oland off the coast of Sweden, found that bumblebees already carrying pollen of the non-rewarding orchid *Anacamptis morio* (L.) R. M. Bateman were more likely to visit this orchid than bees carrying no pollen. Inexperienced bees here were therefore not more likely to act as pollinators of a generalized, food deceptive orchid than experienced bees.

Nilsson (1979) contends that, in addition to general food deception, the floral attractants in the European *C. calceolus* are attuned to other instinctive responses in bees and that very little learning is involved. The floral fragrance has an uncommon composition. In addition to a monoterpene alcohol called linalool, which may elicit a feeding response, it contains acetates and alpha-farnesene. The acetates are found in cephalic (from the head) pheromone secretions of *Andrena* Fabricius bees, and farnesene is a component of the abdominal Dufour gland in female Andrenas (Bergstrom and Tengo 1974; Tengo and Bergstrom 1977; Nilsson 1979). Pheromones are used to odor-mark objects, which then attract bees of the same species. The cephalic hormones draw females and may cause the aggregation of males (Tengo and Bergstrom 1977). Farnesene is found as a lining in the nest and also signals the location of the nest site (Bergstrom and Tengo 1974). According to Butler (1965), females of *Andrena flavipes* Panzer deposit farnesene in the soil surrounding the nest site, and the odor provokes instinctive landing responses in both sexes. The opening in the labellum may mimic the opening of the nest tunnel (Catling and Catling 1991). In addition, as already noted, the hairs within the labellum may absorb pheromones directly from visiting bees as a supplement to the artificial pheromones produced by the orchid (Nilsson 1979).

A survey of nine species of *Cypripedium* in North America, however, found that most differ substantially from *C. calceolus* in their fragrance components (Bergstrom et al. 1992; Barkman et al. 1997). Since pheromone profiles can differ intragenerically among pollinators (Tengo 1979), correlation between differences in fragrance chemistry and primary pollinator species would not be surprising. A varying blend of odor constituents may have evolved to stimulate an instinctive or learned pattern of response on the part of a range of pollinators to food, sexual reproduction, or nest location (Nilsson 1979; Gregg 1983; Vereecken and McNeil 2010).

Reproductive isolation in *Cypripedium* is critically related to the size of the flower: the width of the entrance and especially the diameter of the anther exit holes and the space between the labellar floor and the stigma determine the size of the insect involved in the pollination (Stoutamire 1967; Catling and Knerer 1980). The dorsal-ventral thickness of the insect's thorax appears to be of particular importance. In addition, Nilsson (1981) noted that the depth of the labellum in the European *C. calceolus* must exceed the length of the pollinating bee by a minimum of 3–4 mm or the bee can simply crawl back out through the labellar opening. All of these floral characters are clearly under strong selection pressure in relation to the primary pollen vectors.

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Chapter 3
Section Acaulia

Abstract Section Acaulia is monotypic and based on *Cypripedium acaule.* Although self-compatible, this species reproduces primarily by outcrossing and is pollinated by several species of bumblebee queens. However, visitation rates are low, and comparison of open pollinated and hand pollinated plants indicates that pollinator activity limits fruit and seed production. In *C. acaule* a long-lived perianth, both before and after pollination; a long period of stigma receptivity; and long pollen life compensate for pollinator limitation and maximize sexual reproduction and total fitness through an enhancement of both male and female functions. The implications of pollinator versus resource limitation on long-term evolutionary strategies are discussed.

Keywords *Cypripedium acaule* • Pollinator limitation • Resource limitation • Evolutionary equilibrium • Lifetime fecundity • Reproductive strategies • Seedling recruitment • Male and female fitness • Bumblebees

Section Acaulia is monotypic and restricted to North America.

Cypripedium acaule Aiton (Pink or Stemless Lady's-Slipper)

Distribution and Habitat

Cypripedium acaule is usually found on well-aerated, strongly acidic soils rich in humus. It may occur in a variety of habitats ranging from mixed coniferous-deciduous forest to brushy barrens and wet sphagnum bogs. Although often growing in moderate shade, pollinator visitation, reproductive performance, and population recruitment and growth are all positively related to the amount of sunlight received (Gill 1996). It is distributed across Canada from Newfoundland to Alberta south to

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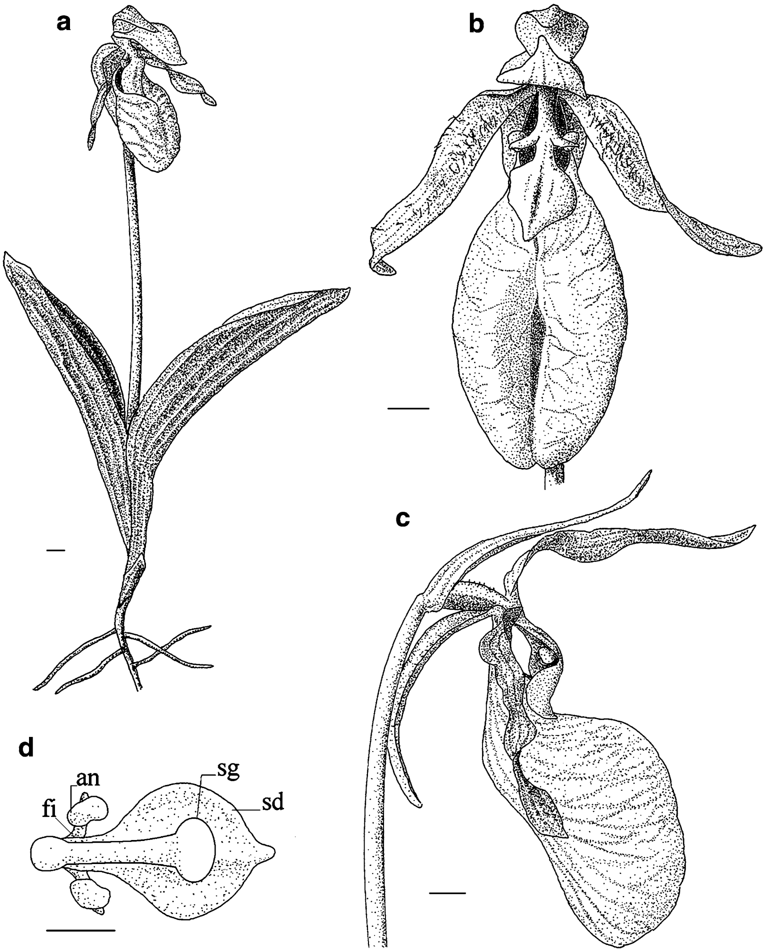

Fig. 3.1 *Cypripedium acaule*. (**a**) Habit, scale bar = 10 mm; (**b**) Flower, front view, scale bar = 5 mm; (**c**) Flower, side view, scale bar = 5 mm; (**d**) column, bottom view, scale bar = 5 mm. *an* anther, *fi* filament, *sd* staminodium, *sg* stigma

Minnesota and Alabama, with a disjunct population in the Northwest Territories (Gill 1996; Cribb 1997; Sheviak 2002).

Floral Morphology

A single flower with a disproportionately large, bladder-like and pendant labellum is produced on a short scape from a pair of basal leaves (Fig. 3.1a) (Luer 1975; Gill 1989; Cribb 1997). Flower height is highly variable (Table 3.1) and in some populations, positively correlated with male, female, and total reproductive success (O'Connell and Johnston 1998). The labellum is magenta to rarely white with

Table 3.1 Data on section acaule Sheviak (2002a)

Character	*C. acaule*
Plant height (cm)	15–61
Flower number	1
Dorsal sepal (mm)	9–52 × 5–22
Lateral sepals (mm)	17–49 × 6–25
Lateral petals (mm)	24–60 × 4–17
Lip length (mm)	30–67
Chromosomes (2n)	20

parallel ridges on either side of a longitudinal, usually closed slit running the length of the lip (Fig. 3.1b) (Sheviak 2002). A pollinator must deliberately force the edges of the slit apart in order to enter, with the opening then closing behind it (Wright 1975). Although labellar length, as a measure of flower size, is positively correlated with plant height, it is negatively associated with reproductive success. The most successful plants combined the advantage of greater height with a smaller labellum. It is possible that smaller flowers improve chances that a pollinator will brush against the anther and stigma with sufficient force to ensure pollen transfer (O'Connell and Johnston 1998). The stigma is sticky and grooved rather than simply papillate as in other species of *Cypripedium* (Luer 1975; Cochran 1986), and the pollen is less sticky and somewhat granular (Gray 1862). Largest among the lady-slippers, the exit holes measure 9.2 (7–11) mm in height and 6.0 (5–8) mm in width, while the distance between the floor of the labellum and the stigma averages 7.2 (6–9) mm. The staminodium (Fig. 3.1b, d) is ovate and green to purple. The lateral petals are deflexed to slightly spreading, more or less twisted, and vary in color from yellow–green to reddish–brown (Fig. 3.1b, c). The sepals are colored like the petals, and the laterals are connate behind the lip (Fig. 3.1c). Stoutamire (1967, 1971) reported that the sepals and petals, along with the lip, produce a sweet odor, which can be detected 5–8 cm away from the flower. Long distance attraction is visual and is related to reflectance of ultraviolet and blue–violet by the labellum and staminodium (Wright 1975). According to Light (2005b), *C. acaule* may occur in groups of 100 or more, and mass blooming may enhance pollinator attraction. The flowers bloom for about 3 weeks but senesce in less than six days when pollinated. Plants may experience periods of subterranean dormancy lasting 1–5 years (Gill 1989).

Compatibility and Breeding System

Outcrossing is the primary mode of reproduction (Stoutamire 1967; Davis 1986). However, the plants are self compatible, and unlike the pollen vectors of most other lady's-slippers, those that pollinate *C. acaule* have been observed to reverse direction after reaching the anther, causing self-pollination (Macior 1974; Wright 1975; Dieringer 1982; Davis 1986). Inbreeding depression appears to be absent: Gill (1996) observed no difference in seed germination (or protocorm growth) between seeds obtained from experimentally self-pollinated or distantly outcrossed flowers. Intrafloral self-pollination in the absence of a pollinator (autogamy) and asexual seed production (agamospermy) are absent (Newhouse in Davis 1986).

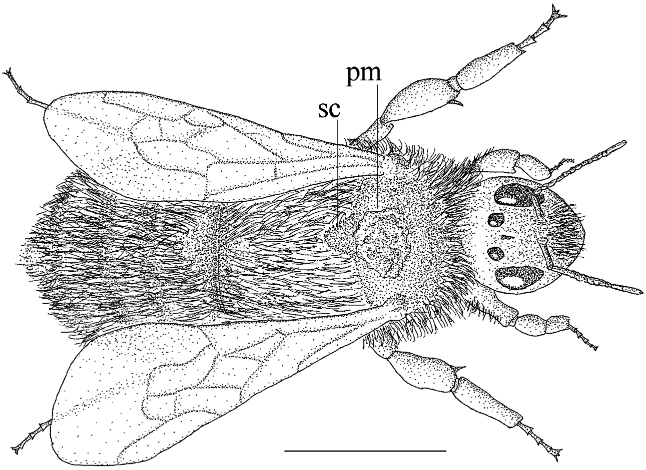

Fig. 3.2 Bumblebee with pollen mass of *Cypripedium acaule* on its dorsal thorax, scale bar = 5 mm. *pm* pollen mass, *sc* scutellum

Pollinators and Pollination Mechanism

This orchid is pollinated chiefly by bumblebee queens (*Bombus* Latreille) (Fig. 3.2) in the spring prior to the emergence of the workers (Stoutamire 1971), a time of the year when pollinators are usually competing for nectar (e.g. Cochran 1986). In a study in Nova Scotia, O'Connell and Johnston (1998) found the number of bumblebees and the pollination rates to be highest in habitats with an open canopy and many blooming ericaceous shrubs, particularly blueberries. In fact, pollination success was more closely related to environmental conditions than to plant characters such as opening bloom date, stem and flower height, and labellum length. Davis (1986) also found a positive correlation between the number of bumblebee visits to *C. acaule* and the presence of blooming ericaeous shrubs in Massachussetts.

Bombus vagans Smith was identified as a pollinator in Michigan (Stoutamire 1967, 1971) and queens of this species have also been collected carrying pollen of *C. acaule* in New Brunswick and Ohio (Table 3.2) (Wright 1975; Plowright et al. 1980; Barrett and Helenurm 1987). In addition, examination of bumblebees in the collection at Michigan State University disclosed the apparent presence of the pollen on several specimens of *Bombus borealis* Kirby (Stoutamire 1967).

Wright (1975) and Davis (1986) also observed four species of *Bombus* queens and two species of *Psithyrus* Lepeltier (now = *Bombus*) traverse the labellum and remove pollen in Ohio and Massachussets (Table 3.2). The average height and width of the thorax in the species of *Bombus* and *Psithyrus* were 11.1 (7.0–13.0) mm and 9.9 (9.0–11.0) mm, respectively (Wright 1975). The relative sizes of the exit holes and the bees permitted the bees to escape, but with sufficient difficulty to insure contact between the thorax and the anther. Similarly, the hinge construction of the labellum allowed the bees to force their way beneath the stigma, while the opposing

Table 3.2 Insects collected bearing pollen of *Cypripedium acaule*

Species	Caste	Locality	Author
Bombus borealis Kirby	? Female	MI	Stoutamire (1967)
B. impatiens Cresson	Queen	OH	Wright (1975)
B. nevadensis auricomus	Queen	OH	Wright (1975)
			Robinson
B. pennsylvanicus (DeGeer)	Queen	OH	Wright (1975)
B. vagans Smith	Queen	NB	Barrett and Helenurm (1987)
B. vagans	Queen	NB	Plowright et al. (1980)
B. vagans	? Female	MI	Stoutamire (1967, 1971)
B. vagans	Queen	OH	Wright (1975)
B. sp.	Queen	MA	Davis (1986)
Psithyrus ashtoni (Cresson)[a]	Queen	MA	Davis (1986)
P. fernaldae (Franklin)[b]	Female	OH	Wright (1975)
Xenoglossodes sp. Ashmead[c]	Female	OH	Wright (1975)

[a] *Bombus ashtonii* (Cresson)
[b] *Bombus fernaldae* (Franklin)
[c] *Tetraloniella* Asgmead

pressure of the labellar hinge assured contact between the stigma and the dorsal thorax of the bees. A female leaf-cutter bee (*Xenoglossodes* Ashmead sp., now *Tetraloniella* Ashmead) although smaller than the exit hole with a thorax averaging 5 mm in height and width, also removed pollen. However, the mean distance between the labellar floor and the stigma exceeded the height of this bee by several millimeters, and Wright (1975) did not consider it an effective pollinator.

Bombus species leave a deposit from their labial glands on flowers they visit (Light 2005b). They can therefore recognize flowers previously explored by other bumblebees. This may account for the frequent landing and immediate departure often seen in bumblebee foraging. The deposit apparently only persists for a limited time, and flowers may be revisited after a day or so.

The primary dependence of a *Cypripedium* on bumblebee queens for pollination is unusual, having been reported elsewhere only for *C. macranthos* Sw. (as *C. m.* var. *rebunense* (Kudo) Miyabe and Kudo) in Japan (Wright 1975; Sugiura et al. 2001). According to Light (2005b), workers also pollinate *C. acaule*, particularly in southern populations. Although its flowers are generally thought to provide no reward, Light (2005a) found pollen of this species in the corbiculae of bumblebees. The pollen may therefore sometimes end up as a component of "bee bread," a food resource for the bee.

Fruiting Success and Limiting Factors

Fruiting success can be limited by a number of factors including the amount and quality of pollen transferred and the quantity of resources (carbohydrate reserves, minerals, water) available for allocation to capsule and seed maturation (Charlesworth and Charlesworth 1987; Sutherland 1987). In orchids requiring an external pollinator, low levels of pollinator availability or activity are often assumed if a significant increase in fruit set is observed among flowers that are hand pollinated compared to those that are left to be pollinated naturally (open pollinated) (Burd 1994, but see Ashman et al. 2004).

Pollen quality is not known to be limiting in *C. acaule*, but pollinator visits are infrequent (e.g. Plowright et al. 1980; Barrett and Helenurm 1987; Gill 1989); in some studies less than 30% of the pollen masses were removed or flowers pollinated or fruit set under natural conditions (Wright 1975; Plowright et al. 1980; Cochran 1986; Davis 1986; Gill 1989, 1996; Gill and Stoutamire 1990; Primack and Hall 1990; Primack et al. 1994; Primack 1996; O'Connell and Johnston 1998). On the other hand, artificial pollinations produced high fruit-set in selfed and cross-pollinated flowers (70–100%; Wright 1975; Cochran 1986; Davis 1986; Barrett and Helenurm 1987; Gill 1989; Gill and Stoutamire 1990; O'Connell and Johnston 1998; Primack and Stacy 1998). *Cypripedium acaule* is therefore highly fertile, and even though supplementary resources might have further enhanced fecundity in these plants (e.g. Campbell and Halama 1993; Brunet 1996; Tremblay et al. 2005), short-term seed production appears to be limited by the effective activity or availability of pollinators rather than a shortage of resources (e.g. Cochran 1986).

Although similar results have been reported in other deceptive, non-rewarding orchids (e.g. Plowright et al. 1980; Dafni 1984; Davis 1986; Barrett and Helenurm 1987; Gill 1989; Primack and Hall 1990; Nilsson 1992), many authors consider pollinator limitation to be an unstable evolutionary state. Resource- and pollen-limitation have different evolutionary implications. A limitation of resources leads to competition among plants for male success and consequent selection on traits that influence the dispersal of pollen. A limitation of pollen leads to selection of traits that enhance pollen receipt (Johnston 1991a, b). According to Haig and Westoby (1988), theory predicts that the effect of these opposing selective forces should produce a balance between resource and pollen limitation. Equilibrium would be expected to evolve as an evolutionarily stable state with individuals experiencing temporary yearly shifts in the balance to accommodate changes in environmental factors. Strategies that increase pollen receipt in pollen-limited species should be favored and should spread through the population (e.g. Cole 1954; Williams 1966; Lloyd 1980a, b; Charnov 1982; Haig and Westoby 1988; Charlesworth 1989; Johnston 1991a, b; Waser and Jones 1991).

A number of strategies have been proposed. Phylogenetic evidence, for example, indicates that nectar-producing orchids have sometimes evolved from deceptive species (Johnson et al 1998). Thus, one possibility for a nonrewarding orchid such as *C. acaule* would be the development of flowers that provide a nectar reward (Gill 1989). This might reverse the negative reinforcement of repeated visitor behavior in non-rewarding flowers (Dafni 1987; Gill 1989). Although the presence or the artificial addition of nectar does not always mitigate pollinator limitation (e.g. Ackerman 1986; Burd 1995; Johnson and Nilsson 1999), it had a significant effect in *C. acaule* (Cochran 1986). Tremblay et al. (2005), in a broad survey of the orchid family, found the median percent fruit set in non-rewarding orchids (20.7%) to be significantly lower than in rewarding species (37.1%). In North America, Neiland and Wilcock (1998) reported that fruit-set figures measuring the relative reproductive success of nectarless and nectar-producing orchids averaged 19.5 and 49.3%, respectively, based on fruit to flower ratios. These authors believe the adoption of nectar production might represent the most effective mechanism for overcoming the reproductive restrictions of pollinator limitation.

On the other hand, an effective, long-term strategy to maximize seed production may require restricted levels of within season pollinator service. Data based on hand pollinations suggest that a prolonged increase in flower and fruit production can limit the resources available for subsequent growth, reproduction, and survival (e.g. Janzen et al. 1980; Lloyd 1980b; Montalvo and Ackerman 1987; Ackerman 1989; Snow and Whigham 1989; Zimmerman and Aide 1989; Ackerman and Montalvo 1990; Primack and Hall 1990; Primack et al. 1994; Primack 1996; Primack and Stacy 1998; Melendez-Ackerman et al. 2000). Thus, an increase in within season pollination rates might not significantly improve overall reproductive success because such increase could have an adverse effect on lifetime fecundity.

Cypripedium acaule has a large and persistent rhizome, and compared to the underground resources available, the costs of reproduction should be relatively low (Primack and Hall 1990). Nevertheless, successive years of artificially increased sexual reproduction and fruiting resulted in a decrease in plant size, and smaller plants were less likely to flower (Primack and Hall 1990; Primack et al. 1994; Primack 1996; Primack and Stacy 1998). This effect was augmented by resource constraints resulting from experimental defoliation.

Cochran (1986), however, considered that the effects of resource limitation on overall reproductive success in this orchid were subordinate to pollen limitation. Based on his data, 2 years of complete pollination would be equivalent to 10–20 years of normal fruit set, and long life spans and low mortality would, in time, permit resource-depleted individuals to resume reproduction. Primack (1996) observed such recovery in several Massachussets populations of this orchid.

Calvo and Horvitz (1990) also consider the costs of reproduction to be secondary to pollen limitation. According to their demographic model, the control of average plant fitness in orchid populations involves more than a simple dichotomy between the costs of reproduction and pollination levels. Increased pollination might, for example, achieve increased fruit set with little or no increase in cost up to some threshold level. In their opinion, experimental results that suggest the presence of resource limitation often involve artificially increased sexual reproduction that raises fruit set to unnaturally high levels. Although maximizing reproduction in favorable years appears to be a selected strategy in many plants where pollination is uncertain (Calvo and Horvitz 1990; Neiland and Wilcock 1998) (see, e.g. *Platanthera blephariglottis*), experimental hand pollinations may exceed the normal range of natural fruit set and may have no significance in relation to the natural ecology of the species.

Studies of reproduction in the orchids *Aspasia principissa* Achb. f (Calvo and Horvitz 1990) and *Tolumnia variegata* (Sw.) Braem (Calvo 1993) were consistent with these predictions. A statistically significant reduction in future growth and flowering was observed only in plants subjected to a high pollination intensity treatment (e.g. in the case of *T. varigata* artificial pollination resulted in a mean fruit set of 72% compared to less than 1% in open pollinated plants). The following year the artificially pollinated plants were on average 30% smaller than the control plants. Simulations indicated that even this cost was insufficient to overcome the potential benefits of higher fruit set. The production of only a few seedlings per fruit could more than compensate the cost of fruiting, and therefore selection for higher levels of pollination should be favored.

Calvo (1993) suggested that the low level of pollination and fruit production frequently observed in nonautogamous orchids might be due to a low correlation between fruit or seed production and seedling recruitment. Selection for increased levels of pollination would be ineffectively low if an increase in seed production was not translated into an increase in the number of reproductive individuals produced in the next generation (i.e. an increase in fitness). Under such circumstances, pollinator limitation might be evolutionarily stable.

Seedling recruitment may certainly be limited by the availability of suitable microsite conditions and other density-dependent constraints (e.g. Fowler 1986; Kull 1998). Keddy et al. (1983), for example, observed a scarcity of microsite conditions suitable for seedling establishment of *C. passerinum* Richardson (sparrow's egg lady's-slipper) among a mosaic of seres (stages of ecological succession) on the north shore of Lake Superior. However, seedling recruitment may not be a problem in *C. acaule.* Gill (1989), for example, reported that approximately 130 new seedlings were produced per year in a Virginia population, despite severe pollinator limitation and very low levels of capsule production. Ackerman et al. (1996) believe that the predicted transition from pollinator toward resource limitation through selection for increased attraction of pollinators should, in any case, be independent of microsite availability. According to this view, populations regulated by density-dependent factors such as the availability of suitable microsites would still experience differential seed production among individual plants, and selection for increased pollinator attraction would be favored because the production of more seeds would enhance the probability of encountering suitable microsites as they became available.

A satisfactory explanation for the prevalence of pollen limitation in sexually reproducing, nonautogamous orchids may remain elusive, but a number of associated life history traits are routinely associated with its presence. In *C. acaule*, the flowers remain attractive for several days following pollination, supplementing the already relatively long blooming time of this species (O'Connell and Johnston 1998). Extended periods of fertilization have been related to low levels of pollination in other orchids. Gregg (1991), for example, found that flowers of some *Cleistesiopsis* (see volume 2) that receive a small amount of pollen fade more slowly than those receiving a large amount, providing a chance for further pollination to occur. In like manner, Neiland and Wilcock (1995) demonstrated that stigmas of some European orchids can remain receptive for at least 8 days following the initial pollination and that later pollinations can lead to seed production. The pollen may also remain viable for a long time, persisting on foraging insects that may only visit non-rewarding orchids intermittently (e.g. Neiland and Wilcock 1995). Prolonged dissemination of pollen from both pollinated and unpollinated flowers, and repeated pollinator visits to pollinated flowers provide a potential for expanded and multiple paternity, pollen tube competition, and selective abortion with a consequent improvement in the quality of seeds produced. A long-lived perianth, both before and after pollination; a long period of stigma receptivity; and long pollen life with protracted dissemination may therefore all contribute to the maximization of sexual reproduction and total fitness through the enhancement of male as well as female functions, even if equilibrium is never achieved.

Other potentially limiting factors include competition from introduced species such as Japanese honeysuckle (*Lonicera japonica* Thunberg) and habitat destruction or alteration through such practices as fire suppression. In an interesting reversal, Gill (1996) reported that the increase in light reaching the forest floor following fire or gypsy moth defoliation of the canopy in Maryland and Virginia stimulated the flowering of food plants and resulted in a temporary local increase in pollinators. This, in turn, led to an increase in the frequency of pollinator visits to *C. acaule* and the production of significantly more flowers, fruits, and plants. He considered that reproduction in this orchid might be highly dependent on disturbances that create such light gaps. Similarly, Stucky (1967) observed an increase in plants of *C. acaule* after brush fires followed by a peak in blooming 10–15 years later. Under other circumstances, Primack et al. (1994) found that fire had a negative effect on *C. acaule* that was further compounded by simulated herbivory. Although early frosts often reduce the number of capsules reaching maturity in the Great Lakes region (Case 1987), a delay in germination (up to 8 months) prevents winter freezing of the tender seedlings (Ballard 1990). The plant is also collected for horticultural and medicinal purposes where it is sometimes used as a sedative. Fortunately, it is still common throughout most of its range.

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Chapter 4
Section Obtusipetala

Abstract *Cypripedium reginae* is a predominantly outcrossing species. However, it is self-compatible, and some geitonogamy occurs. Syrphid flies are primary pollinators. Seed production is pollinator limited. *Cypripedium passerinum* is a colonizing species found in northerly regions. It is self compatible and primarily autogamous over most of its range. Fertility assurance seems to provide the best explanation for the frequently observed high levels of autogamy found in colonial or adverse environments. A model illustrating the advantages of autogamy under these circumstances is discussed. Conditions for seedling establishment and the growth of mature plants differ, and successful sexual reproduction may require a mosaic of successional stages.

Keywords *Cypripedium reginae* • *Cypripedium passerinum* • Colonizing species • Selection for autogamy • Geitonogamy • Fertility assurance • Syrphid flies • Scarab beetles • Leaf-cutter bees

Section Obtusipetala includes three species, one Chinese, two North American.

Cypripedium reginae Walter (Showy Lady's-Slipper)

Distribution and Habitat

Occurring in calcareous fens and along the edges of spruce, cedar, tamarack, or balsam swamps and in a variety of upland sites from elevated bogs to meadows or wooded hillsides, *C. reginae* ranges from the maritime provinces to North Carolina and Tennessee west to Saskatchewan, North Dakota, and Arkansas (Luer 1975;

C.L. Argue, *The Pollination Biology of North American Orchids: Volume 1: North of Florida and Mexico*, DOI 10.1007/978-1-4614-0592-4_4,

Table 4.1 Data on section Obtusipetala (Sheviak 2002)

Character	*C. passerinum*	*C. reginae*
Plant height (cm)	12–38 (–50)	21–90
Flower number	1 (–2)	1–3 (–4)
Dorsal sepal (mm)	11–20 × (7-) 9–15	25–45 × 18–42
Lateral sepals (mm)	6–12 × 6–15	24–42 × 15–37
Lateral petals (mm)	2–20 × 3–6	25–47 × 6–17
Lip length (mm)	11–20	25–53
Chromosomes (2n)	20	20

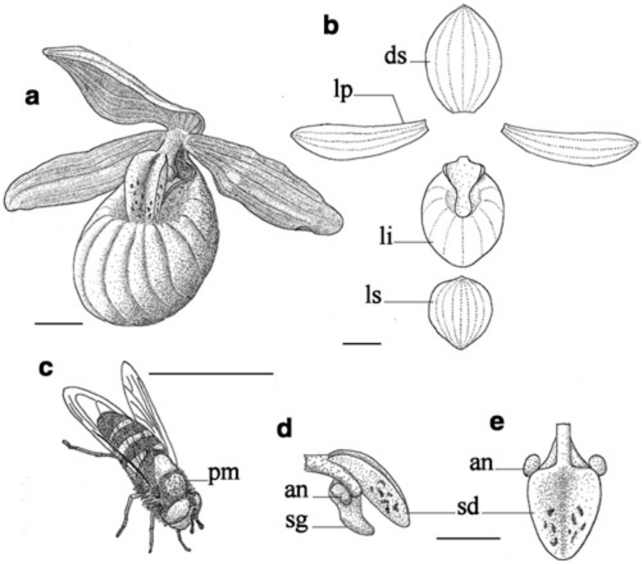

Fig. 4.1 *Cypripedium reginae*. (**a**) Flower, slightly oblique view; (**b**) Flower, exploded view; (**c**) *Syrphus torvus*, syrphid fly with pollen mass on its dorsal thorax; (**d**) Column, side view; (**e**) Column, top view, scale bars = 10 mm. *an* anther, *ds* dorsal sepal, *li* lip, *lp* lateral petal, *ls* lateral sepal, *pm* pollen mass, *sg* stigma, *sd* staminodium

Cribb 1997; Sheviak 2002). It prefers moist soils with a neutral or basic pH (Curtis 1943; Cribb 1997) and grows well in light shade but declines in the decreasing light of a developing canopy (Stucky 1967).

Floral Morphology

Each stem bears one to three, occasionally four large flowers (Table 4.1) (Luer 1975; Cribb 1997; Sheviak 2002). The dorsal sepal is erect or ascending, the lateral petals are spreading, and the lateral sepals are united behind the lip (Fig. 4.1a, b). Both the sepals and petals are white and contrast sharply in color with the subglobose labellum, which is usually a bright rose-pink, sometimes streaked with white. Measurements of the anther exit holes have not been recorded, but the dorsal-ventral thickness of pollinators able to squeeze through the holes appears to have a maximum value of about 3.5 mm (e.g. Vogt 1990). The column (Fig. 4.1d) is 1–1.5 cm long. Its stigmatic surface is coated with fine hairs that function like a "wool card" in pollen removal (Gray 1862; Catling and Catling 1991). The staminode is 1–1.7 cm long and white with a yellow margin and red to purple spots on its apical half (Fig. 4.1a, d, e) (Luer 1975; Cribb 1997). Long distance attraction is probably based on the color and form of the flower. At short range the pollinators apparently respond to a sweet odor produced chiefly by the lateral sepals and petals (Stoutamire 1967). Individual plants do not emerge every year, and prolonged periods of dormancy lasting several years are known (Gregg 2004).

Compatibility and Breeding System

Harvais (1980), in a study in northwestern Ontario, reported 50.6 (35–75)% fruit set in artificially cross-pollinated flowers over a 5-year period and 81.2 (53–100)% fruit set in artificially self-pollinated flowers over 4 years. Similarly, Ballard (1987) observed 95% fruit set in artificially self-pollinated plants from southeastern New Hampshire. Neither author observed any difference in seed germination between capsules of selfed and cross-pollinated flowers. Although Stoutamire (1967) considered *C. reginae* to be a predominantly outcrossing species, it can bear several flowers on each stem and can produce large clones (e.g. Morris and Eames 1929). Some transfer of pollen among flowers of the same plant (geitonogamy) therefore inevitably occurs. Intrafloral self-fertilization in the absence of a pollinator (autogamy) is absent (Catling 1983).

Pollinators and Pollination Mechanism

Cypripedium reginae has large flowers, but according to Stoutamire (1967), its anther exits are smaller than those of *C. acaule* and would offer a more difficult passage for bumblebees. Many insects have been observed to visit plants in their native habitats, including butterflies and beetles; but until recently, only a medium sized, unidentified black bee in Michigan (Stoutamire 1967) and the leaf-cutter bees, *Megachile melanophaea* Smith and *M. centuncularis* (L.) in Ontario (Guignard 1886, 1887), had been reported to enter the flower, follow the prescribed course to the base of the slipper, emerge through the exit hole, and remove pollen from the anther.

Vogt (1990), in a more recent study in Vermont, reported that over 90% of pollinations were performed by syrphid flies and a lesser number by flower beetles. The syrphid flies had a thorax with a dorsal-ventral thickness of 3.5 mm. It usually took a 5–10 min struggle for these flies to squeeze through the anther opening, although they sometimes emerged in as little as 20 s (Vogt 1990). Two collected specimens of *Syrphus torvus* Osten and Sacken carried large pollen smears on their backs (Fig. 4.1c). Like bees, they feed on pollen as well as nectar and may be attracted to the orchid's yellow margined staminodia. One honeybee (*Apis melifera* L.) was found dead in the lip; the 4.2-mm dorsal-ventral thickness of its thorax was apparently too great to allow it to escape through the anther opening.

Both species of leaf-cutter bees that Guignard (1886, 1887) reported as pollinators in Ontario were also present at Vogt's study site in Vermont. Neither, however, visited the flowers. *Megachile centuncularis* has a 3.4-mm thick thorax and should be able to exit through the anther openings (Vogt 1990). However, the thorax of *M. melanophaea* is 4.5 mm thick. Guignard (1887) reported that one individual cut its way out of the labellum, and Vogt (1990) believes its escape by the usual route is unlikely. In his opinion, this species is probably not a legitimate pollinator. He attributed the absence of *Megachile* bee pollination at his study site to a low local density of these insects, a learned avoidance of non-rewarding flowers, or a temporal or geographic variability in the pollination system of *C. reginae*.

Vogt (1990) also described pollination by a single scarab beetle, *Trichiotinus assimilis* (Kirby) (Scarabaeidae). The beetle followed the usual route through the flower and emerged with a pollen smear on its back. It has a thorax with a dorsal-ventral thickness of 3.4 mm, is stronger than the syrphid flies, and forced its way out of the flower with little delay. Smith (1863) also reported beetle pollination for this species, and Guignard (1886, 1887) recorded a closely related species of *Trichiotinus* Casey as a visitor but not a pollinator. Beetle pollination is rare in orchids, occurring in only 1.5% of species examined (van der Pijl and Dodson 1966), and it has not been reported elsewhere in the subfamily Cypripedioideae. Vogt's (1990) observations, along with the other reports of nonhymenopteron pollinators, require a re-evaluation of the postulated bee-pollination syndrome for all *Cypripedium* species in North America (e.g. van der Pijl and Dodson 1966; Stoutamire 1967).

Fruiting Success and Limiting Factors

Large, mature plants had the highest potential for both sexual reproduction and survival (Gregg 2004; Kery and Gregg 2004). In an 11-year study in West Virginia, Kery and Gregg (2004) found that flowering plants were more likely to flower again in subsequent years than vegetative plants, and transition from a flowering to a vegetative state was relatively infrequent. Thus, once a plant had reached the flowering state, resource allocation was apparently sufficient to maintain that state. However, pollen transport may limit fruit and seed production. Mean capsule set in open pollinated flowers varied from 13–16% in Ontario to 8–25% in New Hampshire, much lower than the 51–81% and 95% obtained from these respective sites with hand-pollinated flowers (Harvais 1980; Ballard 1987; Proctor 1998). Similarly, Ballard (1987) reported that open pollinated capsules contained fewer viable seeds than those that were hand pollinated, possibly because of insufficient pollen transfer.

Proctor (1998) found that seed production was largely unaffected by the age of the pollen. The latter remained viable and able to achieve high levels of seed set for about a week following removal from the anther (Ballard 1987; Proctor 1998). Extended pollen viability may here again represent an adaptation to intermittent insect revisitation in a species with nonrewarding flowers. Pollinator limitation might also be implied in a West Virginia population where an upward trend in flower production was accompanied by a downward trend in percent fruit set over the years immediately following elimination of heavy deer predation (Gregg 2004). Still, the fecundity of each capsule (up to 48,000 seeds) and plant lifespans of up to 75 years (Niles 1904) result in the production of countless seeds over the lifetime of an individual, allowing populations to survive or increase over time even though relatively few flowers set fruit.

Germination of seeds from the New England area improved from 16–36% to 70–95% following 2 months of cold treatment at 5 C (Ballard 1990). A period of dormancy would, of course, prevent autumn germination and winter freezing of tender seedlings in northern latitudes. The presence of dormancy in more southerly populations has yet to be examined.

The introduced and abundant European skipper (*Thymelicus lineola* Ochsenheimer), a native skipper (*Polites mystic* Edwards), and other arthropods are often trapped in the pouch of this and other lady-slippers (Arthur 1962; Catling 1974; Barrows 1983; Vogt 1990). Vogt (1990) found them in about one third of the flowers at his study site in Vermont, and Catling (1974) found them in at least half of about one hundred flowers at several Ontario sites. Both noted that they cannot escape and probably interfere with pollination.

Deer predation has been implicated in the extirpation of two populations in Michigan (Waterman 1949). In a systematic, long-term examination of the problem, Gregg (1996, 2004) found deer were a serious threat at a West Virginia site located near the southeastern limits of the orchid's distribution. This population was subject to a range of additional concerns including the presence of competing species, canopy encroachment, and low rates of sexual reproduction. Severe fungal contamination of the seeds in mature capsules also limited reproduction in some populations (Harvais 1980).

Cypripedium passerinum Richardson (Sparrow's Egg Lady's-Slipper)

Distribution and Habitat

Cypripedium passerinum is typically found in the moist acidic or neutral soils of coniferous forests or tundra, often along the shores of lakes and streams. It ranges from Alaska across Canada to Quebec and south into Montana with a disjunct population on the shore of Ille Nue in the Mingan Islands (Luer 1975; Catling and Catling 1991; Cribb 1997; Sheviak 2002). Some northern populations occur at higher and

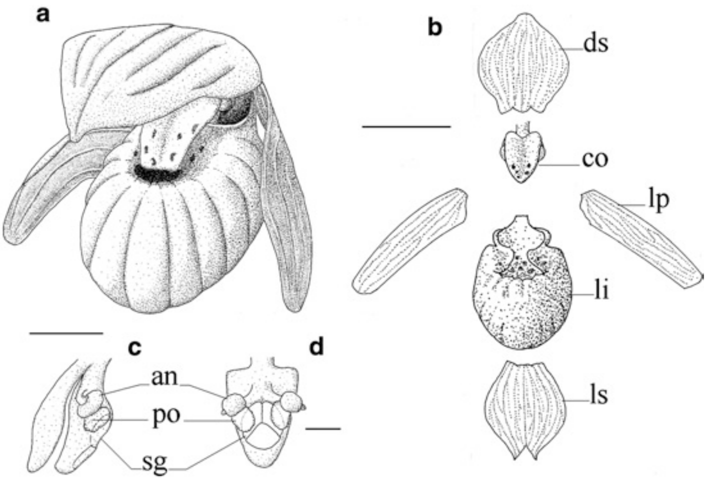

Fig. 4.2 *Cypripedium passerinum.* (**a**) Flower, slightly oblique view, scale bar = 5 mm; (**b**) Flower, exploded view, scale bar = 10 mm. (**c**) Column, side view; (**d**) Column, bottom view, scale bar (**c, d**) = 2 mm. *an* anther, *co* column, *ds* dorsal sepal, *li* lip, *lp* lateral petal, *ls* lateral sepal, *po* pollen mass, *sg* stigma

colder latitudes than any other North American lady's-slipper, with most populations occupying land that was for the most part covered by glaciers less than 10,000 years ago (Catling 1983).

Floral Morphology

Cypripedium passerinum produces one or occasionally two small flowers on a leafy stem (Table 4.1). Sepal color varies from green to white. The dorsal sepal forms a hood over the lip (Fig. 4.2a), while the laterals, sometimes free to the base, are usually partly fused to a bifid apex (Fig. 4.2b) (Luer 1975; Cribb 1997). The resulting synsepal is appressed to the bottom of the lip. The lateral petals, downward curved and spreading, are white, translucent, and flat (Fig. 4.2a, b). Also white, the lip is obovoid or subglobose with minute purple spotting at the orifice and on the inside of the pouch (Fig. 4.2a, b). The column is short with a relatively large stigma (Fig. 4.2c, d). A longitudinally grooved staminode, about 6 mm long, has a white base and a yellow apex with purple to reddish–brown spots (Fig. 4.2b) (Luer 1975; Cribb 1997).

Compatibility and Breeding System

Cypripedium passerinum is self-compatible (Catling 1983; Keddy et al. 1983). Automatic self-pollination and subsequent fertilization (i.e. autogamy) occur over most of its range (Catling 1983).

Pollinators and Pollination Mechanisms

Due to an alteration in the length and curvature of the stigmatic branch and a lateral convergence of the stamens, the anthers develop adjacent to the margins of the stigma (Fig. 4.2c, d) (Catling 1983). The pollen masses are consequently discharged directly onto the stigmatic surface, and no pollen vector is needed for pollination.

The presence of this orchid in areas that were occupied by the last continental glacier indicates a history of colonization. Self-fertilization in the absence of a pollinator (autogamy) is advantageous in a colonizing species because new colonies can originate through the establishment of a single seedling. In addition, the northerly distribution of this orchid suggests that bad weather might sometimes adversely affect pollinator activity. Autogamy may be advantageous when pollinators are rare or inactive in hostile habitats. It may also be advantageous when pioneer plants, located at their distributional margins or in new and temporary, isolated environments, are separated from larger populations that attract pollinators.

Although the genetic similarity of seedlings to parents already adapted to specialized habitats should confer a higher average fitness on the products of autogamy as compared with the more variable progeny of outcrossing (e.g. Stebbins 1970), fertility assurance seems to provide the best explanation for the frequently observed high autogamy levels in plants such as *C. passerinum* found in colonial (unsaturated) or adverse pollinator environments (e.g. Hagerup 1951, 1952; Baker 1955; Arroyo 1973; Catling 1983; Hereford 2010). Lloyd (1978, 1979a, b) chose two extreme situations to illustrate the advantages of autogamy under these circumstances. According to his model, autogamy can be selected in an unsaturated or colonial environment even when the average success of individual autogamous and cross-pollinated progeny is about equal, but less important than the number of seeds produced. It can also be selected if the agents of cross-pollination are unreliable even when individual progeny resulting from cross-pollination have an advantage in fitness. Given a combination of colonizing conditions and unreliable cross-pollination, strong selection for autogamy might be expected (Catling 1990).

Kevan (1972) has successfully challenged the notion of pollinator scarcity in northern regions, although a weather-related reduction in pollinator activity is still significant. Unreliable cross-pollination need not, however, be based on a depauperate pollinator fauna. Competition for pollinator services can also be important. Given sufficient competition and concomitant limitation of reproductive potential, autogamy might be selected in virtually any area, including one having an abundant and rich diversity of pollinators. Levin (1972), for example, has pointed to the presence of autogamous orchids in the tropics amid a wealth of pollinators and predominantly outcrossing orchids.

The flowers of *C. passerinum* open about a week after budding and wilt two to eight (usually four or five) days later (Keddy et al. 1983). Although the size of the exit holes, 2.5–3.0 mm wide, would clearly restrict pollinator size, the presence of sticky pollen and fragrant, open flowers suggest the possibility of occasional cross-pollination. The noted advantages of autogamy (assured fertility and a potential for rapid colonization) might thus occasionally be combined with the advantages of genetic recombination. In this connection, Catling and Bennett (2007) recently discovered a possible relict outbreeding morphotype in the Beringian region of southwestern Yukon. They attributed its occurrence here to the persistent advantage of outbreeding in an area not glaciated for the past several hundred thousand years.

Despite occasional anecdotal accounts to the contrary, only one other *Cypripedium*, *C. dickinsonianum* Hagsater, has, to my knowledge, been demonstrated to be primarily autogamous (Hagsater 1984; Cribb 1997). This species is restricted to the high central massif in eastern Chiapas (Mexico) where it occurs in juniper forest at about 5,000 feet elevation (Cribb 1997). All cultivated plants of this species produced capsules that contained seed with well-developed embryos. As in *C. passerinum*, structural changes in the curvature and length of the stigmatic branch cause the pollinia to contact the stigma (Hagsater 1984; Catling 1990). The similarity is a result of convergence, and the species are not closely related (Albert 1994; Cox et al. 1997).

Fruiting Success and Limiting Factors

In *C. passerinum* nearly all ovaries develop seed. Although sexual reproduction is largely the result of selfing, self-fertilizing species can retain a high degree of heterozygosity (Allard et al. 1968) with no trace of inbreeding depression, and the wide distribution of *C. passerinum* implies no disadvantage based on its level of genetic variability (Catling 1990).

Keddy et al. (1983) studied one population at a site on the north shore of Lake Superior near the Pic River in Ontario. The terrain here is made up of dune complexes stabilized by a variety of vegetation types from shrubland and herbaceous communities to forests. The region is subject to significant variation in rainfall, temperature, soil conditions, and levels of forest disturbance. Most local recruitment of *C. passerinum* is a result of vegetative reproduction. Seedlings are restricted to relatively rare, early successional sites. Given the 15 years or more required for *C. passerinum* to reach reproductive maturity, the availability of suitable conditions for seedling establishment probably has a significant temporal component. Moreover, as succession proceeds habitat conditions often improve, up to a point, for mature plants but deteriorate for the establishment of seedlings. Successful sexual reproduction at this site therefore requires a mosaic of successional stages to accommodate both the establishment of seedlings and their persistence to reproductive maturity.

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Chapter 5
Section Cypripedium

Abstract *Cypripedium parviflorum* is self-compatible, but selfing reduces seed viability, and outcrossing, employing a variety of small bees, represents the principal method of sexual reproduction. *Cypripedium candidum* is self compatible but not autogamous. Outcrossing is the primary method of sexual reproduction, but geitonogamy occurs. Pollinators are small carpenter bees and halictid and andrenid bees. Pollinator visitation is limiting. The breeding system of *C. montanum* has not yet been studied, and the only reported pollinator is *Lasioglossum.* The pollination biology of *C. kentuckiense* also has not been studied. It produces aromatic compounds distinct from other North American members of the genus.

Keywords *Cypripedium parviflorum* • *Cypripedium candidum* • *Cypripedium montanum* • *Cypripedium kentuckiense* • Introgression • Low pollinator fidelity • Seedling recruitment • Carpenter bees • Halictid and andrenid bees

Section Cypripedium is comprised of 14 Old World and four North American species.

Cypripedium parviflorum Salisbury (Yellow Lady's-Slipper)

Until recently, two varieties of *Cypripedium parviflorum* were distinguished in North America: *C. parviflorum* var. *pubescens* (Willd.) O.W. Knight (the large yellow lady's-slipper) and *C. parviflorum* var. *parviflorum* (the small yellow lady's-slipper). Sheviak (1993, 1994) has since segregated a northern variety, *C. parviflorum* var. *makasin* (Forwell) Sheviak, from the typical variety. Although not accepted by all authors (e.g. Cribb 1997), recent studies of allozyme diversity (diversity of enzymes coded by different alleles of a single gene) support the distinctness of these

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varieties from one another and from variety *pubescens* (Wallace and Case 2000). More recently, Sheviak (2010) proposed a fourth variety, variety *exiliens*, to represent the species in the far north. Most of the literature on the breeding system and pollination biology of *C. parviflorum* is based on studies conducted in eastern North America on varieties *pubescens* and *parviflorum.* Some studies on the latter, however, were based on material now assigned to variety *makasin.*

Distribution and Habitat

Cypripedium parviflorum var. *pubescens* is distributed from Newfoundland to western Canada and south to Georgia and Arkansas in the east and New Mexico in the west. Disjunct populations also occur in eastern Wyoming, South Dakota, Nebraska, and Arizona (Sheviak 2002, 2010; World Checklist of Monocotyledons 2008–2010). Found in a variety of habitats including deciduous and coniferous forest, boreal forest, northern prairie, and montane forest and meadow (Sheviak 1996), it shows a preference for slightly acidic to slightly basic soils (Curtis 1943).

Variety *parviflorum* ranges from eastern Nebraska and Oklahoma to Massachusetts and North Carolina, variety *makasin* from western Canada and Washington to Newfoundland and New Jersey with an isolated population in northeastern California (Sheviak 2002, 2010; World Checklist of Monocotyledons 2008–2010). Both distributions are partially sympatric with that of variety *pubescens*, but are largely separate from one another, overlapping slightly in the Midwest and northeastern United States. Variety *parviflorum* occasionally occurs in alkaline bogs and marshes but is more frequently found in deciduous forests on drier and more acidic sites than variety *pubescens*. Variety *makasin* prefers lightly shaded sites, often in calcareous fens and other wet or mesic locations with rich organic or sandy soils (Sheviak 1993, 1994; Cribb 1997).

Variety *exiliens* is the only representative of the species in northwestern Canada and Alaska. The type was growing in limestone talus on mesic to xeric tundra in the Brooks Range. It extends south in the Canadian Rockies into the northwestern United States with a disjunct population in the Black Hills of South Dakota (Sheviak 2010). No specific information is available on the pollination of this variety, and it will not be discussed further.

Floral Morphology

Varieties *parviflorum* and *makasin* usually have smaller flowers than variety *pubescens*, but considerable variation is present, especially in the latter (Table 5.1). Their overall morphology is similar (Luer 1975; Cribb 1997). The dorsal sepal is often undulate to slightly twisted, and the lateral sepals are usually united (Fig. 5.1a). Sepal color can vary from a uniformly dark reddish–brown to yellowish–green with reddish–brown markings. The lateral petals are usually colored like the sepals and are often twisted in spirals. They may be deflexed as much as 45–60° below the

Table 5.1 Data on varieties of *parviflorum* (Sheviak 2002)

Character	*parviflorum*	*pubescence*	*makasin*
Flower number	1–2	1–2	1–2 (–3)
Lip (length) (mm)	22–34	20–54	15–29
Oriface (mm)	12–19	10–23 (–27)	10–17
Chromosomes (2n)		20	20

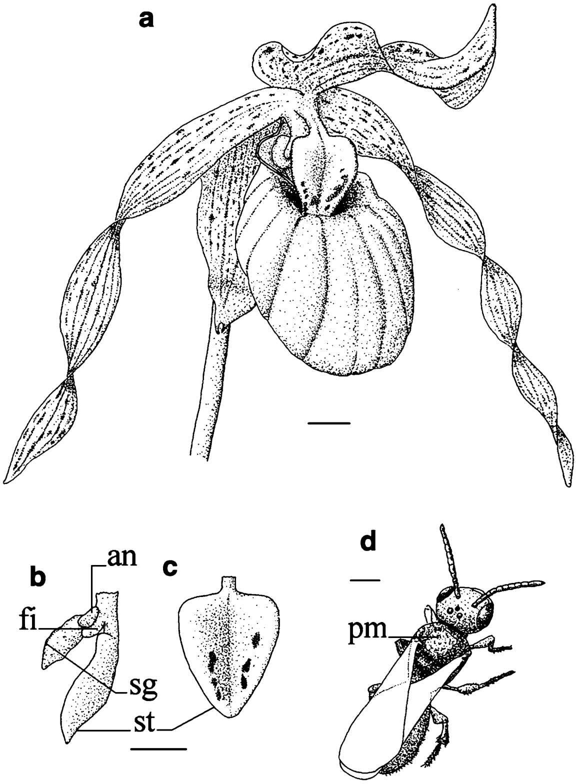

Fig. 5.1 *Cypripedium parviflorum.* (**a**) Flower, slightly oblique view, scale bar = 5 mm; (**b**) Column, side view; (**c**) Staminodium, top view, scale bar (**b, c**) = 5 mm; (**d**) *Ceratina calcarata*, small carpenter bee, scale bar = 1 mm. *an* anther, *fi* filament, *pm* pollen mass, *sg* stigma, *st* staminodium

horizontal. The lip is pouch-like and yellowish with red to purple spots on its inner surface. Column length varies from about 1 cm in variety *pubescens* to about 0.6 cm in the smaller varieties. The staminode is yellow and covered with red or purple spots (Fig. 5.1a–c). In variety *pubescens,* it is 1.0–1.2 cm long, in the smaller varieties, 0.8–1.0 cm long. Both the staminode and the area around the labellar opening are strongly reflective to ultraviolet light, at least in variety *makasin* (Bender 1985b). According to Sheviak (1994, 1996, 2010), the floral fragrance in var. *makasin* is distinct and sweet, while in varieties *parviflorum* and *pubescens* it is faint to moderately strong and often rose-like or sometimes musty in the latter. Plants of variety *pubescens* may be long-lived; Light (1998) reported on a still-living clone believed to be eighty years old. Dormancy is known and according to Shefferson et al. (2005) and Shefferson and Simms (2007), may be adaptive, enhancing the chances of surviving at least short-term environmental fluctuations.

Compatibility and Breeding System

Although Daumann (1968) described high levels of self-incompatibility in the closely related European species, *C. calceolus*, Bender (1985b) found that 85% of seeds in artificially self-pollinated capsules of variety *makasin* from northern Ohio contained mature embryos. Similarly, Tremblay (1994) reported that weights of 5-month-old seedlings in a population of variety *pubescens* from Quebec did not differ among artificially self-pollinated or cross-pollinated, uniparental (pollen obtained from one other specimen) or multiparental crosses. However, seeds from self-pollinated capsules had lower rates of germination than those from uniparental crosses, and both had lower rates than seeds from multiparental crosses, even though the latter had smaller embryos.

A study of pollen flow in variety *pubescens* at the Quebec site using stained pollen failed to detect selfing, either within individual flowers or within members of the same clone. Tremblay (1994) concluded that outcrossing was the principal method of sexual reproduction at this site. The relatively low rate of seed germination in selfed plants of this variety suggests the presence of deleterious recessive alleles, and the rarity of selfing may therefore be adaptive (Tremblay 1994). Electrophoretic analysis of allozyme variation has now confirmed outcrossing as the predominant mode of sexual reproduction in all three varieties (Case 1993, 1994).

Natural hybrids with the small white lady-slipper, *C. candidum*, (*C.* x *favillianum* (J. T. Curtis) Boivin) have been reported throughout the range of variety *pubescens* where these taxa are sympatric (Curtis 1932; Atwood 1975; Luer 1975; Bender 1985b; Niemann 1986). Both are diploids ($2n=20$) (Humphrey 1932; Love and Simon 1968). In one study, Case (1994) determined that 79% of the alleles found in *C. candidum* were also present in *C. parviflorum*. In Iowa, variety *pubescens* usually occurs in woodlands but is sometimes found on prairie sites. Klier et al. (1991) consider that the prairie ecotype here may have resulted from a transfer of genetic information from *C. candidum* by way of introgression (that is, through transfer of genes from *C. candidum* to variety *pubescens* through recurrent backcrossing of the fertile hybrid with variety *pubescens*). Similarly, hybridization with *C. montanum* (C. x columbianum Sheviak) has added diversity to *C. parviflorum* in the Northwest and might account for the origin of var. *makasin* (Sheviak 1992, 1995, 2010). For discussion of additional hybrids, see Sheviak (2002).

Pollinators and Pollination Mechanism

Although disagreements have yet to be resolved on the identity and relative abundance of aromatic compounds comprising the floral fragrances of varieties *pubescens* and *parviflorum*, there are evidently substantial differences between the two (Bergstrom et al. 1992; Barkman et al. 1997). Such differences may imply the involvement of different pollinators, and indeed, according to Proctor et al. (1996), variety *pubescens* is pollinated by halictid bees (Halictidae, sweat bee family) while variety *parviflorum* is pollinated by small carpenter bees (*Ceratina* Latreille; Apidae). However, in northern Ohio, Bender (1985b) observed the halictid *Lasioglossum* (*Dialictus*) *rohweri* (Ellis) (cf. Fig. 6.1c) pollinating variety *parviflorum* (now probably variety *makasin*), and in Michigan, Stoutamire (1967) observed a male *Ceratina calcarata* Robertson (Fig. 5.1d) enter the labellum of variety *pubescens* and emerge from the exit hole carrying a pollen smear on its dorsal thorax. The anther exit holes in varieties *pubescens* (ca. 2 mm) and *makasin* (1.8 × 3 mm) could just accommodate the crawling heights of either *Ceratina calcarata* (2.2 mm) or *Lasioglossum roweri* (2.7 mm) (Stoutamire 1967; Bender 1985b).

Records from elsewhere in North America indicate that other species of *Ceratina* also pollinate varieties *pubescens* and "*parviflorum*" (Stoutamire 1967; Nilsson 1981). In addition to a number of insects recorded only as visitors (e.g. Robertson 1929), Stoutamire (1967), Nilsson (1981), and Case and Bradford (2009) reported that species of *Lasioglossum* Curtiss and *Agapostemon* Guerin-Meneville (both Halictidae); mason bees, *Osmia* Panzer (Megachilidae); *Apis* L. (Apidae); hover flies, *Eristalis* Latreille (Syrphidae); and andrenid bees, *Andrena* (Andrenidae) passed through the labellum and removed pollen from flowers of variety *pubescens* or were collected with pollen smears of this variety on their bodies. As in *C. reginae*, the European skipper, *Thymelicus lineola* and other arthropods are sometimes trapped in the labellum of this variety and may interfere with pollinator movements (Barrows 1983).

Stoutamire (1967) suggested that the preference of the large yellow lady's-slipper for drier upland sites and the small yellow lady's-slipper (probably var. *makasin*) for lower, wetter sites in northeastern North America might correspond with the nesting and foraging habitats of different, ecologically restricted species of bees. A divergence in floral morphology and floral fragrance in these varieties might accordingly reflect an ongoing adaptation to different pollinating agents. Iltis (1965) conjectured that antecedent orchid populations were separated during the Pleistocene glaciation. Isolation and exposure to different groups of pollinators during this period may have led to edaphic and floral specializations, which following the retreat of the ice, plant migration, and limited introgression have produced the variation pattern currently observed in these taxa.

Fruiting Success and Limiting Factors

Ballard (1990) reported less than 10% fruit set in open pollinated flowers of "*C. calceolus* variety *parviflora*" (probably *C. parviflora* variety *makasin*) near Hanover, New Hampshire. Shefferson and Simms (2007) found 43.5% of the plants in a population of *C. parviflorum* in northeast Illinois (also probably variety *makasin* based on distribution (Sheviak 2002)) flowered and 33.5% of these produced fruit. This fruiting correlated with a slight reduction in plant size the following year, which may have resulted in a small cost to survival (Shefferson and Simms 2007). However, fruiting was correlated with an increased chance of future flowering, and high levels of fruiting did not reduce the level of fruiting in subsequent seasons. The priority in resource allocation for reproduction in plants of this variety may therefore be higher than for survival.

Fruit-set in variety *pubescens* showed marked geographic variation: less than 10% of the flowers set fruit in eastern populations while over 90% did so in both small and large populations from the Rocky Mountains of Alberta and British Columbia (Catling and Catling 1991). Fruit production was sometimes also highly variable within populations, ranging between 9 and 32% in successive years at a single site in Quebec (Tremblay 1994).

Information on factors influencing seed quality in variety *pubescens* is limited and the results are often unpredictable (Light and MacConaill 1998). The number of seeds with embryos did not vary significantly when pollen grains from one-quarter, one-half, or a whole anther were placed on the stigma (Proctor and Harder 1994), implying that the pollen load normally transferred on the dorsal thorax of the pollinator might be sufficient to fertilize a large percentage of the ovules present. However, pollen germination was inexplicably variable within and between clones (genets) (Light and MacConaill 1998).

In the seed parent, the age of the flower at the time of its pollination, up to about 10 days, was positively correlated with the percentage of seeds containing fully developed embryos, although, again, considerable variation occurred (Light and MacConaill 1998). The maximum age of flowers capable of setting fruit varied among clones from 2 to 10 days, but the flowers remained in good condition for up to 12 days, and germinable pollen was present in flowers in some clones for up to 15 days (Light and MacConaill 1998).

Thus, a flower can apparently continue to serve as a pollen donor after its capacity to function as a seed parent has expired, an extension of male function that might possibly relate to pollinator limitation. Protracted flower life may also serve to enhance pollinator attraction to younger stems (ramets) of the clone with receptive flowers. Ballard (1990), however, reported no difference in fruit set between hand-pollinated and open-pollinated flowers at his site in New Hampshire. Proctor and Harder (1994) obtained similar results in Alberta, although they noted that limited sampling and high variance might have affected their findings.

Multiparental pollen deposition in *Cypripedium* and other orchids is uncommon (Tremblay 1994), but could be favored by natural selection. According to Kress (1981), superior sporophytic genotypes and phenotypes are produced by pollen phenotypes that are most successful at fertilizing ovules. If pollen tube competition is a significant factor in selection, seeds from capsules receiving pollen from a number of different male parents should have higher vigor compared with those resulting from self or uniparental pollinations (Snow 1990). And, as already noted, multiparental pollination in variety *pubescens* produced seeds with a higher germination rate than those derived from uniparental- or self-pollination. However, the chance of multiparental pollination would obviously be affected by pollinator abundance, and the increase in germination rate may be so slight as to be of no consequence under natural conditions, while greater reproductive success might be realized through investment in increased seed production (Tremblay 1994).

Predation and weather may also limit fruit production in variety *pubescens*. Tremblay (1994), for example, noted that 10–50% of the capsules initiated at his site in Quebec failed to reach maturity due to herbivory, and Light and MacConaill (1998) found capsules that were water stressed during crucial stages of seed development sometimes produced incompletely developed, nonviable embryos. Weather also undoubtedly affects fruit set indirectly through its influence on pollinator activity.

Cypripedium candidum Muhlenberg ex Willdenow (Small White Lady's-Slipper)

Distribution and Habitat

Cypripedium candidum grows in wet to mesic prairies or open fen meadows and prefers loam, peat, or muck soils rich in calcium carbonate (Stoutamire 1967; Sheviak 2002). It spreads vegetatively, frequently producing large clones and develops flowers early in the season, when the surrounding vegetation is still low and the plants are readily visible (Bowles 1983). The amount of sunlight received is directly and positively related to plant size and flower production (Falb and Leopold 1993), although the development of shade-tolerance has been observed in some populations in Iowa. This may be a result of the transfer of genetic information from *C. parviflora* var. *pubescens* (Klier et al. 1991), but the relatively rare *C. candidum* is in no immediate danger of being genetically assimilated by this species (Worley et al. 2009). Distribution extends from southern Manitoba and Saskatchewan east to New Jersey and south to Nebraska, Missouri, Indiana, and Ohio with disjunct populations in Kentucky and Alabama (Klier et al. 1991; Sheviak 2002).

Floral Morphology

Cypripedium candidum produces one or occasionally two medium-sized flowers on a leafy stem (Luer 1975; Bowles 1983; Bender 1985b; Cribb 1997; Sheviak 2002) (Table 5.2). The dorsal sepal is greenish to pale brownish–yellow, usually overspread with reddish–brown spots and stripes. The labellum is obovoid and glossy white with false nectar guides in the form of purple markings inside the pouch and externally around the mouth (Fig. 5.2a). The latter area and the staminode are strongly reflective in ultraviolet light (Bender 1985b). The lateral sepals are united almost to the apex, while the petals are undulate to spirally twisted, spreading, and deflexed 45° from the horizontal; both are colored like the dorsal sepal. The staminode is yellow and decorated with bright red spots. Anthers are borne on distinct filaments on either side of a trilobed stigma (Fig. 5.2b). The anther exit holes measure

Table 5.2 Data on section Cypripedium (Sheviak 2002)

Character	*C. candidum*	*C. montanum*
Plant height (cm)	11–40	25–71
Flower number	1(−2)	1–3
Dorsal sepal (mm)	15–35 × 7–13	33–60 × 8–16
Lateral sepals (mm)	13–35 × 7–15	30–60 × 6–18
Lateral petals	23–46 × 3–5	36–77 × 3–5
Lip length (mm)	17–27	19–33
Chromosomes (2n)	20	

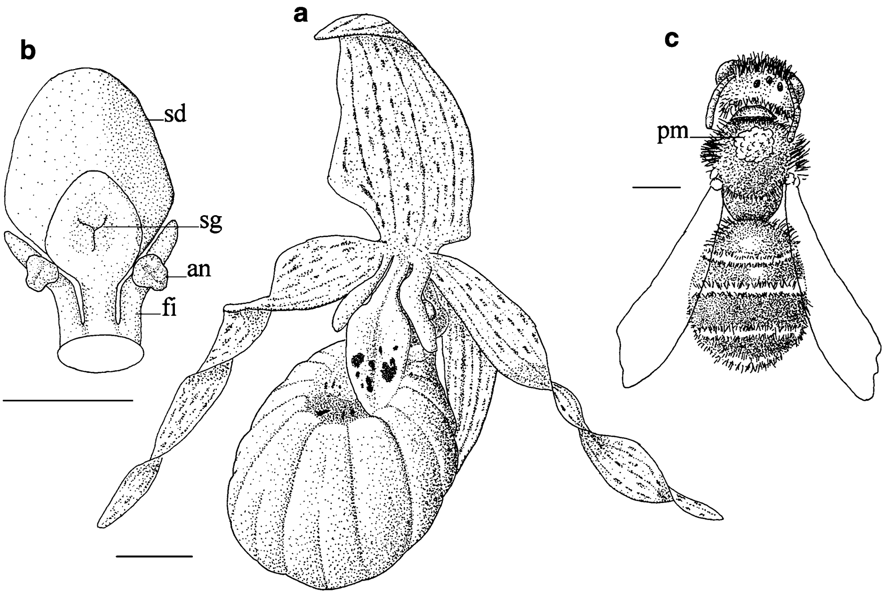

Fig. 5.2 *Cypripedium candidum.* (**a**) Flower, slightly oblique view, scale bar = 5 mm; (**b**) Column, bottom view, scale bar = 3 mm; (**c**) *Halictus confusus*, scale bar = 1 mm. *an* anther, *fi* filament, *pm* pollen mass, *sg* stigma, *sd* staminodium

1.7 (1.0–2.5) mm in height and 1.2 (0.5–2.0) mm in width, while the width of the labellar entrance is 4.1 (3.0–5.0) mm, and the clearance space beneath the stigma is 1.9 (1.5–3.0) mm (Bender 1985b). Flowers last up to 10 days and produce a strong, spicy odor, which emanates chiefly from the sepals and to a lesser extent from the petals and lip (Bowles 1983; Bender 1985b; Stoutamire 1990). Like *C. parviflorum* and many other orchids, this species is prone to periods of dormancy (e.g. Shefferson et al. 2005; Shefferson and Simms 2007).

Compatibility and Breeding System

Cypripedium candidum is self-compatible, but no self-fertilization takes place in the absence of a pollinator (no autogamy) (Bender 1985a, b). It has an outcrossing breeding system (Bowles 1983), but each clone (genet) can produce as many as twenty-five flowering stems (ramets) (Stoutamire 1990), and pollen transfer among clonal flowers (geitonogamy) may occur. Also, as in *C. acaule*, bees occasionally back down into the labellum after contacting the anthers, effecting intrafloral self-pollination (Bender 1985b).

Pollinators and Pollination Mechanisms

Bender (1985b) recorded nine genera of bees and several hemipterids (true bugs) and syrphids (hover flies) as flower visitors during a three-year study in northern Ohio. Insects carrying pollen on their thoraxes were classified as pollinators and included six female hymenopterans (*Halictus ligatus* Say, *Lasioglossum anomalum* Robertson, *L. cressonii* Robertson, *L. rohweri*, *L. cinctipes* (Provancher) (all Halictidae), and *Ceratina calcarata* (Fig. 5.1d) or *C. dupla* Say (small carpenter bees, Apidae)) and one female hemipteran (*Cosmopepla lintneriana* (Kirkaldy), a type of stink bug). All have 2–3 mm crawling heights proportionate to the anther exit holes and clearance space beneath the stigma. The hymenoptera mate as soon as they emerge from overwintering and immediately began to gather nectar and pollen to provision their brood cells (Stephen et al. 1969). The pollination system of the orchid appears to exploit their urgent need for food and their inexperience or lack of long-term memory.

Catling and Knerer (1980) collected a number of additional insects in a southern Ontario native prairie with pollen smears of *C. candidum* on their dorsal thoraxes. These included the female halictids *Augochlorella aurata* (Smith) (=*A. striata* (Provancher), *Halictus confusus*, *L. rohweri*, *L. atlanticum* (Mitchell), and *L. pilosum* (Smith). An andrenid bee, *Andrena ziziae* Robertson, was also captured as it exited a flower through the basal anther opening.

Females of *Augochlorella aurata*, *Andrena ziziae*, and *Lasioglossum rohweri* (all approximately 6–7 mm long), placed inside the labellum, took 5–15 min to find their way out. They spent 2–7 min exploring the distal portion of the lip and 3–8 min moving to and forcing their way out of the exit holes, removing pollen from the anther as they escaped. Catling and Knerer (1980) considered all these bees well suited, both in terms of size and seasonal abundance, for the pollination of this orchid. However, based on frequency of occurrence they believed *Halictus confusus* (Fig. 5.2c) and *Andrena ziziae* to likely be the most important pollinators at their Ontario study site. Possible supplementary pollinators here included the sweat bee, *Sphecodes* Latreille (Halictidae), parasitic on other halictines, a cuckoo bee, *Nomada* Scopoli (Apidae), parasitic on *Andrena*, and other insects such as click beetles (Elateridae) and chalcid wasps (Chalcididae).

Stoutamire (1967) observed another *Andrena*, *A. barbilabris* (Kirby), visiting a cultivated specimen of *C. candidum* in Michigan. It carried pollen from other nearby cultivated flowers of this orchid and functioned as an efficient pollinator, albeit under artificial conditions.

Andrenid females have a short life span and are therefore dependent on relatively few plants. *Andrena ziziae*, for example, relies on food produced by golden alexanders (*Zizia aurea* (L.) W. D. J. Koch) and to a lesser extent on blue-eyed grass (*Sisyrinchium mucronatum* Michx.). Halictine bees such as *Lasioglossum rohweri* and *Augochlorella aurata*, on the other hand, are social and rear a number of successive broods prior to production of males and queens in late summer. These bees accordingly require a continuity of rewarding wildflowers from spring through autumn (Catling and Knerer 1980).

The previously noted hybridization with the yellow lady's-slipper, *C. parviflorum* variety *pubescens*, is common (e.g. Curtis 1932; Marshall et al. 1966; Atwood 1975; Luer 1975; Bender 1985b; Niemann 1986; Klier et al. 1991) and indicates the involvement of some shared pollinator(s). Many solitary bees exhibit a low level of floral fidelity (Free 1966) and could account for the hybridization. Moreover, testing indicates pollen can remain viable long enough to bridge the temporal gap between the peak flowering periods of the two species (Klier et al. 1991). Resulting hybrids appear to have intermediate blooming times, and backcrossing and introgression are apparently frequent (Sheviak 1974).

The absence of pollinator specificity is also evident in the hybridization of *C. candidum* with *C. parviflorum* var. *makasin* (Bowles 1983; Bender 1985b; Stoutamire 1990). Bender (1985b) captured *Lasioglossum rohweri* on *C. candidum*, *C. parviflorum* var. *makasin*, and their hybrid, *C.* x *andrewsii*. Based on its size this bee could transfer pollen among the flowers of all three taxa. It and two other species captured on the hybrids, *Andrena cressonii* Robertson and *Lasioglossum pilosum*, may account, in part, for the hybridization and for reported backcrossing with the parental species (Bender 1985b).

Fruiting Success and Limiting Factors

Catling and Knerer (1980) and Stoutamire (1990) found about 25% of the flowers were naturally pollinated in southern Ontario and 24–70% in northern Ohio, respectively. Studies in Wisconsin (Curtis 1954), Iowa (Carroll et al. 1984), northern Ohio (Bender 1985a, b; Stoutamire 1990), Illinois (Bowles 1983; Shefferson and Simms 2007), and New York (Falb and Leopold 1993) determined that 36–92% of stems (ramets) flowered and 5–62% of these produced fruit, with each fruit containing about 14,000 seeds (Stoutamire 1990). According to Bender (1985b) and Catling and Knerer (1980), the variation in pollination and fruit production may relate to differences in the onset of spring that affect the amount of overlap in the blooming periods of *C. candidum* and plants that attract pollinators to the area by providing a nectar or pollen reward (the aforementioned magnet species effect).

Smaller plants of *C. candidum* and *C. parviflorum* var. *makasin* and their hybrid, *C.* x *andrewsii* A. M. Fuller are more likely to go dormant and less likely to survive dormancy than larger plants (Shefferson 2006). At the same time, Shefferson and Simms (2007) found that fruiting increased the probability of future flowering and that high levels of fruiting did not reduce the production of fruit in subsequent years. Thus, although fruiting levels respond to internal clues such as nutrient uptake or storage as well as the evident effects of pollination, resources may not be limiting, at least in larger plants of *C. candidum*. Bowles (1983) considered resources less significant than pollinators, and Bender (1985b) found only sixty naturally formed capsules from about 3,100 blooming plants (1.9%) at her study site in northern Ohio. Like Bowles, she attributed the low level of fruit production primarily to pollinator limitation.

However, she also reported frequent destruction of seed capsules by both vertebrates and invertebrates and considered herbivory another explanation for the low number of capsules found. Working at the same site, Stoutamire (1990) found a small black weevil (tentatively identified as *Stethobaris ovata* LeConte) responsible for the destruction of about 50% of the developing ovaries.

Wake (2007), in a study in eastern South Dakota, asserted a relationship between pollinator limitation and microhabitat. She obtained 100% seed set in hand-pollinated flowers, 44% in a natural population on an open, exposed site, and 18–22% in two populations on sites with relatively tall, dense vegetation.

Other limiting factors often cited include ecological succession, invasion of exotic species, and human disturbance. Plant resources may be directed toward vegetative growth in years of poor capsule production, and due to reported low rates of seed germination and high seedling mortality in many populations, the production of new ramets may represent a significant component of reproduction in this orchid (Curtis 1943; Bowles 1983).

Cypripedium montanum Douglas ex Lindley (Mountain Lady's-Slipper)

Distribution and Habitat

Reported to prefer well drained, moderately alkaline to neutral soils (Light 1998), *C. montanum* tolerates a wide variety of substrates and habitats. It is found in moist to dry open coniferous or deciduous forest usually at high elevation and is distributed from southeastern Alaska and California to Montana and Colorado (Luer 1975; Cribb 1997; Sheviak 2002).

Floral Morphology

Each plant produces up to three large flowers on a leafy stem (Table 5.2). The sepals and lateral petals are greenish to maroon–brown, and the lip is white with purple

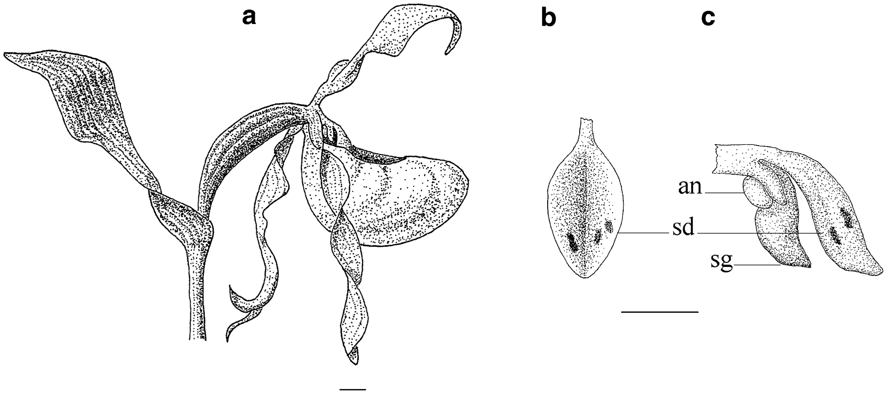

Fig. 5.3 *Cypripedium montanum*. (**a**) Flower, side view, scale bar = 5 mm; (**b**) Staminodium, top view; (**c**) Column, side view, scale bar (**b, c**) = 5 mm. *an* anther, *sg* stigma, *sd* staminodium

spots in the pouch (Cribb 1997). The dorsal sepal is ascending to suberect while the laterals are fused to a bidentate apex; both have slightly undulate margins (Fig. 5.3a). The corolla includes a more or less boat-shaped lip and a pair of spirally twisted lateral petals deflexed 45° from the horizontal. The column is about 1 cm long with a longitudinally conduplicate, with yellow staminode with red spots (Fig. 5.3b, c) (Luer 1975; Cribb 1997). A floral fragrance is produced and has been described as vanilla-like (Urban 1997) or anise-like (Coleman 1995).

Compatibility and Breeding System

The breeding system of this orchid has not been studied. Natural hybrids with *C. parviflorum* (*C. x columbianum* Sheviak) are known (Light 1998; Sheviak 2002). The original cross was probably with *C. parviflorum* var. *pubescens*. These hybrids have a small lip and thus obscure the distinction between the varieties of *C. parviflorum*. See Sheviak's (2002) discussion of the latter for more detailed information.

Pollinators and Pollination Mechanisms

One pollinator may be a small, black-banded bee tentatively assigned to the genus *Lasioglossum* (Halictidae). According to Luer (1975), it entered the lip and later emerged from the exit hole under the anther. A bumblebee (*Bombus* sp.) also tried to enter but was too large to force its way in. Vance (in Bernhardt and Edens-Meier 2010) reported pollination by unspecified, small- to medium-sized bees (5–10 mm long).

Fruiting Success and Limiting Factors

Coleman (1995) found 61(17–83)% fruit set in three large California populations over a four-year period, Vance (in Bernhardt and Edens-Meier 2010) reported that 75–85% produced fruit at an undesignated site, and Kaye (1999) reported 30–50% fruit set over a three-year period in southwestern Oregon. Variation in the latter was attributed, at least in part, to changing climatic conditions. Despite the relatively high levels of fruit production, Kaye (1999) observed very low levels of seedling recruitment in variously managed forest plots over 15-years of observation. Huber (2002) reported a balance of shade and sunshine, as found in small forest openings, to be best for seedling recruitment in northeastern Oregon. Direct sunlight resulted in excessive loss of soil moisture and desiccation of young leaves, while much more than 60% shade inhibited photosynthesis and resulted in soils too cool to stimulate germination.

Resources did not appear to be limiting at Kaye's site. An average of 7–21% of the plants remained dormant, but flowering or fruiting plants were no more likely to go dormant the next year than non-flowering plants. Moreover, reproductive plants were more likely to flower and less likely to die the following year (Kaye 1999).

Urban (1997) reported predation by elk and deer in the Umatilla National Forest of Oregon; however, the lower parts of the plant were not harmed and continued to produce photosynthate for the next flowering season. Human predation, where the plant was picked at ground level or dug-up, was a bigger problem. Additional losses resulted from disturbances such as logging and other forms of habitat destruction (Coleman 1995; Urban 1997; Seevers and Lang 1998).

Cypripedium kentuckiense C. F. Reed (Ivory Lady's-Slipper, Purloined Slipper)

No information is available on the pollination biology of this orchid. In a six-year study of over 1,000 flowers from populations across four southern states, Covell and Medley (1986) found two plusiine noctuid moths, *Polychrysia morigera* (Edwards), a species that is apparently expanding its range from the west, trapped in the labellum of one flower in Tennessee and a single unidentified species of the large carpenter bee *Xylocopa* Latreille in the labellum of another plant in Arkansas.

The very large flowers (lip 53–65 mm long), the ivory to pale yellow lip with a uniquely configured orifice (Sheviak 2002), and the presence of acetates distinct from the floral attractants found in the closely related *C. parviflorum* and similar to those found in the European *C. calceolus* var. *calceolus* (Barkman et al. 1997) suggest that a study of pollination in this species might be of interest.

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Chapter 6
Sections Arietinum and Enantiopetalum

Abstract *Cypripedium arietinum* is an outcrossing species but is chiefly dependent on vegetative reproduction by offshoots. Known pollinating agents are female halictid bees of the genus *Lasioglossum*. Low effective population sizes contribute to genetic drift and a lack of genetic variation within populations. *Cypripedium fasciculatum* is self-compatible, and some clonal transfer of pollen is likely, but the principal mode of sexual reproduction is outcrossing. Autogamy and agamospermy are absent. *Cinetus* is the only known pollinator. The relationship between pollination rates and population size and the relevance of inflorescence size to male and female components of reproductive success are examined along with factors affecting the level of seedling recruitment.

Keywords *Cypripedium arietinum* • *Cypripedium fasciculatum* • Halictid bees • Diapriid wasps • Genetic drift • Glacial bottleneck • Genetic variation • Effective population size • Seedling recruitment

Arietinum

Section Arietinum includes two species. One is found in northern Burma and China; the other is restricted to our flora.

Cypripedium arietinum R. Brown (Ram's Head Lady's-Slipper)

Distribution and Habitat

Showing a preference for cool, well-drained, sub-acidic or neutral soil, *C. arietinum* occurs sporadically on moist hummocks in shady coniferous fens and swamps or in mesic to dry open woodlands. It is distributed from Saskatchewan and Manitoba

C.L. Argue, *The Pollination Biology of North American Orchids: Volume 1: North of Florida and Mexico*, DOI 10.1007/978-1-4614-0592-4_6,

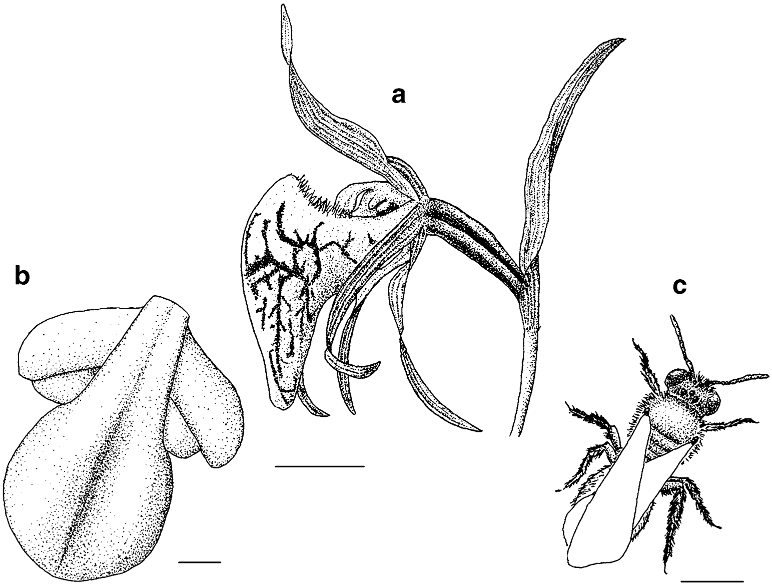

Fig. 6.1 *Cypripedium arietinum.* (**a**) Flower, side view, scale bar = 5 mm; (**b**) Column, top view – note staminodium, filaments, and anthers, scale bar = 1 mm; (**c**) *Lasioglossum coeruleum* female, scale bar = 2 mm

Table 6.1 Data on sections Arietinum and Enantiopetalum (Sheviak 2002)

Character	*C. arietinum*	*C. fasciculatum*
Plant height (cm)	10–35	6–35
Flower number	1(–2)	(1-)2–4(–7)[a]
Dorsal sepal (mm)	15–25 × 5–10	13–25 × 3–8
Lateral sepals (mm)	12–20 × 1.5–4	11–23 × 4–9
Lateral petals (mm)	11–24 × 1–2	10–23 × 6–17
Lip length (mm)	10–16	8–14(–25)
Chromosomes (2n)	20	20

[a] Ferguson et al. (2005) say 1–7, usually 2–3

through the Great Lakes to the Maritime Provinces, New England, and New York (Luer 1975; Cribb 1997; Brzeskiewicz 2000; Sheviak 2002).

Floral Morphology

This orchid produces a small, usually solitary flower on a slender, leafy stem (Fig. 6.1a) (Table 6.1). The sepals are purple green. The dorsal is concave, and the laterals are free and deflexed (Cribb 1997; Sheviak 2002). The lateral petals are erect or deflexed, sometimes spirally twisted, and colored like the sepals. The lip is white and reticulated with purple or crimson markings (Fig. 6.1a). It has a distinctive obliquely conical shape and a small, central opening 1–2 mm in diameter that is further constricted by long trichomes. The exit holes are also small, about 1 mm wide. The column is short, and the staminode is greenish and resembles a fertile stamen (Fig. 6.1b) (Luer 1975; Case 1994; Cribb 1997). The lateral sepals, petals, and labellum generate a light, sweet odor (Stoutamire 1967).

Compatibility and Breeding System

Sexual reproduction occurs by outcrossing (Stoutamire 1967). Autogamy is absent (Catling 1983). *Cypripedium arietinum* produces large numbers of seeds, but according to Stoutamire (1964) and Brower (1977) reproduction is primarily vegetative by means of offshoots. Seed production is, of course, necessary for the establishment of new colonies.

Pollinators and Pollination Mechanisms

Stoutamire (1967) found the pollinating agents in Ontario to be small, short-tongued, female halictid bees of genus *Lasioglossum* (*Dialictus*) (*L. coeruleum* Robertson (Fig. 6.1c) and a second unidentified species). The bees, attracted by scent, landed on or near the signal patch, a contrasting white, pubescent area that surrounds the small opening to the interior of the lip. They then entered the lip, where they remained for one to two minutes and emerged from the anther opening carrying a pollen deposit on their dorsal thorax.

Unfertilized flowers remained in good condition for about a week. However, soon after fertilization, the dorsal sepal closed over the opening in the labellum. Luer (1975) suggested that this functions to prevent the entrance of additional pollinators. Although the inflorescences are usually one-flowered, several stems from a short rhizome may be clustered together (Cribb 1997), and the diversion of a pollinator to unpollinated flowers of the same clone could be positively selected.

Fruiting Success and Limiting Factors

A minimum plant height of about 11 cm seems to be a prerequisite to flowering (Bender 1989). The percentage of plants that produced flowers ranged from 3.6 to 25.3% over an eight-year period in Michigan (Bornbusch et al. 1994) and 22–44% one year in several Wisconsin populations (Penskar and Higman 1999). The levels of fruit production in Wisconsin were also low (Bender, personal communication to Bornbusch et al. 1994). Although some plants became vegetative for one or more years between flowering seasons, the possible effects of resource and pollinator limitation have not been studied.

Low levels of flower and fruit production may reduce the effective size of the population, contributing to genetic drift and a lack of genetic variation within populations (e.g. Bornbusch et al. 1994; Case 1994; Tremblay and Ackerman 2001). According to Tremblay et al. (2005), genetic drift in combination with episodic selection in effectively small, pollen-limited populations with low gene flow may account for much orchid diversity (but see, e.g. Forrest et al. 2004; Waterman and Bidartondo 2008). Although geographic differences apparently occur (Tremblay et al. 2005), Case (1994) demonstrated levels of intraspecific genetic variation within and between Michigan populations of *C. arietinum, C. reginae, C. acaule,* and *C. candidum* that were surprisingly low for animal vectored, obligate cross-pollinating plants. In fact, both Case (1994) and Bornbusch et al. (1994) found a total lack of variation in *C. arietinum*. Although founder effect and genetic drift might be invoked to explain low levels of intrapopulation variation, they cannot account for low species level diversity. Moreover, *C. parviflorum*, with life history features similar to *C. arietinum*, is characterized by high levels of variation (Klier et al. 1991; Case 1994) (this variation is a result of a high level of diversity within each variety, not the inclusion of divergent infraspecific taxa). Case (1994) suggested that glacial disturbances may have contributed to the reduction of variation in ecologically and geographically restricted populations of these four species. That is, today's populations may be derived from genetically depauperate ancestral populations following isolation and a severe reduction in size.

Case cautioned that her findings might apply only to *Cypripedium* populations in the Great Lakes area, but Bornbusch et al. (1994) have obtained similar results in New England populations of *C. arietinum* and *C. acaule*. Further work is needed to fully explain the genetic structure of these populations, but historical events (glacial bottlenecks) and low flower and fruit production (resulting in lower effective population sizes) have characterized *Cypripedium* populations over the long term. Relatively low levels of genetic variation may therefore pose less of a short-term threat than the availability of suitable habitat.

Preferring mid-successional forests, *C. arietinum* can be shaded out by a developing canopy (Case, personal communication to Brzeskiewicz 2000). On the other hand, like many other orchids, it may be intolerant of increased sunlight following excessive thinning and clear-cutting (Ostlie 1990). Many colonies are threatened by forest fragmentation, loss of habitat to development, and changes in drainage patterns (Brzeskiewicz 2000). Predation by insects, cattle, and especially deer is significant in reducing reproductive success in some areas (Brzeskiewicz 2000). Plants damaged by browsing frequently fail to emerge the following year (Ostlie 1990). Next to habitat loss, illegal collecting is perhaps the biggest threat to this and many other orchids. Commercial cultivation of *C. arietinum* in vitro from seed may provide an alternate source (Steele 1998).

Enantiopetalum

Section Enantiopetalum is monotypic and restricted to the western United States.

Cypripedium fasciculatum Kellogg ex S. Watson (Clustered Lady's-Slipper)

Distribution and Habitat

Cypripedium fasciculatum is a small terrestrial orchid of cool, seasonally dry mountain slopes or moist stream terraces, where it occurs on various substrates, often in partially to fully shaded coniferous forest and thickets (Luer 1975; Elliman and Dalton 1995; Cribb 1997; Latham 1999; Sheviak 2002). Small isolated populations are scattered at elevations of 0–3,200 m from Washington to northern California and east in the mountains to Idaho, Montana, Wyoming, Utah, and Colorado (Brownell and Catling 1987; Fowlie 1988; Coleman 1989).

Floral Morphology

A short rhizome produces 2–10 clustered aerial stems, each bearing a variable number of small, musky-smelling flowers closely spaced in a short arching to nodding raceme (Fig. 6.2a, b) (Table 6.1) (Luer 1975; Coleman 1989; Elliman and Dalton 1995; Latham, 1999). The sepals and petals vary in color from purple–brown to yellowish–green with darker, brownish-purple veins. The lateral petals are flat and spreading. The lateral sepals are fused to a bidentate tip, and the dorsal arches over a nearly spherical, dull yellow–green labellum. The latter is streaked and mottled with red to purple markings, especially around its mouth. The column is short, about 3 mm long. A large, papillate stigma is positioned beneath a smaller (2–3 mm long), pale green to whitish staminode (Fig. 1.2d, e) (Kipping 1971; Luer 1975; Cribb 1997). Another exit holes are only 2 mm in diameter, and the opening to the labellum measures about 5 × 7 mm (Coleman 1995; Knecht 1996). Pollinator size is accordingly restricted. All the flowers of an inflorescence open in less than a week, and individual flowers may remain receptive for more than two (Lipow et al. 2002) and up to five weeks (Knecht 1996). Peak blooming dates (i.e. the date with the largest percentage of open flowers) in April and May varied by as many as 25 days over three years at three study sites in southwestern Oregon (Ferguson et al. 2005). Individuals routinely survive more than thirty years (Lipow et al. 2002), and some studies indicate life spans of over 90 years (Niehaus 1974), but emergence and flowering can be sporadic (Harrod 1994).

Compatibility and Breeding System

Cypripedium fasciculatum is self-compatible, and there is no reduction in fruit set in artificially self-pollinated as compared to cross-pollinated plants (Knecht 1996; Lipow et al. 2002). However, autogamy is absent, and agamospermy is unknown

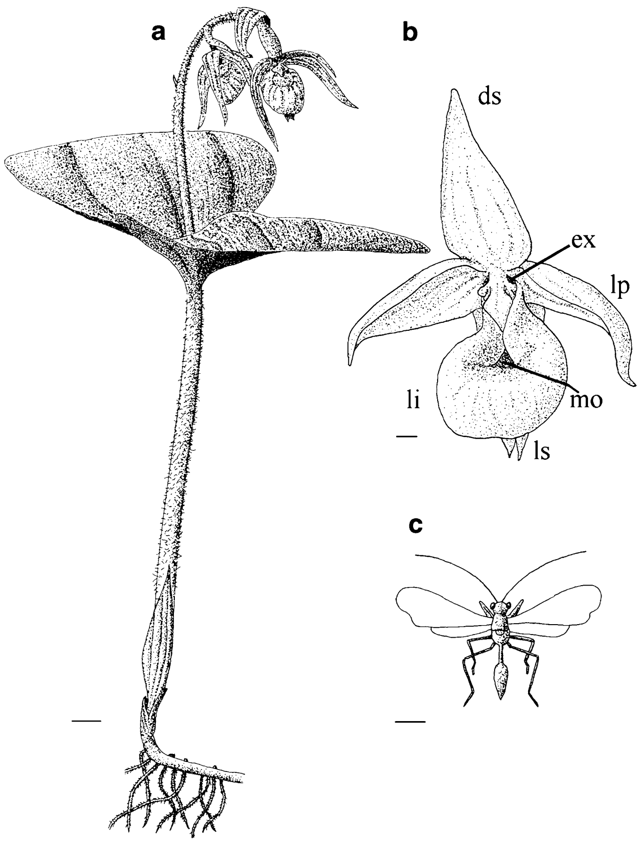

Fig. 6.2 *Cypripedium fasciculatum.* (**a**) Habit, scale bar = 10 mm; (**b**) Flower, front view, scale bar = 1.5 mm; (**c**) *Cinetus iridipennis*, scale bar = 1 mm. *ds* dorsal sepal, *ex* exit hole, *li* lip, *lp* lateral petals, *ls* lateral sepals, *mo* mouth

(Kipping 1971; Harrod and Knecht 1994; Knecht 1996; Lipow et al. 2002; Ferguson et al. 2005).

Although the pollination mechanism in nonautogamous lady's-slippers promotes cross-pollination, the clustered lady-slipper reproduces vegetatively, and some transfer of pollen among members of a single clone undoubtedly occurs. A flowering period with many simultaneously open flowers on each plant provides ample opportunity for pollen transfer among flowers of the same raceme or among racemes of the same clone. Nonetheless, studies of allozyme variation within and between populations imply that the primary mode of reproduction is outcrossing (Aagaard et al. 1999). Either pollination within populations is primarily random or survival of the products of selfing is reduced by some means such as inbreeding depression (Aagaard et al. 1999; Lipow et al. 2002).

Pollinators and Pollination Mechanisms

Recent studies in southwest Oregon identified the pollinator in this area as a tiny (3–4 mm long) parasitic diapriid wasp in the genus *Cinetus* Jurine (Fig. 6.2c) (Ferguson and Donham 1999, 2001; Lipow et al. 2002; Ferguson et al. 2005). This yet-to-be-identified species reached peak activity during anthesis of *C. fasciculatum*, and females were collected carrying pollen smears of the clustered lady-slipper on their sculpted mesonotum (upper surface of the mesothorax or middle segment of the thorax); in one case, the insect was captured emerging from the exit hole at the base of the labellum.

Inconspicuous, purplish–brown flowers with a musky odor are also sometimes pollinated by carrion loving flies, hornets, and beetles (e.g. Kipping 1971; Nilsson 1981; Knecht 1996), but no other insects were seen bearing pollen of this orchid. Although Ferguson and Donham (1999) initially thought that dark-winged fungus gnats (Sciaridae and some Mycetophilidae), found in close association with *C. fasciculatum* and implicated as pollen vectors of other orchids (Mesler et al. 1980), might play a role, they now regard *Cinetus* females as the exclusive pollinators of *C. fasciculatum* in their study area (Ferguson and Donham 2001; Ferguson et al. 2005).

The larvae or pupae of the fungus gnats serve as hosts for diapriid larvae (Gauld and Bolton 1988; Masner 1995). Ferguson et al. (2005) speculate that the flower of *C. fasciculatum* may produce an odor that mimics that of the fungus gnats and that this may prompt female diapriids to enter the labellum in search of their larval hosts. At the same time, wide variation in floral color within populations may increase the number of visits required for diapriids to learn to avoid the flowers.

Ferguson (pers. comm. 2004) has monitored additional populations of clustered lady-slippers in California, Colorado, and Wyoming. Unidentified diapriids show up at all these sites, even though none have, as yet, been found carrying orchid pollen.

Fruiting Success and Limiting Factors

The levels of natural fruit set in *C. fasiculatum* are highly variable. Greenlee (1997) found that a population in Montana's Bitterroot Mountains averaged 0.72 fruits from 2.55 flowers per flowering plant. Knecht (1996) reported that an average of 32% of flowers produced capsules in nine small populations in Washington's Wenatchee Mountains, and Kipping (1971) found 47% of the flowers produced fruit at a site in Nevada County, California. Lipow et al. (2002) recorded levels of fruit set varying from 18% in the White River National Forest of Colorado and 29% in the Nez Perce National Forest of Idaho to 69% in the Siskiyou National Forest of southwestern Oregon. Ferguson et al. (2005) also recorded 56% fruit production from southwestern Oregon, although heavy predation and reduced pollinator activity lowered this level to 13 and 17% in succeeding years.

Experimental studies suggest that pollination service was limiting at several study sites. Lipow et al. (2002) demonstrated a significant increase in fruit set in artificially cross-pollinated as compared to open-pollinated flowers in their Colorado and Idaho populations. Self-pollination experiments, conducted only in Colorado, again produced a significant increase in fruit set when compared to open pollination. Knecht (1996) also observed significantly higher levels of fruit set in hand-pollinated flowers compared to open-pollinated flowers at her study site in east-central Washington. Hand pollinations were not carried out on the Oregon population, but the high level of natural fruit set observed here in some years suggests that fecundity in this population might not always be limited by pollinator visitation rates.

Although more than a one-season study is needed to establish whether pollinators or stored nutrient resources or both are limiting (Campbell and Halama 1993; Primack 1996), we have seen that the pattern of implied pollinator limitation noted by Lipow, Bernhardt, and Vance in Colorado and Idaho and Knecht in Washington has been frequently reported in other orchids that rely on deception. Possible adaptation to pollinator limitation in the clustered lady's-slipper might be further reflected in an observed decrease in fruit set associated with a reduction in pollinator numbers due to fire (Knecht 1996), in synchronous flowering at a time when most other species are not in flower (Latham 1999), and in the long receptivity of the flowers, which maximizes their opportunity for pollination (Primack 1985; Gregg 1991; Neiland and Wilcock 1998).

Lipow et al. (2002) noted that pollination rates were negatively related to population size: the level of fruit set at the Oregon site, where the population was small, greatly exceeded that at the Colorado site, where the population was much larger and denser. A similar inverse relationship is common in other species with non-rewarding pollination systems (Ackerman 1981, 1986; Agren 1996). Presumably, training of the pollinator to the appearance of non-rewarding flowers is more intense and more rapid in larger, denser orchid populations (Lipow et al. 2002; see also Fritz and Nilsson, 1994).

At the same time, the probability of a given flower-producing fruit was not related to the number of flowers present in the inflorescence (Lipow et al. 2002). However, the size of the inflorescence was positively correlated with plant size, and larger plants, with a larger number of flowers, had a higher absolute probability of producing fruit and had more resources to devote to fruit development.

We have noted that low levels of pollination and fruit production in non-autogamous orchids have been associated with a low correlation between fruit or seed production and seedling establishment (Calvo 1993). Knecht (1996) reported both pollinator limitation and poor seedling recruitment for *C. fasciculatum* at her study site in east-central Washington. Plants here produced an average of about 4,300 seeds per capsule, but few were able to establish. Aagaard et al. (1999) speculated that seedlings of this orchid might only become established in the earliest stages of forest succession. The clusters of plants now observed occupying mid- to late-successional stages may represent asexually generated descendents persisting through the production of rhizomatous clones, the apparently separate plants derived by dieback or fragmentation of a branching rhizome. This growth habit and the probable long life span of the clustered lady's-slipper might permit some plants to survive a series of successional stages until suitable habitat for the establishment of seedlings becomes available (Knecht 1996; Aagaard et al. 1999). If so, management to provide early successional habitat would be required for the development of new colonies and the long-term survival of the orchid.

The early succession hypothesis is interesting, but as Aagaard et al. (1999) point out, additional studies are needed to clearly detail how new populations are established and to distinguish between clone members and seedlings in plant clusters sampled from a range of successional stages. Preliminary DNA investigations now suggest that plants more than a few centimeters apart can differ genetically and may be derived from seeds (Liston pers. comm. in Seevers and Lang 1998). Moreover, early successional communities may lack the fungal symbiont(s) necessary for the establishment and early survival of this species (Harrod 1994; Doherty 1997).

Additional studies are also needed on diapriid wasps. The reasons for the dramatic variation in natural fruit set (18–69%) are uncertain, at least in part because diapriid wasp behavior is not understood. Many species of *Cinetus* and other diapriids remain undescribed. The identification and study of individual species and an understanding of their role in the pollination of this orchid across its range must therefore await the construction of a new key to this group.

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Chapter 7
Sections Irapeana and Bifolia

Abstract *Cypripedium californicum* is pollinated by *Ceratina acantha*. Its frequent visits might account for high levels of capsule set in this orchid, but the breeding system has yet to be studied, and the occurrence of autogamy or agamospermy cannot be ruled out. Other visitors include another halictid bee, *Lasioglossum nigrescens,* and a small syrphid fly, *Sphegina occidentalis. Cypripedium guttatum* is pollinated by small halictid bees of genus *Lasioglossum* in China, but none of the implicated bee species are present in North America. Although there are no studies on the pollination of *C. yatabeanum*, apparent introgression with *C. guttatum* indicates the existence of at least one common pollinator.

Keywords *Cypripedium californicum* • *Cypripedium guttatum* • *Cypripedium yatabeanum* • Small carpenter bees • Halictid bees • Syrphid flies • Introgression • Serpentine

Irapeana

Section Irapeana includes four species. One is found in our flora; the others occur in Mexico or Mexico and Central America (Cribb 1997).

Cypripedium californicum A. Gray (California Lady's-Slipper)

Habitat and Distribution

Cypripedium californicum is restricted to northern California and southwestern Oregon where it is often found in forest openings, especially on moist slopes and in marshy areas by mountain streams (Luer 1975; Cribb 1997; Sheviak 2002). It grows on nitrogen-poor serpentine-based soils, frequently in association with the California

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Table 7.1 Data on section Irapeana (Sheviak 2002)

Character	*Cypripedium californicum*
Plant height (cm)	25–120
Flower number	3–8(–22)
Dorsal sepal (mm)	14–20 × 7–13
Lateral sepals (mm)	12–20 × 10–12
Lateral petals (mm)	14–16 × 3–5
Lip length (mm)	15–20

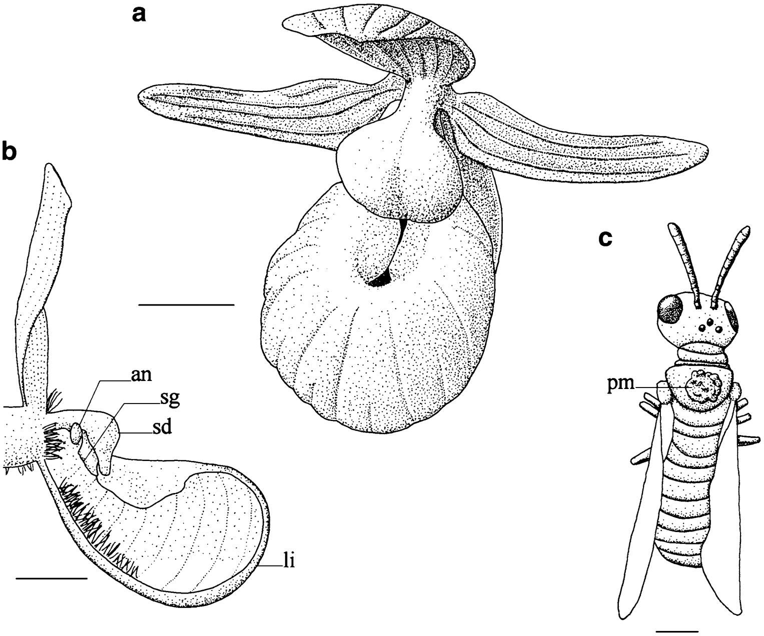

Fig. 7.1 *Cypripedium californicum*. (**a**) Flower, front view, scale bar = 5 mm, (**b**) Flower, sagittal section, scale bar = 5 mm; (**c**) *Ceratina acantha*, scale bars = 1 mm. *an* anther, *li* lip, *pm* pollen mass, *sg* stigma, *sd* staminodium

pitcher plant (*Darlintonia californica* Torrey) (Fowlie 1982; Coleman 1989; Cribb 1997). Limited data are available on its pollination biology.

Floral Morphology

Each leafy stem produces a variable number of small flowers in a loose raceme (Table 7.1) (Kipping 1971; Coleman 1989; Cribb 1997). The lateral petals are yellow–green to pale brownish–yellow and obliquely spreading (Fig. 7.1a). The lip is white and sometimes pinkish or marked with faint purple veins and spots around the orifice. The sepals are colored like the petals; the dorsal is erect, and the laterals are joined below the labellum to a minutely bifid tip. A 5–6 mm long column (Fig. 7.1b) includes a white staminode with green markings. According to Cribb (1997), the floral scent resembles that of *Cyclamen persicum* Mill. or *Convallaria majalis* L. (lily of the valley).

Compatibility and Breeding Systems

No data are available.

Pollinators and Pollination Mechanisms

Kipping (1971) reported that bee visitors were numerous at a study site in Plumas County, California. Small carpenter bees, *Ceratina acantha* Provancher (Fig. 7.1c), visited a single plant with four open flowers 12 times in 1 h. Although only one removed pollen, Kipping considered this insect to be the most likely pollinator at his site. It exhibited unusual behavior including a territorial defense of the area surrounding the labellum that led to attacks against other insects approaching the orchid (Kipping 1971; Nilsson 1979). Kipping (1971) speculated that this behavior was elicited by one or more of the floral fragrance components. Other visitors included another halictid bee, *Lasioglossum nigrescens* (Crawford), and small syrphid flies, *Sphegina occidentalis* Malloch. One of the former was captured as it emerged from an anther exit hole, and several of the syrphids were trapped in labella. Neither species carried any pollen.

Fruiting Success and Limiting Factors

The observed frequency of floral visits might account for the high levels of capsule set observed: 93% of the plants and 76% of the flowers produced fruit. The breeding system, however, has yet to be studied, and the occurrence of autogamy or asexual seed production cannot be ruled out. Abundant fruit production has been unable to compensate for a serious depletion of this orchid by collectors (Coleman 1989).

Bifolia

Section Bifolia includes two closely allied species.

Cypripedium guttatum Swartz (Spotted Lady's-Slipper) and *Cypripedium yatabeanum* Makino (Green Moccasin-Flower)

Cypripedium guttatum occurs outside our flora from eastern Europe to Tibet, *C. yatabeanum*, from Japan to the Kurile Islands. Both have also been reported from boreal regions of North America. *Cypripedium guttatum* is found from Alaska and the Yukon to the Northwest Territories, while *C. yatabeanum* is restricted to Alaska, where it is known from only a few collections (Sheviak 2002). Small halictid bees of genus *Lasioglossum* pollinated *C. guttatum* in southwest China's Yunan Province (Banziger et al. 2005), but none of the implicated bee species are present in North America. There are no studies on the pollination of *C. yatabeanum*; however, the apparent occurrence of introgression with *C. guttatum* (*C.* x *alaskanum* P. M. Brown) indicates the presence of pollen transport between the species and the existence of at least one common pollinator.

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Part II
Subfamily Orchidoideae (Part One)

The subfamily Orchidoideae is a large natural grouping of orchid species with a worldwide distribution. In addition to features not directly related to pollination biology, members share a single bilocular anther and 2–4 sectile pollinia attached by stalks to one or two viscidia. Included are seven tribes and about 3,630 species each commonly having one to many often showy flowers arranged in an erect or arching terminal inflorescence. Two tribes are represented in our flora: the Orchideae, considered below, and the Cranichideae, treated in Vol. 2.

Tribe Orchideae

Members of tribe Orchideae frequently have a three-lobed lip with or without a basal spur, a small rostellum, two viscidia, more or less prominent caudicles, and erect anthers. The tribe includes about 62 genera and roughly 1,800 species common in north temperate and tropical regions of both the Eastern and Western Hemispheres. Nine genera are present in the North American flora north of Mexico and Florida.

Chapter 8
Platanthera L., Introduction

Abstract Preliminary descriptions of pollination mechanisms, breeding systems, floral morphology, and pollinator behavior are provided for the genus *Platanthera*. Viscidia separation and spur length reflect divergent selection for pollinators that extract pollinaria on their proboscises or compound eyes. Reproductive success is often limited by the availability of pollinators and suitable microsites for seedling recruitment. Evolutionary changes in viscidia placement, principal pollinators, flower color, fringing of the labellum, and nectar-spur length are discussed.

Keywords *Platanthera* • Divergent selection • Pollinator limitation • Seedling recruitment • Viscidia placement • Pollinator segregation • Molecular data

Platanthera is a genus of about 500 species widely distributed over Europe, North Africa, Asia, New Guinea, and North and Central America (Pridgeon et al. 2003). About 23 species occur in our flora. The flowers are usually resupinate and occur in solitary, terminal, loose to sometimes dense cylindrical racemes that open acropetally (i.e. with the oldest flowers at the base) (Case 1987; Sheviak 2002). The perianth, often green and inconspicuous, can be very showy in some species. The sepals and petals are free from one another and the latter usually converge with the dorsal sepal to form a hood or bonnet over the column; the lateral sepals are frequently spreading or recurved (Case 1987). The labellum is trilobed, variable in shape, and extended basally into a nectar spur (Sheviak 2002). The column is short and bears an immobile, erect anther with two anther sacs (Luer 1975). These are sometimes called half-anther cells as they are often widely separated by connective tissue (e.g. Figs. 9.2d and 11.1a). Each anther sac produces a club-shaped pollinium attached by a narrow stalk or caudicle to a naked viscidium (i.e. a viscidium not enclosed in a purse-like sac, the bursicle) (e.g. Figs. 9.1d and 9.2b) (Luer 1975; Smith and Snow 1976; Robertson and Wyatt 1990a). The viscidia are borne on rostellar lobes with

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one viscidium positioned on either side of the opening to the nectar spur (e.g. Figs. 9.2d and 10.2a, b). A stigma is located directly above the entrance to the spur and beneath and between the half-anther cells.

Most species of *Platanthera* are adapted to outcrossing or facultative outcrossing. The transfer of pollen within a flower or an inflorescence or a clone can result in reduced fruit set and/or seed viability. Intrafloral self-fertilization in the absence of a pollinator (autogamy) sometimes occurs, but is relatively rare. The most common pollinators are Lepidoptera with Diptera and Hymenoptera, the primary pollinators of several species. Some geographic tendencies are apparent. Smaller moths, wasps, mosquitoes, and flies are more frequent pollinators in arctic and alpine regions, while larger Lepidoptera are relatively more important in the south and may service species with more restricted distributions (Catling and Catling 1991).

The pollination mechanism is similar in all insect-pollinated species. The insect locates the spur opening and inserts its proboscis. The viscidia, borne on rostellar lobes, are positioned to contact and adhere to either the compound eyes or the proboscis of the vector (e.g. Figs. 11.6a, b and 11.7a, b). One or both pollinaria are extracted from the half anther cells as the insect withdraws from the flower (e.g. Smith and Snow 1976; Robertson and Wyatt 1990a, b). As the stalk or caudicle of the pollinarium dries, it rotates, positioning the pollinium to contact the stigmas of subsequently visited flowers (Luer 1975; Cole and Firmage 1984).

Differences in the length of the spurs and the distances between the viscidia reflect divergent selection for different pollinators (Nilsson 1978, 1983, 1988; Sheviak and Bowles 1986). Placement of the pollinaria on the eyes, of course, requires that the relationship of proboscis and spur length results in insertion of the proboscis deep enough to bring the eyes of the pollinator into contact with the viscidia. At the same time, a sufficient separation of the viscidia is needed to bring one or both into contact with the eyes of the pollinator (Sheviak and Bowles 1986). Placement on the proboscis requires a closer spacing of the viscidia but is less sensitive to spur length and unrelated to distance across the eyes.

Sheviak and Bowles (1986) proposed that placement of the pollinaria on the eyes represents the ancestral condition in *Platanthera*. This view, supported by biogeography, seems to make evolutionary sense. Placement on the proboscis permits removal of the pollinaria by a broader range of pollinators and results in less wasteful nectar production when compared to flowers with the more exacting requirements of eye placement. On the other hand, phylogenetic inferences based on a study of nuclear ribosomal DNA (the rapidly evolving internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA (nrDNA) were analyzed) imply that placement of viscidia on the eyes has arisen convergently from placement on the proboscis at least once in each monophyletic group (clade) (Fig. 8.1). Maad and Nilsson (2004) studied pollination efficiency in the Old World species pair *P. bifolia*, with proboscis attachment, and *P. chlorantha*, with eye attachment. Although pollen export was more efficient in *P. bifolia*, pollen import was up to four times faster in *P. chlorantha*. They considered this, along with an associated increase in stigmatic surface area, to provide selective pressure favoring a floral shift from proboscis to eye attachment. Adaptive evolution in both directions is functionally possible (Nilsson 1981), however, and the molecular data suggest that at least two reversals

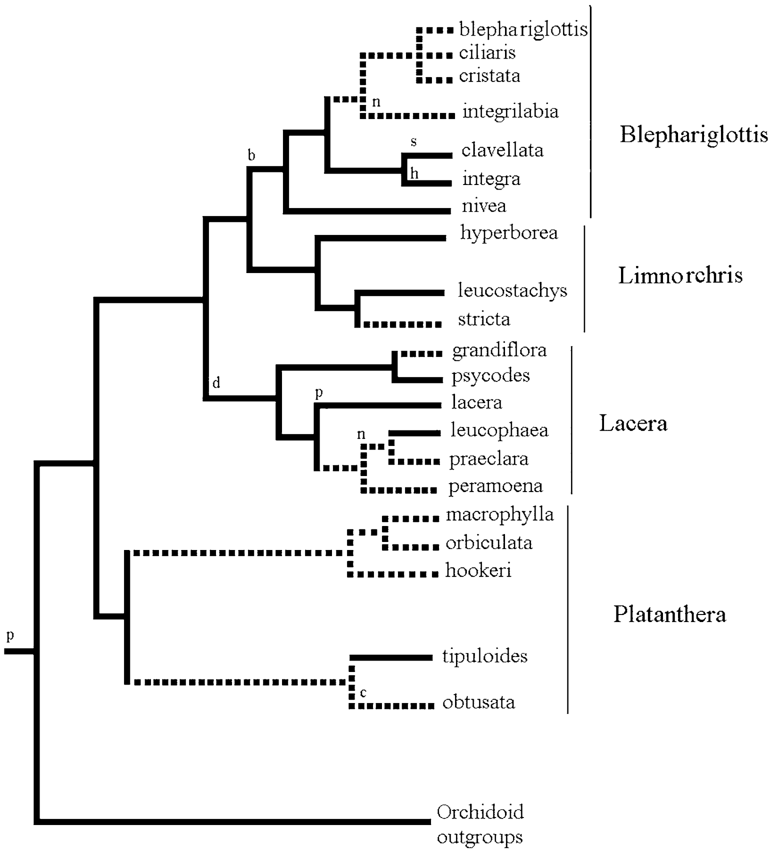

Fig. 8.1 Phylogenetic reconstruction of *Platanthera* species. Solid lines indicate attachment of pollinaria to the proboscis, interrupted lines to the compound eyes. The Platanthera clade is highly condensed. Only 5 of 15 species resolved in this clade are North American, and independent origins of eye placement are shown symbolically at the base of the clade. Letters denote principal pollinators. *b* butterfly, *c* culicid, *d* diurnal sphingid, *h* bee, *n* nocturnal sphingid, *p* nocturnal settling moth, *s* self-pollinated. I thank Cambridge University Press for permitting use of this cladogram, modified and condensed from Hapeman and Inoue (1997)

have occurred in the genus (Fig. 8.1) (Hapeman and Inoue 1997). A more recent hypothesis contends that proboscis deposition may have arisen through neotony, and proboscis and eye deposition may be related through a cyclical speciation system blind to cladistic analysis (Sheviak 2010). In any event, shifts in pollen placement seem to have played an important role in *Platanthera* speciation, leading to closely related species pairs established and maintained by pollinator segregation.

Hapeman and Inoue's (1997) molecular data suggest that pollination by nocturnal settling moths (i.e. noctuids and pyrolids) represents the ancestral condition in the genus (Fig. 8.1). This view is consistent with the interpretations of van der Pijl and Dodson (1966), Nilsson (1983), and Dressler (1993).

A shift to diurnal hawkmoth pollination may have occurred only once, at the base of the Lacera clade (Fig. 8.1). Similarly, butterfly pollination has apparently developed only once, arising from nocturnal settling moth pollination at the base of the Blephariglottis group (Fig. 8.1). In addition to a change in color (discussed below), both of these pollination syndromes required many morphological changes related to the positioning of the viscidia and the presentation of pollinator stimuli (Hapeman and Inoue 1997).

On the other hand, pollination by nocturnal hawkmoths seems to have arisen independently twice among taxa in our flora. It was derived from diurnal hawkmoth pollination in the Lacera group and from butterfly pollination in the Blephariglottis group (Hapeman and Inoue 1997). However, the latter transition remains to be confirmed and may be incomplete (Zettler et al. 1996).

Dipteran pollination arose from nocturnal settling moth pollination in the *Platanthera* group, and although not evident in Fig. 8.1, it occurs in other groups as well. Only minor floral changes are required in the shift from nocturnal settling moths to dipterans, possibly only in odor and length of the spur (Hapeman and Inoue 1997). Flowers pollinated by dipterans are morphologically similar to those pollinated by small moths, and according to Thien and Utech (1970), Voss and Riefner (1983), and Catling and Catling (1991), all *Platanthera* flowers pollinated by flies or mosquitoes are also pollinated by moths.

Hapeman and Inoue (1997) expressed some doubt about the presence of a bee pollination syndrome in *Platanthera*. Although bee pollination occurs in the *Blephariglottis* and *Limnorchis* groups (shown only for the former in Fig. 8.1), butterflies and/or moths pollinate the same species. Even so, Folsom (1984) and Luer (1975, citing Stoutamire without reference) have identified additional members of the Blephariglottis group, including *P. cristata*, that appear to be pollinated primarily by bumblebees (see below).

The primitive flower color in *Platanthera* is green with a transformation to greenish–white occurring a number of times (Hapeman and Inoue 1997). White flowers have arisen independently eight times in five sections. According to Hapeman and Inoue (1997), greenish–white flowers are typically pollinated by moths (noctuids and pyralids) and white flowers by hawkmoths or noctuids. Bright flower colors occur only in diurnally pollinated species: yellow- and orange-colored flowers occur in the Blephariglottis group and purple in the Lacera group (Hapeman and Inoue 1997). Yellow and orange are primarily associated with butterfly pollination and purple with diurnal hawkmoths of the genus *Hemaris* Dalman. Experimental studies with *Hemaris thysbe* (Fabricius) have revealed a strong preference for purple to purplish–pink flowers in other plants (Fleming 1970), and Hapeman and Inoue (1997) believe that diurnal hawkmoth pollination may have exerted strong selection for the evolution of purple flowers in *Platanthera*.

Fringing of the labellum and petals has arisen twice and is convergent in the Blephariglottis and Lacera groups (Hapeman and Inoue 1997). Of nine fringed species of *Platanthera*, seven are pollinated wholly or partly by hawkmoths, and in the Lacera clade, the amount of fringing appears correlated with the frequency of hawkmoth pollination (Stoutamire 1974; Hapeman and Inoue 1997). Since some deeply fringed species of *Platanthera*, including *P. leucophaea* and *P. praeclara*, are apparently pollinator limited (Inoue 1983; Cuthrell 1994), the selection pressure for fringing might be high if it increases pollination frequency (Hapeman and Inoue 1997).

The trend in nectar-spur length has generally been from short to long (Hapeman and Inoue 1997). However, reversals have occurred in species pollinated by dipterans and bees. The evolution of spurs exceeding 2.5 cm in length appears to have occurred independently several times in species pollinated by hawkmoths and papilionid butterflies (Hapeman and Inoue 1997).

Reproductive success in *Platanthera* is often limited by the availability or activity of pollinators, by suitable microsites for seedling recruitment, and by other circumstances to be described below. Additional factors limiting or threatening populations of many species include predation, the invasion of exotic species, erratic flowering, the absence of required fungal symbionts, removal by collectors, and the loss of habitat due to successional changes or agricultural expansion, timber harvesting, and wetland drainage (e.g. Wallace 2002).

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Chapter 9
Limnorchis Group

Abstract *Platanthera aquilonus* is largely autogamous but not agamospermous. Autogamy is facultative, and mosquitoes sometimes act as vectors, the pollinaria attaching to their eyes. *Platanthera dilatata* and *P. huronensis* are outcrossing or geitonogamous with pollinaria positioned to attach to the pollinator's proboscis. *Platanthera huronensis* is pollinated by a variety of insects. *Platanthera stricta* is self-compatible, but outcrossing produces seeds with a higher percentage of normally developed embryos. Autogamy and agamospermy are absent. *Platanthera sparsiflora* is pollinated by small moths. A medial labellar ridge forces lateral entrance to the nectar spur, resulting in pollinaria attachment to the proboscis.

Keywords *Platanthera dilatata/Platanthera aquilonis/Platanthera huronensis* • *Platanthera hyperborea* • *Platanthera stricta* • *Platanthera sparsiflora* • Paternal selection • Restricted pollen acquisition and deposition • Intrasexual competition • Intersexual mate choice • Mosquitoes and small moths

The *P. hyperborea* (L.) Lindley complex historically included a large group of species and varieties with a worldwide distribution and many, often poorly delineated, intermediate forms. Taxonomic approaches have varied from treatment of the entire group as a single polymorphic species to its segregation as a separate genus embracing 20 or more species, a choice supported, in part, by seed morphology (Gammara et al. 2008). Luer (1975) treated the North American taxa as five variable species in a single section (*Limnorchis*). He included *P. dilatata* (Pursh) Lindley (including *P. leucostachys* as a variety), *P. hyperborea* (L.) Lindley, *P. stricta* Lindley, *P. sparsiflora* (S. Watson) Schlechter, and *P. limosa* Lindley. In the World Checklist of Monocotyledons (2008) *P. dilatata* (Pursh) Lindl. ex L. C. Beck is transferred to *Piperia dilatata* (Pursh) Szlach and Rutk. var. *dilatata*, but Sheviak (2002) included it in *Platanthera*, and his treatment is followed here.

Plants in much of North America that were long known as *P. hyperborea* are now recognized as a new species, *P. aquilonis* Sheviak (Sheviak 1999, 2002; Sears 2008).

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Platanthera hyperborea, currently restricted to Arctic and Subarctic regions, is very similar to another species, *P. huronensis* (Nuttall) Lindley, sometimes treated as a variety of *P. hyperborea* (e.g. Luer 1975). It is evidently distinct from the latter at the species level (Sheviak 2011) and intermediate between *P. aquilonis* and *P*. *dilatata* in flower color and morphology (Catling and Catling 1997). In a quantitative analysis of specimens from the Canadian Rocky Mountains, Catling and Catling (1997) found support for a hybrid origin of *P. huronensis*, as proposed by Schrenk (1975, 1977, 1978), and for its recognition as a distinct taxon. According to these authors it arose as a hybrid of *P. dilatata* and *P. aquilonis*, and a study of nuclear and chloroplast DNA markers supports this interpretation (Wallace 2003). Little information is available on the pollination of well-determined plants of *P. hyperborea*; what is known is summarized below under "Other species of the Limnorchis Group."

In addition, *P. tescamnis* Sheviak and Jennings, recently segregated from *P. sparsiflora* (Sheviak and Jennings 2006); *P. purpurascens* (Rydberg) Sheviak and W. F. Jennings (*P. hyperborea* (L.) Lindley var. *purpurascens* (Rydberg) Luer), *P. brevifolia* Greene (*P. sparsiflora* var. *brevifolia* (Greene) Luer), *P. zothecina* (L. C. Higgins and S. L. Welsh) Catling and Sheviak, and *P. yosemitensis* Colwell, Sheviak, and Moore, just distinguished from *P. purpurascens* (Colwell et al. 2007), are treated here as members of this group. *Platanthera convallariifolia* (Fischer ex Lindley) Rydberg, otherwise known from Asia, has been reported from the Aleutians and the Alaska Peninsula. However, these plants intergrade with *P. huronensis*, and it is unclear if they are truly referable to *P. convallariifolia* (Sheviak 2002).

Platanthera dilatata **(Pursh) Lindley ex L. C. Beck (Tall White Northern Bog Orchid),** ***P. aquilonis*** **Sheviak (Northern Green Orchid), and** ***P. huronensis*** **(Nuttall) Lindley (Tall Green Bog Orchid)**

Habitat and Distribution

All three species are commonly found in marshes, fens, wet meadows, and tundra (Luer 1975; Catling and Catling 1997; Sheviak 2002). *Platanthera dilatata* also occurs in bogs and *P. aquilonis* in deeply shaded, mesic, deciduous forest. *Platanthera huronensis* often occupies sites intermediate between the fens and other permanently wet sites occupied by *P. dilatata* and the intermittently dry sites favored by *P. aquilonis.*

Platanthera dilatata is distributed from Newfoundland to Alaska and extends south at high elevations in the West to California and New Mexico. In the East it reaches Minnesota, Illinois, Indiana, Pennsylvania, and New England, becoming increasingly rare toward the southeastern limits of its range. *Platanthera aquilonis* occurs from Newfoundland to Alaska and south to New Jersey, Illinois,

Table 9.1 Data on the Limnocharis group (*Platanthera aquilonis* complex), part 1 (Sheviak 2002)

Character	*P. aquilonis*	*P. dilatata*	*P. huronensis*
Plant height (cm)	5–60	11–130+	10–100+
Dorsal sepal (mm)[a]	3–7 × 1.5–4	3–7 × 1.5–4	
Lateral sepals (mm)[a]	3–9 × 1–3.5	3–9 × 1–3.5	
Lateral petals (mm)[a]	3–8 × 1–4	3–8 × 1.5–4	
Lip (mm)[a]	2.5–6 × 2–3	4–11 × 2–5	5–12 × 2–4
Spur length (mm)	2–5	2–20	4–12
Column (mm)[a]	1.5–2 × 1–1.5	1.5–3 × 1–2	
Anther separation[b]			
Apical/basal	0.06 (0.0–0.2)	1.24 (0.9–2.0)	0.5 (0.1–1.3)
Chromosomes (2n)	42	42	84

[a] Luer (1975)

[b] Catling and Catling (1997)

Nebraska, and New Mexico. *Platanthera huronensis* is found from Newfoundland and Manitoba to New Jersey. Pennsylvania, Michigan, and Minnesota in the East and from southern Alaska and Alberta to New Mexico in the West.

Floral Morphology

The flowers are resupinate, variable in color and size (Table 9.1), and arranged in elongate, cylindrical racemes (Luer 1975; Catling and Catling 1997; Sheviak 1999). The lateral petals and dorsal sepal form a hood over the column (Figs. 9.1a–c and 9.2a, d). The lateral sepals are reflexed or spreading. The lip is rhombic-lanceolate to linear-lanceolate with an obtuse or rounded apex and is variously dilated at its base, more so in *P. dilatata* than in *P. huronensis* or *P. aquilonius.* It is extended below into a decurved, cylindrical to sometimes slightly clavate (club-shaped) nectar spur (Figs. 9.1b, c and 9.2a, d). Significant interspecific differences occur in lip and spur length (Table 9.1). The column is small with the stigma located centrally above the spur opening and a pair of variously diverging half anther sacs positioned above the stigma (Figs. 9.1a, e and 9.2c, d) (Larson 1992; Catling and Catling 1997). A pair of viscidia is located close to but slightly above and to each side of the spur opening. The viscidia are large and oblong in *P. huronensis*, linear to oblong in *P. dilatata*, and orbicular to sometimes lacking in *P. aquilonis* (Figs. 9.1d–f and 9.2b, c) (Larson 1992; Sheviak 2002).

According to Kipping (1971) and Luer (1975), the flowers of *P. dilatata* release a strong and musky-sweet or clove-like floral fragrance. Sheviak (1999) described a sweetly pungent scent of varying intensity in *P. huronensis.* He reported a similar scent for the flowers of *P. aquilonis* except in Alaska where he detected no odor at all. Stoutamire (1968) described flowers of the latter as odorless or ill smelling. Lange (1887) reported a *Dianthus*-like odor; and Porsild (1930), Thien (1971), and Lojtnant and Jacobsen (1976) noted a strong, distinctive aroma emitted at dusk.

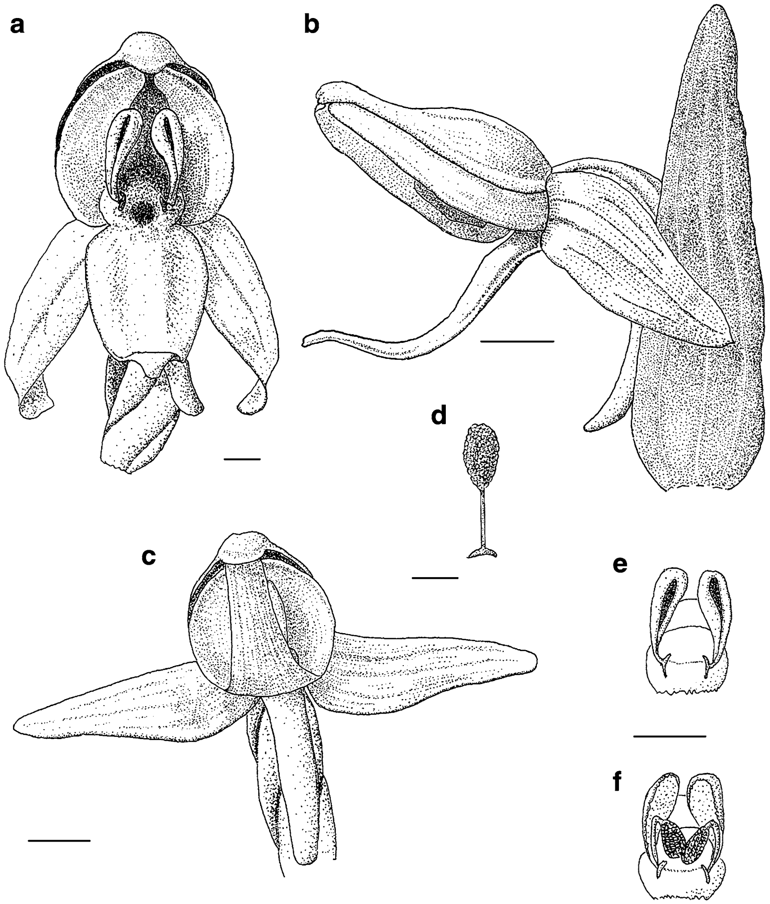

Fig. 9.1 *Platanthera aquilonis*. (**a**) Flower, front view with fully expanded lip, scale bar = 1 mm. (**b**) Flower, side view with fully expanded lip, scale bar = 1.5 mm; (**c**) Flower, front view with lip still in contact with the dorsal sepal, scale bar = 1.5 mm; (**d**) Pollinarium, scale bar = 0.5 mm; (**e**) Column with pollinaria retained in the anther; (**f**) Column showing pollinaria with bent caudicles depositing pollen on stigma, scale bar (**e**, **f**) = 1 mm

Compatibility and Breeding System

Although some outcrossing can occur, *P. aquilonis* is self-compatible and autogamous but not agamospermous (Gray 1862a, b; Guignard 1886; Hagerup 1952; Lojtnant and Jacobsen 1976; Catling 1983; Sheviak 1999; Wallace 2006). According to Catling (1990), it is a colonizing species, and selection might therefore be expected to favor an autogamous breeding system (see discussion under *Cypripedium passerinum*, above, and *Spiranthes ovalis* var. *erostellata*, volume 2). Autogamy

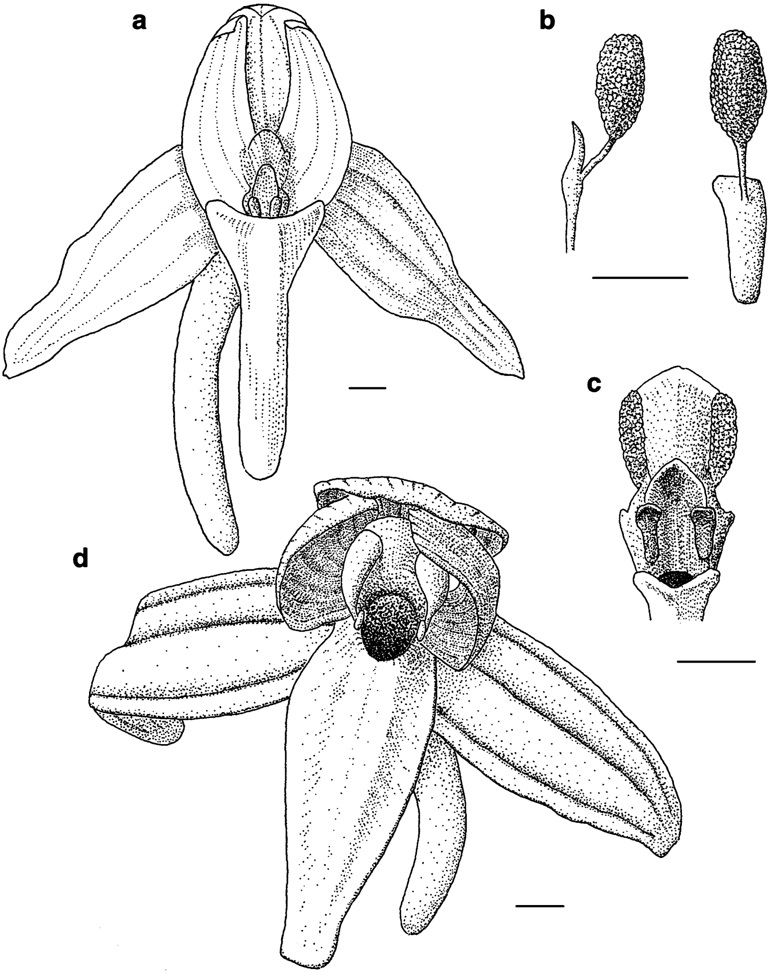

Fig. 9.2 (**a**–**c**) *Platanthera dilatata*. (**a**) Flower, front view; (**b**) Pollinarium, side view (*left*) and back view (*right*); (**c**) Column. (**d**) *Platanthera huronensis*, flower, front view, scale bars = 1 mm

reduces hybridization with *P. dilatata* and *P. huronensis*, and *P. aquilonis* is usually more clearly delineated than either of these species (Catling and Catling 1997).

In contrast to large hybrid swarms reported around the Great Lakes (Luer 1975; Case 1987), Wallace (2006) found that hybridization of *P. aquilonis* and *P. dilatata* (*P.* x *media*) was not a regular occurrence in Maine. She suspects that some plants identified as *P.* x *media* in other studies may have been *P. huronensis* or morphological variants of *P. aqulionis* or *P. dilatata* and recommends further studies to evaluate the cytological and molecular differences between *P. huronensis* and *P.* x *media.* Sheviak (2011) considers them synonymous.

Data on the breeding system of *P. dilitata* are limited, but Gray (1862a) noted that, unlike *P. aquilonis*, the structure and positioning of the column components largely preclude autogamy. Sheviak (1999) studied cultivated plants covering the range of this species, found them to be outcrossing, and confirmed Gray's observations.

Catling and Catling (1989) reported outcrossing and geitonogamy for *P. huronensis*, while Reddoch and Reddoch (1997) reported autogamy. Sheviak (2011) found evidence of effective autogamy in only a few plants from Colorado and Montana. He allows that autogamous individuals might exist elsewhere or that populations in some regions might hybridize with *P. aquilonis* producing offspring that reproduce like the latter (Sheviak 2002). This might account for auto-pollinating plants observed by Catling and Catling (1997) that have anthers characteristic of *P. huronensis* but otherwise closely resemble *P. aquilonis*.

Platanthera dilatata has $2n = 42$ chromosomes, as does *P. aquilonis*, whereas *P. huronensis*, a possible allotetraploid, has $2n = 84$ (Humphrey 1933, 1934; Bent 1969). This difference may serve as one factor maintaining these species against the effects of hybridization. Backcrossing could occur between *P. huronensis* and both *P. aquilonis* and *P. dilatata*, but the latter event is likely to be more frequent because of similar lepidopteran pollinators (see below) as well as the frequent occurrence of auto-pollination in *P. aquilonis* (Catling and Catling 1989, 1991b). Sheviak and Bracht (1998) have found evident hybrids of *P. huronensis* and *P. dilatata* in British Columbia. However, neither hybridization would result in a loss of specific integrity because the hybrids are usually triploid and pollination experiments in cultivated plants have demonstrated that they are sterile (Sheviak 1999).

Pollinators and Pollination Mechanisms

Larson (1992) reported pollination of *P. dilatata* var. *dilatata* by a diurnal noctuid moth, *Anarta* (*Discestra*) *oregonica* (Grote), in the Three Sisters Wilderness Area of Deschutes County, Oregon. This report is based on only a single day's observations but is consistent with earlier records identifying noctuid moths as pollinators of this variety in St. Anthony, Newfoundland and Bruce County, Ontario (Catling 1984; Catling and Catling 1991a). In Nevada County, California, Kipping (1971) reported a nocturnal noctuid moth, *Autographa californica* (Speyer) (cf. Fig. 11.5), bearing pollinaria of *P. dilatata* var. *leucostachys* (Lindley) Luer on its proboscis. Two other nocturnal visitors, *Hyppa indistincta* Smith and a reddish species of *Autographa* Hubner, carried no pollinia. The floral fragrance in this variety is released at dusk and through the evening.

Observations and collections at other sites have revealed the apparent involvement of other insect groups. Catling and Catling (1991a) considered large butterflies including *Papilio zelicaon gothica* Remington (the mount anise swallowtail), *Papilio glaucus* L. var. *canadensis* Rothschild and Jordan (the Canadian tiger swallowtail), and *Vanessa cardui* L., (the painted lady) to be the most important pollinators of variety *dilatata* in the Canadian Rockies. Vogt (1990) also reported *Papilio*

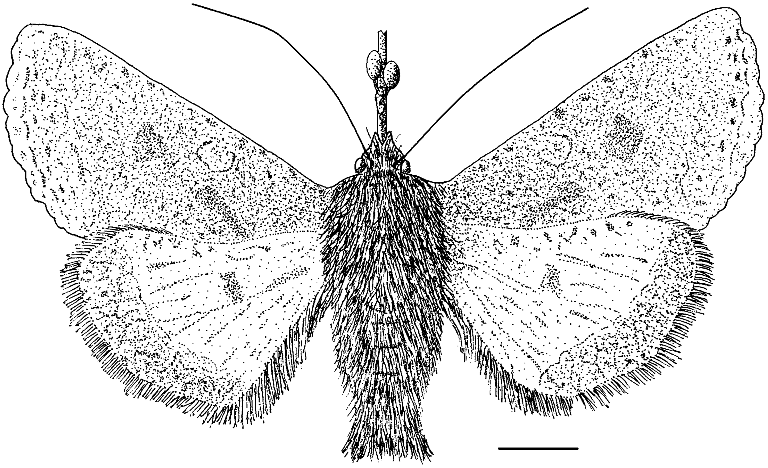

Fig. 9.3 *Anarta oregonica*, dorsal view with two pollinaria attached to base of proboscis (distal part of proboscis not shown), scale bar = 4 mm

glaucus L. (eastern tiger swallowtail) visiting a flower at Woodstock, Vermont, although no attempt to probe the nectary was noted. Patt and Merchant (pers. comm. in Cingle 2001) observed unspecified butterflies visiting the inflorescences of subalpine plants in the Baily Range of Olympic National Park. Luer (1975) mentioned skippers and small brown or gray moths, and Stoutamire (1968), without further comment, noted that hymenoptera as well as lepidoptera may act as pollinators.

The variety of possible pollinators is not surprising considering the variation in spur length found in *P. dilatata.* As Sheviak (2002) has pointed out, variety *dilatata* has a spur of medium length (4–12 mm) and emits a diurnal fragrance suggesting specialization for diurnal lepidopteran pollination. Variety *leucostachys* has a long spur (8–20 mm), and its primarily nocturnal fragrance indicates pollination by moths. Variety *albiflora* (Cham.) Ledeb. has short spurs (2–7 mm), frequently with broader viscidia, and may be pollinated by a wider variety of insects, including bees or flies. Spur length can vary more or less continuously within and between populations with the center of variability located in the northwest (Sheviak 2002). The flowers apparently adapted to different pollinators as populations extended eastward into the boreal forest and southward into the western cordillera (Sheviak 2002).

In Larson's (1992) study, about 15–20 individuals of *Anarta oregonica* (Fig. 9.3) visited the flowers, apparently selecting racemes at random based on visual clues. The relatively large moths (ca. 2 cm long) probed several flowers on each raceme, griping the floral parts of several adjacent flowers while feeding. They usually extracted nectar in a heads-up position with their bodies more or less parallel to the labellum, but other orientations were observed. The depth of probing also varied and may have been a function of the amount of nectar present in the spur. Gross dissections revealed that the nectar level was highly variable. Pollinaria were attached to the dorsal side of the proboscis, a few millimeters from the head.

In a random collection, three moths bore from 1 to 5 pollinaria in this position (Larson 1992). At the time of collection, the caudicle was upright and canted slightly forward in a position that would have brought the pollinia into contact with the stigma of another flower during probing by a moth in an upright position.

Pollen vectors were not required for pollination of *P. aquilonis* populations from Ontario and the northern Peninsula of Michigan, where Catling (1983) found autogamy in 99–100% of the flowers examined. The viscidia in these flowers remained in place following dehydration and opening of the anther cap, but the caudicles, relatively weak near their points of attachment to the pollinia, allowed the latter to bend downward under the influence of gravity, depositing the pollen masses onto the stigmatic surface (Fig. 9.1e, f) (Gray 1862a, 1862b; Catling 1983). This occurred prior to or less than 24 h after the flowers opened. In addition, Sheviak (2001) found that water droplets sometimes disperse the loosely bound massulae across the stigma.

One-third to three-fourths of the massulae remain attached to the caudicle following autopollination. These can be withdrawn by touching a pin to the viscidium (Catling 1983). Thus, insect pollination remains possible (Gray 1862a, b; Catling 1983), and the small orbicular viscidia and short spurs (Table 9.1) suggest that bees or any of a number of smaller insects could act as pollinators (Sheviak 2011). Wallace (2006) established that the pattern of spatial genetic structure in *P. aquilonis* populations from Maine differed from what is typical of other selfing species and suggested that autogamy here might be facultative, permitting limited outcrossing as well as hybridization with *P. dilatata*. This orchid does, in fact, show some characteristics found in species of *Platanthera* pollinated by mosquitoes. The flowers are small and dull colored; the short nectaries are about the right length for mosquito visits; and the length of the pollinium (1.5 mm) matches that of *P. obtusata*, a species known to be pollinated by mosquitoes (see below) (Stoutamire 1968).

The extent to which the flowers open can also vary, and this is relevant to possible mosquito pollination. In some cases, the lip expands fully and is more or less straight at anthesis (Fig. 9.1a) (Stoutamire 1968). In other cases, it remains curved and does not separate completely from the dorsal sepal (Fig. 9.1c), a condition also sometimes seen in *P. dilatata* and *P. huronensis* (Stoutamire 1968; Luer 1975; Sheviak 1999). The result is a mature flower with two lateral openings, a circumstance analogous to the twin openings produced by the swollen callus and associated appendage in such mosquito-pollinated orchids as *P. obtusata* and *P. flava* or the upturned lip and column projection in *P. hookeri* (see below). Stoutamire (1968) suggested that a mosquito probing for nectar might thus be compelled to enter the flower laterally, forcing one of its compound eyes into contact with a viscidium. Pollination by *Aedes pullatus* (Coquillett) has, in fact, been reported for *P. aquilonis* at Great Whale River, Northwest Territories (D. Saville pers. comm. in Catling and Catling 1991a). Hocking et al. (1950) also observed mosquitoes feeding on the flowers on two occasions, but no pollinaria were removed. Although pollination by mosquitoes is possible, some floral features that suggest such pollination could also be considered transitional to obligate autogamy (Stoutamire 1968; Lojtnant and Jacobsen 1976). Reports of a strong, distinctive aroma at dusk along with the absence of an ultra-violet pattern (Kugler 1970; Thien 1971) imply the additional possibility of noctuid and/or pyralid moth pollination (Catling and Catling 1989).

Although the importance of insect pollination in *P. aquilonis* remains in doubt, there is no question about its significance in *P. huronensis*. In a 24-h study of this orchid in southeastern Colorado, Catling and Catling (1989) identified two species of butterfly, *Vanessa virginiensis* (Drury) (American painted lady) and *Erebia epipsodea* Butler (common alpine), three species of noctuid moths, *Trichordestra dodii* (Smith), *Aletia oxygala* (Grote), and *Cucullia intermedia* Speyer, and five species of bumblebees, *Bombus appositus* Cresson, *B. flavifrons* Cresson, *B. occidentalis, B. suckeyi* Green (=*Psithyrus suckleyi* Greene), and *B. insularis* (Smith) (=*P. insularis* Smith), as pollinators. All moved from the base toward the tip of the spike, and all had pollinaria attached to their proboscises.

Except for the noctuid moths, which were mainly seen for a half-hour shortly after dusk (9:15–9:45 p.m.), pollinator visits varied little in frequency between 9:30 a.m. and 6:00 p.m. The bumblebees visited more flowers per inflorescence and more inflorescences than the diurnal lepidoptera. The number of plants visited by nocturnal lepidoptera remains undetermined; some were collected after visiting a second plant, and the behavior of others may have been altered by the use of a flashlight.

If the recorded behavior is typical, bumblebees may effect a higher percentage of geitonogamous pollination than moths whose restricted activity on any one inflorescence may result in a higher ratio of outcrossing. The proportional influence of the butterflies on geitonogamous and xenogamous pollination was not mentioned. However, the younger flowers near the top of the inflorescence have an upturned lip and a differently positioned column, which may limit geitonogamous pollination for all pollinators.

In any event, *P. huronensis* appears to have a pollination strategy that involves more than one group of insects, a strategy that Catling and Catling (1989) consider unusual in *Platanthera*, but which they acknowledge is seen elsewhere among North American species in *P. stricta* (Patt 1986; Patt et al. 1989), *P. obtusata* (e.g. Stoutamire 1968; Voss and Riefner 1983), and *P. blephariglottis* (Cole and Firmage 1984).

Reproductive Success and Limiting Factors

According to Colwell et al. (2007), *P. dilatata* var. *leucostachys* often matures all the fruits on its inflorescence. There is no additional information on fruit set for *P. dilatata* or *P. huronensis* and no data on limiting factors for either species. Details are also lacking for *P. aquilonis*, but autogamy routinely leads to copious seed production, and Gray (1862b) and Hagerup (1952) both reported the production of abundant fruit.

Upturned lips in this complex are thought to allow pollinaria removal while preventing pollen deposition and have been related to protandry and a reduction in geitonogamy (Catling and Catling 1989, 1991a). That is, young flowers at the top of the inflorescence have upturned lips and covered stigmas but accessible pollen, and older flowers at the bottom often have extended lips and exposed stigmas. Many pollinators are known to move in an upward direction when exploring an inflorescence. They may therefore extract pollen from young flowers near the top as they depart one inflorescence and transfer pollen to older flowers with exposed stigmas near the bottom of the next inflorescence visited. Vectors that arrive as pollen donors thus depart as pollen recipients, and selfing and geitonogamous pollinations are reduced while cross-pollination is favored. However, as discussed in connection with possible mosquito pollination in *P. aquilonis*, upturned lips would also force pollinators to enter the flowers laterally. A forced lateral entry should restrict pollen acquisition to a single pollinarium per pollinator visit (Stoutamire 1968; Catling and Catling 1991a). Studies on the Bruce Peninsula of Ontario appear to confirm that such restriction is real. Catling and Catling (1991a) found that young flowers of *P. dilatata* had a higher percentage of single removals while older flowers had proportionately more double removals, presumably as a result of visits by two different pollinators.

Loading of more than one pollinator may be interpreted in relation to the optimization of cross-pollination and/or sexual selection (Harder and Thomson 1989; Catling and Catling 1991a). Cross-pollination can be reduced either by predation of the pollinators or their inability to find more plants of the same species (Catling and Catling 1991a). Increasing the number of pollinators should increase the probability of achieving cross-fertilization in either case. Less obviously, if paternal fitness is limited by the ability to achieve fertilizations (Bateman 1948; Willson 1979), increasing the number of pollen vectors should increase both the number of cross-pollinations and the number of stigmas pollinated and should be favored by sexual selection, resulting in an adaptive expansion of the male role and an increase in male fitness (Catling and Catling 1991a; Gregg 1991). Within the constraints imposed by pollinator service, intrasexual selection might lead to such an increase in the number of potential fertilizations by limiting the quantity of pollen removed during each pollinator visit, as in the present example, and by prolonging the interval during which pollen is available in a flower (see also *Cleistesiopsis*) (Lloyd and Yates 1982; Brantjes 1983; Harder and Thomson 1989; Catling and Catling 1991a; Gregg 1991). Since massive deposits of pollen result in much pollen wastage (Neiland and Wilcock 1995), an increase in the number of potential fertilizations might also be achieved by limiting the amount of pollen deposited on each stigma. Thus, a single pollinator of orchids with soft or mealy pollinia or sectile pollinia with massulae, as in *Platanthera*, may maximize the transfer of pollen from a single source to a number of successive stigmas (e.g. Catling and Catling 1991a). At the same time, stigmas may receive pollen from several males permitting pollen tube competition in the style among pollen grains from different sources. The female, in association with varying levels of resource availability, may then selectively eliminate inferior microgametophytes (through nonrandom fertilization) or inferior zygotes (through abortion) (e.g. Willson and Burley 1983). Both sexes might therefore experience an increase in reproductive fitness through either intrasexual competition (usually male) or intersexual mate choice (usually female).

Platanthera stricta Lindley (Slender Bog Orchid)

Habitat and Distribution

Platanthera stricta is an alpine species commonly growing in either full sun or shade on tundra or mesic sites such as fens (Luer 1975; Patt et al. 1989; Sheviak 2002). It ranges from northern California, Idaho, Wyoming, and Montana to Alaska and the Aleutian Islands.

Floral Morphology

An irregular number of small, green or yellow-green, resupinate flowers are arranged in racemes of varying length (Table 9.2) (Luer 1975; Patt et al. 1989; Coleman 1995; Sheviak 2002). Individual flowers remain receptive for about 14 days, and blooming of a single raceme may last 35 days (Patt et al. 1989). The lateral sepals are spreading or reflexed, and the dorsal sepal and lateral petals form a 3–5 mm long hood over the column (Fig. 9.4a, b). The lip is usually linear or lanceolate to elliptic in shape with an obtuse apex. A 0.8–1.0 mm long stigma is positioned above the opening to the nectar spur. The rostellar lobes are more or less parallel to convergent and bear orbiculate viscidia placed 0.4–0.6 mm apart (Fig. 9.4a). The viscidia usually face downward and are slanted slightly inward toward the opening of the nectar spur.

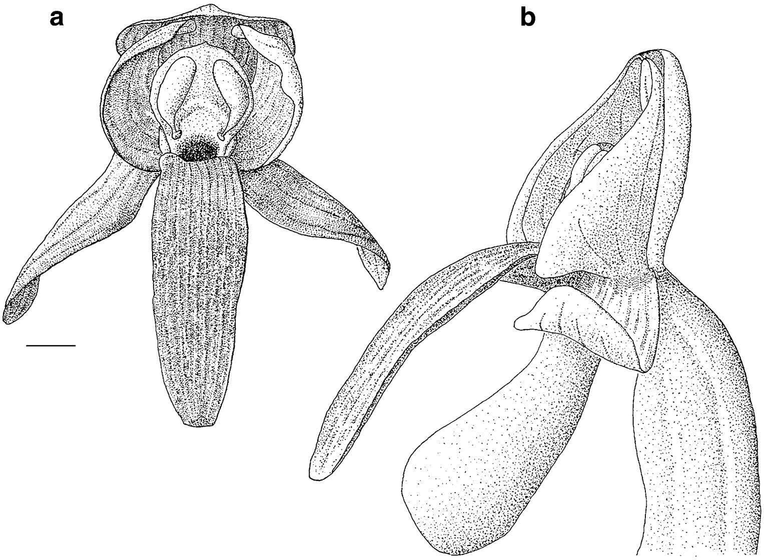

Fig. 9.4 *Platanthera stricta*. (**a**) Flower, front view; (**b**) Flower, side view, scale bars = 1 mm

Catling and Catling (1991a) found a population near Creston, British Columbia, in which the flowers near the tops of the spikes had fused viscidia and thus a single pollinarium. A short nectar spur (Table 9.2) is terminated by a swollen to more or less bilobed sac (Fig. 9.4b) (Luer 1975; Sheviak 2002). Nectar is secreted as small droplets over the inner walls of the spur and can thus be removed by insects with proboscises shorter than the spur (Patt et al. 1989). Individual spurs contain only about 0.1 μl of nectar with an average of about 1.0–3.0 μl per raceme. Analysis of the nectar showed an 8% sugar concentration equally comprised of sucrose, glucose, and fructose. Although low, sugar concentrations in this range are known to appeal to a wide variety of pollinators (Percival 1969; Baker and Baker 1983; Patt et al. 1989). Extrafloral nectaries secrete additional nectar onto the epidermis of the sepals, floral bracts, raceme axis, and leaves. Although Schrenk (1978) was unable to detect any floral scent, Patt (1986) and Patt et al. (1988), using gas chromatography, reported the presence of a number of aromatic compounds thought to induce foraging behavior in many pollinators (Kaiser 1993).

Compatibility and Breeding System

In a 3-year study at Deer Lake Basin (elevation 1,204 m) and Canyon Creek Gorge (elevation 686 m) in Olympic National Park, Washington, Patt et al. (1989) found that bagged, unmanipulated plants produced no capsules. Thus, insects are needed for pollination, and *P. stricta* is probably neither autogamous nor agamospermous. Artificial intrafloral-pollination and geitonogamy resulted in over 90% capsule production, as did artificial cross-pollination. No statistically significant differences were seen among the three treatments. However, mean capsule set in open pollinated plants was significantly lower (52%). On the other hand, both open pollination and artificial outcrossing produced a significantly larger mean percentage of seeds with normally developed embryos than selfing. At the same time, the number of seeds with normally developed embryos was highly variable in open pollinated plants and lower than that obtained in artificially outcrossed plants.

Pollinators and Pollination Mechanisms

Platanthera stricta is unusual among platantheras in the diversity of short-tongued insects that act as pollinators (Patt 1986; Patt et al. 1989). Primary co-pollinators in Olympic National Park included two species of Lepidoptera, fourteen species of empidid flies, and two species of bumblebee (Table 9.3).

The mean lengths of the proboscises in the bumblebees (4.2 ± 0.77 mm) and the geometrid moth (4.6 ± 0.20 mm) are similar to the length of the nectar spur at this site (ca. 4.0 ± 0.25 mm), and these insects could therefore reach any accumulated nectar droplet at the base of the spur. Proboscises for *Greya* Busck (1.6 ± 0.27 mm long)

Table 9.2 Data on the Limnocharis group (*Platanther aquilonis* complex), part 2 (Sheviak 2002)

Character	*P. sparsiflora*	*P. stricta*
Plant height (cm)	20–125+	18–100
Dorsal sepal (mm)[a]	4–7.5 × 3–6	3–5 × 3–4
Lateral sepals (mm)[a]	6–10 × 2–4	4–6.5 × 2–3
Lateral petals (mm)[a]	5–8 × 2–4.5	3–5 × 1.5–2.2
Lip (mm)	4.5–11 × 0.6–3	3–9 × 1–3
Spur length (mm)[a]	5–13	2–6
Column (mm)[a]	2.5–4 × 2–3	2 × 1.5
Chromosomes (2n)	42	42

[a] Luer (1975)

Table 9.3 Primary copollinators of *P. stricta* in Olympic National Park, Washington (Patt et al. 1989)

- Lepidoptera
  - Geometridae
    - *Eustroma fasciata* Barnes and McDunnough (proboscis length 4.6 ± 0.20 mm)
  - Prodoxidae
    - *Greya* Busck, undescribed species (proboscis length 1.6 ± 0.27 mm)
- Diptera
  - Empididae (mean proboscis length for taxa listed, 1.5 ± 0.71 mm)
    - *Anthepiscopus longipalplis* (Melander)
    - *Empis* Linnaeus subgenus *Acallomyia* Melander, 2 undescribed species
    - *E. virgata* Coquillett
    - *E. delumbis* (Melander) as *E. delumba* (Melander)
    - *E. brachysoma* Coquillett
    - *E. laniventris* (Eschscholtz)
    - *Rhamphomyia* Meigen, 7 undescribed species
- Hymenoptera
  - Apidae (mean proboscis length for species listed, 4.2 ± 0.77 mm)
    - *Bombus flavifrons* Cresson
    - *B. melanopygus* Nylander

and empidid flies (1.5 ± 0.71 mm long) were of sufficient length to reach some of the minute droplets of nectar scattered over the inner walls of the nectar spur. Pollinator activity was extensive as reflected in the removal of 57–78% of the pollinaria by the end of the flowering period.

Pollinaria were attached to the glossa (tongue) or labrum (upper lip) of *Bombus*, the compound eyes of the geometrid moth and *Greya*, and usually to the compound eyes and/or proboscis of the empidid flies (Fig. 9.5). According to Patt et al. (1989), the mean separation of the viscidia (0.52 ± 0.080 mm) would accommodate the width of the proboscis in the bumblebees (0.78 ± 0.100 mm), the space between the compound eyes of the geometrid moth (0.50 ± 0.01 mm), and the widths of the heads of both *Greya* (0.79 ± 0.09 mm) and the empidids (0.94 ± 0.31 mm).

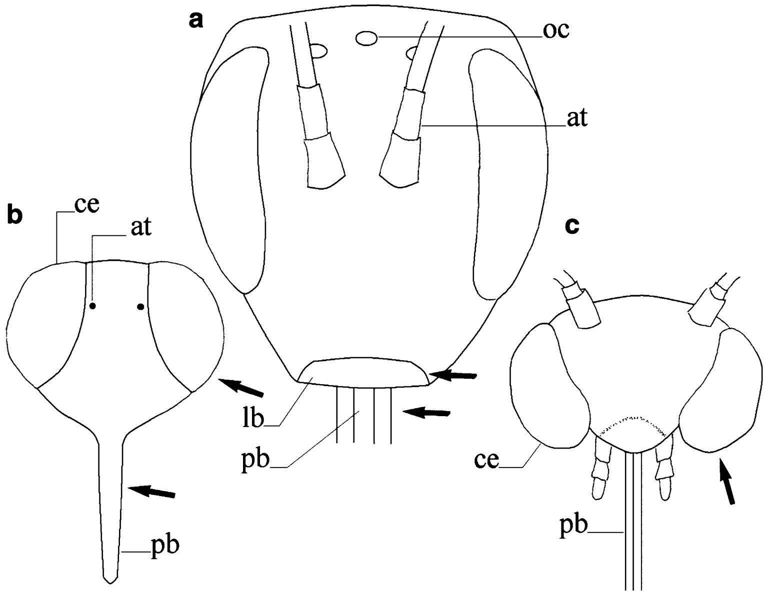

Fig. 9.5 Pollinators of *Platanthera stricta* showing points of pollinaria attachment (*arrows*). (**a**) *Bombus*; (**b**) *Empedid*; (**c**) Moth. *at* antenna, *ce* compound eyes, *lb* labrum, *oc* ocelli, *pb* proboscis

The bumblebees and geometrid moth stationed themselves on the labellum, griped the lateral sepals with their tarsi (distal leg segment), and investigated the nectar spur of each flower with their mouthparts for 2–5 s. Movement was ordered and proceeded from lower to higher flowers with an average of about 1 min spent on each raceme.

Greya and the empidids, on the other hand, moved about more or less randomly on each inflorescence over a period of 5–20 min. They explored the floral tubes for nectar but also fed on the extrafloral sugars. Each spur was repeatedly probed for several minutes as the insect attempted to reach the many minute droplets of nectar scattered over its inner surface. In the process, the mouthparts or eyes repeatedly contacted the stigma and viscidia, increasing the chances of pollination. On some visits, no more than a single flower was sampled. These insects commonly pollinate plants with numerous, closely spaced flowers having well-exposed nectaries (Proctor and Yeo 1972). The concealment of nectar within a nectar spur and the relatively wide spacing of the flowers in *P. stricta* appear poorly suited to *Greya* and the empidids. In this case, the presence of extrafloral nectaries in the raceme may be significant. If these pollinators are attracted and induced to initiate foraging by the floral odor, the extrafloral nectaries may serve to prolong foraging until nectar spurs are located (Patt et al. 1989). A similar strategy has been reported in *Epipactis palustris* (L.) Crantz. (Brantjes 1981), *Listera ovata* (L.) R. Brown, and *Coeloglossum viride* (L.) Hartman (Proctor and Yeo 1972).

Although the empidids and *Greya* usually placed themselves on the labellum while probing the nectar spur, they sometimes approached it from different angles with the result that pollinia were occasionally attached to the thorax and foretarsi (feet) of the flies. Body scales restricted attachment in the moth to the compound eyes; no attachment to the short proboscis was noted (Patt et al. 1989).

The species of pollinators visiting *P. stricta* showed some site and seasonal variation. The nocturnal *Antepirrhoe* (*Eustroma*) *fasciata* Barnes and McDunnough was seen only at the Canyon Creek Gorge site. Nocturnal pollination at Deer Lake Basin may have been prevented by low nighttime temperatures (Patt et al. 1989). Empidid flies were common on other flowering plants throughout the area and spread to *P. stricta* as it came into bloom. *Greya* was observed only at Deer Creek Basin where it appeared to be largely dependent on *P. stricta* as a food source in July and August. Bumblbees only rarely visited *P. stricta* despite their abundance at all sites throughout the study period. This is not surprising considering the small amount of nectar available per spur and its low sugar concentration. However, both bumblebees and *Eustroma*, having once visited the orchid, demonstrated a high degree of floral fidelity within the time frame of a given foraging trip.

Two additional insects, a mosquito (*Aedes* Meigen sp.) and a halictid bee (*Lasioglossum* sp.), may have acted as infrequent copollinators. Three mosquitoes (one female and two males) carried single pollinaria on their compound eyes while a single halictid carried a number of pollinaria on its frons (uppermost part of the head) and compound eyes. These insects along with additional small moths may prove to be important pollinators in other geographical areas (Patt et al. 1989).

Floral scent appears to be the primary attractant, at least for empidids (Patt 1986; Patt et al. 1988). In addition, the visual attraction of the flowers may be augmented by the cellular structure of the tepals and floral bracts, which produces a sparkling effect when seen from certain angles (Patt et al. 1989). Kugler (1951) and Percival (1969) have shown that Diptera in the genus *Lucilia* Robineau-Desvoidy are attracted to glittering items on flowers. Similarly, Nilsson (1978) found that under low light conditions moths are attracted to *P. chlorantha* (Custer) Reichenbach, the greater butterfly orchid, by the subdued sparkle or sheen of its inflorescence.

Fruiting Success and Limiting Factors

The significantly lower capsule-set in open-pollinated as compared to hand pollinated orchids suggests that this species may be pollinator limited, an interpretation not inconsistent with a rarity of aborted capsules in open-pollinated plants (Patt et al. 1989). The variability and reduction of seed fertility in open pollinated as compared to artificially outcrossed plants might also reflect varying levels of intrafloral and intra-racemic pollen transfer and/or differences in pollinator efficiency. Pollinators varied in their position and orientation on the flower, in the time spent probing the nectar spur, and in the number and placement of transported pollinaria. All these variables probably influence the number of massulae deposited on the stigma and the number of ovules fertilized (Patt et al. 1989).

Pollinator limitation could relate to the small amount of nectar produced and its low sugar concentration or to limited pollinator activity during frequent periods of cool, wet weather in northwest Washington (Patt et al. 1989). These circumstances may be partially compensated by the long period of floral receptivity, the extended blooming time of the racemes, and the ability of the flowers to be pollinated by different groups of short tongued, anthophilous (flower loving) insects (Cole and Firmage 1984; Pellmyr 1986; Patt et al. 1989; Colwell et al. 2007).

Reproductive success may also be limited by predation. Patt et al. (1989) found that 20% of the flowering/fruiting orchids tagged at their Olympic National Park study sites were destroyed by grazing mule deer (*Odocoileus hemionus* (Rafinesque)).

Platanthera sparsiflora (S. Watson) Schlechter (Sparsely Flowered Bog Orchid)

Habitat and Distribution

Platanthera sparsiflora is found in wet meadows, marshes, fens, bogs and other moist areas in the western United States (Kipping 1971; Sheviak 2002). It ranges from southwestern Oregon to southern California west to Colorado and New Mexico.

Floral Morphology

A variable number of small, pale greenish, resupinate flowers are sparsely to sometimes densely arranged in a long, slender inflorescence (Table 9.2) (Kipping 1971; Sheviak 2002). The lateral sepals are reflexed or sometimes spreading (Fig. 9.6a, b). The dorsal is more or less erect and in combination with the lateral petals forms a hood over the column. The labellum is fleshy and linear to elliptic-lanceolate with an obtuse tip; a medial ridge, more evident in some specimens than in others, divides the entrance to the cylindrical nectar spur in half (Fig. 9.6a). The spur is slender and sometimes slightly clavate (Fig. 9.6b). The relatively large column (Table 9.2) includes two distinct anther cells and two pollinaria. Prominent, angular rostellum lobes are directed forward and are more or less divergent (Fig. 9.6a) (Sheviak 2002). Each bears an orbiculate to oblong viscidium positioned forward and to either side of the opening to the nectar spur and the viscid stigma. Floral fragrance is released at dusk (Kipping 1971).

Compatibility and Breeding System

Although Kipping (1971) considered *P. sparsiflora* to be primarily cross-pollinated, compatibility data have yet to be published.

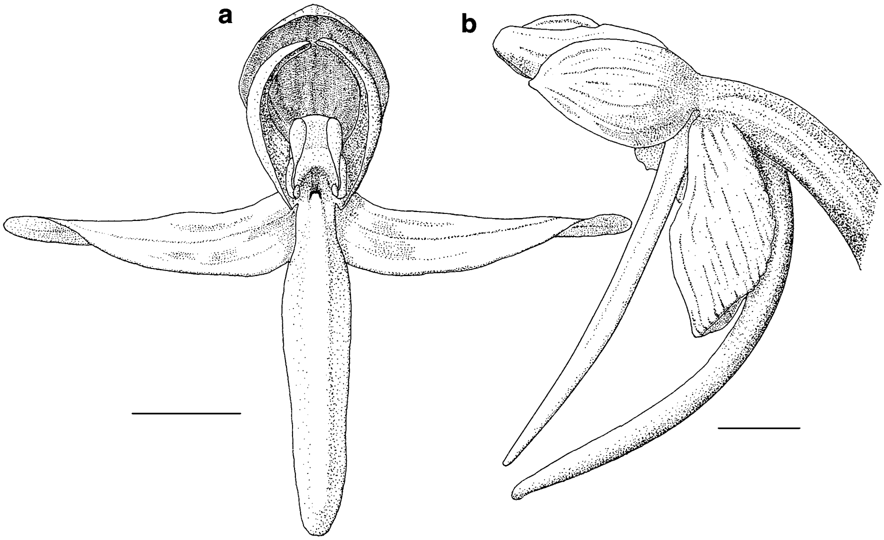

Fig. 9.6 *Platanthera sparsiflora*. (**a**) Flower, front view, scale bar = 3 mm; (**b**) Flower, side view, scale bar = 2 mm

Pollinators and Pollination Mechanisms

Kipping (1971) examined the pollination of this orchid over two seasons in El Dorado County, California. He captured several unspecified, small nocturnal moths of the family Pyralidae on the flowers, one with pollinaria on its proboscis.

According to Kipping, the moth probed the nectary, inserting its proboscis into one of the two nectary openings. Although the orientation of the rostellar lobes is typical of *Platanthera* species that deposit pollinaria on the compound eyes of their pollinators, the medial ridge dividing the entrance of the nectar spur in half forced the moth to enter the spur laterally. The viscidium on the corresponding side contacted and adhered to the proboscis rather than the eye, and the pollinarium was removed as the moth withdrew. On subsequent visits to other flowers the pollinia contacted the viscid stigma centered directly over the opening to the nectar tube, and pollen transfer was accomplished.

Kipping (1971) also observed two plume moths (*Platyptilia* Hubner sp. and *Oidaematophorus* Wallengren sp., Pterophoridae) visiting the flowers. Even though none carried any pollinaria, he thought that they, too, were likely pollinators.

Fruiting Success and Limiting Factors

Colwell et al. (2007) reported that plants of *P. sparsiflora* often fill all the fruits on their inflorescences. Kipping (1971) found that 49% of 197 flowers on six plants produced fruit during the first year of his study, and 82% of 86 flowers on three plants set fruit the second year. He concluded that pyralid moths were effective pollen vectors at his study site. Additional studies on the breeding system and the factors affecting the reproductive success of this orchid are needed.

Other Species of the Limnorchis Group

The columns of *P. brevifolia* and *P. zothecina* resemble the column of *P. sparsiflora* in having rostellar lobes that are more or less divergent and directed forward. Pollination has not been observed, but this orientation is typical of *Platanthera* species that deposit pollinaria on the vector's compound eyes. Both lack the thickened ridge toward the base of the lip seen in *P. sparsiflora*. *Platanthera brevifolia* also has a generally longer spur (9–20 mm) than *P. sparsiflora* (5–13 mm), quite distinct ecological requirements (dry to moist, open coniferous forest), and is probably serviced by different pollinators. Spur length in *P. zothecina* (12–17 mm) barely overlaps that of *P. sparsiflora.* Sheviak (2002) cited this feature in support of its recognition as a separate species and as an indication that it may be specialized for different pollinators.

The rostellar lobes in *P. purpurascens* are strongly divergent, whereas in *P. limosa* they are mostly parallel and closely spaced (Sheviak 2002). The latter also has a long, slender spur (8–25 mm) and a smaller narrower column than *P. brevifolia*, *P. zothecina,* and most populations of *P. sparsiflora*. These morphological differences in structures directly related to pollination again imply the involvement of different pollen vectors.

The column in *P. tescamnis* is small. As in the preceding species, pollination has not been observed (Sheviak, personal communication). However, even though the rostellum lobes again angle outward and forward, they are relatively short, placing the viscidia just next to the upper border of the nectar spur opening, and the viscidia are usually orbicular (Sheviak and Jennings 2006). The pollinaria might therefore attach to the eyes of smaller insects. At the same time, the viscidia are oblong in some populations, suggesting that local adaptation to proboscis attachment may also be possible (Sheviak and Jennings 2006). The only insect visitor Sheviak reported seeing was a hadenine noctuid moth. Hadenines have hairy eyes that prevent pollen attachment, and, indeed, they removed no pollinaria.

Platanthera yosemitensis has yellow flowers with a musky scent and closely spaced viscidia (0.3 mm apart), a combination of characters possibly indicative of a mosquito or fly pollination syndrome (Colwell et al. 2007). Unlike *P. dilatata* var. *leucostachys* and *P. sparsiflora*, this orchid usually matures fruits on only the lower two thirds of its inflorescence. This is particularly true of plants in small populations or on the margin of a population where sometimes only one or two mature fruits are produced (Colwell et al. 2007).

In Greenland, Hagerup (1952) reported germination of the pollen on the stigma of *P. hyperborea* prior to opening of the flowers. Lojtnant and Jacobsen (1976) also observed autogamy in Greenland populations of this species, but were unable to confirm Hagerup's account of cleistogamy (autogamy in closed flowers). According to these authors and Sheviak (1999), the pollinia are highly friable, and individual pollen grains or an entire pollinium can fall from the pollen sac onto the stigma in response to the slightest vibration. In some Icelandic plants, however, the pollinaria were removed, suggesting the activity of pollinators (Sheviak 2011). Although Lojtnant and Jacobsen (1976) found only gland-like hairs within the spur, Hagerup (1952) reported the presence of nectar.

Finally, except for the close resemblance of its flowers to *P. huronensis*, nothing can be suggested about pollination in the questionably distinct Alaskan populations of *P. convallariifolia.*

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Chapter 10
Platanthera Group

Abstract *Platanthera obtusata* is a predominantly outcrossing species pollinated by female mosquitoes of the genus *Aedes*. Geometrid and pyralid moths play a secondary role. Forced lateral entrance of the nectar spur results in attachment of the viscidia to the compound eyes. The viscidia in *P. orbiculata* and *P. macrophylla* are positioned to contact the compound eyes of visiting moths. Floral morphology implies that moths of different size pollinate the two species. *Platanthera hookeri* may be pollinated by nocturnal settling moths or skippers. A forced lateral approach results in pollinaria attachment to the compound eyes.

Keywords *Platanthera obtusata* • *Platanthera orbiculata* • *Platanthera macrophyla* • Eye attachment of viscidia • Pollinator segregation based on size • Mosquitoes • Geometrid moths • Pyralid moths • Crambid and noctuid moths

Luer (1975) considered the *Platanthera* group or section to be comprised of species having one or two basal leaves and a broad anther. More recently, in a study based on molecular phylogenetics, Hapeman and Inoue (1997) resolved fifteen species in a monophyletic *Platanthera* clade. Five of these are found in North America (Fig. 8.1). Detailed information on pollination biology is available for three: *P. obtusata* (Banks ex Pursh) Lindley and the species pair *P. macrophylla* (Goldie) P. M. Brown and *P. orbiculata* (Pursh) Lindley.

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Platanthera obtusata (Banks ex Pursh) Lindley (Blunt-Leaved Rein Orchis)

Distribution and Habitat

Circumpolar in the tundra, *P. obtusata* is found in North America from Newfoundland to Alaska south to Massachusetts and the Great Lakes states in the east and along the Rocky Mountains to southern Colorado in the west (Luer 1975; Sheviak 2002). It occurs on exposed turf and barrens in the north and favors the cold, often moist soils of wooded bogs and coniferous forests toward the southern limits of its range (Luer 1975; Voss and Riefner 1983).

Floral Morphology

A fairly constant number of small, yellowish–green to whitish–green, resupinate flowers are spaced in a spikate inflorescence (Table 10.1) (Thien 1969; Luer 1975; Sheviak 2002). The dorsal sepal is green, and the lateral petals are white. Both lean forward, forming a hood over the column and spur entrance (Fig. 10.1b). The lateral sepals are widely spreading or reflexed. The lip is narrowly lanceolate and pendant or reflexed toward the stem (Fig. 10.1a, b). A grooved callus thickening at the base of the lip ends in a small flap which projects backward into the nectar spur, dividing its entrance into two halves (Fig. 10.1c). The stigma is located directly above the spur entrance between the two half-anthers. The lobes of the rostellum are wide spreading and directed forward (Fig. 10.1a). One orbiculate viscidium is positioned just to the outside of each of the lateral passages into the spur. The latter is downward curving, slenderly conic, and partly or completely filled with nectar.

Compatibility and Breeding System

Thien (1969) found that a pollinator was required for fruit-set in a population from Forest County, Wisconsin, and other studies indicate that outcrossing is the predominant form of sexual reproduction in this species (see below).

Pollinators and Pollination Mechanisms

Platanthera obtusata is pollinated primarily by female mosquitoes of the genus *Aedes* (Fig. 8.1). Geometrid and pyralid moths play a secondary role (Stoutamire 1968; Gorham 1976; Voss and Riefner 1983). Mosquito pollination has been

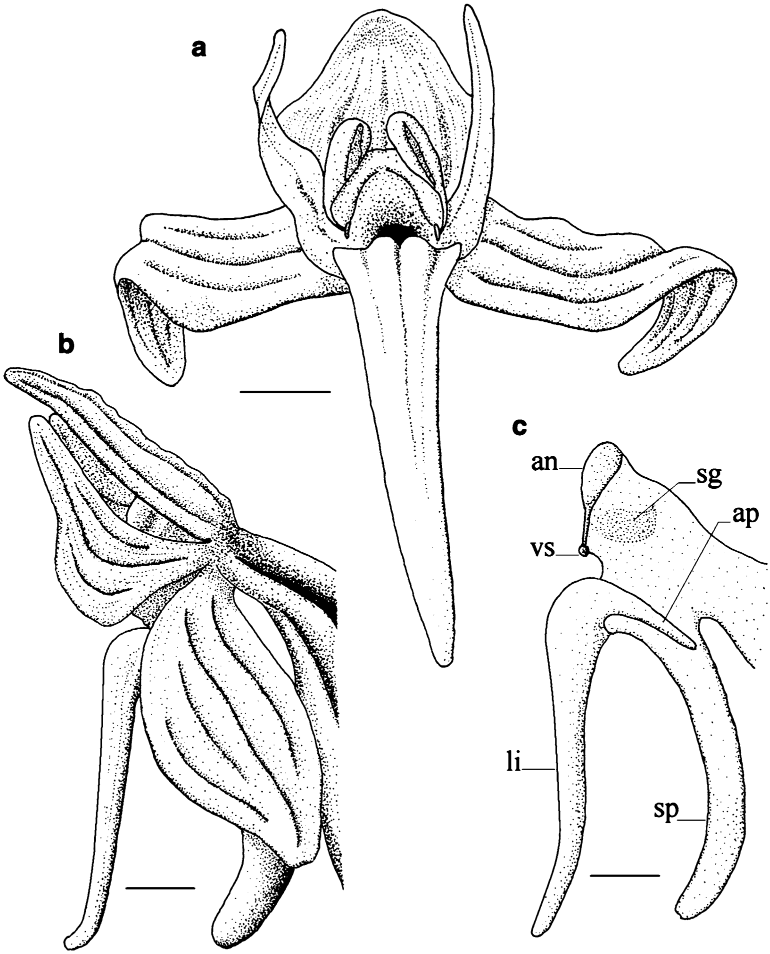

Fig. 10.1 *Platanthera obtusata*. (**a**) Flower, front view; (**b**) Flower, side view; (**c**) Sagittal section of flower, scale bars = 1 mm. *an* anther, *ap* appendage, *li* lip, *sg* stigma, *sp* nectar spur, *vs* viscidium

reported from Michigan (Dexter 1913; Stoutamire 1968), Wisconsin (Thien 1969; Thien and Utech 1970), Manitoba (Hocking et al. 1950; Hocking 1953), The Northwest Territories (Raup 1930; Porsild in Twinn et al. 1948, J. W. Thompson in Stoutamire 1968), and Alaska (Frohne 1955; Gorham 1976). Fifteen or 16 identified species of mosquitoes are known to carry pollinaria attached to their compound eyes (Tables 10.2–10.4).

Stoutamire (1968) collected two species of *Aedes* with attached pollinaria in Michigan (Table 10.2), but saw none actually visiting the flowers. Temperatures were low and this may have inhibited insect activity. In addition, his observations were made during daylight hours, and mosquitoes usually visit the flowers at dusk (Twinn et al. 1948; Hocking et al. 1950; Hocking 1953).

Table 10.1 Data on the Platanthera group (Sheviak 2002)

Character	*P. obtusata*	*P. orbiculata*	*P. macrophylla*
Plant height (cm)	5.5–35	17–62	23–63
Raceme length (cm)		(4) 4–21 (27)[a]	(6) 6–22 (26)[a]
Flower number	(1) 12–15 (17)[b]	(4) 4–31 (51)[a]	4–25 (40)[a]
Dorsal sepal (mm)	2–5 × 2–4[b]	3.3–6.5 × 3.5–7.0[a]	5–9 × 6–8.5[a]
Lateral sepals (mm)	3.5–5 × 1.5–2[b]	6–10 × 3–5[a]	8–13 × 3–6[a]
Lateral petals (mm)	2–4 × 1–2[b]	6–12 × 1.5–3[a]	7–12 × 1.7–4.6[a]
Lip (mm)	2.5–8 (−10) × <1–2	7–17 × 1–2.5	10–23 × 1–2.5
Spur length (mm)	3–8[c] (−10)[d]	14–27	28–46
Column (mm)	2 × 2	4.5 × 5.5[a]	5.4 × 7.1[a]
Chromosomes (2n)	42, 63	42	

[a] Reddoch and Reddoch (1993)
[b] Luer (1975)
[c] Thien (1969)
[d] Stoutamire (1968)

Table 10.2 Mosquitoes from Michigan and Wisconsin carrying pollinaria of *Platanthera obtusata*

Location and species	Author
Michigan	
Mackinac Co., St. Martins Point	Stoutamire (1968)
Aedes vexans (Meigen)	
Marquette Co., Cedar-hemlock bog	Stoutamire (1968)
Aedes intrudens Dyar or *Aedes diantaeus* Howard, Dyar, and Knab	
Cheboygan Co., Rusis Bay	Dexter (1913)
Unidentified	Stoutamire (1968)
Wisconsin	
Ashland, Price, & Oneida Co.	Thien and Utech (1970)
Aedes Meigen sp.	
Aedes canadensis canadensis Theobald	
Aedes communis (DeGeer)	
Aedes punctor (Kirby)	
Aedes sticticus (Meigen)	
Forest Co.	Thien (1969)
Aedes canadensis canadensis Theobald	
Aedes communis (DeGeer)	

Thien (1969) and Thien and Utech (1970) collected four identified and one unidentified species of *Aedes* carrying pollinaria in Wisconsin (Table 10.2). Frequencies varied among vector species and site with up to 15% of *A. communis* (De Geer) and 8.5% of *A. canadensis canadensis* (Theobald) carrying pollinaria.

In Manitoba, Hocking et al. (1950) and Hocking (1953) found pollinaria on 10 species of *Aedes* in the Churchill area (Table 10.3). Two percent to 33% of female *A. nigripes* (Zetterstedt), *A. punctor* (Kirby), *A. excrucians* (Walker), and *A. cinereus* Meigen carried pollinaria. Moreover, the percentages increased over the course of

Table 10.3 Mosquitoes from Manitoba and Northwest Territory carrying pollinaria of *Platanthera obtusata*

Location and species	Author
Manitoba	
Churchill area	Hocking et al. (1950), Hocking (1953)
Aedes campestris Dyar and Knab	
Aedes cinereus Meigen	
Aedes communis s. l. (DeGeer)	
Aedes excrucians (Walker)	
Aedes flavescens (Muller)	
Aedes impiger (Walker)	
Aedes nigripes (Zetterstedt)	
Aedes punctor (Kirby)	
Aedes riparius Dyar and Knab	
Aedes spencerii (Theobald)	
Northwest Territory	
Great Bear Lake, Great Slave Lake, and Lake Athabasca	Porsild in Twinn et al. (1948), Raup (1930)
Unidentified	

Table 10.4 Mosquitoes from Alaska carrying pollinaria of Platanthera obtusata

Location and species	Author
Eielson Air Force Base	Gorham (1976)
Aedes communis s. l. (De Geer)	
Aedes intrudens Dyar	
Mt. McKinley National Park	Frohne (1955)
Aedes communis (DeGeer) (male)	
Sagwon	Gorham (1976)
Aedes Meigen sp.	
Aedes communis Dyar	
Aedes hexodontus Dyar	
Aedes nigripes (Zetterstedt)	
Aedes punctor (Kirby)	

the flowering period, reaching a calculated 80% (based on a compilation of data from different years) 25 days after flowering began (Hocking et al. 1950; Hocking 1953). Peak population levels in *A. nigripes*, *A. punctor*, and *A. communis* may be synchronized with the flowering of *P. obtusata* (Hocking 1953; Thien 1969).

In the Northwest Territory, Porsild (in Twinn et al. 1948) and Raup (1930) recorded mosquitoes with attached pollinaria at Great Bear Lake, Great Slave Lake, and Lake Athabasca, but none were identified.

In Alaska, Gorham (1976) found two pollinaria-bearing species at Eielson Air Force Base and four identified and one unidentified species at Sagwon (Table 10.4). *Aedes communis* and *A. nigripes* were relatively uncommon at Sagwon, comprising only 3.1% and 3.4%, respectively, of 5,727 specimens collected. Yet, 2.8% of *A. communis* and 3.1% of *A. nigripes* carried pollinaria, a much higher percentage than the 0.14–0.20% carried by the other, much more abundant, species.

In a study at Mt. McKinley National Park, Frohne (1955) reported males of *A. communis* carrying pollinaria. This is the only record of male mosquitoes transporting the pollen of this species. Males often sip nectar from a variety of boreal plants, and their usual lack of involvement as pollinators of *P. obtusata* is not understood (Stoutamire 1971). However, according to Stoutamire (1968), their antennae are markedly larger than those of the female and may interfere with the insertion of the proboscis into the nectar spur.

Some responses of mosquitoes to flower features have been described. *Aedes aegypti* (L.), for example, is known to react positively or negatively to different floral scents and to prefer green flowers (Sippel and Brown 1953; Thorsteinson and Brust 1962; Fay 1968). The factors attracting mosquitoes to the flowers of *P. obtusata*, however, are unclear. They lack bright color and are UV-negative (Voss and Riefner 1983). Contrary to Raup (1930), who believed that pollinators were drawn to *P. obtusata* by scent, Stoutamire (1968), Thien (1969), and Voss and Riefner (1983) were unable to detect any odor. Mosquitoes were abundant at Stoutamire's (1968) study sites (Table 10.2) and routinely alighted on vegetation. They may therefore perch in the inflorescence of *P. obtusata* as a matter of course, resting on or near the flowers for some time before responding to a short range-orienting mechanism and feeding stimulant (Stoutamire 1968).

A number of researchers beginning with Dexter (1913) have enclosed inflorescences in glass cages with selected species of mosquitoes in order to observe the pollination process. Thien (1969) used this approach to study the behavior of *Aedes communis* and *A. canadensis canadensis* females collected in northern Wisconsin. He reported that the mosquitoes hovered above the inflorescence of *P. obtusata* for a short time and then landed on newly opened flowers, showing a preference for those containing a large amount of nectar. Their front pair of legs usually gripped the hooded sepal or a petal, their middle legs the petals, and their back legs a petal or another part of the inflorescence. They inserted their 3 mm long proboscis into one of the two lateral openings of the nectar spur and extracted nectar for about 3–5 min. The length of their proboscis in relation to the length of the spur (Table 10.1) explains the preference for newly opened flowers containing a large amount of nectar. The positioning of the mosquito on the flower, imposed by the forced lateral entrance to the nectar spur, resulted in the attachment of a single viscidium to one of the compound eyes; restricted pollen acquisition may here again influence cross-fertilization and/or paternal success. The pollinium was removed from its half-anther during probing or as the insect withdrew from the flower (Thien 1969). The stigma is not receptive in newly opened flowers, but becomes viscid in 2–3 days (Thien 1969). A mosquito bearing pollinaria and visiting a flower at this stage may deposit pollen on the stigma. Only some of the pollen grains adhere, and a single pollinium is capable of pollinating numerous flowers (Thien 1969), the carryover potentially enhancing male success. According to Stoutamire (1968), the presence of pollinaria on a mosquito appears to stimulate it to explore and probe additional flowers. Such a response, if real, would, of course, increase the probability of massulae being deposited on the stigma and indirectly contribute to the reproductive success of the orchid. The question of whether mosquitoes have a problem accessing nectar in 2–3-day-old flowers, when the stigmas are receptive and the spurs may be only partially filled, has not been addressed.

Stoutamire (1968, 1971) conducted a similar study on unidentified, caged mosquitoes collected from the shore of Albany Bay, MacKinac County, Michigan. These mosquitoes also landed on the inflorescence, but particularly on the lateral sepals, where each remained for up to several minutes before beginning an exploration of the flower with its proboscis. Probing initially appeared to be awkward and random on both the front and back of the perianth, but eventually the mosquito settled on the labellum and inserted its proboscis into the nectar spur. Again the appendage which divides the opening of the nectary into 2 halves forced the mosquito to one side of the opening, bringing one of its compound eyes into direct alignment with a laterally positioned viscidium. Several attempts usually preceded a successful insertion of the proboscis followed by a minute or more of feeding. In the process, a viscidium was attached to the eye, and the pollinarium was withdrawn as before. The forward projecting pollinarium was oriented parallel with the proboscis along its right or left side, depending on which side the nectar spur was entered. Following an indefinite interval of rest, the insect proceeded to other flowers which were again extensively probed. Due to interference of the attached pollinarium with surrounding floral structures, the insect was often prevented from inserting its proboscis on the same side of the nectar spur on subsequent visits. During probing and/or insertion of the proboscis, the pollinium contacted the stigma and massulae were deposited on its surface. Although Dexter (1913) and Diets (in Stoutamire 1968) reported mosquitoes carrying up to three or four pollinaria, Stoutamire (1968) found none with more than one on each eye, even after several hours of being caged with the inflorescence.

The initial disorientation and awkwardness of the mosquitoes described by Stoutamire (1968) was not observed by Thien (1969), who suggested that the species used by Stoutamire may differ from those that usually pollinate the plants in nature. Nevertheless, Soutamire's mosquitoes were eventually able to effect pollination. In fact, Stoutamire (1968) demonstrated that females of *A. intrudens* Dyar from populations that occur well south of the range of *P. obtusata* and which had never come into contact with this orchid were attracted to its flowers and were fully capable of feeding on its nectar and of removing its pollinaria.

In addition to mosquitoes, Thien and Utech (1970) collected two species of geometrid moths in northern Wisconsin, *Xanthorhoe abrasaria* (Herrich-Schaffer) and *X. lacustrata* (Guenee), with pollinaria of *P. obtusata* attached to their compound eyes. Forty-five percent of those captured carried pollinaria, and each usually carried a higher number than the mosquitoes. These moths have proboscises from 3.5 to 6 mm long and may have an advantage over the mosquitoes in extracting nectar from spurs that are only partially filled. Several other geometrids have also been reported as pollinators. *Xanthorhoe munitata* (Hubner) visited the flowers and removed pollinaria in Michigan (Stoutamire 1971), and *Mesoleuca ruficilliata* (Guenee) and *Hydriomena renunciata* (Walker) were occasionally observed carrying pollinaria in northern Wisconsin (Thien and Utech 1970).

In addition, Voss and Riefner (1983), in a study in Cheboygan County, Michigan, observed a small crambid moth, *Anageshna primordialis* (Dyar), with pollinaria of *P. obtusata* cemented to its eyes. This insect was seen on a number of occasions perched on the lateral sepals of *P. obtusata*. Following some probing of the flower, it inserted its proboscis into the nectar spur and fed on the nectar. Gorham (1976) also observed a crambid, *Eudonia lugubralis* (Walker), carrying a pollinarium at Sagwon. As Stoutamire (1968) reported for mosquitoes, the floral attractant appears to be short ranged and to come into play after the moth has landed on the inflorescence (Voss and Riefner 1983).

Fruiting Success and Limiting Factors

Thien and Utech (1970) found 10.3–17.4% of flowers in four populations set fruit at their study sites in Wisconsin. They also discovered a correlation between fruit-set and the number of flowers per inflorescence. At least one capsule was formed in a higher proportion of plants with 9–17 flowers than in plants with 1–8 flowers.

Thirty-eight percent of the flowers had pollinaria removed, most only one. But this removal occurred rapidly over only a short time interval near the end of the flowering period. Of the 16–21% of pollinaria removed by the end of the season, nearly all were extracted within the last 7–8 days of a 25–26 day blooming period. The inflorescence is determinate, the first buds open about the same time on large and small inflorescences, and each flower lasts about 10–14 days. The correlation between capsule-set and inflorescence size therefore appears to be a product of the lag in pollination. A similar lag was observed in a population of this orchid at a site in Forest County, Wisconsin (Thien 1969).

The reason for the lag is unclear. There is no correspondence between pollinator abundance and the timing or rate of pollination (Forbes 1948; Siverly and DeFoliart 1968). Thien and Utech (1970) speculate that the pollinators may be feeding on other flowering plants and may transfer their attention to *P. obtusata* when the others stop blooming. Discovery of the means by which the flowers attract their pollinators may shed additional light on this matter.

Platanthera orbiculata **(Pursh) Lindley (Large Round-Leaved Orchid) and *P. macrophylla* (Goldie) P. M. Brown (Goldie's Round-Leaved Orchid)**

Habitat and Distribution

Although *P. orbiculata* is here included in the Platanthera group in accordance with Hapeman and Inoue (1997), Bateman et al. (2009) report that their DNA-based phylogenetic reconstruction does not support this alignment. Often found in the rich,

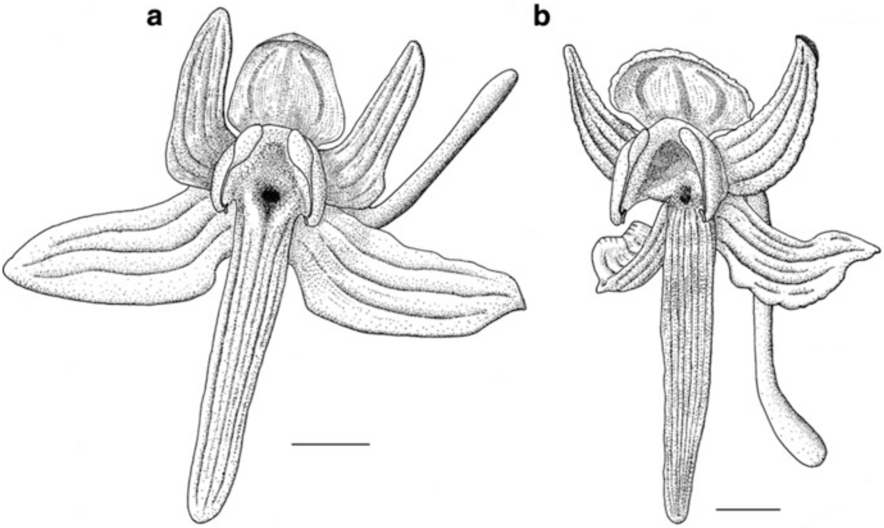

Fig. 10.2 (**a**) *Platanthera orbiculata*, flower, front view; (**b**) *Platanthera macrophylla*, flower, slightly oblique view, scale bars = 3 mm

damp humus of deeply shaded boreal or mixed forests, this orchid also grows in a variety of other habitats varying from balsam-spruce bogs to dry needle litter in pine-spruce woods. In the far north dwarfed specimens occur in the open (Luer 1975; Reddoch and Reddoch 1993; Smith 1993). It is distributed from Saskatchewan and Minnesota to Newfoundland and New Jersey and south in the Appalachians to Tennessee. It also occurs from Idaho and northern Oregon to the Northwest Territories with disjunct populations in southeast Alaska (Sheviak 2002). According to Lesher and Henderson (1998), it is rare throughout most of its range.

Platanthera macrophylla is largely restricted to mesic sites in coniferous and deciduous forests within the eastern range of *P. orbiculata*. It occurs from Newfoundland south to Pennsylvania and west to Ontario and the upper peninsula of Michigan (Brown 1998; Sheviak 2002).

Floral Morphology

A variable number of small- to medium-sized flowers are arranged in lax to dense racemes (Table 10.1) (Luer 1975; Reddoch and Reddoch 1993). The erect dorsal sepal is grayish–green with a light margin. The lateral sepals are reflexed to somewhat spreading (Fig. 10.2a, b) and grayish–green, frequently with nearly white margins. The petals are ascending, the lip pendant. Both are white, sometimes infused with a grayish–green tinge toward the tips. The lobes of the rostellum are directed forward and are wide spreading (Fig. 10.2a, b) (Sheviak 2002). Orbiculate viscidia face one another in front of the nectar spur and are about 4.4 (3.5–4.9) mm apart in *P. orbiculata* and 5.7 (4.0–7.1) mm apart in *P. macrophylla* (Reddoch and Reddoch 1993). In *P. orbiculata,* the pollinia are 3.1–4.7 mm long, in *P. macrophylla*, 4.6–6.2 mm long. The nectar spur is slender and clavate in both but distinctly longer in *P. macrophylla* than *P. orbiculata* (Table 10.1). The latter morphological difference is diagnostic, and molecular phylogenetic studies have further confirmed the distinctness of the species (Hapeman and Inoue 1997; Reddoch and Reddoch 2009). Brackley (1985) reported a faint nocturnal odor from the flowers of both orchids, but Reddoch and Reddoch (1993) were unable to detect it. They suggested however that short papillae on the lip and lateral sepals near the opening of the spur could be osmophores that produce a faint odor in that immediate vicinity.

Compatibility and Breeding System

No experimental data are available. Anecdotal observations suggest that *P. macrophylla* is self-incompatible and that insects transport the pollen of both (e.g. Reddoch and Reddoch 1993; Light 1998).

Pollinators and Pollination Mechanism

The viscidia in *P. orbiculata* and *P. macrophylla* are positioned to contact the eyes of visiting moths (see below) (Fig. 8.1). The difference in the spacing of the viscidia suggests that pollinaria placement in these two species is adapted to differently sized moths (Reddoch and Reddoch 1993). Differences in pollinator size are also implied by the disparity in pollinia and spur length. Pollinator segregation based on the placement of pollinaria on the same body part of differently sized moths contrasts with the mechanism found in other pollinator segregated species of *Platanthera* where pollinaria are attached to different parts of similarly sized moths (see e.g. *P. psycodes* and *P. grandiflora* or *P. leucophylla* and *P. praeclara*, below). A tendency for large lepidoptera to pollinate taxa with relatively restricted distributions and small lepidoptera, taxa with more extensive distributions is apparent in several other pollinator segregated species pairs (Catling and Catling 1991).

Stoutamire (in Luer 1975 without reference) recorded two noctuid moths, *Autographa ampla* (Walker) (cf. Fig. 11.5) and *Diachrysia balluca* Geyer, as pollinators of *P. orbiculata*. According to Reddoch and Reddoch (1993) both could be effective: the distance across their eyes is about 3 mm, and the lengths of the proboscises are 15–20 mm. The eye measurements do suggest, however, that the moths would have to contact one viscidium at a time. The distribution of *Diachrysia balluca* is coincident with most of the eastern range of *P. orbiculata* while that of *Autographa ampla* overlaps all except the northwest part of its range (Lafontaine and Poole 1991).

Luer (1975) mentioned that Sawyer identified a nocturnal hawkmoth, *Sphinx drupiferarum* Smith, as a possible pollinator of *P. macrophylla* (his *P. orbiculata* var. *macrophylla*). van der Pijl and Dodson (1966) attributed the same 1894 observations to Sargent, but Reddoch and Reddoch (1993) were unable to find the original 1894 references. Their examination of this sphinx moth suggested, however, that it probably would not be a very efficient pollinator. Its proboscis ranges from about 44 mm long in the eastern United States (Fleming 1970) to 60 mm long in Colorado (Gregory 1964), or 34–43 mm long in the prairie states (Sheviak and Bowles 1986). In the opinion of Reddoch and Reddoch (1993) the length of its proboscis, presumably in regions where it is relatively long, along with the presence of hair tufts in front of its eyes preclude its playing a significant role.

Fruiting Success and Limiting Factors

Additional studies are needed to establish factors affecting reproductive success in this orchid pair. However, Lesher and Henderson (1998) reported that *P. orbiculata* bloomed for up to eight weeks at a site in Washington, and the previously noted association of protracted flowering with pollinator limitation might be relevant here (e.g. Catling and Catling 1991).

Other Species of the Platanthera Group

Hapeman and Inoue (1997) resolved the North American taxa *P. hookeri* (Torr.) Lindley and *P. tipuloides* (L. f,) Lindley in the *Platanthera* clade. *Platanthera hookeri* is found in coniferous and deciduous forests from Manitoba and Iowa to Newfoundland and New Jersey. Reddoch and Reddoch (2007) found that flowering of this species in southwestern Quebec is positively correlated with rainfall in June and July of the preceding year and negatively correlated with temperature over the same interval. Its column has a downward projection over the entrance to the spur. This in combination with an upturned lip may restrict pollen acquisition, forcing pollen vectors to approach the nectary from one side as in *P. obtusata* (Catling and Catling 1991; Sheviak 2002). The lobes of the rostellum are very wide spreading, the viscidia are suborbiculate, the flowers are greenish, and according to Hapeman and Inoue (1997), it is probably pollinated by nocturnal settling moths. Nilsson (1981), on the other hand, listed skippers (Hesperidae) as the sole pollinator of this species. In either case there is agreement that the pollinaria are positioned to attach to the compound eyes of the vector.

Platanthera tipuloides includes two varieties (Sheviak 2002). Hapeman and Inoue's (1997) study was based on variety *tipuloides* (as *P. tipuloides* f. *nipponica* (Makino) M. Hiroe), distributed from eastern Siberia to Japan. A second variety, *behringiana* (Rydb.) Hulten, is found from Komandor Island to the Aleutians of

Alaska. Little is known about the pollination of the latter, but nocturnal moths and hawkmoths are known to pollinate variety *tipuloides* in Japan and adjacent areas, the pollinaria attaching to the proboscis (Inoue 1983).

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Chapter 11
Lacera Group

Abstract *Platanthera peromoena* is pollinated by *Hemaris thysbe*. The viscidia are positioned to attach to its compound eyes. Both *Platanthera psycodes* and *P. grandiflora* are partially self-incompatible. Autogamy is absent. *Platanthera lacera* is pollinator limited. Low levels of autogamy or agamospermy are present. *Platanthera grandiflora* is pollinated by medium to large-sized lepidoptera with the viscidia attaching to the compound eyes. *Platanthera psycodes* and *P. lacera* are pollinated by smaller lepidoptera with the viscidia attaching to the proboscis. *Platanthera praeclara* and *P. leucophaea* are self-compatible but not autogamous. Both are pollinated by sphingid moths. Differences in the divergence of the rostellar lobes and caudicle movements provide mechanical barriers that minimize interspecific pollen transfer.

Keywords *Platanthera peramoena* • *Platanthera psycodes*/*Platanthera grandiflora*/*Platanthera lacera* • *Platanthera praeclara*/*Platanthera leucophylla* • Viscidia placement and speciation • Partitioning of pollinators • Lepidopteran pollinators • Caudicle movement • Population and inflorescence size effects • Compatibility and hybridization

Members of the *Lacera* group include *P. praeclara* Sheviak and Bowles, *P. leucophaea* (Nuttall) Lindley, *P. grandiflora* (Bigelow) Lindley, *P. psycodes* (L.) Lindley, *P. peramoena* (A. Gray) A. Gray and *P. lacera* (Michx.) G. Don. Although once included in section *Blephariglottis*, Sheviak and Bowles (1986) considered these six species to comprise a natural group, and DNA-based phylogenetic studies have confirmed this view (Fig. 8.1) (Hapeman and Inoue 1997). Pollination has been investigated in all members.

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Platanthera peramoena A. Gray (Purple Fringeless Orchid)

Habitat and Distribution

The purple fringeless orchid occurs in meadows, wet woods, marshes, and roadside ditches from Missouri to New Jersey south to Arkansas, Mississippi, and South Carolina (Sheviak 2002).

Floral Morphology

The inflorescence is a many-flowered raceme with medium sized, densely to loosely arranged flowers (Table 11.1) (Luer 1975; Hapeman 1997; Sheviak 2002). Flower color is basically purple, but can vary from pinkish–purple to deep magenta. The lateral sepals are somewhat reflexed (Fig. 11.1a). The lateral petals have a finely toothed to entire margin, and together with the dorsal sepal extend forward to form a hood over the column. The lip is tripartite from a narrow base with a notched middle segment wider than the laterals (Fig. 11.1a). All segments are cuneate and unlike the other five members of the lacera clade, have only dentate or erose (irregularly notched or jagged) rather than deeply dissected, margins. The slender spur is club-shaped. The lobes of the rostellum are spreading and directed forward, the anther sacs and caudicles diverging (Fig. 11.1a). Orbiculate viscidia about 4 mm apart are positioned to attach to the eyes of the vector. The stigma is located between the viscidia and directly above the opening to the nectar spur.

Table 11.1 Data on the Lacera group, part 1 (Sheviak 2002)

Character	*Platanthera peramoena*
Plant height (cm)	35–105
Raceme length (cm)	6–17 [a]
Flower number	30–50 [b]
Dorsal sepal (mm)	5–9 × 4–7 [b]
Lateral sepals (mm)	6–9 × 4–7 [b]
Lateral petals (mm)	4–8 × 3–6 [b]
Lip (mm)	11–20 × 12–23
Nectar spur length (mm)	20–30
Pollinaria placement	Eyes
Column (mm)	3 × 3
Chromosomes (2n)	42

[a] Correll (1978)

[b] Luer (1975)

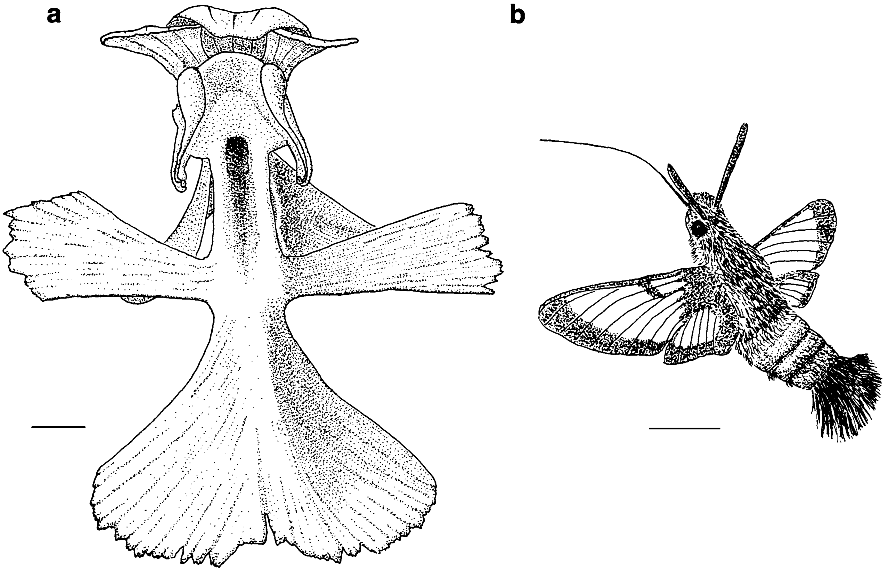

Fig. 11.1 (**a**) *Platanthera peramoena*, flower, front view, scale bar = 2 mm; (**b**) *Hemaris thysbe*, hummingbird clearwing, scale bar = 10 mm

Compatibility and Breeding System

No studies are available on the breeding system of this orchid.

Pollinators and Pollination Mechanisms

Hapeman (1997) found a diurnal sphingid moth, *Hemaris thysbe* (Fabricius) (hummingbird clearwing moth) (Fig. 11.1b), to be the principal pollinator in Dauphin County, Pennsylvania. He considered the orchid to be well adapted to pollination by this moth, and indeed, the distance between its compound eyes exactly matched the distance between the viscidia (4.0 mm). Its proboscis, about 21 mm long, was shorter than the mean length of the nectar spur at this site, 28 mm, with a distance to the nectar surface of about 26 mm. However, despite this discrepancy, the hawkmoth apparently functioned as an effective pollinator. It routinely grasped the lateral lobes of the labellum with its forelegs to gain purchase and forced its proboscis deep into the spur to reach the nectar. This behavior ensured eye contact with the viscidia, removal of the pollinaria, and subsequent contact between the pollinia and the stigma (Nilsson 1988; Hapeman 1997). Immediately following extraction, the pollinia were oriented almost vertically above the eyes of the pollinator. In the course of the next 30 s, they bent downward and inward coming to lie in the correct position to contact the stigma of the next flower visited.

The range of *P. peramonea* is included within that of *Hemaris thysbe*, and the latter has a distinct preference for pink to purple flowers (Fleming 1970; Hodges 1971; Spooner and Shelly 1983). The moth was most active in full sunlight and moved quickly through the population in search of flowers containing adequate nectar (Hapeman 1997). Examined specimens usually bore a number of pollinaria on their compound eyes, averaging 5 per individual.

Another hawkmoth, *Hyles lineata* (Fabricius) (white-lined sphinx) visited the flowers, although less frequently than *Hemaris thysbe*. This species has a long proboscis, 37–38 mm long, and its eyes never made contact with the viscidia. Hapeman (1997) therefore considered it a nectar thief.

Hemaris diffinis (Boisduval) (snowberry clearwing), *Danus plexippus* (L.), (monarch), and *Papilio troilus* L. (spicebush swallowtail) (Fig. 12.3a) also bore pollinaria and probably served as secondary pollinators (Hapeman 1997). Although abundant to common in the area they only rarely visited *P. peramoena*. One of three observed individuals of *Papilio troilus* had two pollinaria attached to one eye and had therefore visited at least two flowers. Although its proboscis is approximately the same length as that of *Hemaris thysbe*, its head is large and not a good fit for the flower. Both head size and column width are variable, however, and *P. troilus* or other species might play a more important role in the pollination of this orchid at other sites. Sheviak (in Homoya 1993) collected the morphologically similar butterfly, *P. glaucus* (tiger swallowtail), bearing a pollinarium of *Platanthera peramoena* in Illinois, and Luer (1975), based on a similarity in column morphology between *P. peramoena* and *P. grandiflora*, also considered swallowtails to be likely pollinators. He recorded visits of *Papilio* as well as two silver spotted skippers, *Epargyreus tityrus* Fabricius and *E. clarus* (Cramer) but did not describe the removal of any pollinaria.

Fruiting Success and Limiting Factors

Even though unopened buds contained ample supplies of nectar, Hapeman (1997) found less than one-half of examined nectar spurs in open flowers contained enough to measure. He suggested that the empty nectar spurs might be the result of visits by *Hyles lineata* and that such nectar thievery might affect the reproductive success of *P. peramoena* by reducing the number of visits by its principal pollinator, *Hemaris thysbe*.

Platanthera psycodes **(L.) Lindley (Small-Flowered Purple-Fringed Orchid),** ***P. grandiflora*** **(Bigelow) Lindley (Large-Flowered Purple-Fringed Orchid), and** ***P. lacera*** **(Michaux) G. Don (Ragged Fringed Orchid)**

Habitat and Distribution

Platanthera psycodes and *P. grandiflora* are sister species (Fig. 8.1). Both are found in wet meadows, bogs, marshes, swamps, and mesic woodlands (Stoutamire 1974; Luer 1975; Sheviak 2002). According to Stoutamire (1974), *P. grandiflora* is more frequently associated with conifers on well-drained, upland soils than *P. psycodes*. The latter is distributed from Minnesota through the Great Lakes to Newfoundland and the southern Appalachians. *Platanthera grandiflora* occurs from Newfoundland to Ohio and at elevation in the Appalachians to southern Tennessee and North Carolina. *Platanthera lacera* is found in swamps, marshes, bogs, riparian meadows, prairies, or open woods from Newfoundland to Manitoba and South Carolina to northeastern Texas (Correll 1978; Sheviak 2002).

Floral Morphology

The raceme in *P. grandiflora* is routinely more than twice as large as that in *P. psycodes*, usually with more loosely arranged flowers (Table 11.2) (Stoutamire 1974; Luer 1975). The lateral sepals are spreading to reflexed in both, while the dorsal sepal and finely toothed lateral petals often stand more or less erect behind the column (Figs. 11.2a and 11.3a, b). The labellum is tripartite from a narrow base

Table 11.2 Data on the Lacera group, part 2 (Sheviak 2002)

Character	*P. grandiflora*	*P. lacera*	*P. psycodes*
Plant height (cm)	27–120	14–80	14–101
Raceme length (cm)	3–25[a]	3–26[b]	8–12+[a]
Flower number[a]	30–60	20–40	30–50
Dorsal sepal (mm)[a]	6–9 × 4–6	4–7 × 3–5	5–6 × 3–4
Lateral sepals (mm)[a]	6–10 × 4–6	4–8 × 3–4	5–7 × 3–4
Lateral petals (mm)	6–10 × 5–6[a]	5–8 × 2[a]	5–7 × 3–6
Lip (mm)	10–25 × 14–26	10–17 × 13–17	5–13 × 5–17
Spur length (mm)	15–35	11–23	12–22
Pollinaria placement	Eyes	Proboscis	Proboscis
Column (mm)	4 × 4[a]	3 × 2	2 × 2
Chromosomes (2n)	42	42	42

[a] Luer (1975)

[b] Correll (1978)

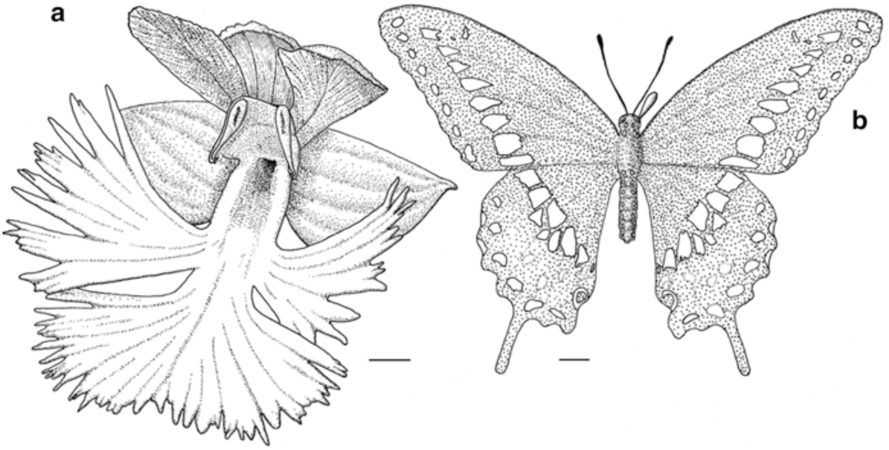

Fig. 11.2 (**a**) *Platanthera grandiflora*, flower, slightly oblique view, scale bar = 2 mm; (**b**) *Papilio polyxenes*, eastern black swallowtail, dorsal view with pollinarium on right compound eye, scale bar = 5 mm

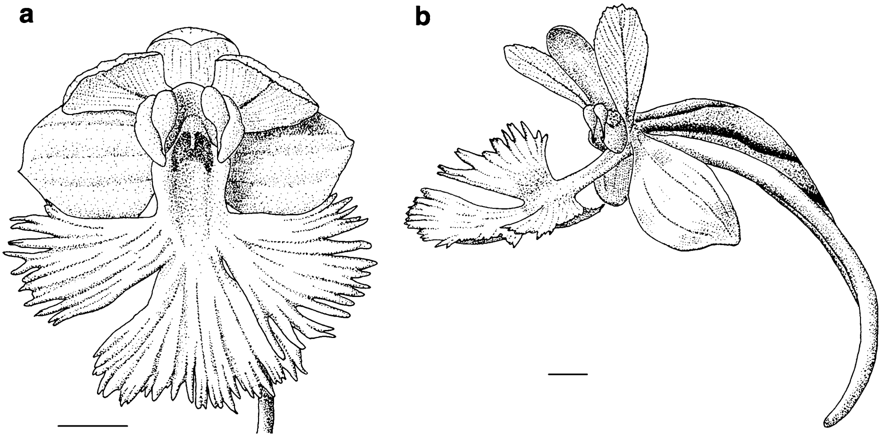

Fig. 11.3 *Platanthera psycodes*. (**a**) Flower, front view; (**b**) Flower, side view, scale bars = 2 mm

(claw) with three cuneate lobes. Both species, but particularly *P. psycodes*, vary in the orientation and dissection of the lateral lobes (Stoutamire 1974). In *P. grandiflora* they are usually deeply fringed and frequently bent toward the front of the flower, whereas in *P. psycodes* they are often shallowly fringed and typically flat or recurved. The sepals, lateral petals, and lip are commonly deep purple to pale lavender or rose lilac, but pure white forms sometimes occur. The labellum claw is occasionally a contrasting white color in *P. grandiflora* and less frequently so in *P. psycodes*. The nectar spur is variable in length (Table 11.2) and slender in both to slightly club-shaped in *P. grandiflora.*

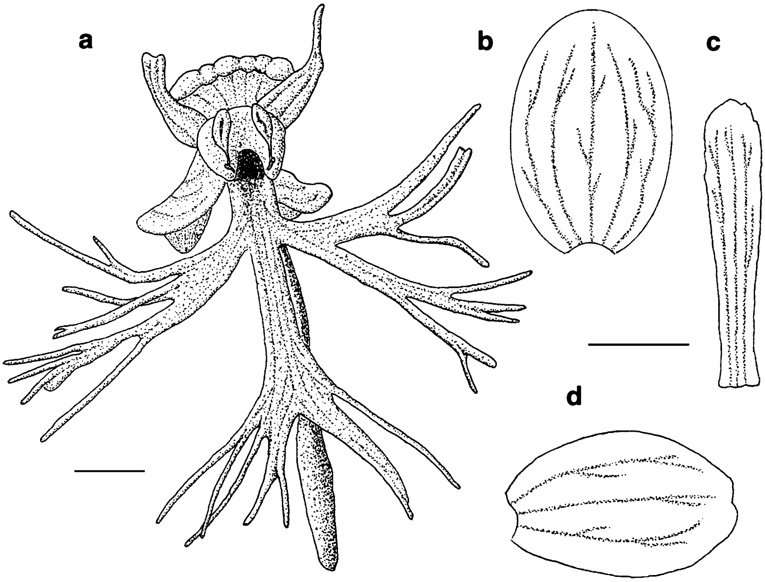

Fig. 11.4 *Platanthera lacera*. (**a**) Flower, front view; (**b**) Dorsal sepal; (**c**) Petal; (**d**) Lateral sepal, scale bars = 2 mm

Interspecific distinctions in column structure are critically related to differences in pollination (Gray 1862; Stoutamire 1974; Sheviak 2002). The relatively small column of *P. psycodes* (Table 11.2) has rostellum lobes that are nearly parallel and directed downwards; the suborbicular to broadly elliptic viscidia are 1–1.5 mm apart and partially enclosed laterally by projecting wings (Fig. 11.3a). The opening to the nectary is oblong in front view and is often partially divided in two by a downward projection from the roof of the nectary (Fig. 11.3a) (Fuller 1933). The distinctness and separation of the resulting openings vary, but they are positioned laterally below the stigma, each under one of the two viscidia (Stoutamire 1974). In *P. grandiflora* the column is relatively broad, and the rostellum lobes are spreading and directed forward; the divergent viscidia are orbiculate, and 4–5 mm apart (Fig. 11.2a). The opening of the nectar spur is located beneath the stigma and is funnel-shaped without a dividing projection (Stoutamire 1974).

The floral scent in *P. psycodes* is sweet and light and although diminished, persists at dusk (Stoutamire 1974). According to Gray (1862) it is distinctly sweeter than that of *P. grandiflora*.

Platanthera lacera bears a variable number of whitish to yellowish green, resupinate flowers in a lax to dense spike (Table 11.2). The lateral sepals are reflexed (Fig. 11.4). The petals are narrow with entire or sometimes apically lacerate margins (Sheviak 2002). The lip is descending and deeply three lobed. The lobes are more or less cuneate and deeply fringed, sometimes more shallowly on the middle than the lateral lobes. The rostelar lobes are short, rounded, nearly parallel, and directed downward. The pollinarium is almost straight with linear viscidia and pollinia that remain enclosed in the anther locule. The spur varies in length (Table 11.2) and is distinctly curved and clavate.

Compatibility and Breeding System

Natural hybrids of *P. psycodes* and the related *P. lacera*, (*P.* x *andrewsii* (Niles) Luer) are known from Minnesota to Newfoundland and south to North Carolina (Stoutamire 1974). All combinations of artificial interspecific crosses involving *P. grandiflora*, *P. psycodes*, *P. lacera*, and *P.* x *andrewsii* produced seed with 20–46% mature embryos (Stoutamire 1974). On this basis, no differences were evident in crosses either among *P. psycodes*, *P. lacera,* and *P.* x *andrewsii* or between members of this group and *P. grandiflora*. However, Stoutamire found only seed from crosses within this group germinated. Seed from crosses involving *P. grandiflora* as a parent did not, suggesting it might be more genetically distinct. The timing of orchid seed germination, however, is often erratic. Past attempts to germinate seeds of *P. grandiflora*, *P. psycodes*, and *P. lacera* have failed, and the number of seeds available were too limited to allow multiple cultures. Stoutamire therefore considered the germination data to be equivocal. Moreover, based on comparisons of nuclear ribosomal segments, *P. psycodes* is more closely related to *P. grandiflora* than it is to *P. lacera* (Fig. 8.1) (Hapeman and Inoue 1997), and Stoutamire (1974) has found a small number of naturally occurring specimens that suggest hybridization between *P. lacera* and *P. grandiflora* (*P. x keenanii* P. M. Brown; Brown 1993, p. 189). Stoutamire (1974) along with Correll (1978) and Fernald (1950) also reported naturally occurring specimens intermediate between *P. psycodes* and *P. grandiflora,* even though Stoutamire (1974) could find little supporting evidence for hybridization of these species based on the examination of column morphology in pressed herbarium specimens.

Despite the ease with which *P. psycodes, P. grandiflora*, and *P. lacera* can be artificially crossed and the occasional natural occurrence of hybrids, Catling and Catling (1994) found it possible to separate *P.* x *keenanii*, *P.* x *andrewsii*, and the putative parents by discriminant analysis and confirmed Stoutamire's (1974) observation that extensive introgression does not occur under natural conditions. Apparently ethological and mechanical or possibly phenological barriers are sufficient to maintain species integrity in this group. Contrary to Dunkelberger (1970), Stoutamire (1974) found no evidence of differing ploidy levels in *P. psycodes* and *P. grandiflora*. The diploid chromosome number for both species was 42 in plants examined from Michigan and West Virginia.

Both *P. psycodes* and *P. grandiflora* are partially self-incompatible. Stoutamire (1974) reported only 16% of the seeds in artificially selfed plants developed mature embryos in *P. psycodes* and 2.5% in *P. grandiflora*. Curiously, there appears to be no experimental data yet on intraspecific outcrossing in either *P. psycodes* or *P. grandiflora*.

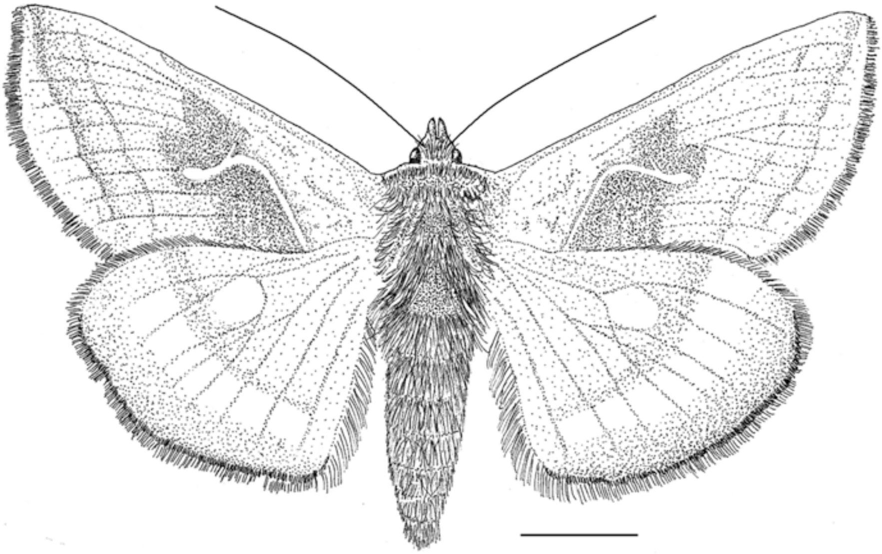

Fig. 11.5 *Anagrapha falcifera*, dorsal view, scale bar = 5 mm

In artificial crosses of *P. lacera* in western Illinois, Little et al. (2005) found 94.1% seed set in selfed and 94.4% seed set in out-crossed flowers. Gregg (1990) also reported high levels of seed set from artificial outcrossing (96%), geitonogamy (71%), and selfing (91%) in a study in West Virginia. Thus this species shows a markedly higher level of self-compatibility than either *P. psycodes* or *P. grandiflora*. Seed set in naturally pollinated populations was lower than in the artificially pollinated plants, ranging from 25.6 to 89.3% over a 5-year period in West Virginia to 71.4% in western Illinois. Although Duckett (1983) and Gregg (1990) found no evidence for autogamy or agamosprmy in Maine and West Virginia, respectively, Little et al. (2005) reported fruit production in 5 of 61 bagged and unmanipulated flowers in western Illinois.

Pollinators and Pollination Mechanisms

According to Moldenke (1949), hawkmoths (e.g. Fig. 12.4b) are the chief visitors to flowers of *P. grandiflora* throughout its range, the pollinaria attaching to the compound eyes (Fig. 8). Insects other than hawkmoths reported as visitors include *Papilio polyxenes* Fabrieius (eastern black swallowtail) (Fig. 11.2b) in New England (Ramsey 1966), *P. trolius* (spicebush swallowtail) (Fig. 12.3a) in Virginia (Wagner in Stoutamire 1974), *P. glaucus* (tiger swallowtail) in West Virginia (Boggs in Stoutamire 1974), and noctuid moths including *Autographa ampla* (cf. Fig. 11.5) at undesignated sites (Luer 1975; Nilsson 1981).

Stoutamire (1974) considered the shape and positioning of the well-spaced viscidia in *P. grandiflora* to be consistent with attachment to the compound eyes of medium to large-sized butterflies or moths, but pollinators were uncommon at his study sites in Vermont and West Virginia, and he failed to observe any visitors. When he removed pollinaria using a glass rod, the caudicles were at first oriented perpendicular to the rod and parallel to one another. They subsequently moved toward each other and forward. In this position, massulae would be properly oriented for deposition in the stigmatic depression located between the anther thecae. The bending was restricted to the area near the juncture of the caudicle and viscidium.

I have observed *Epargyreus clarus* (Crammer) (Silver-Spotted Skippers) pollinating the flowers of *P. psycodes* in northern minnesota (unpublished) Moldenke (1949) noted smaller butterflies visiting the flowers of this orchid, but did not describe the removal of any pollinaria. However, S. I. Smith (in Guignard 1886) found pollinaria attached near the base of the proboscis in *Papilio polyxenes* (Fig. 11.2b) and in two diurnal hawkmoths: *Hemaris thysbe* (Fig. 11.1b) and *H. diffinis*.

Stoutamire (1974) observed one of the same hawkmoths, *H. thysbe*, pollinating roadside colonies of *P. psycodes* in Michigan. He also reported a skipper, *Polites mystic* (long dash), pollinating this orchid in Michigan and Vermont. Both are also pollinators in Wisconsin (Sky Feller in Hapeman 1996). The closely spaced viscidia attached to the 13–15 mm long proboscis of the skipper at a point 1–2 mm from its head. Initially the caudicle orientation was perpendicular to the proboscis, but a forward movement was initiated within 15 s, and it came to lie more or less parallel to the proboscis in about 2 min (Stoutamire 1974). As in *P. grandiflora*, the bending movement was localized to an area at the juncture of the caudicles and the viscidia and progressed through an angle of 25–60°. Similarly, the viscidia attached to the 20-mm long proboscis of the hawkmoth at a point 3–5 mm from its head, and the caudicles underwent similar movements. In either case, attachment of the viscidia to a particular region of the proboscis, rather than randomly along its length, implies that a precise and specifically sequenced series of insect movements was involved (Stoutamire 1974).

Like *P. psycodes*, *P. lacera* normally attaches pollinaria to the vector's proboscis (Fig. 8.1) (e.g. Hapeman and Inoue 1997). Although *P. lacera* is frequently pollinated by nocturnal settling moths (Noctuidae) (Duckett 1983) (Fig. 8.1), on one occasion Stoutamire (1974) found the pollinaria of both orchids on the proboscis of a single specimen of the diurnal hawkmoth, *Hemaris thysbe* (Fig. 11.1b). Intermediate hybrid plants are frequent in the area of Grand Marais, Michigan, and this hawkmoth may be one of the agents responsible for this hybridization.

In their study of *P. lacera* in western Illinois, Little et al. (2005) recorded only five moth visits over 39 h of observation near sunrise and sunset. Two noctuid moths bearing pollinaria were captured between 20.00 and 21.00 h. The chief visitor to the flowers was *Anagrapha falcifera* Kirby (Fig. 11.5). *Allagrapha aurea* was also collected once with pollinaria but was an uncommon visitor. Both moths began their explorations on older flowers at the bottom of the inflorescence and worked up, visiting 2.6 (1–6) flowers per plant. They hovered in front of each flower, inserting their proboscis into the nectar spur. Pollinaria were attached to its base, up to three, in one case, indicating visits to at least two flowers.

Anagraphia falcifera had a proboscis length of 11.1 mm, significantly shorter than the average nectar tube length of 14.3 mm at this site. Nectar tube length was highly variable in the Illinois population, as elsewhere (Table 11.2), but was not correlated with pollinaria removal. Tube length is, of course, less critical for orchids that attach their pollinaria along the length of the proboscis than for those that require precise placement on the eyes or face of a pollinator (Dressler 1981; Hapeman and Inoue 1997). Although placement of pollinaria on the stigma can still require that the pollinator insert its head deep into the flower, no selection differential or significant correlation between nectar tube length and fruit production was observed. Additional visitors included green bottle flies (Calliphoridae) and sweat bees (*Lasioglossum* sp., Halictidae) but none removed pollinaria.

The average length of the nectar tube in *P. psycodes* is more or less constant throughout the north to south range of this species (Stoutamire 1974). However, in *P. grandiflora*, where nectar tube length is more crucial, it is longer in northern than in central and southern Appalachian populations. Stoutamire (1974) believes that this difference may imply a latitudinal variation in pollen vectors, a view that has yet to be confirmed, in part because pollinator visits apparently are so uncommon.

Fruiting Success and Limiting Factors

Light (1998) reported occasional mass flowering of *P. psycodes* in response to high rainfall during the preceding season. Over 75% of the flowers produced capsules, and Light suggested that periodic mass flowering in this species might facilitate gene flow.

Gregg's (1990) report of 96% seed set in artificially cross-pollinated plants of *P. lacera* compared with 25.6–89.2% seed set in naturally pollinated populations over 5 years suggests that pollinator visitation might be limiting at her West Virginia study site. In open pollinated plants, 50% of the seeds contained healthy looking embryos, 3% had small or abnormal embryos, 45% had dead embryos, and 2% were empty. The percentage of healthy embryos varied with the treatment. In addition to the 50% observed in open pollinated plants, artificial outcrossing produced 47%; artificial geitonogamy, 60%; and artificial selfing, 67%. No explanation was put forward to account for the variation. Gregg (1990) reported that disease was also a limiting factor at this site. Thus, over a 6-year period, fungi destroyed 17–95% of the capsules before they reached maturity.

In their study of *P. lacera* in western Illinois, Little et al. (2005) found that 44 open pollinated plants produced 13.9 ± 8.0 flowers and 9.9 ± 7.6 fruits per plant. At least one pollinarium was removed from 84.4% of the 612 flowers produced, and about 70% produced fruit. When compared with the 94% fruit set recorded for artificially outcrossed flowers, this result again suggests the possibility of pollinator limitation at this site. However, the percentage of flowers producing fruit was not significantly correlated with flower number or the number of pollinator visitors, implying that despite a positive correlation between flower number and pollinator visitation, the resources available for allocation to fruit production limited the percentage of flowers producing fruit.

Platanthera praeclara Sheviak and Bowles (Western Prairie Fringed Orchid) and *P. leucophaea* (Nuttall) Lindley (Eastern Prairie Fringed Orchid)

Habitat and Distribution

Although often occupying similar habitats, these species are largely allopatric (Sheviak and Bowles 1986; Sheviak 2002). Populations of *P. leucophaea* are often small and are concentrated in southeastern Iowa, eastern Missouri, Illinois, and southern Wisconsin through the Great Lakes states to Ontario and New York with a few scattered stations in Maine, New Jersey, New York, Virginia, Louisiana, and Oklahoma (Bowles 1983; Sheviak and Bowles 1986; Bowles et al. 2002; Sheviak 2002; Wallace 2003). *Platanthera praeclara* occurs in Manitoba, Minnesota, the eastern Dakotas, and Iowa south through eastern Kansas and western Missouri to northeastern Oklahoma and west through much of Nebraska. A single disjunct population occurs at higher elevation in Wyoming.

West of the Mississippi and throughout much of the prairie peninsula, the species occupy mesic to wet, often calcareous, tall grass prairie remnants and sedge meadows (Bowles 1983). Farther east, however, *P. leucophaea* occurs in a variety of habitats including fens, marshes, and bogs (Bowles 1983; Bowles et al. 2002).

Floral Morphology

The flowers in both (Figs. 11.6a and 11.7a) are oriented horizontally in a single (rarely double) terminal raceme. The raceme in *P. praeclara* is shorter with fewer flowers than in *P. leucophaea*, but the flowers are larger, and the inflorescence appears more compact (Table 11.3) (Sheviak and Bowles 1986; Pleasants and Moe 1993). The dorsal and lateral sepals are green to sometimes slightly whitish in *P. leucophaea*, and the lip and lateral petals are pure white. In *P. praeclara* the entire perianth is creamy white with a faint greenish tinge in the sepals. The lateral petals are apically lacerate in both and frequently emarginated (notched at the apex) in *P. praeclara*. Along with the dorsal sepal, they form a loose bonnet over the column. The lip is comprised of three deeply fringed, fan-shaped lobes arising from a narrow base (Figs. 11.6a and 11.7a). It is extended below into a narrow, clavate (club-shaped) nectar spur, which in *P. praeclara* is one of the longest found among North American species of *Platanthera* (Table 11.3).

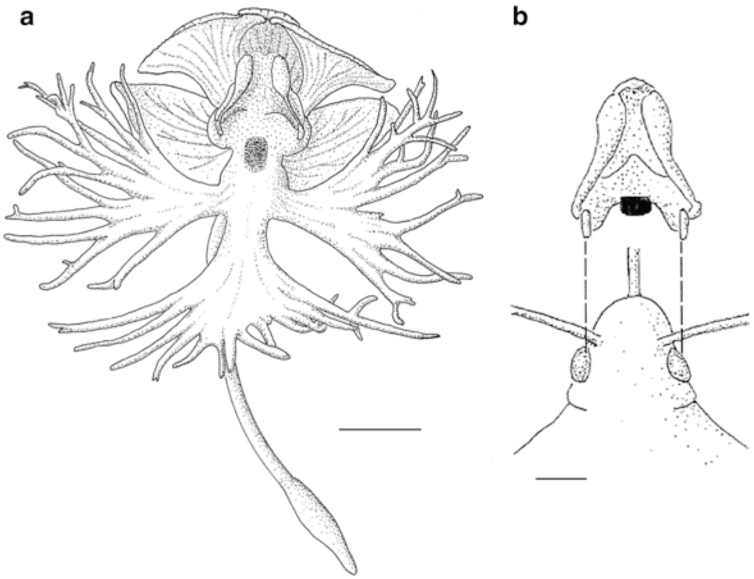

Fig. 11.6 (**a**) *Platanthera praeclara*, flower, front view; (**b**) *Eumorpha achenon* and diagrammatic depiction of the column of *P. praeclara* showing alignment of the viscidia to attach to the compound eyes, scale bars = 5 mm

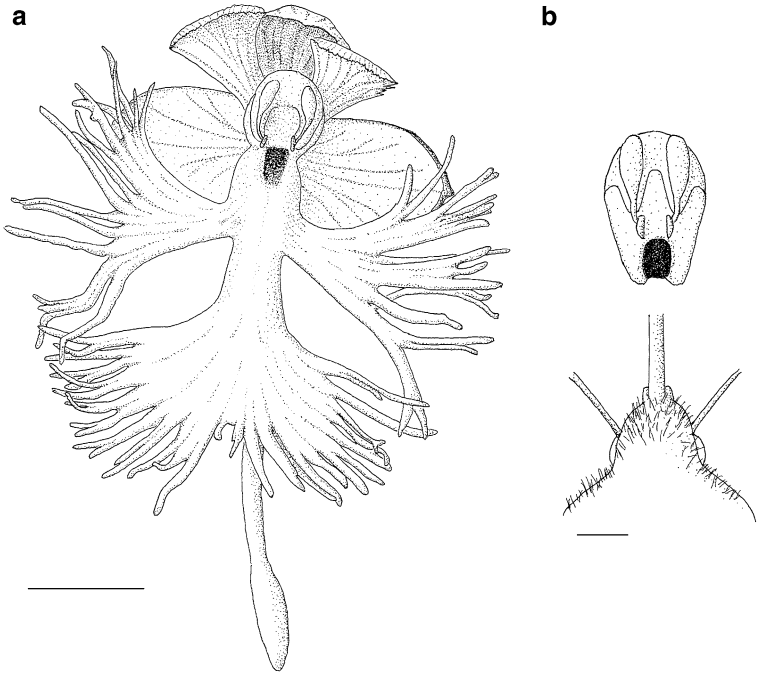

Fig. 11.7 (**a**) *Platanthera leucophaea*, flower, front view; (**b**) *Sphinx eremitus* and diagrammatic depiction of the column of *P. leucophaea* showing alignment of the viscidia to attach to the proboscis, scale bars = 5 mm

Table 11.3 Data on the *Lacera* group, part 3 (Sheviak 2002)

Character	*P. leucophaea*	*P. praeclara*
Plant height (cm)	32–112	38–85
Raceme length (cm)[a]	12.3 ± 4.8	9.2 ± 3.2
Flower number[a]	19.4 ± 7.9	12.6 ± 4.5
Lateral sepals (mm)[a]	8.1 ± 1.2 × 5.0 ± 0.6	12.0 ± 1.1 × 8.3 ± 1.0
Lateral petals (mm)[a]	9.6 ± 1.3 × 5.8 ± 1.2	13.1 ± 1.8 × 9.5 ± 1.9
Lip (mm)	14–22 × 15–29	17–32 × 20–39
Nectar spur length (mm)	28–47	36–55
Pollinaria placement	Proboscis	Eyes
Column (mm)	3 × 3	
Chromosomes (2n)	42	42

[a] Sheviak and Bowles (1986)

Significant differences related to pollination are evident in the structure of the extruded column. The column of *P. leucophaea* is rounded and relatively small with closely spaced pollinaria, short, more or less parallel rostellar lobes, and parallel caudicles (Fig. 11.7a, b). The viscidia, facing each other, are only 1.2–3.2 mm apart and are positioned directly below the pollinia (Sheviak and Bowles 1986). In contrast, the larger, more angular columns of *P. praeclara* have widely diverging rostellar lobes and caudicles directed more or less forward with the viscidia 6.2–7.5 mm apart (Fig. 11.6a, b). The orbiculate viscidia in both species are positioned on either side of the stigma and above the opening to the nectar spur.

Fragrance is most intense at night, and colored nectar-guides are absent. According to Sheviak and Bowles (1986), the fragrance in both is very sweet and light but is spicier in *P. leucophaea* than in *P. praeclara.* The volume of nectar in the latter is known to increase at night without any change in sugar concentration (Westwood and Borkowski in Light 2005).

Flowering within a population is synchronous, flowers can remain receptive for up to about 10 days, and plants can continue to produce flowers sequentially from the bottom to the top of the inflorescence for up to 20 days (e.g. Bowles 1985). According to Sieg and King (1995) and Bowles and Bell (1999), most plants of both species flower only once with the median number of flowering years under three. Sieg and King (1995) claimed that once plants of *P. praeclara* disappear they rarely re-emerge. However, Sather (in Light 2005), in a 19-year tracking study of *P. praeclara* in Minnesota, found that although population size varies, surviving plants experience one to three periods of dormancy lasting from 1 to 8 years.

Compatibility and Breeding System

In a study of *P. praeclara* at the Sheyenne National Grassland in southeastern North Dakota, Pleasants and Moe (1993) found that autogamy was absent and that both artificial cross-pollination and geitonogamy produced fruit. In naturally pollinated

Table 11.4 Breeding system data on *Platanthera leucophaea*

Treatment	Bowles (1985) % Fruit set	Bowles et al. (2002)[a] % Viable seed set	Cuthrell (1994) % Fruit set
Outcrossing	100[b]	70[c], 50[d]	
Geitonogamy	36–67[b]		
Selfing	63	0–15[e]	
Unmanipulated	0[b]		
Open pollination	42–57[f] 22[g]	About 25	49
Study site	Kenoska Co., SE Wisconsin	Lake Co., Illinois	Jefferson Co., SE Wisconsin

[a] Flowers not bagged because entire pollinium placed on stigma excluded subsequent pollination
[b] Flowers bagged
[c] Between populations
[d] Within populations
[e] Based on two plants
[f] Experimental plants
[g] All plants at site

plants, the level of fruit set was positively correlated with the rate of pollinaria removal. Thirty percent of the flowers were pollinated and 33% of all pollinaria were removed. Bowles (1985) reported similar results for *P. leucophaea* in southeastern Wisconsin where 22% of the flowers were pollinated and 33% of the pollinaria removed.

Bowles (1985), Cuthrell (1994), Bowles et al. (2002), and Wallace (2003) examined the breeding system of *P. leucophaea* at sites in Ohio, Illinois, and Wisconsin. Although the numbers were variable, the results of their observations and experimental crosses indicated an absence of autogamy and the presence of a facultative outcrossing breeding system. Because it allows mixed mating, such a breeding system could be susceptible to inbreeding depression, and Bowles (1985) and Bowles et al (2002) observed that selfing and geitonogamy produced lower levels of fruit set than outcrossing and that intrapopulation outcrossing produced lower levels of viable seed set than interpopulation outcrossing (Table 11.4). Similarly, From and Read (1998) reported a reduction in fruit set in selfed as compared to outcrossed plants in Nebraska, and Wallace (2003) found that seed set, relative seed mass, and most particularly seed viability was reduced in selfed as compared to outcrossed capsules (Table 11.5). Under natural conditions, a pollen vector might facilitate self-pollination, geitonogamy, or biparental inbreeding (i.e. crossing between closely spaced, genetically similar plants) as well as outcrossing, and studies of allozyme (enzymes coded by different alleles of a single gene) diversity indicated the presence of high, variable levels of inbreeding within the Ohio populations (Wallace 2002, 2003). According to Wallace (2003), however, outcrossing was the predominant means of reproduction.

Outcrossing in both species is promoted by the time lapse required for caudicle movement and repositioning of the pollinia for stigmatic contact (40–80 s) (Bowles 1983; Bowles et al. 2002). The timing of this movement could be a product of

Table 11.5 Breeding system data on *Platanthera leucophaea* (Wallace 2003)

	Large population			Small population			Large population			Small population		
Treatment	Year	*N*	% Viable seed	Year	*N*	% Viable seed	Year	*N*	% Viable seed	Year	*N*	% Viable seed
Outcrossing	1998	27	62 ± 6.0 (b)[a]	1999	6	46 ± 18.6	2000	33	39 ± 5.8 (b)[a]	2000	9	55 ± 11.4
Selfing	1998	27	16 ± 3.0 (a)	1999	6	31 ± 11.1	2000	30	23 ± 5.6 (a)	2000	9	46 ± 9.7
Open pollination	1998	26	77 ± 5.1 (b)	1999	8	41 + 12.1	2000	33	59 ± 5.6 (c)	2000	9	27 ± 11.9
Unmanipulated, bagged	1998	15	0									

[a] Unlike letters following mean values indicate statistically significant differences between treatments

selection, reflecting the mean duration of pollinator visits to an inflorescence, and higher levels of geitonogamy could be associated with larger inflorescences (Bowles 1985). No data are available on the average time that a pollinator spends at each inflorescence. However, several authors believe selfing or geitonogamy usually occurs only when pollinators revisit the plant (e.g. Barrett and Kohn 1991; Jennersten and Nilsson 1993; Agren 1996; Kunin 1997).

The species are also intercompatible. Sheviak and Bowles (1986) reported that artificial hybridizations at a number of sites in the Midwest produced well-developed capsules with copious and fully formed seed.

Pollinators and Pollination Mechanisms

White, bilaterally symmetrical, horizontally oriented flowers with deeply fringed petals, crepuscular/nocturnal scent production, exposed columns, very long spurs, abundant nectar, and no colored nectar guides immediately suggest moth and more specifically nocturnal sphinx moth pollination (Fig. 8.1) (van der Pijl and Dodson 1966; Faegri and van der Pijl 1971; Hapeman and Inoue 1997). In *P. leucophaea,* the structure of the column, with its closely spaced viscidia, directs attachment of the pollinaria to the proboscis (Fig. 11.7b) while in *P. praeclara* the more widely spaced viscidia on diverging caudicles directs attachment to the eyes (Figs. 8 and 11.6b) (Sheviak and Bowles 1986; Hapeman and Inoue 1997). The proper positioning of the pollinator, in turn, is dictated by the small opening to the nectar spur (Dressler 1981).

Movement of the caudicle following pollinaria extraction differs in the two orchids (Bowles 1983; Sheviak and Bowles 1986; Bowles et al. 2002). In *P. leucophaea* the pollinia, at first attached vertically, bend forward until they are nearly parallel with the proboscis. This permits insertion between the closely spaced lobes of the rostellum that front the recessed stigma. On the other hand, in *P. praeclara* the caudicles rotate slightly inward either to the left or right so as to position the pollinia slightly in front of and above the moth's head. A moth carrying these more laterally oriented pollinaria cannot pollinate the flowers of *P. leucophaea* because the closely spaced lobes of the rostellum (Fig. 11.7a) deflect the pollinia. Similarly, a moth carrying pollinaria of *P. leucophaea*, oriented parallel to its proboscis, does not usually pollinate the flowers of *P. praeclara* because the pollinia are unlikely to contact the more highly elevated stigma. A mechanical barrier to pollination therefore exists between these otherwise compatible species.

In *P. praeclara,* the spurs average about 45.7 ± 5.9 mm. in length, with the bottom 10–15 mm commonly filled with nectar. According to Sheviak and Bowles (1986), if 10 mm is assumed as an average minimum, the maximum proboscis length of a potential pollinator would probably lie in the range of 35–45 (30–50) mm. Based on measurements of proboscis length and eye separation in 19 sphinx moth species common to the prairie, these authors found four that had proboscises of the proper length (34–43 mm) and measurements across the eyes (5.8–6.4 mm) roughly similar to the viscidia separation in *P. praeclara*: *Eumorpha achemon* (Drury) (the achemon sphinx), *Hyles lineata* (white-lined sphinx), *Sphinx drupiferarum* (wild cherry sphinx), and *S. kalmiae* Abbot and Smith (laurel sphinx). Cuthrell and Rider (1993) and Cuthrell (1994) have since collected *Sphinx drupiferarum* and *Eumorpha achemon* carrying pollinaria of *P. praeclara* on their compound eyes at the Sheyenne National Grasslands in southeastern North Dakota, and A. R. Westwood (in Sharma et al. 2003) has reported *Sphinx drupiferarum* and *Hyles galli* (Rottenburg) (bedstraw hawkmoth), both with a proboscis length in the 32–39 mm range, pollinating *P. praeclara* in Manitoba. *Hyles galli* is the more common species here, but it is smaller than *S. drupiferarum* and may be a less effective pollinator (Portman 2003). In addition, C. Jordan (personal communication in Phillips 2003) has observed the introduced *Hyles euphorbiae* L. (leafy spurge hawkmoth) carrying pollinaria at the Sheyenne National Grasslands, and David Ashley (personal communication from N. Sather in Phillips 2003) has found *Paratraea plebeja* (plebeian sphinx) with attached pollinaria at Tarkio Prairie, Missouri. Further regional investigations are needed to establish which hawkmoths are the most effective pollinators and to evaluate their local abundance and pollination activities.

In *P. leucophaea* the distal 10–15 mm of the spur (35.6 ± 4.8 mm long) accumulates nectar. If 15 mm is accepted as a common maximum, the minimum selected proboscis length of a pollinator would be 15.8 mm (Sheviak and Bowles 1986). However, the entire nectar tube can sometimes fill with nectar in unvisited flowers, and insects with shorter proboscises would then have access to the nectar. Short-tongued noctuids and other moths sometimes visit the flowers and may function as at least secondary pollinators (Bowles 1985; Sheviak and Bowles 1986).

Bowles (1983) and Sheviak and Bowles (1986) saw two sphinx moths visiting the flowers of *P. leucophaea* over a 5-year period. *Sphinx eremitus* (Hubner) (the hermit sphinx) was collected while feeding and carried a polliarium attached to the base of its proboscis. *Manduca sexta* (L.) (the tobacco hawkmoth or hornworm) was observed feeding but was not collected. However, a population in Grundy County, Illinois, with *M. sexta* present, had many pollinaria removed. In both cases, numerous seeds were subsequently set, and Sheviak and Bowles (1986) considered both species to be likely pollinators.

Experiments with potted specimens of both orchids and laboratory-reared specimens of *M. sexta* supported the role of this moth as a pollinator of *P. leucophaea* (Sheviak and Bowles 1986). Pollinaria were routinely attached to its proboscis. However, with rare exception, the latter was too long to permit contact of the eyes with the viscidia of *P. praeclara.*

Cuthrell (1994) collected *Eumorpha achemon* carrying pollinaria of *P. leucophaea* on its proboscis in Jefferson County, southeastern Wisconsin. *Platanthera leucophaea* and *P. praeclara* therefore share a common pollinator, but, for the most part, hybridization is probably prevented in areas of sympatry by differences in the mechanics of pollen transfer discussed above.

Robertson (1893) also reported *Eumorpha achemon* along with *Xylophanes tersa* (L.) (the tersa sphinx moth) as pollinators of *P. leucophaea*. His study was conducted long before any distinction was drawn between *P. praeclara* and *P. leucophaea*, but the 2-mm separation he reported for the viscidia identifies his subject as *P. leucophaea*. The proboscis was randomly directed to one side or the other, and usually only one pollinarium at a time was attached to the proboscis. As discussed for *P. dilatata*, separate extraction of the pollinaria might promote cross-pollination and enhance the potential for paternal selection (Bateman 1948; Willson 1979). At the same time, hawkmoths often carry many pollinaria and visit multiple flowers. As a result, numerous flowers probably receive pollen from many different sources, a process that would be complemented by separate extraction of the pollinaria.

Prior to the recognition of *P. praeclara* and *P. leucophaea* as separate species, Stoutamire (1974) proposed two evolutionary lines within the *Lacera* group based primarily on column structure. This feature, as we have seen, is correlated with the positioning of the viscidia on the pollinator. Stoutamire's first evolutionary line included taxa with viscidia that attach to the proboscis (*P. psycodes*, *P. lacera*), the second, taxa with viscidia that attach to the compound eye (*P. grandiflora*, *P. peramoena*) (Fig. 8.1; Tables 11.1 and 11.2). The apparently discordant similarity in gross morphology between *P. psycodes* and *P. grandiflora* was attributed to possible convergence on diurnal lepidopteran pollinators.

Hybridization data consistent with this concept included reports of occasional natural hybrids between *P. psycodes* and *P. lacera* (Ames 1910; Wallace 1951; Voss 1972). In fact, Stoutamire (1974) considered the distinctness of these species to be maintained only by pollinator specialization (Fig. 8.1). At the same time, we have seen that crosses between *P. grandiflora* and *P. lacera* or *P. psycodes* purportedly fail to produce viable seedlings. Stoutamire (1974) considered the column structure in *P. leucophaea* to be intermediate between the *psycodes-lacera* type and the *grandiflora-peramoena* type and derived from the *grandiflora – peramoena* line as a specialization for nocturnal hawkmoth pollination.

Sheviak and Bowles (1986) questioned Stoutamire's (1974) interpretation based on a number of derived similarities shared by *P. psycodes* and *P. grandiflora*, on one hand, and *P. leucophaea* and *P. praeclara,* on the other, despite their dissimilar column structure. In addition, their data indicated probable compatibility between *P. praeclara* and *P. leucophaea*.

Consistent with Sheviak and Bowles (1986), molecular phylogeny has resolved a close relationship between *P. leucophaea* and *P. praeclara* and between *P. psycodes* and *P. grandiflora* and implies that the similarities in column structure between *P. grandiflora* and *P. peramoena* and between *P. psycodes* and *P. lacera* are due to convergence (Fig. 8.1) (Hapeman and Inoue 1997). According to this view, the taxa within each species pair were mechanically isolated from each other through a partitioning of pollinators based on changes in pollen placement, and speciation was a consequence of selection for modifications in column morphology. The members of each pair are partially sympatric and share some common pollinators (Hapeman and Inoue 1997). The difference in column morphology allows the members of each species pair to effectively segregate the pollinators, minimizing interspecific pollen transfer. A European species pair not included in Hapeman and Inoue's study, *P. bifolia – P. chlorantha*, is similarly differentiated primarily by column structure related to placement of the pollinaria (Nilsson 1983).

Sheviak and Bowles (1986) also noted that the viscidia in *P. grandiflora* and *P. praeclara* are round, as is usual in viscidia that attach to the eye. In *P. lacera,* they are linear-oblong, a specialization for attachment to the proboscis. However, in *P. leucophaea* and *P. psycodes,* they are more or less round to only slightly narrowed and may be less fully adapted to proboscis placement than in *P. lacera*. Sheviak and Bowles (1986) accordingly believe that these species are not in the same evolutionary line as *P. lacera*, a view consistent with Hapeman and Inoue's (1997) phylogenetic hypothesis (Fig. 8.1).

Finally, Sheviak and Bowles (1986) suggested that *P. leucophaea* was derived from *P. praeclara* in tallgrass prairies of the Missouri River drainage and that it colonized toward the northeast as the prairie peninsula developed at the end of the Wisconsin glaciation. They considered its acquisition of viscidia attachment to the proboscis as an advance over eye placement, allowing a greater variety of insects to pollinate the flowers. According to Hapeman and Inoue (1997), this placement of pollinaria represents reversion to the primitive condition for the genus and a reversal of the eye attachment originating at the base of the *leucophaea-praeclara-peramoena* clade (Fig. 8.1).

Pleasants and Klier (1995) found that 77% of the alleles of *P. praeclara* were present in *P. leucophaea* while 90% of the alleles of *P. leucophaea* were present in *P. praeclara*. However, they were not able to determine which species possessed a subset of the other and therefore which species might have given rise to the other.

Fruiting Success and Limiting Factors

Wallace (2003) examined the performance of artificially out-crossed, selfed, and open pollinated flowers in one large and one small Ohio population of *P. leucophaea*. She found that the mode of pollination was significantly associated with the percentage of viable seed produced in the large but not in the small population (Table 11.5), and a similar association was observed in the percentage of capsules that set fruit. In the small population, open-pollinated capsules produced a lower percentage of viable seeds than artificially outcrossed capsules. The differences were not statistically significant, but the sample sizes were small (Table 11.5). Pollinator activity could therefore be limiting here. In the large population, the highest percentage of viable seeds consistently occurred in open pollinated capsules (Table 11.5). This was unexpected, and Wallace suggested it might represent an experimental artifact. Namely, the placement of an entire pollinium on the stigma of hand-pollinated flowers (that normally receive only massulae) may have led to an excess of pollen tubes in the style, reducing access to the ovules. Such an interpretation would be consistent with Bowles (1985) and Bowles et al. (2002) who found that open pollination at study sites in Wisconsin and Illinois produced only about half as many viable seeds and fruits as artificial outcrossing (Table 11.4).

Bowles (1985) noted that the simple cellular seed form of this orchid probably requires the allocation of relatively few resources and that the process of flowering and fruiting is partially self-compensating through the production of photosynthate by green capsules and stems of the inflorescence. He considered resource limitation subordinate to pollinator limitation in this species. Vitt (2001), on the other hand, reported that hand pollinating 70% as compared to 30% of the flowers on each orchid led to the production of smaller plants the following year, a result that suggests high pollination rates can reduce the resources available for future growth.

In her investigation of *P. praeclara* in Minnesota, Sather (in Light 2005) found flowering plants had a higher level of survival and were more likely to bloom again than non-flowering plants, suggesting that resources did not limit flower production at her study site. At the same time, From and Read (1998) reported higher levels of fruit set in artificially cross-pollinated than in open pollinated or selfed plants at a site in Nebraska, implying either low levels of pollinator visitation or frequent self-pollination in open pollinated plants.

Reports of natural fruit set in *P. praeclara* varied from 9 to 30% at the Sheyenne National Grassland in North Dakota (Pleasants and Moe 1993; Cuthrell 1994) to 2.1% at the Tall Grass Prairie Preserve in Manitoba (Phillips 2003). Borkowsky and Westwood (2009) were able to increase the level of seed set at the Manitoba site by using ultraviolet light to attract hawkmoths to the orchids. Pollinator attraction may therefore have been a factor limiting seed production here, but the effect of pesticide applications on surrounding croplands needs further investigation (Cuthrell 1994; Phillips 2003).

Pleasants and Moe (1993) believe the positive correlation observed between levels of fruit set and pollinaria removal in *P. praeclara* is also evidence for pollinator limitation. Cuthrell (1994), however, has challenged pollinaria removal as a measure of effective pollinator activity. Pollinaria at his study site were eaten by predatory insects and dislodged in large numbers by the leaf blades of adjacent, wind-tossed grasses. Bowles (1985) also observed a discrepancy between pollinaria removals and fruiting in *P. leucophaea* at his site in Wisconsin and considered that pollinaria might have been removed by non-pollinating floral visitors.

Of course, the noted decrease in fruit set in *P. praeclara* and fruit and seed development in *P. leucophaea* following artificial geitonogamous pollinations and selfing could account for the reductions seen in open pollinated plants. The decrease might reflect various levels of inbreeding depression resulting from geitonogamy and biparental inbreeding rather than low pollinator visitation rates.

Pleasants and Klier (1995) did find measures of genetic variation to be low on an absolute scale for both species based on samples of seven populations of *P. leucophaea* from Illinois and Wisconsin and 14 populations of *P. praeclara* from Nebraska, Kansas, Iowa, Minnesota, and North Dakota. However, neither species appeared to be particularly impoverished when its level of genetic variation was compared to that of other orchids studied.

In Ohio, Wallace (2002) considered inbreeding in *P. leucophaea* responsible for heterozygote deficiency in five of seven populations surveyed and four of seven polymorphic loci analyzed. She suggested, however, that levels of inbreeding depression might prove to be a poor predictor of long-term survival because the large numbers of seed that can be produced by a single capsule could offset reduced seed viability.

Wallace (2003) observed no correlation between inbreeding depression and population size in Ohio populations of *P. leucophaea*, but Bowles et al. (2002) believe that habitat fragmentation and small, effective population sizes in Illinois have led to increased levels of geitonogamy and biparental inbreeding. They reasoned that inbreeding depression might be mitigated in outcrossing species with larger populations and greater genetic diversity (Schaal et al. 1991; Weller 1994), but would likely be more severe in small, isolated populations, where opportunities for outcrossing were reduced (e.g. Washitani 1996; Steffan-Dewenter and Tscharntke 1999). Genetic drift in small populations may also result in a loss of genetic diversity leading to a decline in the fitness of such quantitative traits as seed viability (e.g. Godt and Hamrick 2001).

Preliminary studies in *P. praeclara* also suggest a positive association between population size and heterozygosity (Sharma in Light 2005). Hawkmoth distributions can vary over time and space, and plant populations may be forced to compete to attract them as pollinators. Under these circumstances, small populations of *P. praeclara* may be unable to provide nectar payoffs comparable to other plant populations and may experience a reduction in pollination success (Bowles 1983; Phillips 2003). Pleasants and Moe (1993) also examined the relationship between population size and pollination success in *P. praeclara* but contrary to their expectations found none. They believed that this might have been due to the parameters of their experimental design: some of their distinctions in stand size may have been indistinguishable to sphingid moths.

The effect of stand size in other orchids has produced contradictory or, perhaps, species-specific results (e.g. Schemsky 1980; Firmage and Cole 1988; Fritz and Nilsson 1994). Much additional work is needed to evaluate the activity of pollinators and to clarify the partitioning and maintenance of genetic variation and the changes in inbreeding depression over time and in populations of varying size and genetic structure. For a discussion, see Wallace (2002, 2003) and Phillips (2003).

Studies on the relationship between inflorescence size and pollination success have also produced mixed results. Pleasants and Moe (1993) found no correlation between inflorescence size and pollinia removal per flower or fruit set per flower in a large stand of *P. praeclara* (54 plants) in southeastern North Dakota. However, when all the populations in their study were pooled (about 126 plants) inflorescence size was correlated with fruit set per flower but not with pollinaria removal. Bowles (1985) also reported a positive correlation between the percentage of flowers forming fruit and inflorescence size and visibility above the surrounding prairie canopy in *P. leucophaea* populations from Wisconsin. Nevertheless, large inflorescences were not as common as smaller ones: inflorescence size may have been counter selected by more frequent herbivory, nectar thieving, and geitonogamy or limited by plant age and local environmental conditions. Similar studies of the effects of inflorescence size on fruiting success in other orchids have sometimes shown a positive correlation (Schemsky 1980; Brys et al. 2008), no correlation (Smith and Snow 1976; Cole and Firmage 1984; Firmage and Cole 1988; Patt et al. 1989) or a negative correlation (Smith and Snow 1976).

Vegetative reproduction is uncommon, and some authors consider that populations of both species are maintained by long-term survival of adults and the generation of seeds (Bowles and Kurz 1981; Bowles 1983). Sieg and King (1995), however, believe that *P. praeclara* is probably short-lived and that population decline and extirpation may be related to severe drought or flooding. The presence of a viable seed bank is then essential to the re-establishment of local populations (cf. Sather in Light 2005). Although seed production can be prolific, favorable microsites for seedling recruitment are often scarce and the number of new plants established can be very low (Calvo 1993; United States Fish and Wildlife Service 1996).

The greatest threat to survival of *P. praeclara* and *P. leucophaea* is the continued conversion of prairie to cropland and the drainage of wetlands. Other threats are those shared by many other orchids and include the invasion of exotic species, herbivory, the availability of suitable fungal symbionts, irregular flowering, limited pollination, inbreeding depression, illegal collection, pesticide spraying, and fire suppression (Bowles 1983, 1985; Rasmussen 1995; Smith and Read 1997; Phillips 2003; Sharma et al. 2003).

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Chapter 12
Blephariglottis Group

Abstract *Platanthera blephariglottis* and *P. ciliaris* are self-compatible but not autogamous. The positioning of the viscidia and the length of the nectar spur in both species are adapted for attachment of the viscidia to the compound eyes of long-tongued lepidoptera. Distinct pollinator ecotypes may occur in *P. ciliaris*. In addition to morphological differences, *P. chapmanii*, *P. cristata*, and *P. integra* are separated from one another and other yellow-fringed orchids by pollination biology. *P. integrilabia* is primarily an outcrossing species, but autogamy can occur. The flowers appear to be adapted to nocturnal sphingids, but only diurnal butterflies have been observed as pollinators. *P. clavellata* is self-compatible, and both autogamy and outcrossing are reported.

Keywords *Platanthera ciliaris*/*Platanthera blephariglottis*/*Platanthera chapmanii*/*Platanthera cristata* • *Platanthera integrilabia* • *Platanthera clavellata*/*Platanthera integra*/*Platanthera nivia* • Pollinator ecotypes • Viscidia placement • Visual versus olfactory attraction • Pollen limitation • Inflorescence size and fitness • Population size and seed viability

With removal of the *Lacera* group and addition of section *Gymnadeniopsis* (*Platanthera clavellata*, *P. integra*, *P. nivea*), Hapeman and Inoue (1997) consider the *Blephariglottis* group to be monophyletic (Fig. 8.1). *P. nivia* is not considered in detail here because its pollination biology has yet to be studied. However, a recently recognized species, *P. chapmanii* (Small) Luer emend. Folsom, is added.

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Platanthera ciliaris (L.) Lindley (Yellow-Fringed Orchid) and *P. blephariglottis* (Willdenow) Lindley (White-Fringed Orchid)

Habitat and Distribution

Both species commonly occur in sphagnum bogs, pine savannas, meadows, and prairies (Sheviak 2002). *P. blephariglottis* var. *blephariglottis* is found from Michigan to Newfoundland south to Georgia. A second variety, *conspicua* (Nash) Luer (southern white-fringed orchid), is restricted to the coastal plain from North Carolina to Texas. The habitat of *P. ciliaris* is more varied and includes wet to well-drained sunny or partially shaded sites in open woods, marshes, forest edges, and mountain slopes (Robertson and Wyatt 1990a, b). It is found from Michigan to Massachusetts south to Florida and eastern Texas.

Floral Morphology

Flowers vary in size and are borne on many-flowered, cylindrical, or ovoid racemes (Table 12.1) (Smith and Snow 1976; Cole and Firmage 1984; Sheviak 2002). They are white in *P. blephariglottis* and orange in *P. ciliaris*. The lateral sepals are reflexed (Figs. 12.1a and 12.2a, b). The petals are shorter than the sepals and have lacerate distal ends. The lip is tongue-shaped, commonly with a margin that is fringed in *P. blephariglottis* or deeply filiform-fringed in *P. ciliaris*. It is projected downward into a long, usually cylindric, basal necter spur, often three-quarters filled with nectar (Table 12.1). The amount of nectar can vary significantly within an inflorescence, but the variation is not consistently related to the probability of pollination (Cole and Firmage 1984). The lobes of the rostellum curve forward and are

Table 12.1 Data on the Blephariglottis group, part 1 (Sheviak 2002)

	P. blephariglottis		
Character	var. *blephariglottis*	var. *conspicua*	*P. ciliaris*
Plant height (cm)	8–80	35–110	4–100
Flower number[a]	20–30(40)[b]		30–60
Dorsal sepal (mm)	5–8 × 4–6[a]		4–9 × 3[c]
Lateral sepals (mm)[a]	5–11 × 4–9	8–11 × 5–9	8 × 7
Lateral petals (mm)[a]	3–8 × 1.5–3	5–8 × 1.5–3	6 × 1.5
Lip (mm)	6–13 × 2–9	9–26 × 4–9	8–19 × 4–18
Nectar spur (mm)	15–25	30–50	20–35
Column (mm)[a]	3 × 3	3 × 3	3 × 3
Chromosomes (2n)	40	40	40

[a] Luer (1975)
[b] Cole and Firmage (1984)
[c] Correll (1978)

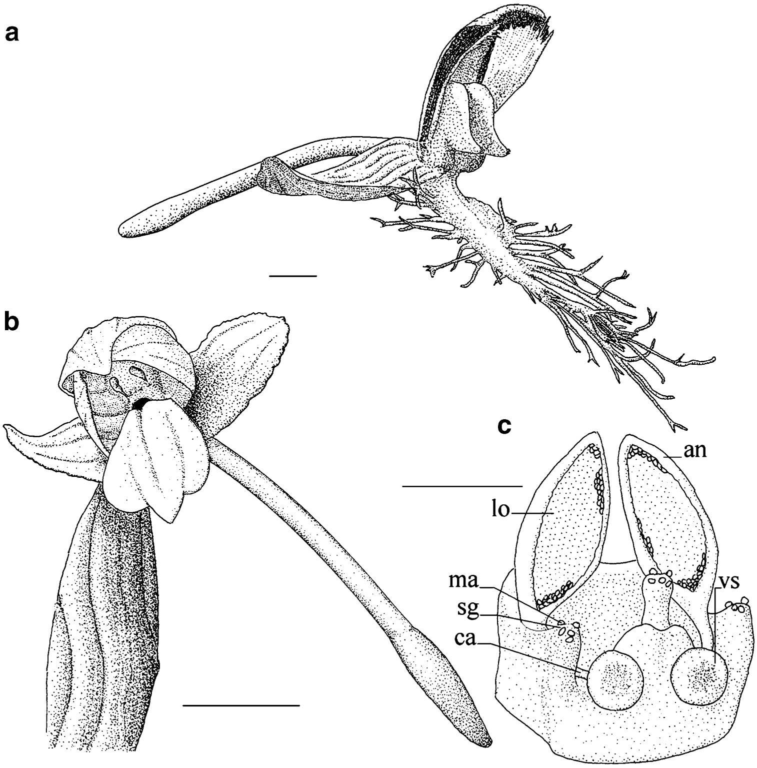

Fig. 12.1 (**a**) *Platanthera ciliaris*, flower, oblique side view, scale bar = 3 mm; (**b, c**) *Platanthera clavellata*. (**b**) Flower, oblique view, scale bar = 3 mm; (**c**) column, slightly oblique view, scale bar = 1 mm. *an* anther, *ca* caudicle, *lo* locule, *ma* massulae, *sg* stigma lobe, *vs* viscidium

slightly spreading (Figs. 12.1a and 12.2a, b). The viscidia are orbiculate to sometimes slightly elliptic and point upward and outward from the flower. One viscidium is positioned on either side of the opening to the nectar spur. A glossy, three-lobed stigma is located directly above the entrance to the spur and beneath and between the half-anther cells (Smith and Snow 1976; Robertson and Wyatt 1990a). Individual flowers remain fresh, secrete nectar, and continue to be receptive for up to 6–7 days in *P. ciliaris* (Robertson 1987) and up to 10 days in *P. blephariglottis* (Cole and Firmage 1984).

Compatibility and Breeding System

Data are available on populations of *P. blephariglottis* var. *blephariglottis* from central Maine (Cole and Firmage 1984) and Michigan (Smith 1975; Smith and Snow 1976) and on populations of *P. ciliaris* from North and South Carolina

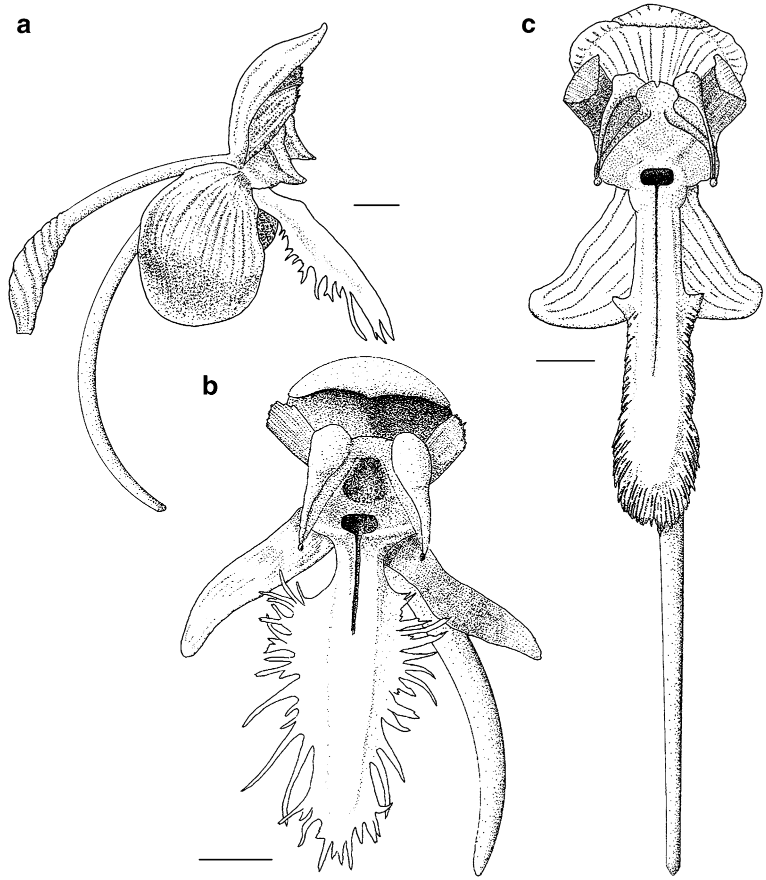

Fig. 12.2 (**a, b**) *Platanthera blephariglottis*, (**a**) flower, side view; (**b**) flower, front view; (**c**) *Platanthera integrilabia*, flower, front view, scale bars = 2 mm

(Robertson and Wyatt 1985, 1990a, b; Robertson 1987), Michigan (Smith 1975; Smith and Snow 1976), and West Virginia (Gregg 1981, 1990) (Tables 12.2 and 12.3). Neither species is autogamous. Experimental transfer of pollen within a single flower, among flowers on the same raceme (geitogamy), or between plants (xenogamy) produced high levels of fruit set in both species (Tables 12.2 and 12.3), as did artificial, reciprocal hybridization between the species.

Smith and Snow (1976) considered seed production in *P. blephariglottis* to be largely the result of geitonogamy and xenogamy and suggested that the former might be more common since pollinators often visited several flowers on a raceme before departing. However, the average amount of time the pollinator remained on the inflorescence, 34 ± 8.2 (2–145) s, was less than the mean time required for the caudicle to rotate and bring the pollinia into position to contact the stigma (about 60 s) (Cole and Firmage 1984). This circumstance might provide a mechanism that

Table 12.2 Percent of flowers setting fruit as a result of experimental treatments indicated for *Platanthera ciliaris*

Species locality	Agamospermy	Autogamy	Selfing	Geitonogamy	Xenogamy	Open pollination	Source
Mountains, NC	0	0	91–94		85–89	84–87	Robertson (1987) and Robertson and Wyatt (1990a, b)
Coastal plain, SC	0	0	72–95		79–100	64–66	
West Virginia		0	87	88	91	15–60/19–74	Gregg (1990)[a]
Michigan							
Open habitat						50	Smith (1975) and Smith and Snow (1976)
Semiopen habitat						27	
Overall		0				46	

[a] Two different results are given for open pollination

Table 12.3 Percent of flowers setting fruit as a result of experimental treatments indicated for *Platanthera blephariglottis*

Species locality	Autogamy	Selfing	Geitonogamy	Xenogamy	Open pollination	Source
Michigan						
Open habitat					23	Smith (1975) and Smith and Snow (1976)
Semiopen habitat					25	
Overall	0	100	100		24	
Maine	0	91	100	99	62 (32–80)	Cole and Firmage (1984)

effectively reduces the incidence of self-pollination in this species (meaning either pollinator-mediated self-pollination within a single flower or geitonogamy). Selfing might occur when pollinators return to or remain on the same inflorescence long enough for rotation of the pollinia to be completed.

Other features also appear to favor cross-pollination. The pollinaria of both *P. blephariglottis* and *P. ciliaris* remain attached to pollinators for several days (Smith and Snow 1976; Folsom 1979), and each pollinator may carry more than one pollinarium (Gregg 1983; Cole and Firmage 1984). Greenhouse tests on *P. blephariglottis* indicate that the pollen remains viable for at least 5 days (Cole and Firmage 1984). When the pollinia are brushed against a stigma, individual massulae often separate from one another, and one to several can be deposited on successive stigmas as the pollinator moves from flower to flower (Luer 1975; Smith and Snow 1976). Prolonged viability of the pollen, its attachment to a pollen vector for an extended time period, and the sequential deposition of one to several massulae on a number of flowers favor outcrossing, as well as an increase in male fitness and an increase in neighborhood size through reduction of biparental inbreeding (e.g., Grant 1977; Cole and Firmage 1984; Sutherland 1986a, b, 1987).

Outcrossing in *P. ciliaris* might be further promoted by a reported variation in the amount of nectar produced among the flowers of an inflorescence (Robertson and Wyatt 1990b). Such variability was considered significant in the movement of pollinators among tropical mass-flowering trees (Frankie and Haber 1983) and Robertson and Wyatt (1990b) thought that it might play a similar role in this species. In addition, they reported that only a few flowers in a given inflorescence were open at any one time in their Carolina populations. This too should lead to a frequent movement of pollinators among plants and a reduction in geitonogamy. Gregg (1983), however, found that butterflies visited from 2 to 26 flowers of *P. ciliaris* per inflorescence, effecting both geitonogamy and xenogamy in a West Virginia population, where most inflorescences had between 25 and 35 flowers. *Papilio polyxenes* (eastern black swallowtail) averaged 13 flower visits per inflorescence at this site during one study year.

Cole and Firmage (1984) reported that on each visit pollinators of *P. blephariglottis* fed on an average of 3.4 (1–19) flowers from the same part of the inflorescence and spent an average of 10 (1.2–39) s on each flower. This behavior was generally repeated on several successive inflorescences interspersed with rest periods of varying duration. Pollinators moved an average of about 3 m between inflorescences, but the distance and the number of inflorescences visited in a particular area were related to the size of the insect. Large butterflies landed on several inflorescences at one location and then flew 10–15 m to another inflorescence. Skippers moved smaller distances and visited more inflorescences per unit area than larger Lepidoptera. This plus their territorial behavior in areas with high orchid density (leading to exclusion or reduction in the number of large butterflies) might result in higher capsule production (Cole and Firmage 1984) and, presumably, a spatial restriction of the pollen component of gene flow (e.g., Beattie 1978) in such areas compared to sites with lower orchid density.

Pollinators also moved between the orchid species, and many authors have reported natural hybrids of *P. blephariglottis* and *P. ciliaris* (*P.* x *bicolor* (Raf.) Luer) (e.g., Hardin 1961; Smith 1975; Smith and Snow 1976; Folsom 1984; Case 1987). Only 2.7% of one mixed population at Booth Lake Bog in southwestern Michigan consisted of hybrids, however, suggesting that pollinator fidelity was high and/or that the difference in phenology (blooming dates) at this site (see below) was a significant impediment to cross-pollination (Smith 1975; Smith and Snow 1976). Hybridization is apparently more frequent elsewhere. Case (1987) reported that hybrids outnumbered parental plants at two other locations in southwestern Michigan. Although a close relationship is not necessarily prerequisite to hybridization among orchids, comparison of nuclear ribosomal segments (Fig. 8.1) (Hapeman and Inoue 1997) and allozyme analysis (Cowden 1993, 1998) do, in fact, suggest that these species are closely allied. Cowden (1993) considered them sufficiently similar to warrant the treatment of *P. blephariglottis* as a variety of *P. ciliaris.* For an update on current taxonomic thinking, see Catling (2011).

Pollinators and Pollination Mechanisms

The positioning of the viscidia and the length of the nectar spur in both species (Table 12.1) imply attachment of the pollinaria to the compound eyes of long-tongued pollinators (Smith and Snow 1976). Orange to yellow flower color is known to attract a variety of vectors including butterflies, whereas white flowers are often associated with moth pollination (van der Pijl and Dodson 1966; Faegri and van der Pijl 1971; Smith and Snow 1976). However, Cole and Firmage (1984) related white flower color in *P. blephariglottis* to butterfly pollination, the contrast making the flowers conspicuous against the darker color of the surrounding bog mat and vegetation. These authors also reported the production of only a weak nocturnal as well as diurnal fragrance in *P. blephariglottis*, a feature not usually associated with moth pollination. However, other floral characters in addition to the white- to cream-colored petals and sepals, including an absence of both nectar guides and an ultraviolet reflectance pattern, are consistent with pollination by moths (Faegri and van der Pijl 1971; Cole and Firmage 1984). Both moth and butterfly pollination have now been reported and may reflect a regional bias in food preferences or differences in the availability of alternative food sources.

In a 2-year study at Booth Lake Bog, Berrien County, Michigan, Smith and Snow (1976) found moths to be the most important pollinators of *P. blephariglottis* and butterflies, the most important pollinators of *P. ciliaris*. They conducted no experiments to test the train of stimuli that led pollinators to the flowers, but based on general observations supposed that the butterflies were initially drawn to *P. ciliaris* by the bright orange flowers and, only on closer approach, by the form of the flower and its fragrance. Nocturnal moths, on the other hand, appeared to be attracted to the flowers of *P. blephariglottis* by their odor and only later, at close range, by their form and color. Nocturnal moths preferentially visited the white *P. blephariglottis* in mixed populations of both orchids, but they followed odor trails to isolated groups of *P. ciliaris* without regard to color. Diurnal moths, on the other hand, appeared more sensitive to color, visiting *P. blephariglottis* and ignoring flowers of *P. ciliaris* present in the same area.

Although these accounts are contradicted by studies that record little or no floral odor in *P. blephariglottis* (Cole and Firmage 1984) and *P. ciliaris* (e.g., Folsom 1984), they are consistent with observations on the mean number of flowers pollinated in two microhabitats (Smith 1975; Smith and Snow 1976). In the first, the racemes of *P. ciliaris* were located in open areas, free of concealing vegetation. In the second, they were surrounded and partly obscured by other plants. The number of flowers pollinated on each raceme in the first habitat was approximately twice that of the second (Table 12.2). Such a result would be expected if a visual stimulus was responsible for attracting the pollinator. For *P. blephariglottis*, approximately the same number of flowers per raceme were pollinated in the two habitats (Table 12.3). If the pollinator in this case was attracted by odor, the presence of surrounding vegetation would have had little influence on pollination.

Papilio troilus (spicebush swallowtail) (Fig. 12.3a) was the most frequent pollinator of *P. ciliaris* in the Michigan study, although this species did occasionally also visit *P. blephariglottis*. Its chief larval food, *Linderia benzoin* (L.) Blume (spicebush), was common in the bog. The emergence of the second (summer) brood of this butterfly corresponded with the peak flowering period for *P. ciliaris*, which occurred 1–2 weeks later than that for *P. blephariglottis*.

Less-frequent pollinators carrying pollinaria of *P. ciliaris* in Michigan included *Papilio glaucus* (tiger swallowtail), *Satyrium liparops* (Leconte) (striped hairstreak), and *Danaus plexippus* (monarch). *Satyrium liparops* only rarely had pollinaria attached. Its chief larval food plant, the blueberry (*Vaccinium*), was common in the bog, and its July emergence occurred during anthesis of *P. ciliaris*. Thus, it might be expected to play a role, but even though its proboscis is of sufficient length to reach the nectar, its head is small and may not always come into contact with the viscidia. *Danaus plexippus* was probably no more than an incidental pollinator. It travels over a wide area, and its larval foods were not found in the bog. *Hyles lineata* (white-lined sphinx) (Fig. 12.4b), a nocturnal species, was seen to visit the

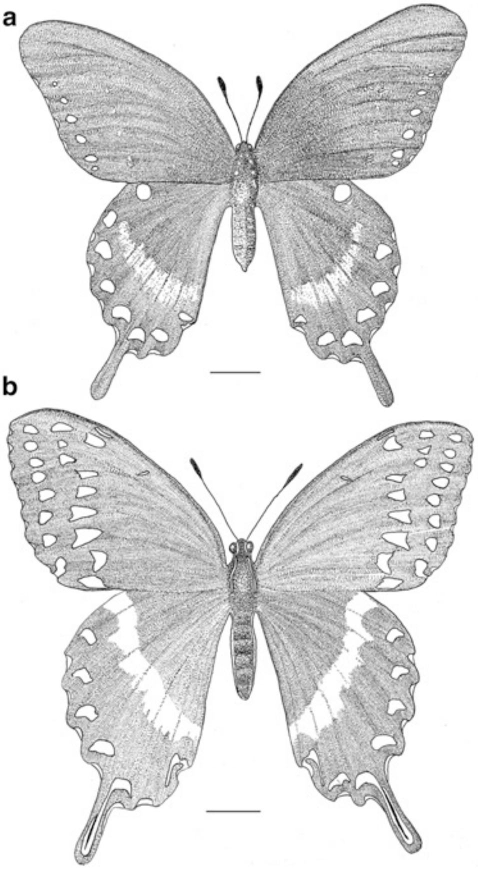

Fig. 12.3 (**a**) *Papilio* (*Pterourus*) *troilus*, spicebush swallowtail, dorsal view; (**b**) *Papilio* (*Pterourus*) *palamedes*, palamedes swallowtail, dorsal view, scale bars = 10 mm

flowers, and Smith and Snow (1976) considered it a probable pollinator even though it was not observed carrying pollinaria.

Smith and Snow's (1976) data on the pollinators of *P. blephariglottis* did not reveal any one vector with the primacy observed for the spicebush swallowtail on *P. ciliaris*. Moths found with attached pollinaria included *Hemaris thysbe* (hummingbird clearwing) (Fig. 11.1b) and *Darapsa versicolor* (hydrangia sphinx). Both were daytime visitors and expected residents of the bog as the larval foods of these species (*Cephalanthus occidentalis* L. [buttonbush] for the sphinx moth and *Lonicera* sp. [honeysuckle] and *Viburnum* sp. [cranberry] for the clearwing) were present in the bog. In addition, spicebush swallowtails (Fig. 12.3a) and bumblebees (*Bombus*) along with a single monarch butterfly were observed with pollinaria attached. As was the case for *P. ciliaris*, the monarch was probably no more than an incidental pollinator here. Catling and Catling (1991), however, found it to be the sole pollinator during a 24-h period of observation in Parry Sound District, Ontario, with the pollinaria attaching to its eyes.

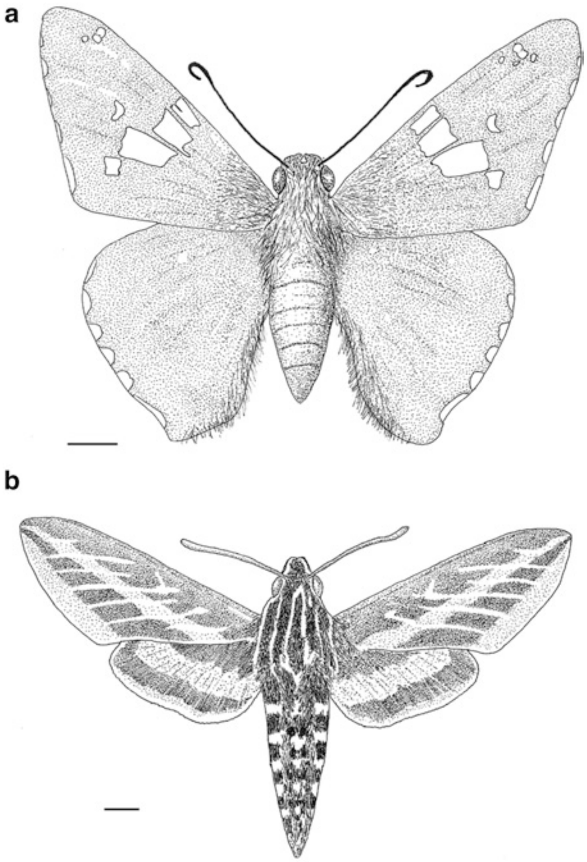

Fig. 12.4 (**a**) *Epargyreus clarus,* silver-spotted skipper, dorsal view; (**b**) *Hyles lineata*, white-lined sphinx, dorsal view, scale bars = 5 mm

Other insects classified by Smith and Snow (1976) as possible to probable pollinators but not observed with attached pollinaria included *Apis mellifera* (honeybee) and three night-flying moths: *Hyles lineata* (Fig. 12.4b), *Manduca quinquemaculata* (Haworth) (five-spotted hawkmoth, tomato hornworm), and an unidentified species of *Agrotis* Ochsenheimer (cutworm moths, Noctuidae). The honeybee has a short proboscis, and Smith and Snow (1976) described its attempts to locate the nectary as awkward. Similarly, *Agrotis* is probably too small to be effective in transferring pollen. Both were considered unlikely pollinators. The larval food plants of *M. quinquemaculata* (*Lycopersicum* and *Nicotiana*) are not bog plants, and it most likely did not visit *P. blephariglottis* regularly. *Hyles lineata* may be expected as a frequent night visitor since *Epilobium* (willow herb), one of its larval food plants, occurred in the bog. As was the case for *P. ciliaris*, it carried no pollinaria, but Smith and Snow (1976) again believed it to be a likely pollinator. It appears, in fact, to be the only plausible nocturnal candidate observed by these authors.

The overall percentage of *P. ciliaris* flowers pollinated in Michigan was about twice that for *P. blephariglottis* (Tables 12.2 and 12.3). This may have been due to cool nighttime temperatures. According to Smith and Snow (1976), night-flying moths were inactive when temperatures dropped to 15°C. Based on this measure, only 9 nights out of the 28-day flowering period were warm enough for night-flying moth activity. However, if *Hyles lineatea* is found to be a pollinator, Heath and Adams (1967) in a study of the physiology of this moth reported that it could, through muscle vibration, maintain body temperatures at 34–38°C against air temperatures of 10–30°C. Daytime temperatures were never low enough to interfere with the activity of butterflies, bees, or diurnal moths.

Smith and Snow (1976) found the percentage of flowers pollinated in *P. blephariglottis*, as measured by fruit set, to be inversely related to the size of the raceme. Such a relationship could be associated with resource limitation, but according to these authors, it resulted because pollinators spent about the same amount of time on large and small racemes. In *P. ciliaris*, on the other hand, the smaller racemes, those with 10 or fewer flowers, showed a lower percentage of pollination than larger racemes. Smith and Snow (1976) suggested that butterflies, depending on sight to find the orchid, might have overlooked racemes with fewer flowers present. In addition, the mean number of flowers in each raceme was higher for *P. ciliaris* than for *P. blephariglottis* (Table 12.1), a feature which Smith and Snow (1976) also believed might be due to the visual basis of butterfly attraction, resulting in selection for larger racemes.

Based on the number of flowers of *P. blephariglottis* pollinated on the bottom, middle, and upper thirds of the raceme, as measured by fruit set, Smith and Snow (1976) concluded that pollination rates were more or less constant throughout the blooming period. These authors believed that pollinator numbers were essentially constant throughout and that the pollinators, chiefly moths attracted by scent, could detect the presence of a few flowers at the bottom of the raceme about as well as a fully blooming raceme. On the other hand, they reported that pollination was 55% greater in the top third as compared to the bottom third of the raceme in *P. ciliaris*. They concluded that the number of visually directed pollinators increased in parallel with the number of open flowers and that fully blooming racemes were most readily detected.

More recently, Cole and Firmage (1984), in a 3-year study at the Colby Marston Preserve, a bog in Kennebec County, Maine, significantly expanded the list of known pollinators for *P. blephariglottis*. In contrast to the results of the Michigan study, these authors found butterflies and skippers to be much more important than moths and the almost exclusive pollen vectors for this species in their study area. Both small and large pollinators were observed throughout the flowering period, but some seasonal change was noted with the former being relatively more abundant early and the latter increasing toward the end of the season. Seventy nine percent of the visitors and pollinators at this site were butterflies and skippers and 15% were bees. Nearly half of all insects observed on the flowers (46%) were true skippers (Hesperiidae), and nearly a quarter (22%) were of a single species, *Epargyreus claurs* (silver-spotted skipper) (Fig. 12.4a). Other skippers carrying pollinaria included *Euphyes ruricola* (Boisduval) (dun skipper), *Polites coras* (Cramer) (peck's skipper), and *P. mystic* (long dash), the latter previously identified as a pollinator by

Luer (1975). Also collected with pollinaria were two Pieridae, *Colias philodice* Godart (clouded sulfur) and *Artogeia rapae* (L.) (=*Pieris rapae* (L.)) (cabbage white) as well as *Strymon melinus* (Hubner) (gray hairstreak) (Lycaenidae), *Papilio glaucus* (tiger swallowtail) (Papillionidae), an unknown species of *Hemaris* (Sphingidae), and two bumblebees, *Bombus vagans* and *B. fervidus*.

Only diurnal pollinators were detected. No moths, other than the day-flying *Hemaris*, were seen with attached pollinaria during the 3-year study, and *Hemaris* was seen on only two occasions. Microclimatic differences in the form of cold air drainage sometimes reduced nighttime temperatures in the Maine bog to below 15°C, which could again have inhibited nocturnal moth activity. However, light trapping and observation on warm nights also failed to reveal the presence of moths with attached pollinaria. Catling (1984) also failed to observe any nocturnal moth pollination for this species at a number of undesignated sites in Canada.

Although Smith and Snow (1976) classified *Papilio troilus* (spicebush swallowtail) and *Danaus plexippus* (monarch) as incidental pollinators and *Apis mellifera* (honeybee) as an unlikely but possible pollinator, Cole and Firmage (1984) listed them as only flower visitors. Similarly, Cole and Firmage (1984) identified *Speyeria atlantis* (Edwards) (atlantis fritillary) as a visitor even though Stoutamire (cited in Luer 1975 without reference) apparently considered it a pollinator.

Both Smith and Snow (1976) and Cole and Firmage (1984) identified species of *Bombus* as pollinators of *P. blephariglottis*, but because their tongues are short for the spur, Cole and Firmage believed that they played a minor role. They were implicated in the pollination of *Kalmia angustifolia* L. (sheep laurel), which stopped flowering before *P. blephariglottis*. *Bombus* then switched over to the orchid. In fact, except for this overlap in certain years, *P. blephariglottis* provided the only significant source of nectar during its blooming period. Thus, unlike the Michigan site where *P. ciliaris* was also common, butterflies at the Maine site would often have been dependent on *P. blephariglottis* and had little competition for the available nectar.

In contrast to Smith and Snow's (1976) report of constant pollination rates on the bottom, middle, and top thirds of the inflorescence, Cole and Firmage (1984) found significant differences in these rates. Thus, some factor or combination of factors, such as the number of pollinators or the level of pollinator activity, varied throughout the season at the Maine study site. Similarly, Cole and Firmage (1984) were unable to confirm any consistent negative correlation between raceme size and percentage capsule set, except for a weak one during the first year of the study when a relatively large number of racemes were in bloom.

Cole and Firmage (1984) also saw little difference in percentage capsule set between orchids growing on open mat or hidden among shrubs or trees. They considered that although these plants may have been difficult to locate visually from ground level, most would not have been obscured from potential pollinators flying over them. In any case, butterflies and skippers had no difficulty in locating and pollinating orchids surrounded by vegetation despite their reliance on visual rather than olfactory clues.

The subject of both the Michigan and Maine studies was *P. blephariglottis* var. *blephariglottis*. The flowers of variety *conspicua* tend to be larger with a more elaborate filiform fringe on their lip and distinctly longer spurs (Table 12.1) (Sheviak 2002). These differences, particularly in spur length, imply specialization for different pollinators. In addition, variety *conspicua* appears to bloom somewhat later than variety *blephariglottis* in the limited area where they are sympatric (Sheviak 2002).

In a 2-year study, Robertson and Wyatt (1990a, b) found marked differences in the pollination of two widely separated populations of *P. ciliaris.* One was located in the Francis Marion National Forest on the coastal plain of South Carolina and the other at the Coweeta Hydrologic Laboratory in the Appalachian mountains of western North Carolina. Although the species differed, the pollinators of primary importance at both locations were large butterflies. No other insects carried pollinaria and no other insects were observed as consistent visitors.

As in Michigan, the most important pollinator in the mountains during both years of the study was *Papilio troilus* (spicebush swallowtail) (Fig. 12.3a). It was the most frequently observed visitor and usually had pollinaria attached to its eyes; each carried an average of 5.9–6.8 over the 2 years. *Battus philenor* (L.) (pipevine swallowtail), a reportedly toxic species (Howe 1975), is similar to and was sometimes lumped with *Papilio troilus*, its putative mimic. However, *Battus philenor* proved to be a far less frequent pollinator than *Papilio troilus*. *Papilio glaucus* (tiger swallowtail) visited *P. ciliaris* both years and carried pollinaria (three times) during 1 year of the study. *Phoebis sennae* (L.) (cloudless sulfur) was noted only once. It bore a single pollinarium.

On the other hand, the most frequent pollinator on the coastal plain of South Carolina both years was *Papilio palamedes* Drury (palamedes swallowtail) (Fig. 12.3b); over 80% of those examined had pollinaria attached, and each carried an average of about 3.5. The North American distribution of this species is restricted to the southeastern USA, the lower Mississippi Valley, and Mexico (Howe 1975), and its range does not normally extend to the mountain population of *P. ciliaris* (Robertson 1987). *Phoebis sennae* also visited coastal plain populations of *P. ciliaris* during both years of the study, but only about one-third carried pollinaria, and the average number of pollinaria carried per individual (2.5) was lower than that observed for *Papilio palamedes*. Within an area where both butterflies were active simultaneously the majority of palamedes swallowtails bore pollinaria, whereas only a minority of cloudless sulfurs did. *Papilio troilus*, the predominant pollinator in the mountains, was occasionally observed on the coastal plain but did not commonly visit *P. ciliaris*, although 1 year it was recorded three times, once with a single pollinarium attached. It was often seen on *Liatris graminifolia* Willd (blazing star) at a site near the location of *P. ciliaris*. *Papilio palamedes* and *Phoebis sennae* also frequently visited the flowers of *Liatris.*

Effective pollinator activity, evaluated in terms of the rate of deposition and removal of pollinaria, was lower on the coastal plain than in the mountains. This was true both years even though the frequency of pollinator visits in relation to plant population size was higher on the coastal plain during 1 year of the study (Robertson 1987). Pollinators on the coastal plain visited fewer plants and spent less time on each flower and inflorescence. Moreover, fewer carried pollinaria, and those that did carried a lower number, on average, than the pollinators in the mountains.

The separation of the viscidia was more or less constant at both sites and matched the distances between the compound eyes of the pollinators. However, the length of the nectar spurs differed. The average length in mountain populations (23.8 mm) closely approximated the average lengths of the proboscises in the primary pollinator, *Papilio troilus* (23.3 mm), and the secondary pollinators, *Papilio glaucus* (19.5 mm) and *Battus philenor* (24.9 mm). In coastal plain populations, on the other hand, average spur length (25.6 mm), although already significantly longer than in mountain populations, was shorter than the proboscises of either the primary pollinator, *Papilio palamedes*, or the secondary pollinator, *Phoebis sennae* (both nearly 29 mm).

Robertson and Wyatt (1990a) considered that the coastal plain and mountain populations of *P. ciliaris* might represent distinct pollination ecotypes in which differences in floral morphology reflect an evolutionary response to differences in principal pollinators. They further suggested that ongoing selection might be occurring for increased spur length in the coastal plain population in response to the longer proboscises of the pollinators at that site. Indeed, during 1 year of the study, reproductive success as measured by percent fruit set was positively correlated with spur length in coastal plain plants. However, reciprocal transplant studies were inconclusive, and further research is needed to clearly establish the genetic basis of the differences in floral morphology between mountain and coastal plain populations.

Experiments conducted to test for nocturnal pollination found none occurring at either site. *Xylophanes tersa* (tersa sphinx moth) carried no pollinaria but stole nectar from the flowers of *P. ciliaris* on the coastal plain. It hovered from plant to plant just after dark and extracted nectar with its long proboscis (32.0-mm long in one individual) without contacting the viscidia. Sometimes, other apparent nectar thieves, possibly carpenter bees, made slits near the bottom of the spurs at both sites and extracted most of the nectar.

In the mountains, neither sphinx moths nor other nectar thieves with long tongues were observed. Again, moth activity could have been limited by low temperature: nighttime minimums during the flowering season averaged 14.2°C as compared to 20.5°C on the coastal plain. If visits of sphingid moths at the coastal plain site are frequent enough and if they are indeed absent or rare in the mountain population, sufficient nectar could be extracted at the former site to cause some difference in effective pollinator activity (Robertson and Wyatt 1990a).

Frame and Gregg (1981) and Gregg (1981, 1984, 1990) examined the pollination of *P. ciliaris* in north-central West Virginia. The list of pollinators from this study site was similar to lists compiled from Michigan (Smith and Snow 1976) and North Carolina (Robertson and Wyatt 1990a, b), except for the presence of one additional vector of secondary importance, *Papilio polyxenes* (eastern black swallowtail).

Fruiting Success and Limiting Factors

Firmage (1990) examined factors affecting flowering in a 11-year study of a *P. blephariglottis* population in Maine. He found that each plant flowered in about 40% of the seasons that it lived. The number of flowers produced was negatively related to the amount of shading and positively related to ramet weight. The size of new ramets was, in turn, inversely related to the percentage fruit set or the weight of fruits produced in the previous season. However, although a reduction in the biomass of the overwintering ramets and shaded microhabitats reduced the number of flowers that bloomed, productivity was not lowered enough to reduce flowering frequency. In fact, Cole and Firmage (1984) found that plants flowering in one season at the Maine site were more likely to flower again the next year and in subsequent years than plants that did not flower; capsules were well-developed even in inflorescences with more than 40 flowers; and no abortion of capsules was observed. Cole and Firmage inferred that the level of fruit production at the Maine site was not determined by the availability of resources and cited a series of observations favoring pollinator visitation rates as the primary limiting factor in this species.

They found, for example, that artificial pollination markedly increased the percentage capsule set compared to open-pollinated controls. Ninety one to one hundred percent of artificially selfed and outcrossed plants regularly set capsules compared to a mean of 62.4% in control plants (Table 12.3). Smith (1975) and Smith and Snow (1976) obtained similar results in Michigan, where 100% of hand-pollinated plants produced fruit compared to a mean of 24% in open-pollinated controls (Table 12.3).

Also suggesting pollinator limitation, the percentage of fruit set was higher in years when relatively few inflorescences were produced. Moreover, an increase in the number of inflorescences was associated with an increase in the number of plants that set no capsules and a decrease in the number of plants with 100% capsule set. When the number of plants with 100% capsule set was examined over a 3-year period, it suggested that a decrease in the number of inflorescences was correlated with an increase in the number of pollinators visiting each plant.

P. blephariglottis bloomed late in the season at the Maine study site and usually lacked competition from other plants for its pollinators. Comparable sequential patterns of flowering in bog communities have been related to a limited availability of pollinators (Judd 1958; Pojar 1974; Reader 1975; Heinrich 1976), and Cole and Firmage (1984) proposed a similar interpretation for *P. blephariglottis*. Moreover, although they gathered data for 6–7 h per day on 70% of the days when *P. blephariglottis* was blooming, no pollinators were seen on many days and, when present, they were usually sparse.

As inflorescence size increased, there was a corresponding increase in the number of capsules up to an average of 10–11 per plant. The percentage capsule set remained more or less constant within this range. Larger inflorescences occurred, but generally produced no mean additional increase in capsule numbers. Although this could again be related to resource limitation, Cole and Firmage (1984) considered that large inflorescences of *P. blephariglottis*, those with more than 20 flowers, probably produced a higher percentage of capsule set when and only when they received repeat pollinator visits. Larger inflorescences presumably did not usually produce any mean additional increase in capsule numbers because vectors in Maine, like those in Michigan, did not usually increase the number of flowers visited per inflorescence with increasing inflorescence size, and pollinator limitation generally restricted the number of visits per inflorescence.

However, during 2 years of their study, when relatively few flowers were in bloom, the percentage fruit set for larger and smaller inflorescences did not differ, indicating an increase in the number of pollinator visits with increasing inflorescence size (Cole and Firmage 1984). Thus, larger inflorescences may, under some circumstances, increase the frequency of pollinator visits (Stephenson 1979; Udovic 1981).

An increase in the number of fertile progeny produced by each plant through an increase in the number of pollinator visits would obviously improve fitness (Calvo and Horvitz 1990). The amount of nectar remaining in flowers of *P. blephariglottis* after one to a few visits differed very little from that in unvisited flowers. Thus, ample reward remained to promote the visits of subsequent pollinators, and the flowers are long-lived and continue to accumulate nectar throughout the blooming period. Calvo and Horvitz (1990) believe that maximizing fruit production in favorable years when pollinators are abundant, the weather is good, and resources are sufficient might be the best response to uncertain pollination. Despite the cost, the production of large inflorescences might permit a substantial, short-term increase in the number of seeds produced in such years (Cole and Firmage 1984; Sutherland 1986a, b, 1987; Calvo and Horvitz 1990; Maad 2000). Large inflorescences might also increase chances for additional fruit set by prolonging the blooming period and would permit the abortion of capsules with inferior seed and the allocation of resources to high-quality fruits (Cole and Firmage 1984; Montalvo and Ackerman 1987).

In addition, a larger number of flowers in a primarily outcrossing, hermaphroditic species might improve reproductive success through an increase in pollen donation (male fitness). Hermaphroditic flowers that produce fruit may contribute to both male and female success, whereas those that produce no fruit can contribute only to male success (e.g., Sutherland and Delph 1984). If the allocation of resources to “extra” flowers (i.e., those that do not produce fruit) increases male fitness, through pollen donation, more than it diminishes female fitness, through reduction in fruit maturation, the production of “excess” flowers should be selected (e.g., Sutherland 1986a, b, 1987; Burd and Callahan 2000 and references therein). Firmage and Cole (1988), for example, found that male and female reproductive success in *Calopogon tuberosus* increased in parallel with increasing inflorescence size in plants with small inflorescences (1–4 flowers), but male reproductive success continued to increase with further increase in inflorescence size while female success leveled off.

Pollinator visitation rates also appeared to limit seed and capsule production in *P. ciliaris*. Gregg (1990) reported that natural seed set in a West Virginia population ranged from 15 to 74% over a 5-year period, whereas hand cross-pollinations produced a 91% seed set (Table 12.2). Similarly, Robertson (1987) and Robertson and Wyatt (1990a, b) found that open-pollinated plants usually had a 6.5–13.5% lower fruit set than hand-pollinated plants and that the levels of effective pollinator activity in disjunct coastal plain and mountain populations were highly correlated with fruit production at these sites. Percent fruit set averaged about 20% lower on the coastal plain than in the mountain population in both study years (64 and 66% versus 84 and 87%; Table 12.2), and these figures closely paralleled data on the percentage of flowers that had pollinia removed from their anthers (64 and 59% on the coastal plain versus 84 and 78% in the mountains) or deposited on their stigmas (64 and 68% on the coastal plain versus 82 and 84% in the mountains). At the same time, the number of fruits produced per plant was variable and positively correlated with flower number, both results contrary to expectations in plants where resources might be limiting.

Other factors that appeared to affect the reproductive success of both species included competition with woody plants, alteration of the water supply, and the collection of flowers or entire plants (Stucky 1967; Gregg 1990). Leaves, stems, flowers, and fruits of *P. ciliaris* in West Virginia were destroyed by herbivores, probably deer, in some years but not in others (Gregg 1990). Robertson (1987) also identified several insect predators, including a number of beetles, weevils, and grasshoppers, that damaged the flowers and leaves of this species in the Carolinas. In West Virginia, fungal pathogens destroyed 3–75% of the capsules in *P. ciliaris* over 3 years and reduced embryo size and capsule weight by about 33% compared to fungus-free capsules (Gregg 1990). Stucky (1967) reported that rabbits cropped *P. blephariglottis* to ground level at some sites in Rhode Island, but Cole and Firmage (1984) found that capsule predation was uncommon in Maine. However, early frost, occurring in 2 of the 3 years of the Maine study, prevented capsule development in young flowers of late-blooming plants. Reproductive success at this site was also affected by winter rain and perhaps by the availability of mycorrhizal fungi (Firmage 1990).

Other Yellow-Fringed Orchids

A limited amount of information is available on the pollination of several other species of the yellow-fringed orchid complex. *P. cristata* (Michx.) Lindl. (including *P. pallida* P. M. Brown, cf. Sheviak 2002; McGrath 2008) (crested-fringed orchid or orange-crest orchid) (Table 12.4) is similar to *P. blephariglottis* and *P. ciliaris*, but often has smaller, deeper orange to sometimes yellow flowers (Luer 1975; Folsom 1984). It is found in damp pine forests and low, wet meadows from Massachusetts to Florida and west to Texas (Luer 1975; Brown 1998).

P. chapmanii (Small) Luer emend Folsom (Chapman's fringed orchid) (Table 12.4), intermediate in many ways between *P. cristata* and *P. ciliaris* and long confused with their hybrid (*P.* x *channellii* Folsom), was recognized as a distinct species by Folsom (1979, 1984). It occurs in northern Florida, southeastern Georgia, and eastern Texas (Folsom 1984).

Table 12.4 Data on the Blephariglottis group, part 2 (Sheviak 2002)

Character	*P. chapmanii*	*P. cristata*	*P. integra*
Plant height (cm)	30–77	18–90	20–75
Flower number[a]	30–60	10–80	30–60
Dorsal sepal (mm)[a]		4.5 × 3.5	4 × 3
Lateral sepals (mm)[a]		4 × 4	5 × 4
Lip (mm)	5–10 × 4–9	4–8 × 4–8	3–5 × 1.5–4
Nectar spur (mm)	8–17	4–10	5–10
Column (mm)[a]		2 × 2	1 × 2
Chromosomes (2n)	42	42	

[a] Luer (1975)

In addition to morphological differences (Folsom 1984 and below), *P. chapmanii* and *P. cristata* are separated from one another and other members of the complex by pollination biology. In a study conducted on the coastal plain of Florida and Alabama, Folsom (1984) found that *P. chapmanii*, like *P. ciliaris*, is pollinated by long-tongued butterflies: *Phoebis sennae*, *Papilio troilus*, *Papilio palamedes*, and *Eurytides marcellus* (Cramer) (as *Papilio marcellus*) (zebra swallowtail). However, the spur in *P. chapmanii* is only 8–17-mm long (Sheviak 2002), and due to a bend in the column the viscidia converge and face the labellum (Folsom 1984). This positioning and the short nectary result in the attachment of the pollinaria to the butterfly's proboscis rather than to its compound eyes.

The small flowers of *P. cristata* have an even shorter spur, 4–10-mm long (Sheviak 2002). The viscidia are closely spaced and face forward. Their alignment and positioning are adapted for attachment of the pollinaria to the head of a bee, and *Bombus pennsylvanicus* (DeGeer) is reportedly its chief pollinator (Folsom 1984).

The latter has also been indicated as a pollinator of another possible member of this complex, *P. integra* (Nutt.) Gray ex Beck (Stoutamire in Luer 1975 without reference), a species Morong (1893) considered to be autogamous. *P. integra* is found chiefly in swamps, wet meadows, and pine forests from New Jersey to east Texas (Luer 1975). Its yellow–orange flowers are similar to those of *P. cristata* in size and general morphology, but are distinguished by a relatively entire to slightly crenulate lip. The pollinaria again are close together and more or less parallel. The viscidia, located directly above the opening to a 5–10-mm long nectar spur, are positioned to attach to the bee's proboscis (Luer 1975; Nilsson 1981; Sheviak 2002).

Platanthera integrilabia (Correll) Luer (Monkey-Face Orchid)

Habitat and Distribution

This orchid is usually restricted to deeply shaded bogs and damp hardwood forests in the southern Appalachians and Cumberland Plateau (Luer 1975; Zettler et al. 1996). Once common from Kentucky and North Carolina to Mississippi and

Table 12.5 Data on the Blephariglottis group, part 3 (Sheviak 2002)

Character	*P. clavellata*	*P. integrilabia*
Plant height (cm)	8–47	50–80
Flower number[a]	3–15	6–15
Dorsal sepal (mm)[a]	4×2.5	8×6
Lateral sepals (mm)[a]	4×2.5	9×7
Lateral petals (mm)[a]	5×2	7×2.5
Lip (mm)	3–7×3–4	10–15×2.5–4
Nectar spur (mm)	7–13	35–60
Column (mm)[a]	1×1.5	5×5
Chromosomes (2n)	42	

[a] Luer (1975)

Georgia, the species has now declined, and only one population in McMinn County, southeastern Tennessee, remains comparable in size to those once present throughout its range (Zettler and Fairey 1990; Shea 1992).

Floral Morphology

A relatively constant number of nocturnally fragrant, resupinate, white flowers are spaced in a short, broad, terminal raceme (Table 12.5) (Luer 1975). The lateral sepals are reflexed against the ovary while the dorsal converges with the lateral petals to form a hood over the column (Fig. 12.2c). The lip is spatulate-lanceolate; the distal two-thirds is expanded and has a finely saw-toothed margin. Basally, it is projected downward into a long, slender, curved nectar spur (Table 12.5). A large column bears two widely divergent anther sacs (Fig. 12.2c). The stalks of the pollinaria are curved forward, and the viscidia are orbiculate.

Compatibility and Breeding System

Apparently adapted to outcrossing, *P. integrilabia* is also self-compatible. In some cases, a membrane surrounding the pollinia deteriorated 6–9 days after flower opening, permitting the pollinia to contact the stigma (Zettler and Fairey 1990). Autogamy may, therefore, supplement insect pollination and add to fruit set in ageing, unpollinated flowers. However, some evidence suggests that a level of self-incompatibility may be present in some populations (see below).

Pollinators and Pollination Mechanisms

The white flowers with their long spurs (Table 12.5) and nocturnal fragrance would appear to be adapted to pollination by moths, especially nocturnal sphingids (Faegri and van der Pijl 1971; Dressler 1981; Grant 1983). However, in a study conducted in early August in southeastern Tennessee, Zettler et al. (1996) found pollinaria on only three diurnal butterflies: *Epargyreus clarus* (silver-spotted skipper) (Fig. 12.4a), *Papilio glaucus* (tiger swallowtail), and *P. troilus* (spicebush swallowtail) (Fig. 12.3a). Of 11 observed individuals, 8 were swallowtails. In all cases, they carried pollinaria on only one compound eye. Both the skipper and the swallowtails foraged from the lower and mature flowers at the base of the inflorescence upward toward the younger flowers, but the skippers appeared awkward and inserted their proboscises into the nectar spur openings with difficulty. The swallowtails were also slow, but they were deliberate and had less trouble locating the openings.

Although the butterflies clearly functioned as pollinators, their efficiency was low. Multiple visits were, in fact, required to extract the pollinaria. Thus, for example, a single skipper visited 13 flowers on 7 different plants before it carried away a single pollinarium. Similarly, one spicebush swallowtail investigated all of the flowers on two inflorescences twice before removing a pollinarium. The mean distance between the viscidia of *P. integrilabia* is 0.47 cm. The mean distance between the outer margins of the two compound eyes in the skipper and swallowtails are 0.45 cm and 0.42–0.44 cm, respectively. These insects could, therefore, probe the nectar spur without contacting the viscidia with their compound eyes.

A number of other insects visited inflorescences but did not carry pollinaria. Included here was a single 2:00 a.m. visit to two inflorescences by an unidentified species of sphingid in the genus *Manduca* Hubner (Zettler et al. 1996). Perhaps, a yet unobserved role for nocturnal sphingids might explain a discrepancy between the high rate of fruiting success (see below) and the noted slow and inefficient removal of pollinaria by the diurnal pollinators. Zettler et al. (1996) suspect that sphingid activity in their area may have been sporadic and/or delayed until late in the flowering season (late August–early September) and that they missed it. Certainly, the cycle of floral fragrance production implies a crepuscular or nocturnal pollinator. The rate of emission increased beginning at 7:00 p.m. and slowly faded after 11:00 p.m. with the highest intensity at dusk from 8:00–10:00 p.m. On the other hand, no significant variation was observed in mean nectar concentration (17.2–20.8% sugar) or volume (2.9–7.5 μl) over a 24-h period, suggesting that *P. integrilabia* might be adapted to both diurnal and nocturnal pollinators. Based on entomological records, Zettler et al. (1996) identified ten local species of sphingid moths in eight genera with eye measurements ranging from 0.40–0.70 cm, flight times corresponding with the blooming period of *P. integrilabia*, and larval food sources located in or near the Tennessee site (Selman 1975; Covell 1984). Those with more widely spaced compound eyes would presumably be more efficient than the butterflies at removing one or both pollinaria.

Fruiting Success and Limiting Factors

Fruit matures about 2 months following flowering (early October) (Zettler et al. 1996). At the southeastern Tennessee site, about 57% of the flowers set fruit, averaging 4.7 capsules for each inflorescence. About 3,400 seeds were produced per capsule or about 16,000 seeds per inflorescence. There were 577 inflorescences in the study area for a calculated total of over 9 million seeds.

Fruit set in smaller populations in Georgia and South Carolina ranged from only 6.9 to 20.3% (Zettler and Fairey 1990). In addition, seeds obtained from smaller populations had significantly lower germination rates than those from the southeastern Tennessee site. Zettler et al. (1996) suggested that these differences may be a result of higher cross-pollination rates in the large population and that self-pollination and inbreeding depression may be significant in small populations. Coupled with the observation that this species is unable to establish more than 3% of its seeds either in vitro (Zettler and McInnis 1992) or in its natural habitat (Zettler 1994a), it is possible that large seed production, and therefore large populations, may be necessary to overcome high rates of seed/seedling mortality (Zettler et al. 1996). Inflorescence and tuber predation by deer and feral hogs (Zettler 1994b) and human activities, such as logging and orchid poaching, also limit the future prospects for this orchid (Zettler and Fairey 1990; Zettler et al. 1996).

Platanthera clavellata (Michaux) Luer (Little Club-Spur Orchid)

Distribution and Habitat

This species ranges from Newfoundland south to Florida and west to Ontario, Minnesota, and Texas. It may occur in sphagnum bogs, meadows, marshes, low woods, or swampy forests (Sheviak 2002). Open habitats are preferred in the northern part of its range and at heights in the Appalachian Mountains (Luer 1975).

Floral Morphology

The flowers are rotated less than 180° and are borne at an angle (Fig. 12.1b) (Luer 1975; Sheviak 2002). The petals are a paler green than the sepals and, along with the dorsal sepal, converge about the column. The lip is pale green, oblong, and truncate with an obscurely three-lobed tip; it is extended basally into a slender nectar spur with an expanded or bifid tip (Table 12.5). The column is short and broad with projecting auricular lobes directed downward. The stigmatic surface is three-lobed (Fig. 12.1c) (Gray 1863), and the anther cells are short and nearly parallel. The viscidia are positioned above and on either side of the opening to the nectary.

Compatibility and Breeding System

P. clavellata is self-compatible, and apparently both autogamy and outcrossing occur (Gray 1862, 1863; Catling 1983; Gregg 1990). It is a colonizing species, and as discussed elsewhere selection can favor the development of autogamy in such taxa (Catling 1984). Rare hybrids with *P. blephariglottis* are known (*P.* x *vossii* Case) (Sheviak 2002).

Pollinators and Pollination Mechanism

Luer (1975, p. 208) reported that in situ pollinia developed “cellular processes” that grew directly onto the lateral lobes of the stigma. Gray (1862, 1863), on the other hand, found that the pollinia lacked coherence and that massulae routinely fell from the anthers onto the three stigmatic lobes, where the pollen grains germinated and penetrated the stigma (Fig. 12.1c). However, he suggested that some pollen might also be removed by insects. When he contacted the viscidia with a bristle and removed the pollinaria, a large portion of the pollen mass remained attached to the caudicle. Subsequently, the caudicle rotated, positioning the pollinia to contact the stigmatic surface.

Catling (1983, 1984) studied *P. clavellata* in Ontario and Nova Scotia. Like Gray, he found that a lack of coherence of the massulae led to autogamy. He further noted that some pollinaria lacked a well-developed caudicle and viscidium. Although insect pollination might supplement autogamy even in the absence of a caudicle and viscidium, it would probably be far less significant than in plants with fully developed pollinaria (Catling 1983). No pollinators have yet been identified.

Fruiting Success and Limiting Factors

Catling (1983) reported autogamy and 100% seed set in populations of this orchid from Ontario and Nova Scotia. Gregg (1990) observed seed set ranging from 65 to 72% in a West Virginia population during a 3-year period with 50% of the seed set based on autogamy. Thirty-two percent of the seeds had healthy embryos, 48% had small or abnormal embryos, and 20% had either empty seeds or seeds with dead embryos. Fungi limited fruiting success, destroying 4–11% of the capsules over 2 years.

Other Possible Members of the Blephariglottis Group

According to Hapeman and Inoue (1997), the white flowers of *P. nivea* are pollinated by butterflies with viscidia attaching to the proboscises (Fig. 8.1). They resolved this species as sister to other members of the *Blephariglottis* clade. However, the flowers are nonresupinate, and this along with a combination of column and/or tuberoid features shared with *P. integra* and *P. clavellata* suggested to Sheviak (2002) that these species might comprise a group apart from *Platanthera*. Brown (2002) resurrected Rydberg’s old genus *Gymnadeniopsis* to accommodate them, but this transfer has not yet been widely accepted.

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Chapter 13
Platantheras of Unknown Alignment

Abstract *Platanthera flava* is pollinated primarily by unidentified mosquitoes of the genus *Aedes*. Central partitions divide the opening to the nectar spur in half and may represent an adaptation to restrict pollen acquisition. Pollinaria are attached to the proboscis. Small moths may act as secondary pollinators. *Platanthera chorisiana* includes autogamous, geitonogamous, and outcrossing populations. Insect pollination and outcrossing are thus far known only in Japan. Examined North American plants are exclusively autogamous, perhaps as a result of intense competition for pollinators or harsh weather conditions and restricted pollinator activity.

Keywords *Platanthera flava* • *Platanthera chorisiana* • *Aedes* mosquitoes • Small moths • Restricted pollen acquisition • Autogamous populations • In situ germination

Data on pollination biology are available for two additional species of *Platanthera*, both of uncertain alignment. One provides an additional example of dipteran pollination, and the other of geographical divergence in the mode of sexual reproduction.

Platanthera flava (L.) Lindley (Tubercled-Orchid)

Habitat and Distribution

The tubercled-orchid occurs in wet habitats including low woods, swamps, bogs, meadows, flood plains and streambeds in the eastern United States and Canada from Nova Scotia to Minnesota and south to Florida and east Texas (Stoutamire 1971; Luer 1975; Sheviak 2002).

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Table 13.1 Data on unaffiliated species of *Platanthera* (Sheviak 2002)

Character	*P. chorisiana*	*P. flava*
Plant height (cm)	4–29 (–30)	13–65
Flower number	5–20[a]	10–40[a]
Dorsal sepal (mm)	1.5 × 1[a]	4 × 3[a]
Lateral sepals (mm)	2 × 1[a]	3.5 × 2[a]
Lateral petals (mm)[a]	1.5 × 1.5	4 × 2.5
Lip (mm)	1.5–2.5 × 1.2–2	2–6 × 1.8–5
Nectar spur (mm)	0.7–1.25	4–8 (–11)
Column (mm)[a]	1 × 1	1.5 × 2
Chromosomes (2n)	42	42[b]

[a] Luer (1975)

[b] Variety *herbiola* (R. Brown) Luer

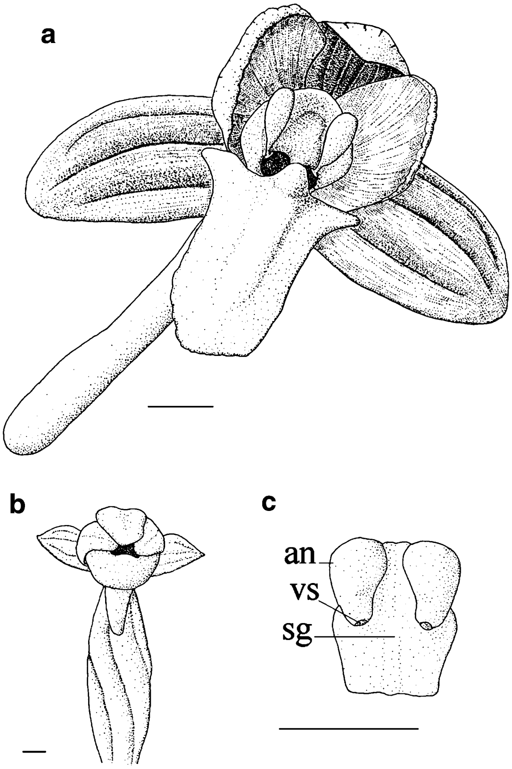

Fig. 13.1 (**a**) *Platanthera flava*, flower, front view; (**b, c**) *Platanthera chorisiana*; (**b**) Flower, front view; (**c**) Column, front view, scale bars = 1 mm. *an* anther, *vs* visidium, *sg* stigmatic area

Floral Morphology

A variable number of small, yellow–green, resupinate flowers are borne in a slender to stout spike (Table 13.1) (Stoutamire 1971; Luer 1975; Sheviak 2002). A dark-green dorsal sepal and yellow–green petals form a hood over the column (Fig. 13.1a).

The lateral sepals are dark green and spreading to reflexed. The lip is yellow–green and descending to commonly reflexed. It is broadly ovate to oblong with a pair of basal lobes and a rounded or emarginated, entire to slightly crenulate apex. The nectar spur is club-shaped. Its entrance is divided in two by a fin-like tubercle projecting upward from the lip just in front of the opening and by a ridge projecting downward from the roof of the nectary (Fig. 13.1a). Each of the two resulting channels is located directly below a viscidium. The viscidium is elongated and curved, forming a hemispherical canal over each opening. It is clearly adapted to clasp the shaft of any cylindrical object inserted into the nectar tube.

Compatibility and Breeding System

Experimental crosses have yet to be conducted, but the pollination mechanism suggests that this orchid is chiefly cross-pollinated (see below).

Pollinators and Pollination Mechanisms

According to Stoutamire (1968, 1971), *P. flava* is pollinated primarily by unidentified female mosquitoes of the genus *Aedes*, which behave much as *Aedes* mosquitoes on the flowers of the blunt-leaved rein orchis (*P. obtusata*). They discover the entrance to the nectary only after extensive exploration of the flower with their proboscises. The central partitions divert entrance to one or the other of the two lateral openings beneath the strap-shaped viscidia. Partitioning may here again represent an adaptation to restrict pollen acquisition (see discussion under *P. dilatata*). Unlike *P. obtusata*, a viscidium attaches to the cylindrical shaft of the proboscis rather than a compound eye, and the pollinarium is pulled from the anther sac as the insect withdraws from the flower. If the polliniarum is subsequently transported to another flower, massulae may be deposited on the stigma as the insect again probes for nectar. As in *P. obtusata*, secondary pollination by geometrid moths may also occur (Stoutamire 1971). Light (1998) also mentions pollination by a crambid moth, *Anageshna primordialis*, with the pollinia attaching to the base of the proboscis. This is the same moth that Voss and Riefner (1983) observed carrying pollinaria of *P. obtusata* on its compound eyes.

Fruiting Success and Limiting Factors

No data are yet available.

Platanthera chorisiana (Chamisso) Reichenbach (Chamisso's Orchid)

Distribution and Habitat

Platanthera chorisiana is found in wet meadows, bogs, and tundra along the Pacific from northern Washington and the coastal islands to Alaska and across the Aleutians through Kamchatka to Honshu (Luer 1975; Inoue 1983; Catling 1984; Sheviak 2002). Although considered of uncertain alignment here, Bateman et al. (2009) included this orchid in the Platanthera clade.

Floral Morphology

A variable number of incompletely rotated, tiny greenish flowers are arranged in a lax to dense spicate inflorescence (Table 13.1) (Luer 1975; Inoue 1983; Sheviak 2002). The lip is approximately spherical, concave, and fleshy with an entire margin and a short, truncated spur (Fig. 13.1b). The lateral sepals are slightly spreading, but the dorsal sepal, petals, and lip are more or less closed around the column, forming a small, 3–4 mm sphere with a tiny opening at the tip (Fig. 13.1b). Minute anther sacs diverge only a little to either side above the stigma (Fig. 13.1c). In some, a rostellum is absent, and the viscidia are either absent or poorly developed (Catling 1984), in others, the rostellum is well developed with oblong viscidia present and functional on very short to almost obsolete caudicles (Fig. 13.1c) (Inoue 1983).

Compatibility and Breeding System

Self-compatible, autogamous (Catling 1984), and geitonogamous or outcrossing populations are known (Inoue 1983).

Pollinators and Pollination Mechanism

Based on a study of herbarium specimens from the Queen Charlotte Islands and Vancouver Island, Catling (1984) concluded that plants from this area are obligately self-pollinating and require no pollen vectors. The pollinia lie in contact with the stigmatic surface. Pollen grains in massulae adjacent to the stigma germinate in situ, forming an interwoven mass of pollen tubes extending to the stigma.

Insect pollinated populations of *P. chorisiana* are so far unknown from North America, but Inoue (1983), in a study on Rebun Island, Hokkaido, Japan, reported diurnal pollination by a small beetle, *Oedemeronia lucidicollis* (Motschulsky) (Oedemeridae). Even though the beetle has a short tongue, the length of the spurs (Table 13.1) allowed it to reach the nectar. The beetle may also feed on the pollen. Pollinaria were attached near the mouth and on the head between the antennae. Inoue (1983) noted that floral morphology does not exclude pollination by other small insects at other sites.

The apparent geographical differences in pollination may be related to environmental influences. Factors that favor the development of autogamy on the Queen Charlotte Islands and Vancouver Island might include weather conditions that restrict the activity of pollinators during the flowering period or competing plants that have a more abundant or richer supply of nectar (e.g. Levin 1972; Jain 1976).

Fruiting Success and Limiting Factors

No data are available, but abundant seed-set in all ovaries might be expected where autogamy is present (e.g. Catling 1983).

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Chapter 14
Other Orchideae

Abstract Outcrossing in *Piperia* is promoted by pollinator behavior and protandry. Autogamy and agamospermy are absent. Crepuscular or nocturnal moths are principal pollinators. *Galearis spectabilis* is pollinated by bumblebee queens, with pollinaria attaching to the medial frons area below the ocelli. *Pseudorchis albida* variety s*tramenia* is routinely autogamous in the far north. The brightly colored flowers of *Dactylorhiza* are nectarless and may attract pollinators by deceit. A wide variety of insect pollinators are recorded for *Coeloglossum*, with the pollinaria attaching to the head. Studies on *Dactylorhiza* and *Gymnadenia* demonstrate pollinator-mediated selection. Floral morphology suggests that *Habenaria quinquiseta* is pollinated by sphingid moths and *H. repens* by smaller, short-tongued moths.

Keywords *Piperia* • *Galearis* • *Pseudorchis* • *Amerorchis* • *Dactylorhiza* • *Coeloglossum* • *Gymnadenia* • *Habenaria*

Piperia Rydberg

According to a recent hypothesis based on molecular phylogeny, *Piperia* is nested well within *Platanthera*, and a revised classification recognizes it as a section of this genus (Bateman et al. 2003). However, the genera are here maintained as distinct in accordance with their treatment in the "Flora of North America" (Ackerman and Morgan 2002) and in deference to current, widespread, conventional usage. *Piperia* is also recognized in Kew's World Checklist of Monocotyledons (2008). Synonymization of *Piperia* into *Platanthera* is available in Bateman et al. (2003, 2009).

Ten species of *Piperia* occur in North America (Ackerman and Morgan 2002). Specific information on pollination biology and the breeding system is available for *Piperia elegans* (Lindl.) Rydberg (elegant peperia), *P. elongata* Rydberg (chaparral orchid, wood rein-orchid), *P. unalascensis* (Sprengle) Rydberg (Alaska piperia, slender-spire orchid), and *P. yadonii* Morgan and Ackerman (Yadon's piperia, Monterey piperia).

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Table 14.1 Data on *Piperia*, part 1 (Ackerman and Morgan 2002)

Character	*P. elegans*	*P. elongata*
Plant height (cm)	12–73 (–100)	14–130
Raceme length (cm)	2.5–40	6–70
Flower number[a]	to >100	to >100
Flower color	Mostly white	Green
Dorsal sepal (mm)	3–7 × 1.6–3	2.4–6 × 1–3
Lateral sepals (mm)	3–7 × 1.6–3	2.4–6 × 1–3
Lateral petals (mm)	4–6 × 1.5–2.5	3–6 × 1.5–2.5
Lip (mm)	2.5–7 × 1.5–3.5	2.1–5 × 1.2–3.4
Spur length (mm)	7–14[b]/3–6[c]	7–18
Chromosomes	42	42

[a] Coleman (1995)
[b] Subspecies *elegans*
[c] Subspecies *decurtata*

Habitat and Distribution

All ten species have their center of diversity in the California Floristic Province (Dunn 1988; Morgan and Glicenstein 1993). *Piperia transversa* occurs on road banks and in dry, open, coniferous or mixed evergreen forest, oak woodlands, and chaparral. *Piperia elegans* is also found in coniferous and mixed evergreen forest as well as on sunny coastal bluffs and in coastal scrub and prairie. Both are distributed from California to British Columbia with the range of *P. elegans* extending east to northern Idaho and northwestern Montana (Coleman 1995; Ackerman and Morgan 2002). *P. elongata* is usually located some distance from the ocean in dry sunny areas, among chaparral shrubs, in mixed coniferous or oak forest, and on roadcuts. It occurs over much the same area as *P. elegans*. *P. unalascensis* grows in open, mixed, or coniferous forest, manzanita shrubland, and roadcuts in full sun to partial shade. It is distributed continuously from California to the Aleutian Islands and east to Utah, Wyoming, Montana, and southwestern Alberta. Disjunct populations are also reported from Colorado, New Mexico, South Dakota, Michigan, Ontario, Quebec, and Newfoundland. *P. yadonii* is found in Monterey pine forest and coastal chaparral and is restricted to northern Monterey County, California.

Floral Morphology

All species of *Piperia* bear numerous small, white to green flowers in a racemose inflorescence of variable length (Tables 14.1–14.3). The lateral sepals are united with the lip at their base and are spreading to variously recurved or sometimes more or less reflexed (Coleman 1995; Ackerman and Morgan 2002). The petals are

Table 14.2 Data on *Piperia*, part 2 (Ackerman and Morgan 2002)

Character	*P. transversa*	*P. unalascenis*
Plant height (cm)	12–57	9–70
Raceme length (cm)	3.5–32	9–44
Flower number[a]	to >90	to >100
Flower color	White, green veins	±Translucent green
Dorsal sepal (mm)	2.5–4.5 × 1–2	2–4.2 × 1–2.6
Lateral sepals (mm)	2.5–4.5 × 1–2	2–4.2 × 1–2.6
Lateral petals (mm)	2–5 × 1–2	2–5.5 × 0.6–2
Lip (mm)	2.2–5.3 × 1–2.5	2–5 × 1–3
Spur length (mm)	7–12	2–5.5
Chromosomes (2n)	42	

[a] Coleman (1995)

Table 14.3 Data on *Piperia*, part 3 (Ackerman and Morgan 2002)

Character	*P. yadonii*
Plant height (cm)	10–50 (–80)
Raceme length (cm)	(2–)5–15 (–30)
Flower number	to > 100[a]
Flower color	Green and white
Dorsal sepal (mm)	3–5.5 × 1–2.5
Lateral sepals (mm)	3–5.5 × 1–2.5
Lateral petals (mm)	3–5 × 1.5
Lip (mm)	2.5–5 × 1.2–2.5
Spur length (mm)	2–5

[a] Coleman (1995)

erect and, like the sepals, spreading to sometimes recurved or reflexed (Fig. 14.1a). In *P. yadonii*, they curve toward the dorsal sepal, all three segments occasionally touching at their tips. The lip has a medial ridge and is usually recurved to more or less deflexed. It varies in shape from oblong to triangular-lanceolate (Fig. 14.1a). The spur contains nectar and is relatively long in *P. transversa*, *P. elegans,* and *P. elongata* (Fig. 14.1a) (Tables 14.1–14.3). It is usually curved and bent more or less abruptly downward but is straight and essentially horizontal in *P. transversa.*

The rostellum is blunt in all five species. Two pollinaria are present per flower (Fig. 14.1b). Each consists of an oblong to ovoid viscidium with two attached pollinia containing pollen aggregated into massulae (Fig. 14.1c). A stigma is located directly under (i.e., proximal to) the pollinaria.

Floral odors are usually generated at night, but linger during the day in *P. unalascensis*. According to Ackerman and Morgan (2002), scent production is diurnal in *P. yadonii*, but Doak and Graff (2001) contend that it increases perceptibly at night.

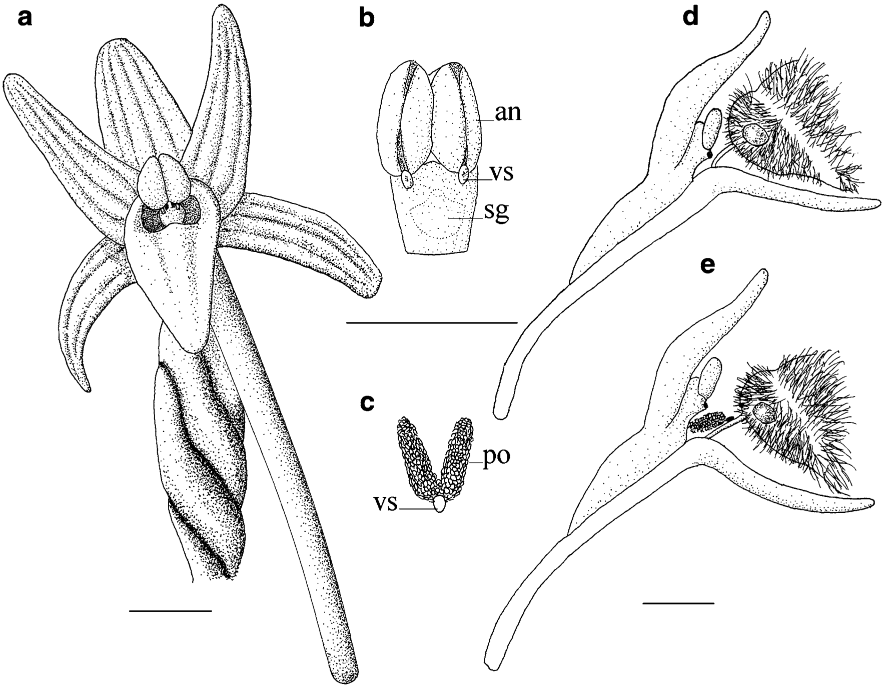

Fig. 14.1 *Piperia elongata*. (**a**) Flower, front view, scale bar = 2 mm; (**b**) column with anther cap removed, front view; (**c**) pollinarium, scale bar (**b, c**) = 1 mm; (**d**) sagittal section of young flower showing viscidium positioned to attach to the pollinator's proboscis; (**e**) sagittal section of older flower following separation of the lip and column with stigma positioned to receive pollen, scale bar (**d, e**) = 2 mm. *an* anther, *po* pollinium, *sg* stigmatic area, *vs* viscidium

Compatibility and Breeding System

In a study of four species of *Piperia* conducted in northern California, Ackerman (1977) examined the percentage of seeds with mature embryos produced in open- and hand-pollinated flowers (Table 14.4). He had difficulty maintaining the vigor of potted plants employed in the hand pollinations. *P. elegans* did relatively well, but the number of successful interspecific crosses and the percent seed viability involving the other species as female parents may have been affected. He considered hybridization results using *P. elegans* as the female parent to be the most reliable. Although it is apparent that some level of interspecific fertility was present in all crosses attempted (Table 14.5), Ackerman (1977) and Morgan and Ackerman (1990) failed to detect hybrids among sympatric groupings in Oregon and California, including all paired combinations of the four species.

Based on artificial selfing, the species are self-compatible, and artificial outcrossing in *P. elegans* produced a higher level of viable seed than open pollination (Table 14.4). At the same time, no fruit was produced among over 1,200 unmanipulated, caged

Table 14.4 Percentage of seeds of *Piperia* with mature embryos produced by indicated treatments based on the number of fruits with viable seeds/number of pollinations made, part 1 (Ackerman 1977)

Treatment	*P. elegans*	*P. elongata*	*P. transversa*	*P. unalascensis*
Autogamy	0	0	0	0
Selfing	34.4 (6/6)	4.3 (1/5)	2.1 (1/3)	1.6 (1/5)
Outcrossing	57.0 (2/5)	3.9 (1/3)	4.1 (1/5)	9.0 (1/5)
Wild population	46.2 (10/–)		55.2 (10/–)	25.6 (8/–)

Table 14.5 General/percentage of seeds of *Piperia* with mature embryos produced by indicated treatments based on the number of fruits with viable seeds/number of pollinations made, part 2 (Ackerman 1977)

Treatment	*P. elegans*	*P. elongata*	*P. transversa*	*P. unalascensis*
Hybridization				
P. elegans (male//female)	–			
P. elongata (male//female)	8.9 (5/7)//1.1 (3/5)	–		
P. transversa (male//female)	11.3 (3/3)//NC	97.6 (1/1)//NC	–	
P. unalascensis (male//female)	31.5 (4/5)//NC	NC//NC	NC//NC	–

NC no cross made

flowers of the four species, and autogamy and agamospermy are therefore probably absent (Table 14.4) (Ackerman 1977).

In a study of *P. yadonii* populations in Monterey County, California, Doak and Graff (2001) reported a mixed system that included transfer of pollen between flowers within an inflorescence (geitonogamy) and between plants (cross-pollination). Although artificial geitonogamous and cross-pollinations did not differ in the number of fruits produced per plant, outcrossing gave rise to a significantly higher mean proportion of viable seed per fruit. At the same time, naturally pollinated flowers produced a lower mean proportion of viable seeds per fruit than artificially outcrossed flowers but failed to differ significantly in this respect from artificial geitonogamous pollinations. Autogamy and agamospermy again were absent. Vegetative reproduction was also absent. Although *P. yadonii* is sympatric with a number of other species of *Piperia*, no intermediates are known (Morgan and Ackerman 1990; Doak and Graff 2001).

Pollinators and Pollination Mechanism

According to Ackerman (1977), the lip in young flowers of *Piperia* is horizontal with little space between it and the column. An insect attempting to access the spur at this stage is likely to contact the viscidium with its proboscis and remove pollinaria as it withdraws (Fig. 14.1d). However, the opening is probably too narrow to

Table 14.6 Pollinators of *Piperia*

Pollinators	*P. elegans*	*P. transversa*	*P. unalascensis*	authors
Geometridae (Geometrid moths)				
Eupithecia. Curtis sp.			Upper Peninsula, MI	Stoutamire in Ackerman (1977)
Thallophaga taylorata (Hulst)	Humboldt Co., CA			Ackerman (1977)
Noctuidae (Noctuid moths)				
Autographa Hubner sp.	San Mateo Co., CA			Kipping in Ackerman (1977)
Plusia nichollae (Hampson)[a] Humboldt Co. CA				Ackerman (1977)

[a] As *Chrysaspidea* (sic) *nichollae* (Hampson)

Table 14.7 Pollinators of *Piperia yadonii* in Monterey Co, CA (Doak and Graff 2001)

- Apidae
  - *Bombus* Latreille sp.
- Cullicidae
  - Mosquito species
- Geometridae (Geometrid moths)
  - *Drepanulatrix baueraria* Sperry
  - *Elpiste marcescaria* (Guenee)
  - *Semiothisa* Hubner sp.
- Noctuidae (Noctuid moths)
  - *Agrotis ipsilon* (Hufnagel)
- Pyralidae (Snout moths)
  - *Pyrausta perrubralis* (Packard)
  - *Udea profundalis* (Packard)

allow insertion of a proboscis bearing an attached pollinarium, and pollen deposition on the stigma is avoided. In older flowers, the lip and column separate. An insect carrying pollinia can now easily deposit pollen on the stigma, but the distance between the lip and the viscidia is likely to prevent removal of additional pollinaria (Fig. 14.1e). A similar mechanism based on protandry is present in *Goodyera* and *Spiranthes* (Cranichideae, volume 2), but its occurrence in the *Habenaria* alliance is apparently restricted to *Piperia*.

Ackerman (1977), Doak and Graff (2001), Kipping (in Ackerman 1977), and Stoutamire (in Ackerman 1977) all recorded moth pollination for *Piperia* (Tables 14.6 and 14.7). Although Ackerman observed very few pollinators, all those he did see were moths and all appeared during an interval of 1–3 h just after sunset. Doak and Graff (2001) found the greatest moth activity on *P. yadonii* occurred between the hours of 8:30 p.m. and 10:00 p.m. According to Ackerman (1977), the moths moved upward on the inflorescence, pollinating the older flowers at the base and extracting pollinaria from the younger flowers above. Thus, protandry and pollinator behavior may increase the probability of outcrossing as in *Goodyera* and *Spiranthes* (volume 2) (Darwin 1862; Gray 1862). Ackerman (1977) reported that Kipping (1971) also observed three pyralid moths and two plume moths pollinating *P. unalscensis* in the Sierra Nevada. However, the plant that Kipping was referring to here was not *P. unalscensis* but *Platanthera sparsiflora*.

Several, often morphologically diverse moths may pollinate a single species of *Piperia*, but no shared pollinators have as yet been detected (Tables 14.6 and 14.7). Moth-pollinated orchids in subtribe Orchidinae (all genera included here under Orchidoideae, except *Habenaria*) are often visited by multiple species (e.g., Thien and Utech 1970; Smith and Snow 1976); however, van der Pijl and Dodson (1966) believe that effective isolating mechanisms are present in the subtribe that result in a degree of pollinator specificity. Those mentioned include differences in odor, spur length, and the point of attachment of viscidia on the pollinator. In *Piperia*, the viscidia are only known to attach at one place, the proboscis (Ackerman 1977; Doak and Graff 2001). Moreover, the range in size and morphology found among the pollinating moths implies that the level of specialization needed to remove the pollinaria is likely to be low. *P. unalscensis* and *P. yadonii* have shorter spurs than other species considered here (Tables 14.1–14.3), and this might lead to some level of reproductive isolation. Blooming dates vary with habitat, elevation, and latitude but might, for example, separate sympatric populations of *P. unalascensis* from *P. elongata* and *P. transversa*. *P. yadonii* also apparently blooms earlier than sympatric *P. elegans*, *P. elongata*, *P. michaelii*, and *P. transversa* (Wilkin and Jennings 1993). However, according to Ackerman (1977), phenology does not, in most cases, isolate the taxa. No investigation of scent components has yet been published, but Ackerman (1977) believes that such studies may be the key to understanding the biology of these species.

In addition to moths, Doak and Graff (2001) found a night-flying mosquito with pollinaria of *P. yadonii* attached to its proboscis. The only diurnal pollinator noted was an unidentified species of *Bombus*. It visited the flowers of *P. yadonii* rarely, but Doak and Graff believe that it is possible that a few active bumblebees could account for a significant percentage of the pollinations in some small populations.

Fruiting Success and Limiting Factors

Allen (1996) and Yedon (in Crowell 2002) reported that 5% or fewer vegetative plants of *P. yadonii* flowered while Doak and Graff (2001) found that 0.4–22% did so over 2 years with 21–49% of the blooms setting fruit. The effects of herbivory and interpopulation variation made precise analysis of the factors affecting fruit and seed production difficult. Differences noted between artificial selfing and outcrossing in *P. elegans* and *P. yadonii* could indicate the presence of inbreeding depression at the level of seed production (e.g., Ackerman 1977; Doak and Graff 2001). The fact that artificial outcrossing in *P. yadonii* and *P. elegans* produced a higher level of viable seed than open pollination, in turn, suggests the possibility of pollinator limitation or high levels of geitonogamy in open-pollinated plants. Pollen deposition rates are poorly correlated with measures of fecundity in *P. yadonii*, implying that factors other than pollination limitation are important. Further studies comparing pollinator limitation, nutrient availability, and genetic variation among populations are needed.

According to Doak and Graff (2001), the most severe limitations on the reproductive success of *P. yadonii* are herbivory, fungal infection, and the invasion of nonnative plants, although habitat fragmentation, development, and recreational activities might be of equal, long-term importance. Populations are genetically divergent probably due to fragmentation and limited gene flow. Each population should, therefore, be protected to preserve the overall diversity of the species (George et al. 2009).

No information is available on the reproductive biology of the five remaining species of *Piperia*: *P. candida* Morgan and Ackerman, *P. colemanii* Morgan and Glicenstein, *P. cooperi* (S. Watson) Rydberg, *P. leptopetala* Rydberg, and *P. michaelii* (Greene) Rydberg.

Galearis Rafinesque

Galearis is a genus of two (Sheviak and Catling 2002a) to possibly six (Pridgeon et al. 2001) species found in North America, China, Japan, and the Himalayan region. A single species, *Galearis spectabilis* L. (showy orchis), occurs in our flora.

Habitat and Distribution

Galearis spectabilis is usually found in mesic hardwood forests on well-drained, rich loam, or decaying humus (Luer 1975; Case 1987; Smith 1993). It ranges from New Brunswick to Minnesota and south to South Carolina, Arkansas, and southeastern Oklahoma (Luer 1975; Sheviak and Catling 2002a).

Floral Morphology

A variable number of showy, medium-sized flowers are loosely arranged in a solitary terminal raceme (Fig. 14.2a; Table 14.8) (Luer 1975; Case 1987; Sheviak and Catling 2002a). The sepals and the lateral petals are purple and usually connivent to form a helmet over the column (Fig. 14.3a, b). A contrasting white lip is linear-ovate to rhombic in shape with an obtuse tip and entire, wavy margins (Figs. 14.2b and 14.3a). It is extended behind into a 9–20-mm long, slightly club-shaped nectar spur (Fig. 14.3b). The column bears separate, erect anther cells, each with a single pollinium, caudicle,

Fig. 14.2 *Galearis spectabilis*. (**a**) Habit; (**b**) flower, exploded view, scale bars = 10 mm

Table 14.8 Data on *Galearis* (Sheviak and Catling 2002a)

Character	*Galearis spectabilis*
Plant height (cm)	5–20
Flower number	2–15
Dorsal sepal (mm)	10–20 × 4–6
Lateral sepals (mm)	10–20 × 4–6
Lateral petals (mm)[a]	12–18 × 3
Lip (mm)	10–18 × 6–15
Nectar spur (mm)	9–20
Column (mm)[a]	7 × 4
Chromosomes (2n)	42

[a] Luer (1975)

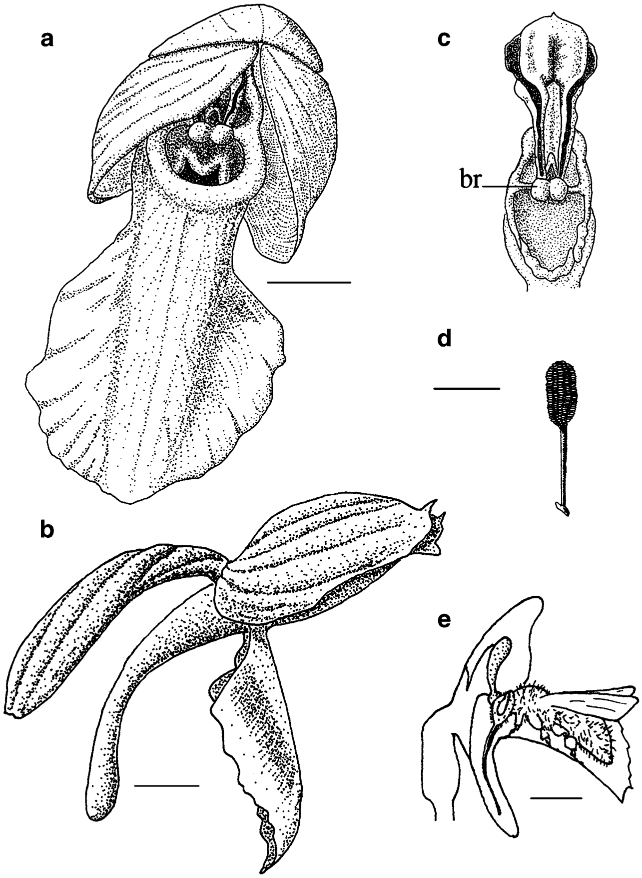

Fig. 14.3 *Galearis spectabilis*. (**a**) Flower, front view, scale bar = 4 mm; (**b**) flower, side view, scale bar = 4 mm; (**c**) column, front view; (**d**) pollinium, scale bar (**c, d**) = 2 mm; (**e**) bee contacting the viscidia, scale bar = 5 mm. *br* bursicle

and viscidium (Fig. 14.3c, d). The two viscidia are contained within separate sacks of a divided bursicle (Fig. 14.3a, c). The stigma is concave and located behind the bursicle (Sheviak and Catling 2002a).

Compatibility and Breeding System

In a study in Summit and Portage Counties, northeast Ohio, Dieringer (1982) obtained no fruit from unmanipulated, caged flowers, one fruit from twenty-five experimental self-pollinations (4%), no fruit from one geitonogamous pollination, and one fruit from one cross-pollination (100%). In a second study conducted in Maryland, Zimmerman (pers. comm. in Whigham and O'Neill 1991) found that 53.5% of open-pollinated flowers and 65.4% of artificially self-pollinated flowers produced fruit. The level of self-incompatibility varied over the distribution of this orchid (Zimmerman in Tremblay et al. 2005). On the basis of these data, it appears that pollinators may be needed for fruit set and that selfing and outcrossing are possible means of sexual reproduction. Delayed caudicle movement favors outcrossing (see below), but self-pollination or geitonogamy could, of course, occur if pollinators revisit flowers or remain on an inflorescence long enough to permit bending of the caudicles. Dieringer (1982) believes that this possibility in conjunction with a distribution in small, disjunct populations in northeastern Ohio may have resulted in varying levels of inbreeding.

Pollinators and Pollination Mechanisms

Wright (1975) observed *Bombus impatiens* Cresson and *B. vagans* queens carrying pollen of *Galearis spectabilis* on their heads in Hocking County, southeastern Ohio, and Dieringer (1982) found queens of *B. vagans* to be the sole pollinator of this orchid at his study sites in northeastern Ohio. It was the most common bumblebee present when *Galearis spectabilis* was in bloom. Eight individuals visited the orchid during 34.5 h of observation extending over the course of two spring seasons. Four of the eight queens merely landed on the lip and then flew away. The remaining four probed the flowers, inserting their heads into the nectar spurs (Fig. 14.3e). In three of the four flowers, the pollinaria had been extracted earlier. In the fourth, the bumblebee removed both pollinaria as it withdrew its head from the flower, the viscidia attaching to the center of the frons area (forehead) below the ocelli (simple eyes). By analogy with artificial pollinations using a pencil point, the bumblebee apparently ruptured the bursicula as it thrust its head into the nectar spur. The viscidia were cemented to the bee and the pollinia were pulled from their enveloping sheaths as the bee departed. The caudicles immediately began to move forward and downward, and over the course of about 3 min, positioned the pollinia to contact the stigmas of subsequently visited flowers.

A number of other bees have been identified as potential or actual pollinators. C. Robertson (1929) listed females of *B. griseocollis* (DeGeer) (as *B. separatus* Cresson) and *B. pennsylvanicus* (as *B. americanorum* Fabricius) as flower visitors, and Macior (personal communication in Dieringer 1982) found pollinaria attached to the heads of *B. fervidus*, *B. nevadensis auricomus* (Robertson), and *B. pennsylvanicus* queens. The length of the proboscis in all species varies from 10.4 to 13.9 mm (Macior 1978; Dieringer 1982). Although the nectar spur in flowers of *Galearis spectabilis* from northeastern Ohio was 18 (16–19)-mm long, it was filled to varying depths, and nectar would frequently have been accessible to *B. vagans* and other bees with tongues distinctly shorter than the spur (Dieringer 1982).

Unlike *B. vagans* which nests in woodlands, *B. fervidus*, *B. pennsylvanicus*, *B. nevadensis auricomus*, and *B. griseocollis* live in meadows and open fields (Macior 1978; Dieringer 1982). *Galearis spectabilis*, often described as a woodland orchid (e.g., Luer 1975), can also occur in old fields (Sheviak and Catling 2002a) and may be dependent on both meadow and woodland nesting species of *Bombus* for chance pollination.

Reproductive Success and Limiting Factors

Dieringer (1982) examined open pollination over 2 years at two Ohio sites. At one, 17% of the plants flowered both years and the percentage of flowers producing fruit varied between 9 and 11%. At the second site, 15–21% of the plants flowered and fruit production ranged from 0 to 1%. Although Dieringer's (1982) previously mentioned artificial outcrossing experiment was based on only a single pollination, his results are consistent with Zimmerman's (pers. comm. in Whigham and O'Neill 1991) report of lower fruit set in open-pollinated compared to hand-pollinated flowers.

Competition for pollinators was intense in Ohio, and *Galearis spectabilis* received fewer visits than synchronously flowering plants of *Iris pseudacorus* L. and *Geranium maculatum* L. According to Dieringer (1982), the flower of *Iris*, with its large fall, contrasting pattern and high ultraviolet reflectance, may have been more attractive to the bees. Heinrich (1975) noted that flowers with the most conspicuous signals seem to be the first to attract foraging insects. In addition, the flowers of *Iris* and *Geranium* were borne at heights comparable to the surrounding vegetation and higher than those of *Galearis spectabilis*. Dieringer (1982) suggested that bumblebees might forage consistently at only one particular level. Such horizontal flight patterns have been demonstrated in foraging honeybees and other insects (Levin and Kerster 1973; Handel and Peakall 1993; O'Connell and Johnston 1998; Maad 2000).

Although capsule set might be pollinator limited, Dieringer (1982) does not think that pollinator limitation explains the locally restricted occurrence of *Galearis spectabilis* in northeastern Ohio. The largest existing population studied in this area consisted of 280 plants. Each capsule produced about 7,000 seeds in experimentally self- and cross-pollinated as well as open-pollinated plants. A single capsule is, therefore, potentially capable of producing more than enough seed per season to replace the largest population observed.

According to Stebbins (1952), *Galearis spectabilis* is sensitive to disturbances in the relatively constant habitat conditions of stable climax forests, and Auclair (1972) considers that human alteration of these conditions may threaten its survival. However, its noted occurrence in old fields suggests a wider range of ecological tolerance.

Pseudorchis Seguier

Pseudorchis is a monotypic genus distributed in boreal and temperate regions of Europe and Asia, extending via Iceland to North America (Pridgeon et al. 2001), where *Pseudorchis albida* (L.) Love and Love is represented by the subspecies *stramenia* (Fernald) Love and Love (Fig. 14.4a, b). It has strongly scented yellow–green or creamy colored, nectariferous flowers. The column is suberect with a small, three-lobed rostellum and two pollinaria. Viscidia are concealed within the lateral lobes of the rostellum (Fig. 14.4b, c). It occurs on limestone barrens and tundra in

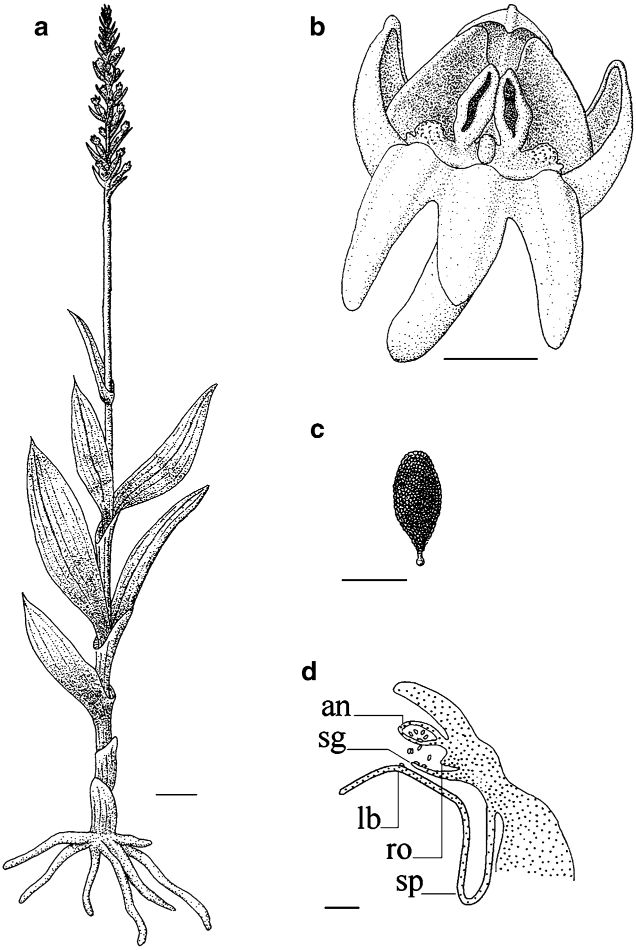

Fig. 14.4 *Pseudorchis albida*. (**a**) Habit, scale bar = 10 mm; (**b**) flower, front view, scale bar = 1 mm; (**c**) pollinarium, scale bar = 0.5 mm; (**d**) sagittal section of flower, scale bar = 1 mm. *an* anther, *lb* labellum, *ro* rostellum, *sg* stigma, *sp* nectar spur

southern Greenland, Quebec, Newfoundland, and Labrador, but is also found in northern Europe, Iceland, and the Faeroes (Lojtnant and Jacobsen 1976; Sheviak 2002a).

European populations of *Pseudorchis albida* subsp. *albida* may be pollinated by moths (Fritsch 1933) or butterflies (Muller 1881; Kunth 1898–1905, Ziegenspeck 1936; Fuller 1978; Reinhard et al. 1991). Reports of insect pollination are consistent with Darwin's (1862) observation that pollinia are often removed. However, visitors are rarely seen, and Fuller (1978), who recorded a fruit set of 93%, attributed high fecundity to facultative autogamy. Harmsen (1943) found no evidence of self-pollination, but Summerhayes (1951) and Ziegenspeck (1936) also mentioned spontaneous self-pollination.

Hagerup (1952) considered subspecies *stramenia* to be routinely autogamous in the far north, where, despite a scarcity of pollinator activity, partly closed flowers produced abundant fruit and large quantities of seed. He found massulae detached and loose within the partially dehisced anthers of unopened flower buds. In newly opened buds, the massulae were dispersed within the flower but were most abundant on the stigma located directly beneath the anther. The rostellum is short and narrow and does not obstruct movement of the pollen (Fig. 14.4d). Manipulation of the flowers during examination was sufficient to scatter the massulae, and Hagerup considered that similar movement probably occurred when the bud was shaken in the wind. Nevertheless, the anther in anthesis still contained many massulae that could potentially be transferred to other flowers by insect vectors.

Amerorchis Hulten

Bateman et al. (2009) consider that *Amerorchis* is better incorporated into *Galearis* than retained as a monotypic genus. Kew's World Checklist of Monocotyledons (accessed May 2010), on the other hand, includes it in *Platanthera.* Pending additional work on Old World species of *Galearis* and related taxa, the present treatment follows Sheviak and Catling's (2002b) recognition of *Amerorchis* as a distinct, monotypic genus based on *Amerorchis rotundifolia* (Banks and Pursh) Hulten. It is found in fens, white-cedar swamps, calcareous coniferous forests, and tundra from southern Greenland and Labrador to Alaska and south to New York and Wyoming (Sheviak and Catling 2002b). According to Cingle (2001), the flowers produce neither nectar nor scent, and reproduction is chiefly vegetative; however, seed production does occur. In Minnesota's Lake Itasca State Park and in Michigan, *Amerorchis* appears to be monocarpic (i.e., dying after seed production) and is found at different sites from year to year (Penskar and Higman 1999, Argue, unpublished).

Little detailed information is available on the pollination biology of this orchid. The column in each of its 1–12 racemose flowers bears two pollinaria comprised of a sectile pollinium, a stalk (caudicle), and a basal viscidium (Fig. 14.5a). The viscidia are enclosed in a solitary, two-lobed bursicle positioned above the orifice to the nectary. According to Proctor and Harder (1994), pollinators may remove one or both pollinaria, and one or more massulae may be deposited on each stigma. A few

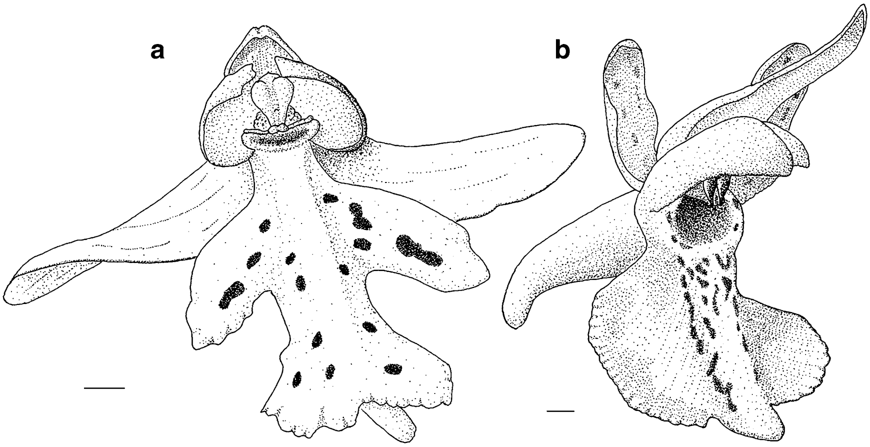

Fig. 14.5 (**a**) *Amerorchis rotundifolia*, flower, front view – note the narrow ends of stigma flanking bilobed bursicle; (**b**) *Dactylorhiza praetermissa*, flower, oblique view, scale bars = 1 mm

massulae pollinate as many as 20 ovules, and every pollinium contains 50–100 massulae. They considered that selection has acted on massula size rather than pollinarium size and has led to the production of sufficient pollen in a few massulae to pollinate all the ovules in a flower. The many massulae normally removed with each pollinarium are then utilized in the complete pollination of a number of successively visited flowers. Seed viability is highly variable, ranging from 0 to 78% per capsule. A closely related species, *Orchis morio* L., also produced many sterile seeds, an observation that Nilsson (1984) attributed to inbreeding depression in a small founding population.

Dactylorhiza Necker ex Nevski

Dactylorhiza includes about 50 (Pridgeon et al. 2001) to 75 (Sheviak et al. 2002) species widely distributed in boreal, temperate, and Mediterranean climates from Iceland to eastern Siberia. Two species are found in North America. *Dactylorhiza aristata* (Fischer ex Lindley) Soo (Fischer's orchid) is restricted to the open tundra, meadows, and bogs of Alaska, and *D. praetermissa* (Druce) Soo (=*D. majalis* (Reichenbach) P. F. Hunt and Summerhayes var. *junialis* (Verm.) Senghas) (broad-leaved orchid, leopard marsh orchid) (Fig. 14.5b) is introduced and found on seepage slopes in Ontario and in bogs in Newfoundland (Sheviak et al. 2002; World Checklist of Monocotyledons 2008).

No studies are available on the reproductive biology of either orchid in North America. However, a level of self-incompatibility, as reflected in biparental inbreeding, was reported in French populations of *D. praetermissa* (Ferdy et al. 2001). Both species are nectarless, and their brightly colored flowers may attract pollinators by deceit. A lack of reward may be compensated to some extent by variation in floral color. Sheviak et al. (2002) found that pigmentation in the flowers of *D. aristata* from Alaska ranged from magenta to pink or white. Such variation might stimulate different components of the pollinator's visual system or merely extend the time needed to learn avoidance (Nilsson 1980, 1981a). Few fragrance compounds are produced, and this may force the pollinators to recognize the flowers by color alone (Heinrich 1979; Nilsson 1981a). According to Kugler (1935), newly emerged bumblebees, the probable pollinators in our flora, depend on sight to recognize their first food flowers. If so, natural selection may have minimized expenditures through a reduction of scent production (Nilsson 1981a). Disassortative pollination, in which inexperienced pollinators move between the different color morphs, might serve to stabilize polymorphism in the population (Kay 1978; Nilsson 1980). Frequency-dependent selection on petal color has been documented in *D. sambucina* (Gigord et al. 2001).

In Eurasia, species of *Dactylorhiza*, including *D. aristata*, are frequently pollinated by insects. Sietvold et al. (2010) found that bumblebee workers mediated effective selection on *D. lapponica* (Laest. ex Hartm.) Soo for taller plants with more flowers and longer spurs but no selection on corolla size or flowering start. Bumblebees are also frequent pollinators of other species (e.g., Summerhayes 1951; Nilsson 1981a). Sugiura et al. (2002) identified two bumblebee pollinators on Rebun Island, Japan, with the pollinaria attaching to their face. Both lacked pollen loads on their back legs, indicating that they had not yet produced their first brood and were inexperienced foragers. Flies or beetles function as efficient secondary pollinators – or primary pollinators in isolated populations as in the Faeroe Islands – with the pollinaria attaching to the head or base of the antennae (Darwin 1862; Muller 1873, Macleod in Kunth 1898–1905, Hagerup 1951; Nilsson 1980; Voth 1983; Gutowski 1990). The possibility of occasional lepidopteran pollination is suggested by the occurrence of hybrids between *Dactylorhiza* and *Gymnadenia conopsea* (L.) R. Br., the latter with characteristic lepidopteran flowers (Cingle 1995). Pollinator limitation has been reported in some species as in *D. lapponica* (Sietvold et al. 2010) or *D. purpurella* (T. Stephenson and T. A. Stephenson) Soo, where levels of fruit set can be increased by hand pollination (Neiland and Wilcock 1995). In addition, both autogamy (caused by bending of the caudicle) and facultative apomixes have been recorded for *D. maculata* (L.) Soo (Martens 1926, Gustafssen 1946–1947 in Fryxell 1957).

Apparently, not all species are unrewarding. Thus, for example, Dafni and Woodell (1986) found that *D. fuchsii* (Druce) Soo produces a sucrose-rich stigmatic secretion that can be exploited by honeybees but not by bumblebees, and Voth (1983) reported that beetles (Cerambycidae) feed on papillae in the lip and spur of this species (identified in Voth (1983) as *D. maculata* (L.) Soo subsp. *meyeri* (Rchb. F.) Tournay).

Although ethological barriers may sometimes restrict the level of introgression (Heslop-Harrison 1958), pollinator specificity is often low, and this is reflected in the frequent occurrence of hybrid swarms among widely interfertile Old World species of *Dactylorhiza* (Pridgeon et al. 2001). Such hybridization and the production of amphidiploids may have played an important role in the formation of new species (Cingle 2001; Sheviak et al. 2002; Hedren et al. 2007).

Coeloglossum Hartman

According to phylogenrtic studies based on DNA sequences (nuclear ribosomal DNA (nrDNA) internal transcribed spacer (ITS) sequences and DNA sequences in the chalcone gene family were analyzed), *Coeloglossum* is embedded within a strongly supported, monophyletic *Dactylorhiza* (Pridgeon et al. 1997), and a formal transfer has been proposed (Bateman et al. 1997). Sheviak and Catling (2002c) and Sheviak et al. (2002), however, continue to recognize *Coeloglossum* and *Dactylorhiza* as distinct but closely related taxa, and a study which combines sequences of the internal and external transcribed spacers of nrDNA supports *Coeloglossum* as a sister clade to a monophyletic *Dactylorhiza* (Devos et al. 2006). *Coeloglossum* is, therefore, provisionally recognized here as distinct, pending further evaluation of its status. It includes a single, circumpolar species.

Coeloglossum viride (L.) Hartman (*Dactylorhiza viridis* (L.) R. M. Bateman, Pridgeon, and M. W. Chase) is present in a broad range of habitats in North America through much of Canada, Alaska, the northern USA and, at elevation, to New Mexico, Tennessee, and North Carolina (Sheviak and Catling 2002c).

Up to 40 flowers are borne in a dense inflorescence with conspicuous bracts. The sepals form a hood over the column with the lip descending beneath (Fig. 14.6a, c). Darwin (1862) reported that access to the nectar contained in a short saccate spur (Fig. 14.6c) is restricted by a narrow slit in an overlying membrane, which the exploring insect finds only after repeated probing. The proper positioning of the insect is guided by the curved margins of the lip (Fig. 14.6a, b). One or both pollinaria, each with a single pollinium (Fig. 14.6a), attach to its head as it feeds on the nectar or as it withdraws from the flower. Extrafloral nectaries are also present and may prolong foraging until the floral nectar is located (Proctor and Yeo 1972). According to van der Pijl and Dodson (1966), nectar from the spur can flow out over the lip, but unlike *Listera cordata* with similar pollinators (volume 2), no nectar groove is present. Nilsson (1981b) related this to different requirements for positioning of the insect in the presence of viscidia as compared to explosive rostella. Bending of the caudicles following extraction positions the pollinia to contact the stigma of subsequently visited flowers. Delay in rotation again increases the probability that the pollen will be deposited in the flower of a different plant (Darwin 1869).

Hagerup (1951, 1952), in a study in the Faroes, also found the entrance to the spur covered by a thin membrane. However, he mentioned no slit and believed that the membrane excluded all insects that lacked strong, biting mouthparts, including butterflies and small diptera. Although there was indirect evidence of insect visitation and pollen transfer in the Faeroes and elsewhere (Silen 1906a, b; Godfery 1931; Hagerup 1951, 1952), Hagerup (1952) noted that the anthers opened before the flower and that the massulae were incoherent, allowing them to fall out and onto the stigma when the flower was shaken in the wind or visited by an insect. Autogamy or insect-mediated selfing is, therefore, probable. Autogamy would be advantageous in the Faroes, where insect service is limited. However, as Hagerup pointed out, the breeding system has not been examined, and self-compatibility has yet to be established.

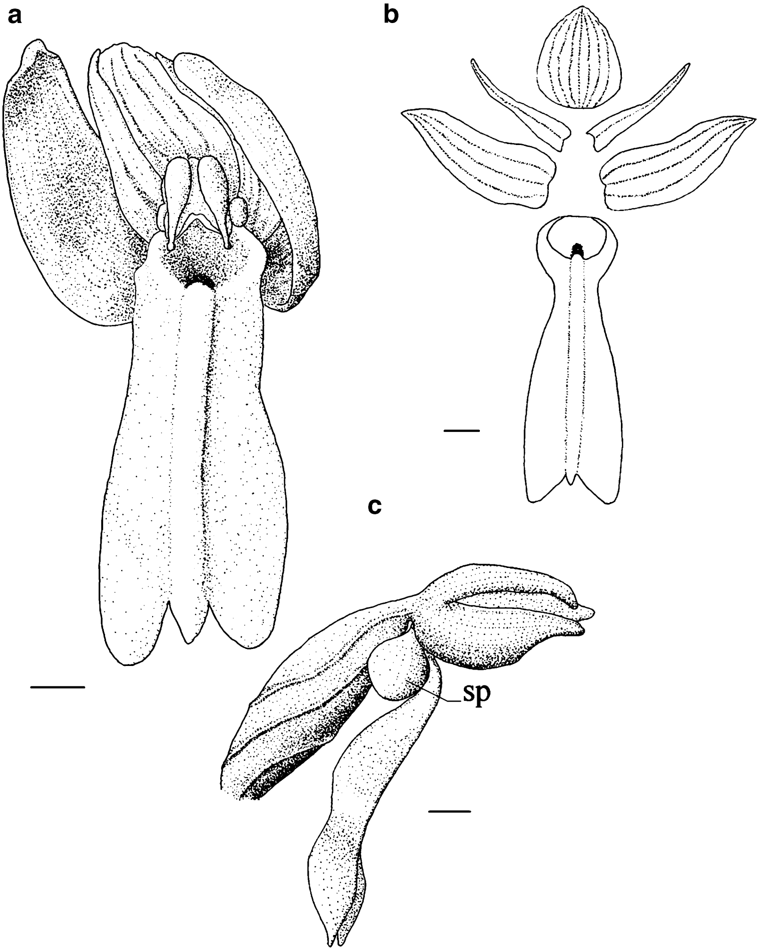

Fig. 14.6 *Coeloglossum viride*. (**a**) Flower, front view; (**b**) flower, exploded view; (**c**) flower, side view, scale bars = 1 mm. *sp* nectar spur

Elsewhere in Europe, the flowers are pollinated by insects, such as ichneumons (for example, species of *Cryptus* Fabricius), saw flies (*Tenthredopsis* Costa), small bees (Apideae), crane flies (*Tipula* L.), and beetles (species of *Cantharis* L., *Athous* Eschscholtz, and *Rhagonycha fulva* (Scopoli)) with pollinaria attaching to their heads (Silen 1906a, b; Godfery 1931; Peitz in Fuller 1980; Reinhard et al. 1991). Fuller (1980) remarked that the small column and narrow spur entrance in *C. viride* would be well-suited to pollination by Lepidoptera. None, however, have ever been observed as pollinators.

Willems and Mesler (1998) found plants of this species to be short-lived in the Netherlands with highly variable levels of annual recruitment and mortality. Fifty percent of the population produced flowers, but only ten percent produced seed.

Seed production nevertheless plays a critical role in the population dynamics of this species, vegetative reproduction being of minor significance.

Gymnadenia R. Brown

Gymnadenia is a genus of about 16 Eurasian species. *Gymnadenia conopsea* (L.) R.Br., a nectariferous, European to temperate East Asian species, was found once in Connecticut, but might now be gone. Old World members are usually pollinated by butterflies and hawk moths and reflect a continuity of characters between moth and butterfly flowers (van der Pijl and Dodson 1966). In an important study on *Gymnadenia conopsea* in central Norway, Sietvold and Agren (2010) found that insects mediated directional selection for taller plants with more flowers, larger corollas, and longer spurs. This study and another on *Dactylorhiza lapponica*, discussed above, demonstrate that pollinators can mediate selection on characters that are likely to affect both pollinator attraction and pollination efficiency (cf. pollination ecotypes in *Platanthera ciliaris*).

Habenaria Willdenow

Habenaria is an artificial (polyphyletic) genus of about 600 species occurring in tropical and subtropical regions of both the Eastern and Western Hemispheres (Pridgeon et al. 2001; Bateman et al. 2003). Sheviak (2002b) recognizes four North American species. Two occur north of Florida in the coastal southeast and Gulf States: *H. quinqueseta* (Michaux) Eaton (long-horned habenaria or Michaux's orchid) and *H. repens* Nuttall (water-spider orchid, floating orchid, or water orchid).

No information on pollination is available for either, but floral morphology implies that moths may act as vectors. The flowers are white or greenish-white, nectar is contained in a labellar spur, and the lateral petals and labellum are dissected into filiform segments (Table 14.9) (Fig. 14.7a) (Sheviak 2002b). Structure

Table 14.9 Data on *Habenaria* (Sheviak et al. 2002)

Character	*H. quinqueseta*	*H. repens*
Plant height (cm)	26–90	10–90
Inflorescence length (cm)[a]	7–25	6–28
Dorsal sepal (mm)	6–13 × 5–10	3–7 × 3–4
Lateral sepals (mm)	8–16 × 4–7	3–7 × 3–4
Lateral petal lamina (mm)	6–15 × 2	3–7 × 1
Lip		
Middle lobe (mm)	8–20 × 2–3	5–11
Lateral lobes (mm)	± = to > 2× middle lobe	4–7 × 1
Spur length (cm)	4–10	0.8–1.4

[a] Correll (2003)

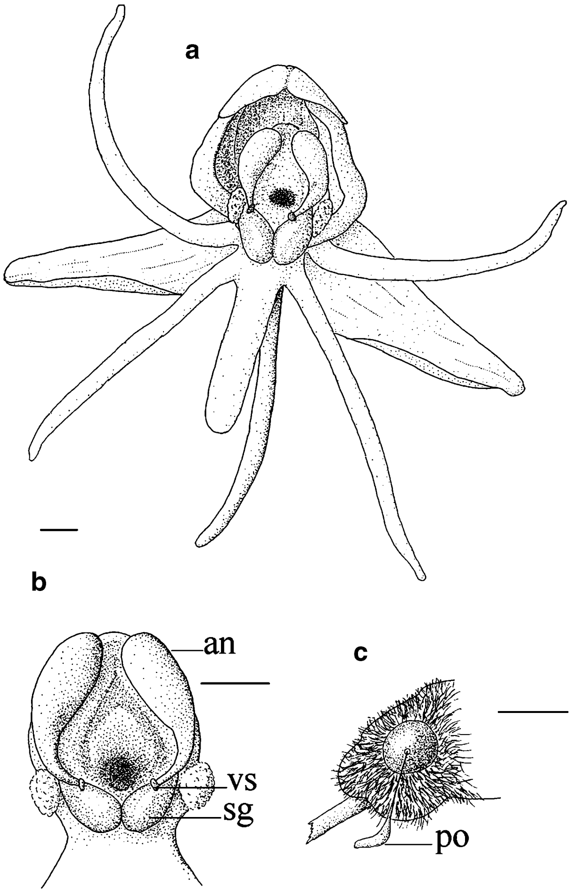

Fig. 14.7 *Habenaria repens*. (**a**) Flower, front view; (**b**) column, front view; (**c**) position of pollinarium on moth pollinator, scale bars = 1 mm. *an* anther, *po* pollinia, *sg* stigma, *vs* viscidium

of the column suggests that the pollination mechanism may be similar to that described for *H. gourlieana* Gillies ex Lindley from South Africa (Singer and Cocucci 1997). As in our species, the caudicles are long and slender near the viscidia but thick and strong near the pollinia (Fig. 14.7b). Extracted pollinaria consequently hang down near their point of attachment on the eyes while the pollinia are held in a nearly horizontal position at the opposite end (Fig. 14.7c). During insertion of the proboscis, the distal ends of the pendulous pollinaria are dragged over the stigmatic arms (Fig. 14.7b) and some massulae from the forward-directed apices of the pollinia (Fig. 14.7c) adhere to the sticky surface. Singer and Cocucci (1997) suggest that the extended, upturned perianth lobes obstruct lateral access to the flower. A hovering moth carrying pollinaria is, thus, forced to approach from the front, promoting effective contact of the pollinia apices with the stigmatic arms. Apical contact may be important because massulae at the caudicle end are less well-developed (Hesse and Burns-Balogh 1984), and contact of the larger lateral surface with the stigma in other *Habenaria* sometimes results in a level of adhesion that pulls the entire pollinarium from the pollinator (Singer and Cocucci 1997). The 40–100-mm long spur of *H. quinqueseta* appears adapted to sphingid moth pollination. The smaller flowers of *H. repens*, with 8–14-mm long spurs, may be pollinated by smaller, short-tongued moths (Table 14.9).

Vogel (1954), Nilsson and Jonsson (1985), Galetto et al. (1997), and Singer and Cocucci (1997) have observed moths pollinating *Habenaria* species in South Africa, central Argentina, northern Chili, and Madagascar. Female crane flies, mosquitoes, and butterflies have also been reported as pollinators (e.g., Moreira et al. 1996; Singer and Cocucci 1997; Singer 2001). The pollination mechanism is similar to that described above for *Platanthera*, and the pollinaria usually attach to the eyes or sometimes the proboscis. Apparent exceptions are Kunth's (1898–1905) report of sternotriby (attachment to the ventral surface of the insect) and Vogel's (1954) documented transfer of pollinaria on the front tarsi (distal-led segment) of hawk moths as well as his proposed example of viscidia attachment to the ventor (ventral part of the abdomen) based on rostellar morphology.

The breeding systems in *H. quinqueseta* and *H. repens* have also not been investigated, and few studies are available for other *Habenaria* species. Moreira et al. (1996) found that autogamy was absent and pollinators were necessary for fruit set in the Brazilian species, *H. pleiophylla* Hoehne and Schltr. Singer (2001) found another South American species, *H. parviflora* Lindl, to be self-compatible but again neither autogamous nor agamospermous. Artificial outcrossing in the latter species was about as successful as selfing (both >93%), and pollinator behavior suggested that geitonogamy might be important. According to Singer (2001), however, the massulate pollinia and broad, convex stigmatic surfaces favor outcrossing, improving both the dispersal and receipt of pollen. Outcrossing might also be promoted by a delay in the movement of the caudicles as, for example, in *H. decaryana* H. Perr from Madagascar (Nilsson and Jonsson 1985).

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Glossary

Abaxial The side of an organ (leaf, bract, or floral part) directed away from the main axis, normally the outer or lower surface.

Acropetal A process that begins at the base and proceeds toward the apex.

Adaptation The modification of an organism, a character, or a habit to fit the environment.

Adaxial The side of an organ (leaf, bract, or floral part) directed toward the main axis, normally the inner or upper surface.

Adnate United to a part or organ of a different kind as stamens to petals; cf. connate.

Adventitious Organs that develop in unusual places such as roots that arise from the stems or leaves; also applied to structures in the seed that are embryo-like but develop from outside the true embryo and often abort.

Adventitious embryony A form of agamospermy whereby the diploid embryo develops from vegetative propagation and multiplication of cells of the nucellus or cells surrounding the egg, usually resulting in polyembryony.

Agamospermy A form of apomixes in which seeds and embryos are produced asexually from a diploid cell with no fertilization.

Allele Genes that occur at the same locus on homologous chromosomes and affect the same characteristics in different ways.

Allogamy Cross-fertilization or outbreeding.

Allopatric Species or populations that occur in different, non-overlapping geographic areas.

Allopolyploidy A type of polyploidy arising through the combination of chromosome sets from two or more different species.

Allozyme In our sense, the variants of an enzyme genetically coded by different alleles of a single gene as distinguished through electrophoretic analysis of enzyme phenotypes.

Amphidiploid An allopolyploid that as a result of retention or duplication of chromosome sets only forms bivalents at meiosis and thus acts like a diploid.

C.L. Argue, *The Pollination Biology of North American Orchids: Volume 1: North of Florida and Mexico*, DOI 10.1007/978-1-4614-0592-4,

Angiosperms A class of vascular plants that characteristically produce seeds enclosed in an ovary, flowering plants.

Annual A plant that germinates from a seed, grows, flowers, produces seeds, and then dies within a single year; cf. perennial.

Anther The part of the stamen or male organ that produces pollen.

Anther cap A structure covering the pollinia in orchids.

Anthesis Specifically the opening of the stamens, but more generally, the stage when the flower bud opens and the period during which the flower remains open and functional.

Anthophilous Attracted to flowers, often as a food source.

Apex (pl. apices, adj. apical) The tip or terminal point of a perianth part, leaf, bract, or stem.

Asexual Reproduction by vegetative means.

Auricle Projecting lobes at the base of a leaf, bract, or petal; in orchids often a small, lateral outgrowth of the column, possibly part of a sterile anther.

Autogamy Intrafloral self fertilization without the aid of a pollen vector.

Auto-pollination Self pollination without the aid of a pollen vector.

Bifid Forked or cleft into two parts.

Bilaterally symmetrical Shaped so that only a cut through one plane will divide the object into matching halves.

Biogeography Study of the global distribution of organisms.

Bract A scale-like or leaf-like structure at the base of a flower, flower stalk, or inflorescence branch; located below the pedicel in orchids.

Bursicle (or bursicula) A sac-like or purse-like structure enclosing a viscidium in some Orchids.

Calcareous Composed largely of calcium carbonate or growing on a sustrate composed chiefly of calcium carbonate (limestone, chalk).

Callus A fleshy or other protuberance; for example, of the labellum.

Calyx The collective term for the sepals comprising the outer whorl of the perianth.

Cantharophily (cantharogamy) Floral syndrome with features suggesting pollination by beetles.

Capsule A dry, dehiscent fruit opening along one or more sutures.

Carpel The female floral organ comprised of the stigma, style, and ovary that bears and encloses the ovules in flowering plants.

Caudicle A slender extension of the pollinium (derived within the anther) usually composed of viscin and some pollen, connecting the pollinia to the stipe or, in the absence of a stipe, directly to the viscidium.

Cephalic Of or relating to the head.

Chloroplast A green, intracellular organelle or plastid that contains chlorophyll and other pigments essential to photosynthesis; the site of photosynthesis.

Chromosome A rodlike body that contains DNA, histones, and other proteins and regulates cell function, development, and the transmission of genetic information.

Clade A monophyletic group of any size or rank.

Cladistic analysis A method used to reconstruct phylogenies on the basis of shared, derived characters and to construct classifications based on the recognition of clades and their alliances.

Classification The placement and delimitation of taxa within divisions of a hierarchical system.

Clavate Shaped like a club, thick above and tapering to the base.

Claw The narrowed basal part of a sepal, lip, or other petal in some plants.

Cleistogamy Self-pollination (autogamy) in closed flowers.

Clinandrium The part of the column under or surrounding the anther; the anther bed.

Clone A population of genetically identical individuals derived by asexual reproduction.

Clypeus A shield-like plate on the front of an insect's head.

Column A centrally positioned organ of the orchid flower formed by the partial or complete fusion of the male and female parts.

Column-foot A ventral extension of the column base in some orchids that is attached to the labellum.

Column-wing Projections on both sides of the column in some orchids thought to possibly represent sterile anthers.

Competition Activity occurring when two or more individuals belonging to the same or different species vie with one another for some limited resource.

Conduplicate With a single longitudinal fold down the middle.

Connate United to a part or organ of the same kind as one petal to another; cf. adnate.

Connivent Parts or organs that are convergent and touching but not fused.

Conspecific Two or more organisms belonging to the same species.

Convergence Process involving the independent evolution of a similar character in two species or the occurrence of a similar character in a set of species that was not found in their common ancestor, a convergently evolved character.

Co-pollinator Term applied to pollinators where more than one kind is effective in the pollination of a plant; sometimes used in reference to pollinators playing a minor rather than a primary role.

Corbicula (pl. Corbiculae) A smooth area on each hind tibia of a bee that is edged with a fringe of stiff hairs and functions in the collection and transport of pollen, the pollen basket.

Cordate Heart-shaped, indented at the base.

Corm A short, enlarged fleshy base of a stem, usually underground or near the surface.

Corolla Collective term for all the petals of a flower comprising the inner whorl of the perianth when a calyx is present.

Cost of reproduction The energy invested in the production of offspring.

Cotyledon The initial leaf or leaves of the embryo inseed plants.

Crenate A margin with rounded teeth.

Crenulate A margin with very small, rounded teeth, diminutive of crenate.

Crest An elevated line or ridge, usually on some part of a flower.

Crisped (cripate) A margin that is irregular, wavy, or ruffled.

Cross-fertilization Union of an egg with sperm from a different plant following cross-pollination.

Cross-pollination Transfer of pollen from the anther of one plant to the stigma of another.

Cuneate Wedge-shaped and narrowed toward the base.

Deception In our sense, simulation of non-existent rewards to attract pollinators.

Deciduous Leaves or other plant parts shed naturally prior to winter or the dry season or at a prescribed developmental stage.

Deflexed Bent or turned sharply downward.

Dehiscence The spontaneous splitting open of certain plant organs (e.g., anthers, fruits) along prescribed lines to discharge their contents.

Delimit To establish limits or boundaries.

Deltoid Triangular, of leaves and floral parts with the point away from the base.

Demographic data Data on the dynamic balance of a population, especially with regard to age structure, density, and capacity for expansion or decline.

Dentate A margin with outward pointing teeth.

Denticulate Diminutive of dentate, finely toothed.

Derived A relative term referring to a feature that has evolved from another.

Diandrous Possessing two fertile stamens.

Diploid Possessing two sets of chromosomes in each somatic cell nucleus, indicated as “2n.”

Disc As used here in reference to orchids, the upper surface of the lip.

Distal The part of a structure farthest away from the point of attachment; cf. proximal.

DNA (Desoxyribonucleic acid) the stuff of which genes are made and the genetic code is written.

Dolabriform In the shape of an axe-head.

Dorsal The outer or underside of leaves, bracts, and floral parts, synonymous with abaxial

Drift See genetic drift.

Dufour gland Gland on the abdomen of bees.

Ecotype Organisms of a population sharing a specified genotype or a particular characteristic in one environment that is not shared by other populations of the same species in other environments.

Edaphic Bearing on soil, most particularly the various physical, chemical, and biological features of the soil that affect the life of organisms associated with it.

Elastoviscin A viscous material responsible for the coherence of pollen grains in orchid pollinia.

Emarginate Having a notch at an obtuse apex, usually in reference to leaves and floral parts, synonymous with retuse.

Embryo In plants a young individual in early stages of development following differentiation of the proembryo into suspensor and embryo.

Embryo sac The female gametophyte in angiosperms, containing the egg cell and a number of other haploid cells.

Endemic An organism with a restricted distribution native to a certain geographic area.

Entire A margin that is continuous, smooth, and undivided, lacking lobes or teeth, said of leaves and perianth parts.

Entomogamy, entomogamous The floral syndrome based on insect pollination.

Entomophilous Pollinated by insects; cf. entomogamy.

Ephemerals A plant or flower that is short-lived.

Epichile The distal (terminal) part of a labellum differentiated into a hypochile, (mesochile), and epichile.

Epidermis The outermost cell layer covering the primary plant body, usually a single cell layer thick but occasionally comprised of several layers.

Epiphytic The condition of a plant attached to and growing on another plant or object but not parasitic.

Erose A margin that is irregularly eroded, notched, or jagged, as if it had been chewed.

Ethological isolation Barrier to pollen exchange based on behavioral differences of the pollinators.

Evolution A process of genetic change in biological populations in response to environmental changes (see natural selection).

Extrafloral nectaries A sugar secreting gland outside the flower.

Falcate Curved as in a sickle; usually applied to leaves or perianth parts.

Fecundity The production or the capacity to produce offspring in abundance.

Female fitness The differential contribution of the female to the production of viable offspring; the relative reproductive success of genes contributed by ovules as compared to pollen.

Female function Seed production.

Fen An open plant community on flat land generally growing on alkaline or neutral wet peat.

Fidelity A constancy where a pollinator is particularly attracted to a narrowly adapted type of flower.

Filiform Thread-shaped.

Filament The slender, sterile part of the stamen that supports the anther, part of the column in most orchid flowers.

Fitness A measure of differential reproductive success among members of the same species in their contribution to the gene pool of the next or to succeeding generations.

Food-flower mimic A usually unrewarding flower that mimics the appearance of flowers that provide a reward such as nectar and/or pollen.

Founder effect The proposition that a small, pioneer community established in genetic isolation from the main population will possess only a small fraction of the genetic variation present in the parent population.

Frons A segment of an insect's cranium usually positioned between and below the antennae and above the clypeus; the anterior, uppermost part of the head of an insect, forehead.

Fugaceous Early withering or dehiscence of a plant part.

Galea Part of an insect's maxilla, the outer lobes.

Gametes Sex cells, eggs and sperm.

Gamopetalous Having the petals united (sympetalous) to form a corolla tube.

Geitonogamy Fertilization of a flower with pollen from a different flower of the same plant or clone.

Gene flow In plants the movement of genes from one population to another conspecific population by cross-pollination.

Gene pool All the genes present in a breeding population or species at one time.

Genet A term describing a single plant comprised of a number of vegetatively produced, genetically identical stems (ramets), a clone.

Genetic drift Changes in gene frequency entirely as a result of chance rather than natural selection; most likely to occur in very small populations where the probability of non-random mating is high.

Genotype The genetic makeup of an individual or the shared genetic makeup of a group of individuals as contrasted with physical appearance (phenotype).

Gland An organ comprised of one or more cells that secretes specific chemical compounds.

Globose Spherical, globe- or ball-shaped.

Glossa A tonguelike structure in the labium of an insect.

Gynoecium All the female components of a flower, the carpels.

Gynostemium See column.

Hamulus A kind of stipe derived from an upwardly curved, distal extension of the rostellar apex.

Hand pollination The transfer of pollen to stigma by human hand, artificial as opposed to natural or open pollination.

Hemipollinarium A term applied to each half of a pollinarium when each has its own viscidium and is capable of being removed separately from the other half, e.g., *Platanthera.*

Herbaceous Pertains to plants with little woody tissue, particularly if the above ground parts endure less than a year.

Hermaphroditic A flower having both male and female reproductive structures or a plant with only perfect flowers.

Heterotrophic An organism that is not able to synthesize food and receives its nourishment from the consumption or absorption of organic substances.

Heterozygous Describing an organism with contrasting alleles of a single gene.

Hexaploid An organism having six sets of paired chromosomes in each nucleus, termed "6n."

Homolog(ous)(y) In a phyletic sense, a trait reflecting inheritance from a common ancestor as contrasted with traits of independent origin.

Humus The dark organic matter in soil derived from the decomposition of plant or animal matter.

Hybrid An individual produced from genetically different parents; as used here from different species, genera, or other taxonomic groups.

Hybridization The production of hybrids by natural or artificial means.

Hypochile The basal part of a lip that is divided into two or three parts, the hypochile, (mesochile), and epichile.

Inbreeding Selfing or breeding with closely related individuals.

Inbreeding depression A decline in vigor in normally outcrossing species resulting from inbreeding and problems associated with homozygous recessive lethals and semilethals.

Incumbent Resting on or bending downwards, as the anthers of many orchids that bend downward during development.

Incurved Bent or curved toward the center of an organ.

Inflorescence A cluster of flowers or flowering branches that may include bracts but not foliage leaves.

Integument Protective cell layers enclosing the nucellus of the ovule, maturing to become the seed coat.

Intergeneric Between genera.

Intrageneric Within genera.

Introgression The transfer of genes from one species to another through recurrent backcrossing of a fertile hybrid with one of its parents.

ITS (For internal transcribed spacer) a piece of non-functional DNA located between structural ribosomal DNAs.

Keeled (Keel) A ridge, usually centrally positioned and parallel to the long axis of the organ.

Labellum (1) The median petal in an orchid flower, usually differing in size, shape, and/or color from the others, also known as the lip. (2) a fleshy pad terminating a fly's proboscis.

Laciniate A margin that is irregularly and deeply divided into narrow divisions or lobes.

Lamella (pl. lamellae) A thin layer, plate, or elevation.

Lamina The usually broad, flat, expanded part of a lip, petal, or leaf.

Lanceolate Longer than wide with the maximum width toward the base and tapering toward the apex.

Larva An independent, immature feeding stage of an insect, usually in reference to one undergoing complete metamorphosis.

Lateral Pertaining to a structure positioned on either side of a medial line dissecting a flower into two halves; e.g., "lateral petal."

Lax Loosely arranged, not dense or crowded.

Ligulate Shaped like a tongue or strap.

Limb In orchids, the expanded, flat part of the lip; in general, the expanded part in a gamopetalous corolla above the throat.

Lip See labellum.

Locule A cavity in an anther where pollen grains develop or in an ovary where ovules develop.

Magnet species The idea that species with flowers very attractive to pollinators can increase the local abundance of pollinators and thereby increase visitation to sympatric species having less attractive or non-rewarding flowers.

Male fitness The differential contribution of the male to the production of viable offspring; the relative reproductive success of genes contributed by pollen as compared to ovules.

Male function Pollen donation.

Massula (pl. Massulae) A mass or packet of pollen grains in orchids having sectile pollinia.

Medial Located in or near or pertaining to the middle of something.

Median In a series of recorded values that quantity having an equal number of observations on either side of it or an average of two middle values when the number of values recorded is an even number.

Megagametophyte The female gametophyte or haploid generation.

Megasporocyte A special cell of the megasporangium also known as the megaspore mother cell that undergoes reduction division or meiosis to produce four haploid megaspores within the ovule.

Megasporogenesis The process leading to formation of the megaspore and embryo sac in angiosperms.

Melittophily Floral syndrome with features suggesting pollination by bees.

Mentum A chin-like extension at the base of some orchid flowers resulting from a fusion of the lateral petals with the base of the lip or column (column-foot).

Mesic Related to or adapted to a moderately moist environment.

Mesonotum The middle portion of the dorsal surface on an insect's thorax.

Microgametophyte The stage in pollen grain development following mitotic division of the haploid microspore nucleus to give rise to a tube cell (or nucleus) and generative cell, the latter ultimately dividing to form two sperm cells.

Mimicry A resemblance between two unrelated species advantageous to one (Batesian mimicry) or both (Mullerian mimicry) and therefore favored by natural selection.

Monad(s) A single pollen grain, not attached to other grains as in tetrads.

Monandrous Having only one functional anther in each flower.

Monocotyledons A presumably monophyletic subclass of the angiosperms, sometimes placed in class Liliopsida, having embryos with a single cotyledon (absent in most orchids), narrow parallel-veined leaves, flower parts usually inserted in threes, a fibrous root system with adventitious roots, a stele with scattered vascular bundles, and phloem plastids with deltoid protein inclusions.

Monophyletic Referring to organisms derived from a single progenitor, including all descendants of that progenitor, and characterized by one or more synapomorphies; a natural group.

Morphology The study of form in organisms, especially external features.

Multiparental pollination The receipt on a stigma of pollen from more than one other plant.

Mycetomyophily Floral syndrome with features suggesting pollination by fungus gnats and fungus-loving flies.

Mycorrhiza An association between the roots of higher plants and an infecting fungus, often regarded as symbiotic.

Myophily (Myiophily) Floral syndrome with features suggesting pollination by flies.

Natural selection Differential survival and reproduction in a population based on an increase in frequency of entities best adapted to the environment compared to those less well adapted; the entities could be genotypes of individuals, subsets of genotypes, or alleles.

Nectar guide Structures or contrasting colors, sometimes in the ultraviolet range, on the lip or other petals that indicate to a flower visitor where to search for the nectar.

Nectar tube A variously shaped but often more or less cylindrical tube derived from the lip and/or other perianth parts that may or may not contain nectar.

Nectary A gland that secretes nectar, often part of the lip in orchids.

Nodding To droop or bend downward.

Non-resupinate Flower orientation in orchids with the lip uppermost.

Nototriby (Nototribic) Stamens and style positioned to come into contact with the dorsal surface of the pollinator; cf. sternotriby.

Notum In an insect, the dorsal part of each thoracic segment.

Nucellus In seed plants, the diploid tissue lying between the embryo sac and the integuments.

Oblong Longer than wide with nearly parallel sides.

Obovate Longer than wide with an outline like that of an egg, the broader end apical; cf. ovate.

Obtuse Blunt or rounded at the tip, the sides meeting at an angle of more than 90°.

Ocelli In insects, the simple as opposed to the compound eyes.

Ontogeny Development of an individual or organ from the zygote to the adult stage; cf. phylogeny.

Orbicular More or less roundish or circular.

Ornithophilly Floral syndrome with features suggesting pollination by birds.

Osmophore(s) Specialized scent producing glands or cells, usually on a flower.

Outcrossing As used here, a cross between two nonclonal individuals of the same species.

Ovary The basal part of the pistil which contains the ovules and develops into the fruit (in orchids a capsule).

Ovate Having an outline like that of an egg, the broader end basal (below the middle); cf. obovate.

Ovoid A solid in the shape of an egg.

Ovule A sporangium containing the female gamete and other haploid nuclei in a central embryo sac, the surrounding nucellus or megasporangium, and one or two layers of protective integument; develops into a seed following fertilization.

Papilla (pl. papillae),
papillose A small rounded projection or nipple-like structure, usually from an epidermal cell, often considered a type of trichome.

Parasitism (parasitic) A relationship between two different species in which one (a parasite) profits at the expense of the other (the host).

Pedicel The stalks immediately beneath single flowers attaching them to the main axis (peduncle) of an inflorescence.

Peduncle The primary stalk of an inflorescence or of a solitary flower.

Perennial A plant that survives year after year.

Perianth The sepals and petals or tepals of a flower.

Petal An individual segment of the corolla generally positioned just inside the sepals when both are present, often colorful and showy.

pH A measure of acidity or alkalinity based on the hydrogen ion concentration; a reduction in pH represents a decrease in alkalinity and an increase in acidity.

Phalaenophily The floral syndrome associated with pollination by small moths (moths other than sphingids).

Phenology The science studying the influence of seasonality on the recurrence of such annual phenomena of animal and plant life as bird migration, budding etc.

Phenotype The appearance of an organism determined by the interaction of the genotype and the environment and between dominance and epistatic relationships within the genotype.

Pheromones Any of a class of substances secreted by one insect that influences the behavior of another of the same species.

Phototaxis (Phototactic) Movement toward or away from light.

Phylogenetics/Phylogeny A reconstruction of the relationships and evolutionary history of organisms.

Phylogenetic analysis A procedure that attempts to infer phylogeny; particularly cladistic analysis.

Pistil The female and seed-bearing part of the flower, typically consisting of the stigma, style, and ovary.

Pleistocene The first part of the Quaternary, lasting from about two million to about ten thousand years ago.

Pollen Initially one-celled microspores produced by microsporogenesis in anthers, subsequently giving rise to the male gametophytes.

Pollen-tube An outgrowth from the pollen grain that usually emerges through an aperture in the pollen wall and grows through the styler tissue toward an ovule where it enters and releases its gametes.

Pollinarium (pl. pollinaria) A functional unit of pollen transfer usually consisting of pollen packets (pollinia), a stalk, and a viscidium.

Pollination biology Study of the mechanisms and processes involved in the pollination of flowers.

Pollination syndrome A complex of floral characters that tend to reflect adaptation to the morphology and behavior of a primary class of pollinators.

Pollinator limitation The condition in which the number of pollinator visits limits the number of seeds or fruits produced.

Pollinium (pl. Pollinia) A coherent and more or less compact mass of pollen grains.

Polymorphism The presence of two or more discontinuous variants within a species that are not related to gender.

Polyphyletic Reference to an artificial group that includes taxa descended from more than one ancestral species.

Polyploidy The condition in which the nucleus contains more than two complete sets of chromosomes.

Primitive An ancestral or pleisiomorphic feature; the term is relative and the same character may be primitive in one group and derived or advanced in another.

Proboscis (pl. Proboscises) In insects, elongate, beaklike mouthparts adapted for sucking or piercing

Protandrous (Protandry) Condition where the anthers dehisce before the pistil in the same flower reaches maturity.

Protocorm A transitional, multicellular body produced by early divisions of the germinated orchid seed that gives rise to the first true shoot and root.

Proximal Denoting the part of an organ situated nearest to the point of origin or attachment to the main body.

Psychophily Floral syndrome with features suggesting pollination by butterflies.

Pseudopollen Pollen-imitating structures on the flower that attract pollinators by deception or nutritive, granular, pollen-like cells offered as a floral reward.

Pubescent Provided with short hairs, especially when soft and down-like.

Raceme A simple, indeterminate inflorescence with pedicelled flowers on a common, more or less elongate central axis.

Racemose In racemes or having a raceme-like inflorescence.

Ramet A stem and apparently individual plant belonging to a genet or clone.

Recombination A major source of variation that arises during meiosis through crossing over and the reassortment of entire chromosomes.

Recurved Curved backward or downward.

Reflexed Abruptly bent downward or backward.

Reproductive success The relative production of fertile offspring by a particular genome.

Resource limitation Limitation of the number of seeds or fruits produced as a result of insufficient nutrients, water, or light.

Resupinate Twisting or bending of the orchid pedicel or ovary so that the lip, which is uppermost in the bud, is positioned on the lower side when the flower is mature.

Reticulate Veins, markings, or thickenings arranged in a netlike pattern.

Retuse Leaves or floral parts with a notch at a rounded apex.

Rhizome An indeterminate, prostrate or subterranean stem that in plants such as sympodial orchids is made up of the bases of successive aerial shoots.

Rostellum A structure that separates the stigmatic surface from the anthers and that produces a glue that attaches the pollinia to the pollinator.

Saccate Deeply concave, pouch- or sac-shaped.

Sapromyophily (Sapromyophilous) The floral syndrome associated with pollination by carrion- and dung-flies attached by dark colors and putrid odors.

Scape A leafless flowering stalk arising from the ground and carrying a single flower or inflorescence.

Scutellum In insects, the posterior part of the second and third dorsal thoracic segments, the mesonotum and metanotum; usually used in reference to the mesonotum as it is much reduced on the metanotum in most insect groups.

Scutum In insects, the second and largest part of the upper surface of a thoracic segment. It is preceded by the prescutum and followed by the scutellum.

Sectile Referring to pollinia that are subdivided into small packets (massulae) interconnected by elastic threads.

Selection pressure The intensity with which natural selection alters the genetic composition of a population.

Self-compatible Capable of producing seed by self-pollination.

Self-incompatible (Self-sterility) Incapable of producing seed by self-pollination.

Self-pollination The transport of pollen from the anthers to the stigma of the same flower, a flower on the same inflorescence, or a flower on the same genet.

Sepal An individual component of the outermost whorl of the perianth.

Serpentine A soil rich in magnesium silicate, often characterized by the presence of a distinctive flora.

Sessile Attached without any kind of stalk.

Sister groups (sister taxa) Groups (clades) of any rank that have split from an immediate common ancestor.

Spatulate (Spathulate) Having a broad, rounded apex tapering to a narrow base; spatula-shaped.

Speciation The formation of new species.

Sphingophily The floral syndrome associated with pollination by moths of the family Sphingidae (sphinx or hawk moths).

Spike A type of simple, indeterminate inflorescence with sessile flowers borne on a more or less elongate common axis.

Spur A hollow tubular or sac-like extension of the labellum or other floral part that may or may not contain nectar.

Stamen The male or pollen producing organ of the flower typically comprised of an anther, filament, and connective, but variously modified in orchids.

Staminode, staminodium (pl. staminodia) A sterile stamen, sometimes modified to produce a petal-like or shield-like structure.

Sternotriby (Sternotribic) Stamens and style positioned to come into contact with the vented surface (sternum) of the pollinator; cf. nototriby.

Stigma The part of the carpel on which pollen lands and germinates.

Stipe, Stipes (pl. Stipites) (1) In orchids, a stalk of the pollinarium derived from the rostellum, not the anther, connecting the viscidium to the caudicle or pollinium. (2) in insects, a mouthpart, specifically, a stalk-like component of the maxilla distal to the cardo and bearing the maxillary palps.

Style The portion of the pistil between the ovary and stigma, in orchids a part of the column.

Subspecies A subdivision in the taxonomic hierarchy with a rank subordinate to species.

Superposed Positioned on top of one another; said of pollinia that are flattened parallel to the long axis of the clinandrium or anther bed.

Symbiont An organism that lives in a symbiotic (mutually beneficial) relationship with another organism.

Sympatric Refers to populations or species distributed in the same or overlapping geographic areas; cf. allopatric.

Syndrome A group of functionally correlated characters reflecting adaptation to a particular combination of environmental or biotic conditions.

Synsepal A perianth part comprised of fused or united sepals.

Tapetum Cells lining the interior of the anther locule that supply material to the developing pollen grains.

Tarsi A segment of the insect leg distal to the tibia.

Taxon (pl. Taxa) Any named taxonomic group such as a species, genus, or family.

Tegula A kind of stipe or pollinium stalk derived from the dorsal epidermis of the rostellum; cf. hamulus.

Tepal An individual segment of the perianth in flowers having sepals and petals that are similar in appearance.

Terrestrial In reference to plants, growing in soil on the ground; cf. epiphytic.

Tetrad A group of four cells formed by meiosis; as applied to pollen, four pollen grains that remain attached as a unit at maturity.

Tetraploid An organism or cell with four complete sets of chromosomes in each nucleus.

Theca (pl. Thecae) In reference to plants, a pollen sac; there are two thecae per anther each comprised of a pair of locules.

Thorax In insects, the middle subdivision of the body positioned between the head and abdomen and bearing the legs and wings (when present).

Tibia The fourth segment and lowermost long segment of an insect's leg.

Trap-blossom A flower which effects pollination by temporarily trapping and retaining its pollinators.

Trichome An often microscopic, unicellular or multicellular outgrowth from an epidermal cell which can be hairlike, scalelike or peltate, glandular or nonglandular.

Tripartite Comprised of three parts.

Truncated Having an apex or base that is terminated abruptly, as if squared off by a transverse cut.

Tuber A thickened subterranean stem or root usually modified for storage; a stem tuber has buds or "eyes", a root tuber does not.

Ultra-violet Electromagnetic radiation with wavelengths (between about 40 and 400 nm) that are invisible to humans but visible to many pollinators.

Undulate Having a wavy margin or surface; cf. sinuate.

Vegetative reproduction A type of asexual reproduction in which specialized organs such as rhizomes, tubers, corms, bulbs, pseudoblubs, and gemmae generate new growth.

Ventor In insects, the lower or ventral part of the abdomen.

Ventral In plants, the inner or upper side of lateral organs such as leaves, bracts, or petals (adaxial).

Viscidium (pl. Viscidia) The sticky part of the rostellum, often connected to the pollinia and functioning in its attachment to a pollinator.

Viscin An elastic, more or less glutinous, often thread-like material which binds pollen together in the pollinia and caudicles.

Viscous A fluid with little tendency to flow; thick, glutinous, sticky, adhesive.

Xenogamy The transfer of pollen between different genets.

Zygomorphy Bilaterally symmetrical, usually applied to a flower.

Zygote A cell formed by the fusion of two gametes prior to the initial divisions of embryo development.

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