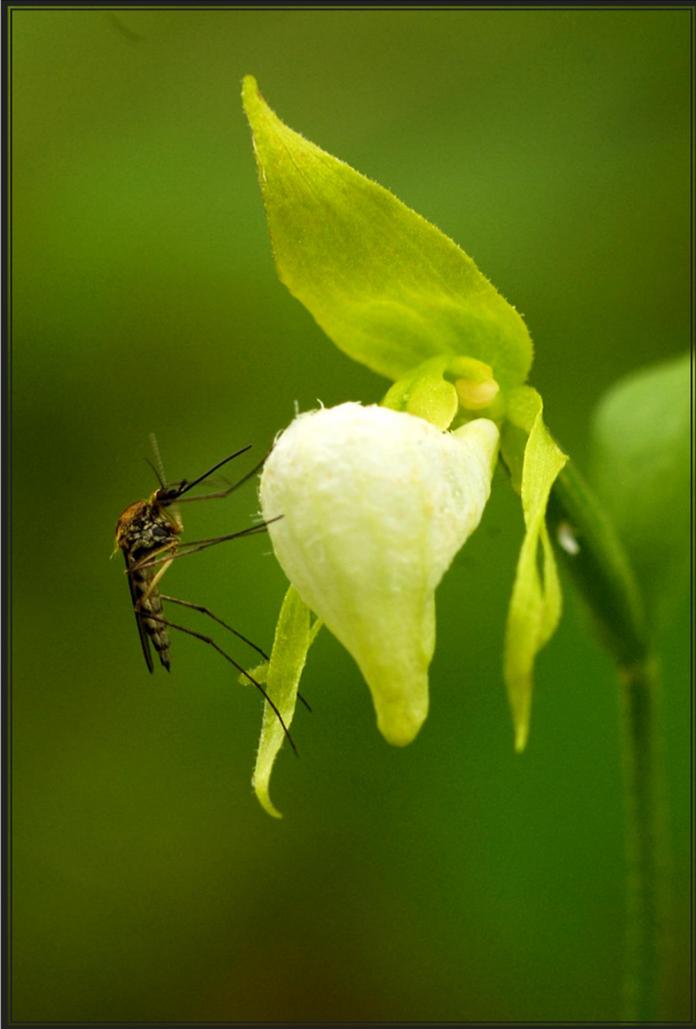


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# **The Pollination Biology of *Tipularia discolor* (Pursh) Nuttall (crane-fly orchid)<sup>1</sup>**

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## **DISTRIBUTION AND HABITAT**

*Tipularia discolor* is a perennial wintergreen orchid native to the shady, humus-rich forest soils of eastern North America. Although it ranges from southeastern Massachusetts and southern Missouri to northern Florida and eastern Texas (Whigham and McWethy 1980, Brown 1998, Catling and Sheviak 2002), studies of its pollination biology are currently restricted to a single site in North Carolina and the Smithsonian's Chesapeake Bay Center for Environmental Studies near Annapolis, Maryland.

## **FLORAL MORPHOLOGY**

Small, greenish-yellow to greenish-purple flowers are loosely arranged on a single, slender raceme (Figure 1, Table 1). The number of flowers in an inflorescence is variable (Catling and Sheviak 2002) but can be relatively constant at a given site (e.g., Snow and Whigham 1989, Whigham and O'Neill 1991). Individual flowers exhibit unusual asymmetry with the column directed either to the right or to the left of the nectary opening. Both left- and right-handed flowers occur on each raceme (Stoutamire 1978). The sepals and petals also have an altered and irregular orientation, with one or more often asymmetricaly positioned in the perianth (Figure 2a, b) (Luer 1975, Stoutamire 1978). It is the only North American orchid that shows such modified symmetry. The lip is trilobed with small, rounded, lateral lobes and a narrow central lobe, slightly

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<sup>1</sup> Modified from *The Pollination Biology of North American Orchids*, vol. 2, Springer, New York (2012).



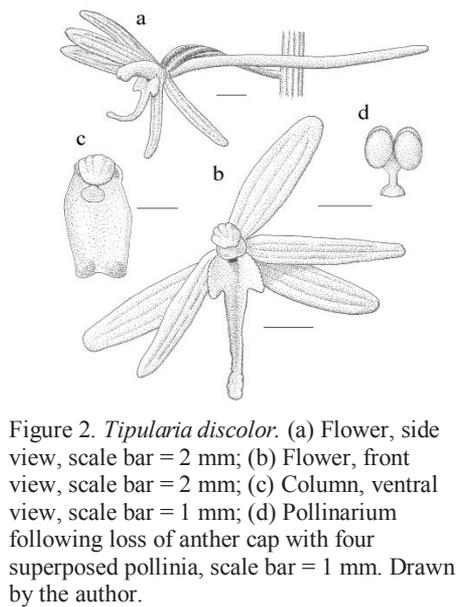
Figure 1. Raceme of *Tipularia discolor*. Photo by David G. Smith (<http://www.delewarewildflowers.org>), used with permission.

spreading at the tip (Figure 2b) (Luer 1975). It is extended basally into a long, narrow nectar spur (Figure 2a, Table 1) (Luer 1975). A slightly curved, 2.5-4 mm long column bears one terminal, incumbent anther containing two pairs of hard, superposed, yellow pollinia (Figure 2c, d). All four pollinia are attached to a single 1 mm long, elastic stalk with a basal viscidium, the latter enclosed in a bifid flap of the rostellum (Luer 1975, Catling and Catling 1991, Dressler 1993, Catling and Sheviak 2002). The stigma is sticky, entire, and located behind the anther (Whigham and McWethy 1980). The flowers produce a perceptible, nocturnal fragrance (Stoutamire 1978), which Schnell (1997, p. 438) described as “a very faint fruity or citronella odor.” The leaves emerge in autumn and persist until early summer of the following year. Flowering occurs following senescence of the leaves in mid-to late summer when relatively few other forest herbs are in bloom (Taylor 1974, Whigham and McWethy 1980), but the number of plants flowering each year is highly variable, and individual plants differ in the number of times they flower and the intervals between flowering (Whigham and O’Neill 1991).

## COMPATIBILITY AND BREEDING SYSTEM

Whigham and McWethy (1980) examined the reproductive biology of this orchid in a two-year study at the Smithsonian site in Maryland. They reported that natural populations were

maintained primarily by vegetative reproduction, and Whigham and O'Neill (1988) observed no seedling recruitment over eleven years at this site. Nevertheless, a study of genetic markers supports the occurrence of gene flow among populations (Smith et al 2002), and Coke (1990) reported high germination rates and high levels of seedling survival in laboratory experiments. A more recent field study at the Smithsonian site has revealed that the spontaneous germination of *Tipularia* seeds and the natural distribution of its seedlings are associated with the presence of decomposing wood (Rasmussen and Whigham 1998). Seedlings were found growing on rotting stumps and fallen logs; none were found growing on soil. When seeds



were experimentally sown in soil at sites where adult plants were common no germination occurred. In a second experiment germination was found to occur much more frequently in plots amended with decomposing wood than in plots with unamended, ambient soil. It thus

**Table 1. Data on *Tipularia* (Catling and Sheviak 2002)**

| Character           | <i>Tipularia discolor</i> |
|---------------------|---------------------------|
| Plant height (cm)   | 10-65                     |
| Raceme length (cm)  | 8-28                      |
| Flower number       | (5-) 10-55 <sup>1</sup>   |
| Dorsal sepal (mm)   | 5-8 x 1.5-2.8             |
| Lateral sepals (mm) | 5-8 x 1.5-2.8             |
| Lateral petals (mm) | 4-7 x 1-1.8               |
| Lip (mm)            | 5-8 x 2.5-3               |
| Spur length (mm)    | 10-23                     |
| Column (mm)         | 2.5-4                     |

<sup>1</sup>Snow and Whigham (1989) report 20-30 flowers.

appears that seedling recruitment occurs only if the proper substrate is available, and that the substrate, and perhaps the fungal symbiont, changes during the life history of the orchid (Rasmussen and Whigham 1998).

Experimental crosses in Whigham and McWethy's (1980) study indicated that pollinator-mediated intra-floral selfing, geitonogamy (i.e., crosses between flowers on the same plant), and cross pollination all have the potential for seed production. Artificial intra-floral self-pollination resulted in seed-set in 91% of the flowers. Geitonogamy and cross-pollination produced seed in 84% and 69% of the flowers, respectively. The lower percentages in the latter two treatments were attributed to abortion of developing fruit for unknown reasons one year. However, in a later two-year investigation at the same site, Snow and Whigham (1989) reported a similar level of seed set with 47-89% of artificially cross-pollinated flowers developing capsules. Capsule development in open pollinated flowers in both studies was significantly lower (see below). Examination of unemasculated and emasculated flowers enclosed in insect-proof netting indicated that autogamy (intra-floral self pollination in the absence of a pollinator) and agamospermy (a form of asexual seed formation) are probably absent.

## POLLINATORS AND POLLINATION MECHANISMS

Whigham and McWethy (1980) found a large, night-flying, noctuid moth, *Pseudaletia unipuncta* (Haworth) (Figure 3), to be the sole pollinator of *T. discolor* at the Maryland site. Two smaller geometrid moths (*Protoboarmia porcelaria* (Guenee) and *Xanthorhoe ferrugata* (Clerck)) were occasionally seen visiting the flowers, but neither deposited or removed any pollinaria or extracted any nectar.

Stoutamire (1978) also identified three species of noctuid moths as pollinators near Statesville in North Carolina: *Plusia oxygramma* Geyer, *P. precattonis* Guenee, and *Cucullia convexipennis* Grote and Robinson. The moths began their explorations just before complete darkness and continued to visit for about 45 minutes. Pollinators in both Maryland and North Carolina were presumably attracted to the inconspicuous, nocturnally fragrant flowers by their scent. According to Whigham and McWethy (1980) the random flight pattern of *Pseudaletia* was suddenly altered as individuals ventured within 3-5 meters of a *Tipularia* inflorescence, when they moved directly to the flowers.

The moths observed by Stoutamire (1978) had 15 mm long proboscises which were used to extract nectar from 18-20 mm deep nectar tubes. The moths oriented their bodies at right angles to the ground rather than in the plane of the column and inserted their heads into the throat of the flower to reach the nectar (Schnell 1997, Whigham and McWethy 1980). The distance

between the opening to the nectar spur and the column tip (1.5-2 mm) in *T. discolor* corresponded to the distance between the base of the proboscis and compound eyes of the noctuids. As the moths withdrew they extracted a pollinarium on either their left or right eye, depending on the orientation of the angled column. A moth carrying a pollinarium on its right eye could only pollinate another right-handed flower and visa-versa. Stoutamire (1978) suggested that asymmetry here might represent an adaptation to lateral, as opposed to mid-line, attachment of the viscidium in an orchid having only a single pollinarium.

In all cases the moths passed quickly from flower to flower, grasping the sepals and petals and maintaining a continual fluttering motion of their wings (Stoutamire 1978, Whigham and McWethy 1980). Stoutamire (1978) reported that movement proceeded from the base toward the top of the raceme. According to Whigham and McWethy (1980), only a few flowers on each inflorescence were visited, and although nectar was taken, not all the visited flowers had pollinaria removed. They considered that the chances of a compound eye contacting the viscidium increased with decreasing nectar volume, forcing the moths to insert their proboscises deeper into the nectar spurs.

Whigham and McWethy (1980) also suggested that self-pollination might occur when, following attachment of the viscidium to the moth's eye, the insect forced its head deeper into the flower. This would bring the pollinia into contact with the sticky stigmatic surface, positioned just posterior to the anther sac. However, because the surface of the viscidium is turned inward and faces the center of the flower, it probably is affixed to the back of the compound eye as the moth withdraws (Catling and Catling 1991). Even if the viscidium is attached as the moth enters the flower, the anther cap, which surrounds the four pollen masses on the end of the pollinarium, is usually retained for some minutes following extraction, and pollinia are not generally deposited on a stigma until after the anther cap falls off (Snow and Whigham 1989, Catling and Catling 1991). Since the moths quickly visit only a few flowers on any given inflorescence before moving on to another plant, the period of anther cap retention provides a mechanical barrier during this interval that should promote outcrossing and prevent or greatly reduce the chances of geitonogamous pollination (Stoutamire 1978, Whigham and McWethy 1980, Snow and Whigham 1989, Catling and Catling 1991). No data are available on possible return visits to the same plant. Following loss of the anther cap (Figure 2d), 1

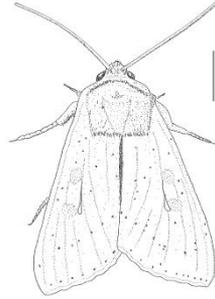


Figure 3. *Pseudaletia unipuncta* (army worm), a pollinator of *Tipularia discolor*, scale bar = 5 mm. Drawn by the author.

or 2 of the 4 transported pollinia may attach to and remain on any contacted stigmatic surface (Catling and Catling 1991). Each pollinarium is therefore able to contribute pollen to 2-4 flowers.

Pollinator activity was related to the amount of nectar present. Whigham and McWethy (1980) found that moth visits at their study site began 4 to 5 days after anthesis and continued for 13 to 15 days, peaking on the 11<sup>th</sup> to 13<sup>th</sup> day. By about the 16<sup>th</sup> day when nectar had dropped to approximately 20% of its maximum volume, very few pollinators visited the flowers, even though they remained open with some nectar content for an additional 3 to 15 days. Apparently *Pseudaletia unipuncta* was sensitive to the total amount of nectar available and broke off visits when this amount fell below some undetermined, minimum level. Willson and Bertin (1979) recorded similar behavior of this moth on *Asclepias*, where it functioned as a common pollinator for only one week of an extended flowering period.

The pollinators not only responded to the overall cycle of nectar production but also were able to concentrate their attention on the portion of the inflorescence that produced the most nectar. Both nectar production and anthesis occurred acropetally (*i.e.* maturation proceeded from the base toward the apex). Pollinator visits were initially restricted to the basal portion of the inflorescence. After about 5 days nectar production was equally dispersed along the length of the inflorescence, and pollinator visits were also equally dispersed. After 10 days nectar production was largely limited to the upper flowers, and pollinator visits were then concentrated in this area. All inflorescences were visited during the blooming period with a maximum of 25-45% of available flowers visited daily.

## FRUITING SUCCESS AND LIMITING FACTORS

Snow and Whigham (1989) found 18 to 25% of the flowers on naturally-pollinated plants set fruit with each plant producing an average of 6 to 8 fruits per year over two years in Maryland. Eleven percent of the flowering plants produced no fruit, 68% produced 1 to 10 fruits, and 6% produced over 15 fruits.

Whigham and McWethy (1980) reported that once pollinators successfully transferred pollen to the stigmatic surface, flowers produced fruit an average of 71 - 94% of the time. However, pollinators were scarce during the mid-summer flowering period, and fruit was set in only 24% of unbagged, emasculated flowers. This result lies within the range of variation observed for open pollinated, unemasculated plants in Snow and Whigham's 1989 study. If it is assumed that the experiment excluded the transfer of pollinia among ramets of

the same clone, the reported level of fruit set would be compatible with a prevalence of cross-pollination in this species.

Based on comparisons with hand pollinated flowers, both studies imply that fruit-set in open pollinated plants is limited by pollinator service. However, Snow and Whigham (1989) found that the potential advantage of increased pollination might not translate into an increase in lifetime fecundity. Fruit and flower development reduced the stored reserves available for corm and leaf growth, and levels of sexual reproduction were correlated with corm size and leaf area (Snow and Whigham 1989, Whigham 1990, Efrid 1987). Plants that produced 1-10 fruits, as in most naturally pollinated individuals, were more likely to flower the following year than those with many fruits: 23% did so compared to only 3% of those with over 10 fruits (Snow and Whigham 1989). Plants that produced less than 10 fruits also showed a reduction in leaf area the following season compared to nonfruiting plants. Additional studies of seasonal allocation patterns and photosynthetic characteristics of *Tipularia* have verified the importance of carbohydrate storage in the corm for future growth and reproduction (Zimmerman and Whigham 1992, Tissue et al. 1995). The average production of 6-8 fruits per year may represent a compromise between the chances of immediate and future reproductive success, but predation is high at some sites, and additional data on survivorship and age-specific fecundity of both parents and clonal descendants are needed to evaluate the trade-off in fitness between the numbers of fruits produced per season and the number of reproductive seasons (Cole 1954, Schaffer and Gadgil 1975, Whigham and O'Neill 1988, Snow and Whigham 1989).

High fruit-set also had a significant effect on vegetative reproduction. Vegetative reproduction can affect fitness by producing additional flowering ramets which attract more pollinators to the plant (genet) (e.g., Firmage and Cole 1988) and by dispersing the risk of mortality over a larger area (e.g., Cook 1979). Such reproduction in *T. discolor* occurs by branching. Plants that do not branch produce a single leaf, whereas those that branch produce two. Branching was observed in 75% of the plants with no fruit (pollinated flowers removed), 50% of those with less than 10 fruits, and 34% of those with higher fruit set (Snow and Whigham 1989, cf. Efrid 1987). Since it occurred in half the plants that exhibited average levels of fruit production, development of a second leaf was common in *Tipularia* and could potentially compensate for the reported negative effects of flowering and fruiting on leaf and corm size (Snow and Whigham 1989, Whigham and O'Neill 1991).

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## Sicily 2013 – *Ophrys* Heaven

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I met Tom Miranda at a North American Native Orchid Conference meeting some time ago, and we talked about a future outing to Sicily. So when Tom got in touch with me earlier this year and asked me to lead such a trip, it was a nice surprise. However, since he requested going from April 27 - May 8, a bit late for most orchids, the planning was something of a challenge. The weather was in our favor and the flowering of the orchids was delayed and the weather during our visit was perfect. Tom and Jason Gedeik, both from the Washington D.C. area, had the job of searching for suitable accommodations for our stay. They managed to find us a luxury villa near Taormina at the base of the foothills of Mount Etna, and places to stay at two working farm bed and breakfast ranches near Palermo.

These were two excellent areas as they were good for orchids and also close to the major archaeological sites. It seemed like an organizational nightmare as there were enthusiasts coming from all over the USA and Ontario, Canada. Tom contacted all the participants and offered advice on flights to enable everyone to get to the villa in time. Somehow it worked, and everyone had wonderful stories to tell of how they managed to get to the Catania (eastern side of the island) or Palermo (northwestern side) airport while we got acquainted and enjoyed a BBQ and several bottles of local wine around the luxurious swimming pools.



*Ophrys tenthedrinifera*  
with ash from the previous  
day's eruption of Mt. Etna.  
[DE]

My own travel experience was not trouble-free. I and my English friend Barry Chambers could only get an evening flight from London, England and that was late arriving in Catania. We were rather dismayed to be told by other car rental agencies that our car hire company staff had finished for the day and gone home. After a phone call we learned that the company has two offices at

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1. Photographs by Tom Sampliner [TS] and Duane Erdmann [DE] as noted.

the airport. We had gone to the wrong one. Obviously their competitors were not going to enlighten us! Our frustration was compounded when we were charged extra for being late! At least we had companionship through this since Tom had arranged to meet us at the Catania airport and Duane Erdmann, the editor of the *Native Orchid Conference Journal*, had also turned up late having had flight problems coming from the States. Once we finally picked up our nine-seater van we probed our way through the jungle of Catania on a Saturday night which was not a lot of fun. The rest of the group had already collected a similar van and a car which together hopefully would be sufficient for the 19 of us to go to all the sites as well as doing some independent side trips.

We arrived at the villa in the early hours but were still up to set off at a reasonable time in the morning for two interesting orchid sites around Castiglione and Linguaglossa. It was wonderful watching my new friends discovering their first *Ophrys*. This was *O. sicula* which is mainly yellow and named after the island. We also found *Anacamptis longicornu* and *A. picta*, members of the green-winged orchid family; and *Anacamptis papilionacea*, the European pink butterfly orchid, at this site. We saw these orchids many times on our travels but the *A. longicornu* was usually past its best. I was pleasantly surprised to see the milky orchid, *Neotinea lactea*, still in bloom. It is very pretty and stands out like a beacon. It was a little difficult at times to identify the many scattered species and varieties since Tom Sampliner and Bob and Amy Sprague, all from the United States, were the only people who had experience with European orchids. Tom S. had been to Crete and was especially knowledgeable.

There were lots of *Orchis italica* which is also called the naked man orchid for resembling just that – and we saw these at many sites. There were some *Ophrys* from the *fusca* section which were challenging for both Tom S. and me to place in their various categories. Otherwise, we had the small *O.*



*Ophrys laurensis* [DE]



*Ophrys oxvrrhynchos* [DE]



*Ophrys incubacea* [DE]



A typical *Ophrys* plant is no more than a foot tall; *Ophrys lunulata* [DE]

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*bombyliflora* hiding amongst the vegetation looking like a small bumblebee and *Neotinea tridentata*, the toothed orchid, just emerging at a number of sites. There were some lovely stands of *O. tenthredinifera* beside the road showing off their wonderful yellow borders. It is also known as the sawfly orchid due to its pollinator. A small number of *O. passionis* var. *garganica* was found at just one site during our travels and we saw our first *Serapias*, *S. bergonii*.

At Linguaglossa, going towards Etna, was the only site where we found *Dactylorhiza romana* in its red and yellow forms. The site also yielded a possible hybrid with *D. sambucina* and some plants that looked like a red *D. markusii*. A good day!

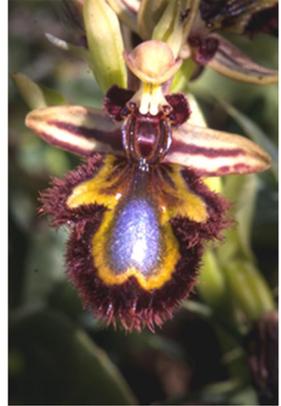
The following day was even better! We travelled south and headed towards Ferla. After stopping several times en route we found some of the prettiest *Ophrys*, *O. speculum*, and *O. bertolinii* which both have very vivid blue speculums (reflecting surface). We also found the endemics *O. oxyrrhynchos* and *O. biancae*, two very similar looking orchids which differ only in the small details of lip size and markings. Even more surprising was that *O. apifera* was



*Ophrys passionis* var.  
*garganica* [TS]



*Ophrys biancae* or hybrid  
with *O. oxyrrhynchos* [DE]



*Ophrys speculum* [DE]



*Ophrys calliantha* [DE]



*Ophrys grandiflora* [DE]



*Ophrys lutea* with  
pollinator [DE]



*Ophrys incubacea* or  
*O. exaltata* [TS]



*Ophrys lacaitae* [DE]



*Ophrys gackiae* [TS]

in bloom. This is the well-known bee orchid which is found all over Europe but is usually later flowering. In addition to the orchids seen the day before, there were two more types of the yellow bee orchid, *O. lutea* and *O. phryganea*, as well as three more *Serapias* to put on our list, namely *S. orientalis*, *S. vomeracea* and *S. parviflora*.

On a bend going towards Ferla we found an array of more new orchids. The endemic *Ophrys lunulata* looking like a half-shaped moon which, strangely, was only seen here. *Orchis anthropophora*, the man orchid, which has perfect manikin flowers, put on a good show here and it had hybridised with *Orchis italica* producing beautiful flowers with colors ranging between red and yellow. Here, too, was *Ophrys panormitana*, a member of the *O. exaltata* group, which we saw at most sites. The name means “from the region of Palermo”. They were really well past their best as they are the early spider orchids that start blooming in March.

Our next stop was the archaeological site near Ferla where we were both surprised and delighted to find the pretty *Ophrys lacaitae*, a very yellow orchid which is much sought after and often missed because of its rarity and lateness. While driving in the van we noted the large form of the giant orchid, *Himantoglossum robertianum*, a very early flowering species which, as we expected, was well past its best but a welcome addition to our growing list.

We wondered if the next day could be any better, but first we all needed a rest so we made our own plans to do so. Taormina was on our doorstep and so were all the interesting archaeological sites at Catania (Syracuse). One group consisting of Doug and Terri Kennedy and Marlene Young from Ontario; Alice Jenson from Tennessee; Cheryl and Alan Mizak from Connecticut; and

| Table 1.<br><i>Ophrys</i> seen in bloom |  |
|---|--|
| <i>apifera</i>                          | <i>lunulata</i>                        |
| <i>bertolinii</i>                       | <i>lutea</i>                           |
| <i>biancae</i>                          | <i>mirabilis</i>                       |
| <i>bombyliflora</i>                     | <i>obaesa</i>                          |
| <i>calliantha</i>                       | <i>oxyrrhynchos</i>                    |
| <i>calocaerina</i>                      | <i>pallida</i>                         |
| <i>exaltata</i>                         | <i>panormitana</i>                     |
| <i>flammeola</i>                        | <i>passionis</i> var. <i>garganica</i> |
| <i>gackiae</i>                          | <i>phryganea</i>                       |
| <i>grandiflora</i>                      | <i>sabulosa</i>                        |
| <i>incubacea</i>                        | <i>sicula</i>                          |
| <i>lacaitae</i>                         | <i>speculum</i>                        |
| <i>laurensis</i>                        | <i>tenthredinifera</i>                 |
| <i>lucifer</i>                          |  |

## THE BEE ORCHIDS

*Ophrys* is a genus of terrestrial orchids in the alliance *Orchis* and sub-tribe *Orchidinae*. Its species are found as far north as Finland ranging southward to the Canary Islands Eastward through Europe and along the North, South and Eastern Mediterranean to southern Turkmenistan. The greatest diversity is eastern Aegean, Mediterranean Turkey and southern mainland Greece, Rhodes, Lesbos, and to some extent Crete. Sicily offers a wide array of *Ophrys* taxa providing for a rich field experience as to varieties, forms and hybrid swarms. Therefore, while the island may not have as many species as the eastern portions of the range, it is one of the more desirable destinations.

Bee orchids capture our attention because of their evolved traits designed to attract and deceive naïve male insects into attempting to copulate with the orchid flower. Solitary bees are the main pollinators of *Ophrys spp*; however two species are pollinated by wasps and one by a beetle species. The extent to which these flowers have evolved various traits to entice their pollinators seems like science fiction. The orchids produce cocktails of aromatic compounds that mimic exactly the sexual hormones of the female of the pollinator species. This is the long distance attractant for the male pollinators that regularly emerge from their winter dormancy a few weeks earlier than their female counterparts.

Color patterns, position of flower parts and shapes further enhance the impression on the pollinator that he is approaching the lady of his dreams. Upon alighting, the pollinator is further deceived by the textures, shape and contours of the lip. Hairs, for example, give tactile confirmation. A hairless shiny zone, commonly called the mirror or speculum visually replicates either the female insect wings or abdomen.

Bee orchids arise from underground tubers and roots. There are usually two tubers; one gathers starch and water providing nourishment to the plant over the winter and the beginning of the next seasons' growth. It then withers and a new one enlarges and supplies the following year's growth. Above ground the stem arises from the center of a rosette of bluish-green leaves just above ground and rises up to support one or many flowers, depending on the species. Leaves may or may not be spotted, and may or may not have wavy margins.

Each flower will have an outer whorl of three sepals that are always hairless and more or less ovate. The inner whorl consists of lateral petals that are variously narrow or wide, single colored or bicolored, positioned horizontally or upwards at a forty-five degree angle; each species varies. The third petal, the lip, is larger than the other petals and is highly modified to look like the female of a specific insect. It acts as the attractant and the landing pad for the pollinator.

Most Bee orchids prefer open, warm and dry, sunny habitats in nutrient-poor, calcareous soil. Grazing by goats and sheep presents a constant danger in many areas. Throughout their range development and population sprawl present another threat.

The number of Bee orchid species has ranged from over three hundred in one orchid text to a more conservative number of under thirty in another. The upper number reflects small differences in observable characters that led some to propose hosts of new species. Recently comprehensive studies of *Ophrys* spp throughout their range, along with molecular studies, point to some lower number of highly variable species that manifest multiple subspecies and varieties. This view is the current trend accepted by those influenced by molecular studies. Those that still favor field work and observations of all aspects that affect taxonomy such as pollinator relationships favor the more liberal interpretation of species.

— Tom Sampliner

(Continued from page 13)

three Texas participants namely Allison Galloway, Deborah Greer and Richard Schmidt, had a good day exploring these sites. The other contingent included Americans Steven Cirafesi, Victor Lentini and Tom Miranda. They all had an affinity with Sicily as this was the land of their ancestors, so it was nice that they could go back to see where their families had originated.

Barry and I decided to go with Tom M. and Tom S. to Tyndaris and en route, under the trees, we did see some purple *Limodorum abortivum*, *Neotinea maculata* (the dense flowered orchid) and banks of *Orchis provincialis* – another yellow orchid that likes acid soils. While Tom M. was visiting his family, the rest of us in this small group went around the local archaeological site. Later in the week, while some went to the island of Lipari near the volcano of Stromboli, some of us visited Roccella Valderone and found more *Ophrys lacaitae* and the only site for *Anacamptis laxiflora*, the lax flowered orchid, which is another late bloomer.

In our remaining time before heading across the island, we all went to Santa Rosalia primarily to see *Ophrys mirabilis* and *Orchis brancifortii*. The elusive *Ophrys mirabilis* is another *O. fusca* type but with hairy arms which makes it unique. *Orchis brancifortii* only seems to grow on the Mount Etna lava slopes. It is much like the four-spotted orchid but has a smaller range and can only be found in Sicily and Sardinia. After a little searching we found both species but only a single plant of the *Orchis brancifortii*. Fortunately it was a good specimen. Finally we ventured up Mount Lauro to see yet another type of *Ophrys fusca*, this time one with a pretty yellow border on the lip, *O. laurensis*. We had admired the stands of *O. tenthredinifera* at the start of our trip but on Mount Lauro we were treated to specimens of *O. grandiflora*, a larger version of the beautiful sawfly orchid. Other orchids seen here were the pyramidal orchid, *Anacamptis pyramidalis*, and a type of late spider orchid, *Ophrys calliantha*, which is much like *O. candica*.

## Other Sicilian Orchids Seen



*Orchis italica* [TS]



*Orchis anthrophora*  
“Man orchid” [TS]



*Neotinea maculata* [TS]



*Orchis brancifortii* [TS]



*Anacamptis*  
*papilionacea* [DE]



*Anacamptis morio*  
subsp. *picta* [TS]



*Anacamptis pyramidalis*  
[DE]



*Limodorum abortivum*  
[DE]



*Serapias lingua* [DE]

On our journey to Ficuzza we stopped to admire the Roman mosaics of the Villa Romana di Casale at Piazza Armerina, and on a later day some of us went south to Agrigento to explore Greek and Roman archaeological sites.

After settling in at the two B&B farm houses we toured the Ficuzza forest. Unfortunately the famous peonies were past blooming, but we did find the rare type of *Ophrys fusca*. *O. pallida*, which is endemic to the area. It proved to be a good area for *O. fusca* types, and we were able to add *O. flammeola*, *O. gackiae*, *O. obaesa*, *O. lucifer*, *O. sabulosa* and possibly *O. calocaerina* to our list. (See Table 1 for a list of *Ophrys* species seen.) The last new orchid to add to our list was the saprophytic orchid *Limodorum abortivum*, which was present in pine stands. (See Table 2 for a list of other orchids seen.)

We had a wonderful trip, in spite of the lateness of the visit, and managed to see everything we were looking for. It was a pleasure to lead a group of fellow enthusiasts ... and seeing Mount Etna erupting on our first day, was a bonus especially for the photographers.



Mt. Etna eruption [TS]

Table 2.  
**Other Orchids Seen in Bloom**

|   |  |
|---|--|
| <i>Anacamptis morio</i> var. <i>picta</i>     | <i>Neotinea lactea</i>                     |
| <i>Anacamptis laxiflora</i>                   | <i>Neotinea tridentata</i>                 |
| <i>Anacamptis lonicornu</i>                   | <i>Neotinea maculata</i>                   |
| <i>Anacamptis papilionacea</i>                | <i>Orchis brancifortii</i>                 |
| <i>Anacamptis pyramidalis</i>                 | <i>Orchis anthropora</i>                   |
| <i>Dactylorhiza markusii</i>                  | <i>Orchis italica</i>                      |
| <i>Dactylorhiza romana</i>                    | <i>Orchis provincialis</i>                 |
| <i>Dactylorhiza romana</i> × <i>sambucina</i> | <i>Orchis italica</i> × <i>anthrophora</i> |
| <i>Himantoglossum robertianum</i>             | <i>Serapias lingua</i>                     |
| <i>Limodorum abortivum</i>                    | <i>Serapias begonii</i>                    |
|   | <i>Serapias parviflora</i>                 |
|   | <i>Serapias orientalis</i>                 |
|   | <i>Serapias vomeracea</i>                  |

## FATHER OF WILDLIFE CONSERVATION

Aldo Leopold (1887-1948) is considered by many to have been the most influential conservation thinker of the 20<sup>th</sup> century and is acknowledged by many as the father of wildlife conservation in the United States. After graduate school, Leopold worked for the US Forest Service, where he saw policies being enacted without scientific information: policies that in many cases resulted in more harm than good. Over time in articles and speeches he espoused a philosophy of wilderness, believing that vast areas of nature should be road free, where citizens could lose themselves in nature. As a result Leopold is credited with establishment of the first wilderness area within the national forest system.

The University of Wisconsin was his home from 1933 until his untimely death at age 61. He wrote extensively on forestry, wildlife management, conservation and restoration biology, literature and even esthetics. Leopold's most famous book, *The Sand County Almanac*, published in 1949 has sold over two million copies and is a must read for anyone interested in ecology and the natural world.

Leopold was a strong proponent of orchid conservation and he wrote an article that helped to protect the Faville Grove Prairie, one of the best and most extensive examples of unploughed and ungrazed prairie in Wisconsin (Leopold 1940a,b, see also a biography by C.D. Meine). This is explained in the video documentary (<http://wisplants.uwsp.edu/favilleprairie.html>) called "Aldo Leopold and the Wild Prairie Orchids." The natural *Cypripedium* hybrid, *×favillianum* Curtis (Rhodora 34: 242. 1932) is named after the same Stoughton W. Faville whom the prairie is named after, it formerly being his land (and he being a wildflower expert). It may also be of interest to readers that Wisconsin has an online interactive orchid flora ([http://www.botany.wisc.edu/orchids/Orchids\\_of\\_Wisconsin.html](http://www.botany.wisc.edu/orchids/Orchids_of_Wisconsin.html)) as well as the older publication by Fuller (1933).

Every year on the first Saturday of March the University of Wisconsin celebrates Leopold Day, a full day of readings from Leopold, hikes and musical performances. The purpose is to get the public thinking about conservation and expanding their personal actions to protect our natural resources.

— Hal Horwitz

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Leopold, A. 1940. Exit orchis: A little action now would save our fast disappearing wildlife. [Wisconsin] Wildlife 2: 2 (Aug 1940), 17. Reprinted in Am. Wildlife 29: 5 (Sept-Oct 1940), 207; reprinted in Wisc. Acad. Rev.: 9: 1 (Winter 1962), 26-27.

Leopold, A. 1940b. Faville prairie preserve. Wild Flower 18:4 (Oct 1941), 67-68 .

## Conservation Efforts for *Cyrtopodium punctatum*

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The Cigar Orchid (*Cyrtopodium punctatum*) occurs as far south as South America, and reaches the northernmost extent of its range in extreme south Florida. It is North America's largest and one of the most dramatic species of native orchids. Flowering from late March through late April, large plants can produce 500 golden yellow, orange, and brown flowers that emit a wonderfully sweet fragrance. The Cigar Orchid's preferred habitat is that of cypress strand swamps and cypress sloughs. It grows as an epiphyte in the western parts of south Florida typically on Bald Cypress (*Taxodium distictum*), or Pop Ash (*Fraxinus caroliniana*).

Because of south Florida's sub-tropical climate, there are distinct wet and dry seasons. These plants are perfectly adapted to take advantage of large amounts of tropical moisture during their growing season (May-Oct.) and then go completely dormant during the very dry months (Nov.-May). They have adapted specialized root systems that form large 'mats' of fine branching roots. During the dry season, plants shed all of their foliage. The large mass of fine roots is an effective way for these plants to scavenge the air during almost daily morning fog events through this otherwise dry part of the season.

Unfortunately, because of their wonderful adaptive qualities and their astounding beauty, they have been the target of many decades of illegal poaching and over-collecting. In addition, former haunts of this species were heavily logged for their productive stands of cypress timber, thus nearly exterminating the large host trees required for this species. Today, remnant native populations of this once commonly seen orchid remain elusive to even the most experienced orchid biologists. The Atlanta Botanical Garden has been assisting in the recovery of this species at the Fakahatchee Strand Preserve State Park since 2008. Fewer than 20 plants were known to occur in this park at the onset of the project. By cross-pollinating wild plants and growing them from seed in our laboratory and greenhouses, we have succeeded in reintroducing over 600 plants into the 85,000 acre State Preserve in recent years. Future efforts between partners (Florida Dept. of Recreation and Parks, Florida Fish and Wildlife Conservation Commission, Florida International University, and Atlanta Botanical Garden) will include further population augmentation, and continued collection of data for essential ecological restoration, and GIS analysis.

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1. This topic was covered in a talk given by the author at the 2013 Native Orchid Conference meeting in Oroville, CA.

## **Pollinators of Ram's-Head Lady's-Slipper Orchid (*Cypripedium arietinum*) in Eastern Ontario and Notes on the Pollination System**

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To gather information on pollination of *C. arietinum*, flowers were observed over a period of 40 hours of appropriate conditions in their natural habitats, and insects were captured in two malaise traps over a three-day period. Five pollination records were obtained, all involving small bees [three *Lasioglossum* and two *Ceratina*]. No visitors were observed. With two previous records of *Lasioglossum* pollination, the importance of small bees is supported. The flower of *C. arietinum* is treated as a non-model mimic with the possibility of *Viola* spp. in particular serving as important magnets, and *Actaea* spp., *Maianthemum stellatum* and *Tiarella cordifolia* possibly also being important. Additional evidence is required to support Batesian mimicry. Clarification of the pollination system of *C. arietinum* may provide an improved understanding of evolution involving deception due to the very unusual flowers and primitive position of *C. arietinum* in the genus.

It is widely reported that various species of bees are the pollinators of North American Lady's-Slipper Orchids (Cypripedioideae, Catling and Catling 1991, Cingel 2001, Argue 2011). One species, Ram's-Head Lady's-Slipper Orchid (*Cypripedium arietinum* R. Br., see Horwitz 2009 for a valuable summary of information) stands out in this group as unique in having a lip that is funnel-shaped, has a densely pubescent orifice and is white with purple veins and madder purple below. The coloration and hair are often associated with fly-pollination (Pijl and Dodson 1966). However, the very limited information on pollination of *C. arietinum* (Catling and Catling 1991, Cingel 2001, Argue 2011) suggests that the pollinators of this primitive Lady's-Slipper (Atwood 1984, Perner 1998) are bees. Stoutamire (1967) observed two bees of the genus *Lasioglossum* (*Dialictus*), one of which was *Lasioglossum coeruleum*, emerging from lips with pollen on the thorax. Pijl and Dodson (1966, Fig. 21) also included an illustration of a bee in the basal opening of the lip which may be a female of the genus *Hylaeus* based on the two white marks on the head.

These few observations (2 bees) are too few to characterize the pollination of *C. arietinum* with certainty. It seems to be the one of the few species of *Cypripedium* where we may expect to find pollinators other than bees. The less

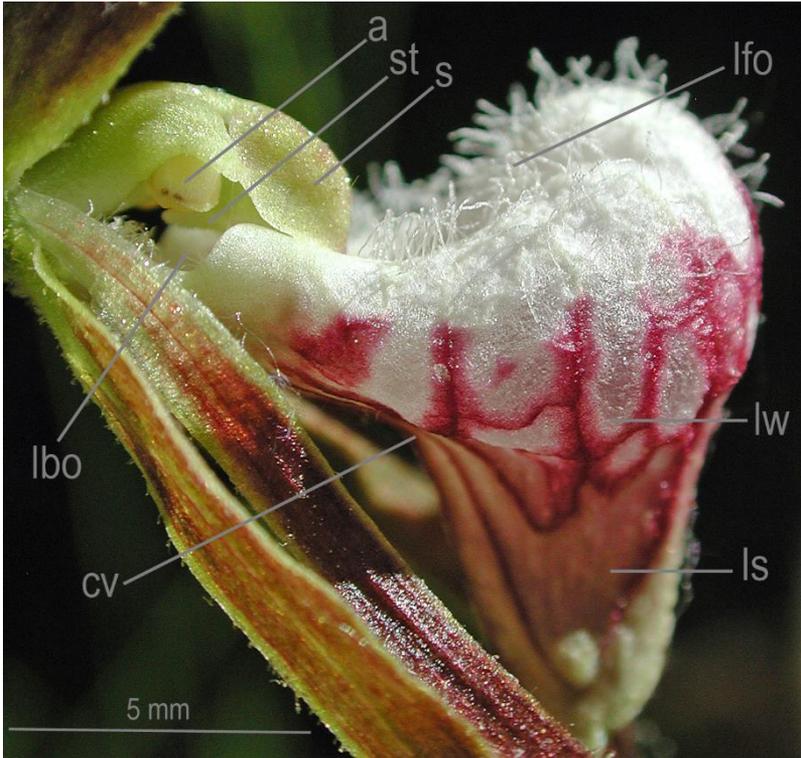


Figure 1. Flower of *Cyripedium arietinum* in lateral view. a, anther; cv, converging veins; lbo, basal opening of lip; lfo, frontal opening of lip; ls, lip spur; lw, lip window; s, staminodium; st, stigma. Photo by P.M. Catling, taken in Marlborough Forest, south of Ottawa, 3 June 2011.

unique Clustered Lady's-Slipper (*Cyripedium fasciculatum*) is now suspected of being pollinated by a single group of wasps (Diapariidae, - Ferguson and Donham 1999, Argue 2007).

The lack of observation of pollination is not surprising. Although there has been disagreement on the subject, *Cyripedium* orchids do not obviously provide anything for pollinators (Dressler 1993) although individual flowers may possess a wide range of attractants (Nilsson 1979). The flowers control the pathway of the pollinator which enters through the large frontal opening of the pouch-shaped lip (Figure 1. lfo ) then passes the stigma so that it first deposits pollen that it is carrying and then it picks up a new load on the only way out through one of the basal openings of the lip (Figure 1. lbo) below the anther. Many species and groups of orchids are food-deceptive, and when they occur in low numbers the plants may often not be visited by pollinators (Li et al.

2008). For those that are visited, the pollination event is often difficult to observe because flowers are often not visited at all or because the pollination event can happen very quickly within a fraction of a minute over a flowering period that may last up to 60 hours of appropriate daylight. Obtaining 18 pollination records in 60 hours seems high in the study of Li et al (2008) but their observations included a large population, more than one observer and extended over a two year period. In late May 2011, we witnessed a pollination event unexpectedly and then decided to collect additional information on the pollen vectors. The results are reported here and they are of interest with respect to the larger subject of the evolution of the floral structure and pollination in *Cypripedium*.

## METHODS

### Study area

The study area in Marlborough Forest south of Ottawa approximately at 45.0706, -75.8328, included an area of mostly Eastern White Cedar (*Thuja occidentalis*) woodland in shallow soil over limestone rock. There were adjacent Cedar-Balsam Fir (*Abies balsamea*) swamps and marshlands and woodlands including Trembling Aspen (*Populus tremuloides*) and White Spruce (*Picea glauca*). Wildflowers blooming at the same time as the orchids in the surrounding areas included (in order of scientific name): Baneberries (*Actaea* sp.), Wild Sarsaparilla (*Aralia nudicaulis*), Goldthread (*Coptis groenlandica*), Wild Strawberry (*Fragaria virginiana*), Canada Mayflower (*Maianthemum canadense*), Starry False Solomon's – Seal (*Maianthemum stellatum*), Fringed Polygala (*Polygala paucifolia*), Foamflower (*Tiarella cordifolia*), Starflower (*Trientalis borealis*), White Violets (*Viola blanda*, *V. macloskeyi*, *V. renifolia*), and Blue Violets (*Viola cucullata*, *V. nephrophylla*, *V. sororia*).

### Capturing pollinators

To obtain pollinators we sat within one meter of patches of 10 – 30 flowers and waited to observe pollination events. Insects were captured after visiting one or two flowers. Insects entering flowers were allowed to escape from the basal openings of the lip before being enclosed within a bottle. Observations and collections were made during sunny conditions over a period of 40 hours between 28 May and 5 June.

On 29 May 2011, two malaise traps approximately 2 m long by 1.5 m high were set out near a part of the population of approx. 500 plants. The traps funneled flying insects into a container of 95% alcohol. Captured insects were examined for the pollen of *Cypripedium*. Any found was considered attributable to *C. arietinum* because flowers of Yellow Lady's-Slipper (*Cypripedium parviflorum* Salisbury var. *pubescens* (Willdenow) O.W. Knight) in the area

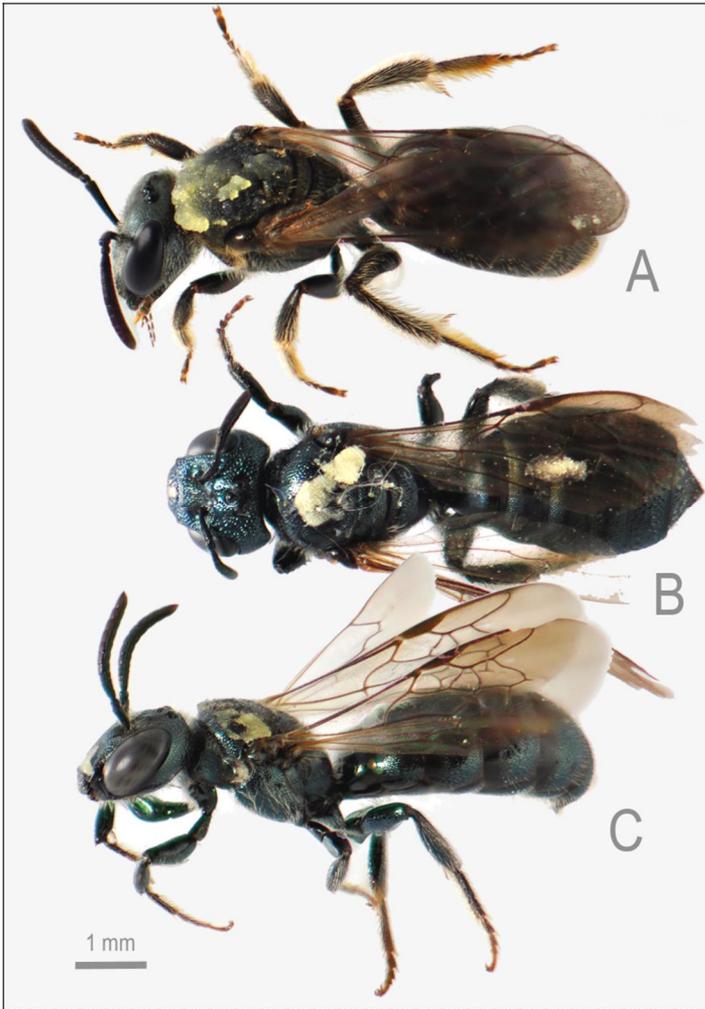


Figure 2. Pollinators of *Cypripedium arietinum*, all with pollen on the dorsal surface of the thorax. A, *Lasioglossum* (subgenus *Dialictus*) sp., female B, *Ceratina* sp., female C, *Ceratina calcarata*, male. Photo by P.M. Catling.

had not yet opened. At the end of the period of observations on 5 June, all flowers still receptive were hand pollinated with pollen from flowers at least 50 m away.

Identifications of pollinating insects were made using Gibbs (2010), Mitchell (1960, 1962) and the “Discover life” website (Id-nature guides – bees <http://www.discoverlife.org/mp/20q> [Updated: 2011-12-15]).

## RESULTS

There were three direct observations of pollination: (1) On 28 May 2011, it was 18° C with sun around 5 pm after five days of cool, cloudy and rainy weather. A small bee emerged from a flower with pollen on the thorax, approached another flower 20 cm away, landed, crawled through outer opening into lip pouch, crawled around inside, was sometimes quiet, and emerged through side exit within 20 seconds. The small bee, 7.5 mm long, evidently a female of a species of *Lasioglossum* (Figure 2A) spent about 5 seconds in one of the basal openings of the lip. There it struggled, apparently due to a tight squeeze, and perhaps also due to the sticky pollen mass attached to its thorax. (2) On 30 May 2011, on a sunny afternoon with 23° C, a small bee with pollen on the thorax landed on a lip, crawled inside the distal opening, remained in the pouch for 10 minutes and then exited easily through a side opening. It was 8 mm long and identified as a female of a species of *Ceratina* (Figure 2B). (3) On the same day, a small bee with pollen on the thorax, landed on another flower, crawled around inside the pouch, often resting, and after 80 seconds, exited out of one of the basal pouches. This bee was 7.5 mm long and identified as a male of *Ceratina calcarata* (Figure 2C).

In all three cases above, the bee entered the lip within a few seconds of landing on it and did not flail as though falling. They were also relaxed inside the flower. There were no other pollinators or visitors.

Two small bees (7.5 mm long) with *Cypridium* pollen on the thorax here were found in the malaise traps on 29 May prior to the flowering of *C. parviflorum* var. *pubescens* so were assumed to be carrying *C. arietinum* pollen. Pollen of these two species could not be distinguished using simple microscope equipment. No other insects in the malaise traps carried *Cypridium* pollen. One of these bees was a female of a species of *Lasioglossum* (subgenus *Dialictus*) and the other a female of a species of *Ceratina*.

## DISCUSSION

### Pollinators and Pollination

The five pollination records of small bees reported here for *C. arietinum* more than doubles the pollination records. No other pollinators or visitors were observed during the study. Along with Stoutamire's (1967) two records of *Lasioglossum*, the importance of species of that genus is confirmed but *Ceratina calcarata*, and related species may also be important.

The sister species of *C. arietinum* in China (Chen 1983, Perner 1995), *C. plectrochilum* Franch.), with a more inflated and paler lip, is also pollinated

by small bees including species of *Lasioglossum* and *Ceratina* (Li et al. 2008). The observations reported here of the relaxed and purposeful entry into the flower and relaxed movement inside are similar to those of Li et al. (2008) for *C. plectrochilum* and contrary to observations of *Osmia* and *Megachile* bees entering and within lips of *C. parviflorum* var. *pubescens* (pers. obs.). It appears that it is the lip itself that is the attractant

Li et al. (2008) showed that there can be very high (approximately 50%) capsule set as a result of pollination of *C. plectrochilum* by *Lasioglossum* spp. in China. This is unusually high for a lady's-slipper in North America (pers. obs.). He attributed this high fecundity to a biodiversity-rich environment with many spring ephemerals that benefitted the bee pollinators in the genus *Lasioglossum*. The idea that a nectarless species benefits from growing in the vicinity of one or a group of nectar-containing species is often referred to as the "magnet species theory." A number of studies have rejected the theory (e.g. Lammi and Kuitunen 1995) while others have supported it (e.g. Pellegrino et al. 2008).

## Floral mimicry?

Knowing the pollinators and their their behavior and considering these with regard to the flower of *C. arietinum* helps to develop hypotheses that may enable further understanding of the pollination system. In this case it may involve evolution, by any of several processes (Ackerman 1986, Nilsson 1992), to resemblance of violet (*Viola* spp.) flowers. In most places where *C. arietinum* grows (largely a Great Lakes region endemic), there are violets of some species present (pers. obs.), most often and obviously *Viola sororia sensu lato* (or *Viola nephrophylla*), but also many white violets. Small bees of the genera *Lasioglossum* and *Ceratina* are frequent visitors to flowers of violets in some places where the orchid is also present (pers. obs.). Bees of similar size were reported in Beattie's (1971) classic study to be pollinators of similar species of *Viola* in Europe. To obtain pollen or nectar from the violet flower these bees often have to push past a dense mass of hairs at the base of the petals, and are led by converging veins into a floral tube where both nectar and pollen may be accessible. These hairs are on the base of lateral petals of many species of violets and also on the basal (spur-bearing petal) of some. It may seem unlikely that a flower like that of *C. arietinum* is a mimic of a violet flower, which seems at first to be very different, yet when one considers the known activities of the pollinator and the parts of the *C. arietinum* flower, it is an interesting possibility. Although Pelligrino et al. (2008) reported floral mimicry in the case of *Viola aethnensis* and the orchid, *Dactylorhiza sambucina*, this involved general color as most reports of floral mimics have.

In the flower of *C. arietinum*, the bee lands on the lip and pushes past the hairs into the frontal opening where converging veins are brightly lit in the



Figure 3. Flower of *Viola nephrophylla*. A dense mass of hairs and conspicuous venation below it is also seen in the flower of *Cypripedium arietinum*. Modified from a photo by Joshua Mayer taken at Snow Bottom Natural Area, Wisconsin (Flickr Creative Commons).

floor of the lip by windows of clear tissue on the side of the lip. Having entered the lip, the only way out is by either of the two basal openings due to the inflexed margin of the frontal opening. The spur is dark and may function to reduce attraction to the central part of the lip and enable vein convergence in the basal part of the lip. Otherwise its function is unclear and it may be relict. Inside the lip, veins and more hair lead to the lateral openings. The process involving pushing past a mass of hair, and potential influence of converging veins, and then an enclosed tubular space, is the same for both some violets and *C. arietinum*, suggesting the possibility of floral mimicry of the former by the latter. This kind of mimicry has been referred to as “model-mimicry” in orchids (Ackerman 1986) and is a category of Batesian mimicry. There are several examples in the Orchidaceae including that of the unrewarding *Anacamptis israelitica* as mimic of the rewarding lily, *Bellevalia flexuosa* (Dafni and Irvi 1981).

It is possible that the whitish hairy flowers of *C. arietinum* would also attract pollinators visiting other co-blooming whitish flowers with linear floral parts, including particularly *Actaea* spp., *Maianthemum stellatum*, and *Tiarella cordifolia*. This would correspond to “non-model” mimicry (Dafni 1984, Nilsson 1992) that is believed to be the case in many deceptive orchids (Pelligrino et al. 2008). Members of the genus *Cypripedium* have been generally regarded as belonging to this category of generalist (non-model) food mimics (Pelligrino et al. 2008). Johnson et al. (2003) suggest that most European deceptive orchids have not yet evolved species-specific Batesian mimicry, the evidence suggesting generalized magnet species resemblance. This interpretation may be applied to *C. arietinum* pending evidence to the contrary, such as

close-matching spectral reflectance, incapacity of the pollinators to distinguish the mimic from the model, higher fecundity of the mimic in the presence of the model, etc. It was suggested by Li et al. (2008) that the Chinese sister species of *C. arietinum*, *C. plectrochilum*, is also a non-model mimic that resembles a number of co-blooming vernal species of woodlands including species of *Claytonia*, *Erythronium*, *Fragaria*, *Hepatica*, *Trillium*, and *Viola*.

Within the general concept of non-model mimicry involving exploitation of a group of unrelated co-blooming plants, there is often one, or sometimes a guild, that seems to be the most important and that a particular deceptive orchid may resemble most closely. In the presence of this particularly important species model, the deceptive orchid experiences a reproductive benefit (Johnson et al. 2003).

It may be difficult to draw the line between model-mimicry and non-model mimicry because “important” species bridge the gap. At present, it is appropriate to treat *C. arietinum* as a non-model mimic, despite the possibility of *Viola* spp. being a model to some degree. There are also possibilities of other explanations such as the flower of *C. arietinum* appealing to a bee as a nest entrance (as well as a violet blossom).

Based on its unusual flower, Atwood (1984) resurrected Rafinesque’s distinctive genus name *Criosanthes* for *C. arietinum*, treating it as the basal branch of evolution in the genus *Cypripedium*. Although *C. arietinum* was not supported as the most primitive lady’s-slipper by later authors (Cribb 1997), it still occupies a lower level in the tree and learning more about its pollination system may help to understand co-evolution involving deception.

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## Thank You

Thanks to Janet Novak for her work designing our new user-friendly website [www.nativeorchidconference.info](http://www.nativeorchidconference.info) It has been a long time coming and we appreciate the time and effort Janet devoted to this project. It is hoped that this website can be easily accessed by those even with a minimal level of interest or curiosity; we know it will inspire them to learn more and perhaps register for the Yahoo group site.

— Bob Sprague

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