ISSN 1554-1169

The Native Orchid Conference

Volume 11(2) April - June 2014

Volume 11, Issue 2

Contents

Native Orchid Conference Journal is published four times a year by the Native Orchid Conference, Inc., a non-profit [501(c)3] organization, as a service to its members. The organization is devoted to fostering the study, conservation, and enjoyment of orchids native to North America. Membership dues are: US individual – ($30), US Family – ($35), student – ($15), and non-US Individual or Family – ($40). Address inquiries about membership, back issues of this journal, and requests for copies of the bylaws to the Treasurer: Jim Hayward, NOC, Inc., P.O. Box 13204, Greensboro, North Carolina 27415-3204, USA; nativeorchids@yahoo.com OR ncorchid@yahoo.com.

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The Pollination Biology of *Malaxis paludosa* (L.) Swartz (bog adder's-mouth) (=*Hammarbya paludosa* (L.) Kuntze)[1]

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Habitat and range

Malaxis paludosa is usually found in open, sunlit black spruce (*Picea mariana* (Mill.) Britton, Sterns, and Poggenb.) bogs or swamps on hummocks of *Sphagnum* L. or occasionally *Mnium* L. moss (W. R. Smith 1993). Reeves and Reeves (1984) consider it an epiphyte on mosses. Circumboreal in distribution, this small and inconspicuous plant has been collected at a few North American sites in Alaska, western Canada, Ontario, Manitoba, and Minnesota, but probably occurs undiscovered in numerous bogs in between (Catling and Magrath 2002).

Floral morphology

A highly variable number of minute, greenish-yellow flowers are evenly spaced in a terminal raceme (Table 1) (Luer 1975, W. R. Smith 1993). The nearly-microscopic yellowish lip is striped with green and stands erect due to a 360-degree twist of the pedicel and ovary (Figure 1a). It is more or less ovate with an acute or sometimes constricted apex giving rise to a small, acuminate tip. The lower margins clasp the column resulting in a tubular entrance to the flower (Figure 1b). The lateral petals are recurved and about as long as the lip. The column is short and erect (Table 1) (Luer 1975, Dressler 1993). Two pairs of waxy, leaf-like pollinia are produced in a terminal, two-celled anther (Figure 1c, e). The anther opens while the flower is still in bud, and the anther membrane contracts toward the base of the column, exposing the pollinia (Darwin 1862). The pollinia remain cradled in the cup-like clinandrum and

[1] Modified from *The Pollination Biology of North American Orchids*, vol. 2, Springer, New York (2012).

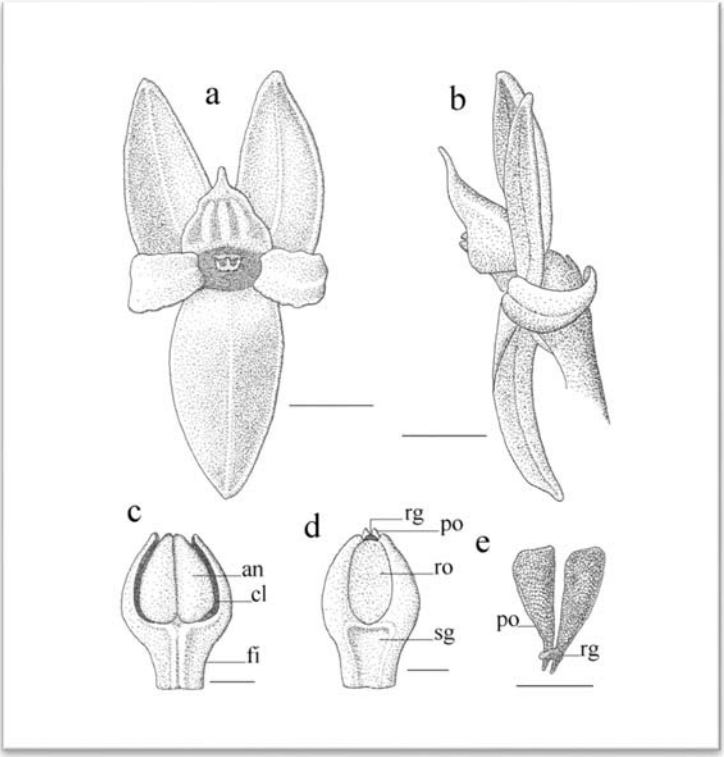

Figure 1. Malaxis paludosa. (a) Flower, front view, scale bar = 1 mm; (b) flower, side view, scale bar = 1 mm; (c) column, back view, scale bar = 0.2 mm; (d) column, front view, scale bar = 0.2 mm; pollinia (two shown) held together by a drop of rostellar glue, scale bar = 0.2 mm. (c)-(e) Modified from Darwin (1862). *an* anther, *cl* clinandrum, *fi* flilament, *po* pollinia, *ro* rostellum, *rg* rostellar glue, *sg* stigma

shriveled anther membrane at their base. The attenuate upper ends project slightly beyond the top of the rostellum, and as the bud opens they contact the posterior surface of a small drop of viscid matter or rostellar glue which projects slightly above the rostellum (Figure 1d). The pollinia are bound together by the glue, which shrinks and becomes more viscid over time (Figure 1e). Caudicles are absent. The stigma, located on the front half of the column at the base of the rostellum (Figure 1d), is covered by a film of viscous fluid (Darwin 1862).

Flowering begins at the bottom of the inflorescence and buds are produced from the apex throughout the flowering period. The first flowers to open remain fresh for the length of the blooming period, about 4-5 weeks, whereas late flowers may bloom for only a few days (Reeves and Reeves 1984). Only

Table 1. Data on *Malaxis* (Catling and Magrath 2002)

Character	*Malaxis paludosa*
Plant height (cm)	3-23
Raceme length (cm)	0.5-9
Flower number	2-55
Dorsal sepal (mm)	(1.6)2-2.5 x 1-1.6
Lateral sepals (mm)	(1.6)2-2.5 x 1-1.6
Lateral petals (mm)	1.4-1.9 x 0.5-1
Lip (mm)	1.2-1.8 x 0.7-1
Column (mm)	(0.3)0.5-0.7 x (0.3)0.5-0.7
Chromosomes (2n)	28

the lip wilts; the sepals and other petals on both the unfertilized flowers and developing fruit remain fresh and green into late August. The leaves of this tiny orchid are smaller than in other American species of *Malaxis*, and Reeves and Reeves (1984) suggest the photosynthetic contribution of the enduring green perianth may be significant. Flowers of *M. unifolia* Michaux. and *M. monophyllos* (L.) Swartz are not similarly persistent. A minute film of nectar, insufficient for analysis, is produced in an area at the base of the lip and column. The floral odor is sweet and cucumber-like and most detectable about 15 cm away from the plant. It is produced throughout the blooming period, although it is more noticeable early on. Foliar embryos may sprout from the margins and tips of the leaves to supplement seed reproduction and creeping and rooting annual growth (Taylor 1967).

Compatibility and breeding system

Autogamy is known in a handful of *Malaxis* species scattered from the Western Hemisphere to Asia and the South Pacific (Ridley 1888, King and Pantling 1898, Schlechter 1911-1914, J. J. Smith 1928). However, in a study in Beltrami County, Minnesota, Reeves and Reeves (1984) reported that open pollinated plants of *M. paludosa* produced fruit, but plants bagged to exclude pollinators did not. The orchid, therefore, is probably neither autogamous nor apomictic. Catling (1983) also found no evidence for autogamy in a plant from

the Queen Charlotte Islands. Rostellar development here was sufficient to effectively separate the pollinia and the stigma. In any case, the self-compatibility of this orchid has yet to be established. Self-incompatibility is known in at least one *Malaxis*, *M. massonii* (Ridl.) Kuntze, from Puerto Rico (Aragon and Ackerman 2001).

Pollinators and pollination mechanisms

Reeves and Reeves (1984) found pollinia attached to a single, 2.5 mm long, male fungus gnat, *Phronia digitata* Hackman (Diptera, Mycetophilidae). Attachment was at the ventral-anterior part of the thorax behind the mouthparts (Figure 2). According to these authors, the insect probably perched on the lowermost sepal and reached over the column to extract nectar from near the base of the lip and column with its proboscis. In the process the area behind its mouthparts contacted the viscid droplet on the pollinia. If the column had been approached from the lip, the pollinia would have been attached elsewhere. In older flowers the lip bends downward and the lowermost sepal upward, leaving entry from the lowermost sepal the only one possible (Reeves and Reeves 1984). When another flower is visited the pollinia are likely to contact and adhere to the viscous fluid on the surface of the stigma. Reeves and Reeves (1984) observed pollinia in this position with emerging pollen tubes penetrating the stigmatic tissue. The pollinia were not inserted into a stigmatic pocket as reported by Darwin (1862).

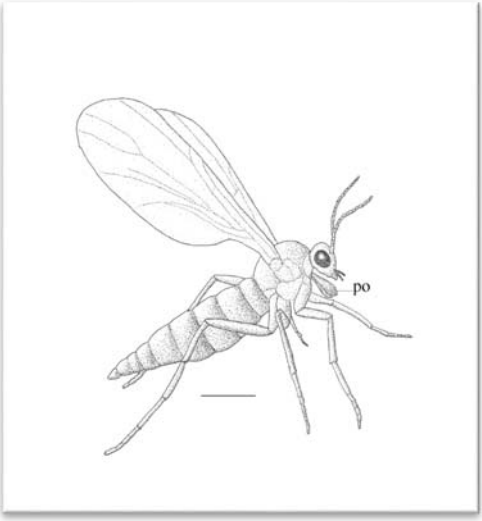

Figure 2. Fungus gnat with pollinia of *Malaxis paludosa* attached to the anterior ventral thorax, scale bar = 0.3 mm. po pollinia

Reeves and Reeves (1984) also observed a mosquito, *Aedes* sp. (Diptera, Culicidae), possibly probing for nectar near the base of the lip and column. No pollinia were found on mosquitoes, however, and these authors believe they are too large to either contact the pollinia or bring about pollination. Five other species of dipterans and two hymenopterans were observed or collected on the plants but none carried pollinia. The smaller European version of *M. paludosa* is apparently pollinated by tiny bog flies (Davies et al 1988).

Fruiting success and limiting factors

Even though pollen vectors were only rarely observed, both Darwin (1862) and Reeves and Reeves (1984) reported that pollinia were removed from most flowers. Reeves and Reeves (1984) found that 20.5% of the flowers in their study area produced fruit in 1983 with a mean of 3.64 fruits per plant and a maximum of 7. In 1984 this average dropped to 2.17. The modal number for the two years was 4 and this number was produced by about 28% of the plants. In 1983 64% of the plants produced 4-7 fruits compared to 22% in 1984 with the variation provisionally attributed to differences in rainfall. Although the sample was very limited, Darwin (1862) reported an even higher level of natural fruit set with 13 of 21 flowers (62%) on one spike producing capsules. The level of fruit production can therefore be substantial, although seed viability and seedling recruitment remain to be examined. By way of comparison, fruit set in a deceptive, obligately outcrossing, and reportedly pollinator-limited, Puerto Rican species, *M. massonii* (Ridl.) Kuntze, was only 1.8% (Aragon and Ackerman 2001).

Predation, probably by rodents and insects, accounted for fruit losses ranging from about 34-39% over the two years of the Minnesota study (Reeves and Reeves 1984).

Additional species of *Malaxis*

Malaxis unifolia is sympatric with *M. paludosa* in Minnesota, Ontario, and Manitoba, and its resupinate flowers bloom at about the same time. In Minnesota, Reeves (in Christensen 1994) observed a cecidomyiid gall midge with a pollinium attached to its head crawling upward on the labellum toward the column of *M. uniflora.* The two species may therefore be pollinated by different insects carrying pollinia on different parts of their bodies. Other visitors to *M. unifolia* included species of *Bradysia* Winnertz (Sciaridae), *Aedes* (Culicidae), and *Trioxys* Haliday (Braconidae).

Based on flower size and phenology, Reeves (in Christensen 1994) believes that fungus and gall gnats may pollinate *M. soulei* L. O. Williams (now *M. macrostachya* (Lex.) Kuntze), *M. corymbosa* (S. Watson) Kuntze (now *M. brachystachys* (Rchb. f.) Kuntze), *M. porphyrea* (Ridley) Kuntze, and *M. tenuis* (S. Watson) Ames (now *M. abieticola* Salazar and Soto Arenas) in southern Arizona. Similarly, Hapeman (1996) thinks that flower size and color as well as habitat indicate that fungus gnats probably pollinate the North American *M. monophyllos* var. *brachypoda* (Gray) Morris and Eames in Wisconsin. In an abstract, Reeves and Reeves (1985) noted the presence of insect pollinators as well as isolating mechanisms for this variety in Minnesota, but failed to identify the pollinators or provide any additional detail. Light (1998) reported that it produced 5 mm long, seed bearing capsules at an unspecified site in Canada.

Tests in Ontario showed no evidence for autogamy in this orchid or in *M. unifolia*; both have well developed rostella separating the stigma and pollinia (Catling 1983). However, the largely Old World *Malaxis monophyllos* var. *monophyllos* (= var. *diphyllos* (Cham.) Luer), also found in Alaska and British Columbia, is reported to be mostly autogamous in Europe, although tiny flies may sometimes act as pollinators (Davies et al 1988). So far as I am aware nothing has been published on pollination of the three remaining North American species of *Malaxis*, *M. wendtii* Salazar, *M. bayardii* Fernald, and *M. spicata* Swartz, although again, flower size and color imply the involvement of small flies such as fungus gnats.

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Close-up of *Malaxis paludosa.* Photo by Ian Ward.

Malaxis paludosa plants. Photo by Lorne Heshka

Pollination of Great Plains Ladies'-tresses (*Spiranthes magnicamporum*) Near Ottawa, Ontario

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In the fall of 2013 Great Plains Ladies'-tresses (*Spiranthes magnicamporum* Sheviak) was discovered on the relict alvar grasslands near Almonte in Burnt Lands Provincial Park, west of Ottawa in eastern Ontario (Reddoch *et al.* 2013). These grasslands are thought to be remnants of open prairie-like habitat that was more widespread in early postglacial times. Here *S. magnicamporum* grows in an open meadow dominated by Prairie Dropseed grass (*Sporobolus heterolepis* (A. Gray) just as it does in parts of the tallgrass prairie in southern Manitoba. The orchids were first observed on 18 Sept. and by 26 Sept. 520 plants had been found in an area of almost one square mile. Observations of seven bumble bees visiting consecutive plants, i.e. serving as pollinators, over a two hour period were reported by Reddoch et al. (2013) who reviewed the information on pollination of the species which suggested bumble bees, but with few observations.

Here the visitation and pollination observations at the new site near Ottawa are extended based on records and collections made on mild, sunny days between 18 and 26 Sept. 2013. The information was gathered over a three hour period from noon until 3 PM on each of 7 days during random walks through the population.

Pollination and visitation: Over the period there were 54 observations of bumble bees (*Bombus* spp.) and one of a Honey Bee (*Apis mellifera* L.) visiting the flowers of *S. magnicamporum*. In addition to this, 20 observations were made of bumble bees serving as pollinators and an additional 15 bumble bee pollinators (visiting two or more consecutive plants) were collected. Of the collected bumble bees, 10 were *Bombus vagans* Smith (7 males, 3 females) and 5 were *Bombus impatiens* Cresson (3 males, 2 females). All bees were identified using Laverty and Harder (1988).

Pollination mechanics: The bees climbed upward in the inflorescence probing the flowers as has been reported previously (Figure 1A). The pollinia were attached to the dorsal surface of the galea (Figure 1B). These aspects of

behaviour and positioning have been reported previously for bumble bees pollinating species of *Spiranthes* (Catling 1983). Most captured bees carried 3-7 pollinia but some carried only one.

High fecundity and potential apomixis: All examined plants in the wild set abundant seed suggesting that pollinators were not limiting. However, this particular population may not be pollinator-dependent. In fact it may be apomictic based on the observation that three plants with flowers in bud when collected, bloomed as typical and fragrant *S. magnicamporum*, but also produced abundant seed from flowers that had not been pollinated. Examination of this seed showed some extruded embryos and polyembryonic seed, indicative of adventitious embryony, but these features were not evident to the extent frequently seen in *S. cernua.* Other locations have been reported for apomictic *S. magnicamporum* in Ontario (Catling 1982) and it may be that the eastern disjunct populations are all apomictic compared to those of the western plains and prairies (Catling 1982, Figure 5) where distribution may have been more or less continuous.

Characteristics of the flowers: The flowers of the population near Almonte were typical of *S. magnicamporum* in all respects but less fragrant than some plants in Illinois and North Dakota. They may also have averaged a little less yellowish and had larger basal calli, but data are insufficient to confirm this. A reduced fragrance may be anticipated in an apomictic population. How-

Figure 1. Pollinators of *Spiranthes magnicamporum*. A, Female *Bombus vagans* probes a flower; B, Female *Bombus impatiens* showing position of pollinia (yellow, upper right) on galea. Photos by author.

ever, the promise of a nectar reward was apparently real. A test of the liquid (a partial drop) at the base of the lip (below the calli) using indicator strips suggested a high concentration of glucose (over 100 mmol/L, Bayer Diastix Reagent strips used for testing glucose in urine). Since glucose is not the only form of sugar in nectar (which may contain sucrose and fructose, etc.), these flowers may have been a much more valuable energy source than the simple test suggested.

Pollinator fidelity: At the time of year when *S. magnicamporum* was flowering, there were few other flowering plants in the open alvar and adjacent alvar woodland. In 2013 the only other flowering plants over much of the area were Gray Goldenrod (*Solidago nemoralis* Aiton) and Northern Heart-Leaved Aster (*Symphyotrichum ciliolatum* (Lindl.) Á Löve and D. Löve) which had become more conspicuous than usual, perhaps as a result of increased growth due to the decline of competing woody plants during the drought of the previous year. The only one of these that was visited much was *Aster ciliolatus* and the primary visitor was *Bombus impatiens*.

Significance of the observations: The northeastern-most disjunct population of *S. magnicamporum* is committed to and effectively pollinated by two species of bumble bees despite the presence of apomixis by adventitious embryony (asexual reproduction by the development of viable seeds). Possibly disjunct eastern populations have required a dual breeding system to survive in isolated patches of habitat or their move eastward from the prairies was significantly facilitated by fertility assurance of apomixis.

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Spiranthes magnicamporum (Great Plains Ladies'-tresses) – the Manitoba Population

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Examination of the Flora of North America range map for *Spiranthes magnicamporum* reveals that this species is found in a number of disjunct locations in Eastern North America and through a broader range in the mid-west, from Texas to its most northerly range in southeastern Manitoba. The Manitoba population extends to approximately 20 kilometers north of the 49th parallel.

Although this orchid is commonly known as the Great Plains Ladies'-tresses, this name may be somewhat misleading as it has been recorded from as far northeast as the Burnt Lands Provincial Park near Ottawa, Ontario. The latter location is about a thousand miles east of the Great Plains. In Manitoba, this orchid does live up to its common name with populations found principally in tall grass prairie remnants of the Great Plains.

In Manitoba, the only other orchid found blooming in the same habitat and at approximately the same time, and that may be mistaken for this species, is *Spiranthes romanzoffiana*. There are, however, at least two principle characteristics that can be used to separate these two species. The first is that the leaves of *S. magnicamporum* normally wither before the flowers are in peak form while those of *S. romanzoffiana* remain fresh. The second requires careful examination of the lip of the flower. The lip of *S. romanzoffiana* is constricted – making it appear fiddle shaped, with the lip turning down sharply near its apex; the lip of *S. magnicamporum* does not exhibit this characteristic.

With a genuine concern for this species, the Province of Manitoba has designated *S. magnicamporum* as an endangered species. Fortunately a number of populations of this rare orchid are located in the protected habitat of the Tall Grass Prairie Preserve in southeastern Manitoba. Some of these populations are considered small, with five to ten individuals, while other populations in a good year, may include a hundred or more blooming stems. In addition, the region outside of, but near the preserve has widely-scattered populations found primarily in roadside ditches.

The plants bloom in autumn and a mid September to early October excursion to the Tall Grass Prairie Preserve can be an exhilarating experience. With a cloudless sky, and a temperature of around 15C, it is without question the perfect time to make a trip to the prairie. My wife Joan accompanies me on most of my orchid excursions, and has her own term for this type of day. She aptly calls it “a magnicamporum day”. During a bug-free stroll along the well-marked trails of the preserve, the wonderful fragrance of this orchid most often reveals its presence long before it is observed.

Without question, however, our favorite population of this orchid occurs outside of the preserve, in a grassy roadside adjacent to a pioneer Ukrainian cemetery. This cemetery, along with the adjacent roadside, receives a mid-summer mowing. The mowing, completed prior to flower stem development of the orchid, controls weed and grass growth but does not impact the orchid negatively. When blooming in this habitat, the orchids are easy to find and are indeed a visual delight.

Finally, as a bonus, it is not uncommon to see large bumble bees collecting nectar and simultaneously pollinating the orchids. On several occasions these large bumble bees have been observed falling to the ground from the orchids, as they attempt to remove the pollen that has accumulated on their bodies.

Spiranthes magnicamporum spiral looking down. Photo by Lorne Heshka.

In Plain Sight: Discovering Insect Herbivores of Orchids

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Our long term studies of terrestrial orchids in Gatineau Park, Québec, Canada, have provided insight into the incidence and diversity of indigenous insect herbivores including the leafmining fly, *Parallelomma vittatum* Meigen (Diptera: Scathophagidae) that uses *Cypripedium parviflorum* var. *pubescens* (Willdenow) Knight, *C. reginae* Walter, and *Epipactis helleborine* (L.) Crantz (Orchidaceae) as hosts (Light and MacConaill 2011). This leafminer is holarctic in distribution: it can be found in north temperate regions of Asia, Europe, and North America (McAlpine 1987; Pitkin et al. 2011a). In Europe, including the British Isles, *P. vittatum* has been reported to infest several orchid genera including *Cypripedium*, *Epipactis*, and *Neottia* (syn. *Listera*) (Pitkin et al. 2011b). As far as we are aware, our 2011 article was the first report of *P. vittatum* using orchids as hosts in Canada.

The first available orchid host for this leafminer in our study area is the May-flowering *C. parviflorum* var. *pubescens* followed by *C. reginae* and *E. helleborine*, from mid June and mid July, respectively. No

Figure 1 (upper) Typical leaf mine with back lighting to show larvae on *C. parviflorum* var. *pubescens*.

Figure 2. Field view of a developing blotch mine on *C. reginae*.

Figure 3. Developing mine on leaf of *E. helleborine*.

infestations have been seen with other orchids that grow in the general vicinity including *C. acaule*, *Platanthera aquilonis* and *P. clavellata.* Despite the infestations being sparse and patchy, we can easily spot communal blotch mines while conducting field work (Figures 1–4). The white eggs, 1-2mm long, adhere tightly to the leaf undersurface, hatching within five days (Figure 5). Mature larvae have distinctive mouthparts (cephalopharangeal skeleton), and a pair of prominent respiratory openings (posterior spiracles) (Figure 6). These structures, as well as aspects of the life history such as site of oviposition and larval stage duration, help to distinguish infestations by *P. vittatum* from that of other miners that might be found infesting plants that share the orchid habitat in Gatineau Park, including *Maianthemum canadense*, *M. racemosum*, and *Polygonatum pubescens* (Smith 1989). Larvae of *P. vittatum* feed actively for about 10 days. Then they leave the mine, dropping to the ground to pupate in litter. The pu-

Figure 4. Detail view of eggs and mine on *E. helleborine*.

Figure 5 (upper left). Clutch of leafminer eggs that . have recently hatched and begun feeding within a leaf of *C. reginae*.

Figure 6. Backlighting to reveal two larvae feeding within a leaf *of C. reginae*.

Figure 7. Mature larva of *P. vittatum* after clearing to show structural details including the pair of posterior spiracles that are characteristic of this insect.

Figure 8. Lateral and dorsal views of a puparium of *P. vittatum* reared from *E. helleborine*.

paria are reddish brown with a pair of distinctive posterior spiracles similar to that seen with mature larvae (Figures 7, 8). Adult flies, (Figure 9), hatch about two weeks after pupation, but since most larvae have already been parasitized by a small, as yet undescribed, host-specific wasp, *Utetes sp*. (Hymenoptera: Braconidae), (Wharton, personal communication), a wasp emerges in place of a fly (Figure 10). Attrition from parasites and other causes can be as high as 90%.

In 2007, we were able to rear an unparasitized larva to obtain an adult fly, which was identified as *P. vittatum* and deposited as a voucher specimen in the

Canadian National Collection (Ottawa). In that same collection, we discovered some specimens with labels revealing that they had been reared from *Neottia* (syn. *Listera*) *cordata* (Linnaeus) Richard by Dr. G. C. D. Griffith who had collected in the Yukon and Alaska in 1969. This information led us to examine herbarium specimens for evidence of leafminer activity in *Neottia* species including *N. cordata.* We examined specimens of six *Neottia* species in three major Canadian herbaria: the National Herbarium of Canada, Canadian Museum of Nature (CAN), Agriculture and Agri-Food Canada Vascular Plant Herbarium (DAO), and the Herbier Marie-Victorin, Université de Montréal (MT): *N. auriculata* (Weigand) Szlachetko (syn. *L. auriculata*), *N. banksiana* (Lindley) Reichenbach (syn. *L. caurina*), *N. bifolia* (Rafinesque) Baumbach (syn. *L. australis*), *N. borealis* (Morong) Szlachetko (syn. *L. borealis*), *N. convallarioides* (Swartz) Richard (syn. *L. convallarioides*), and *N. cordata*. Eggs, mines, or larvae present in leaf mines were found with specimens of *N. auriculata* (4/33 specimens, NF, ON; Figure 11), *N. banksiana*, (7/52 specimens, BC;

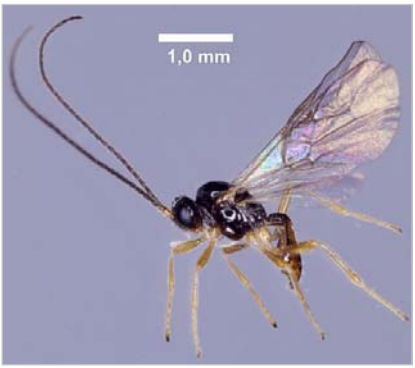

Figure 9 (upper left). *Parallelomma vittatum* adult.

Figure 10 (lower left). The wasp, *Utetes sp.*, is a parasite of *P. vittatum.*

Figure 11. Part of an herbarium specimen of *N. auriculata*, CAN 16759, Algoma District, ON, showing a mine with one larva.

Figure 12 (upper left). Part of a herbarium specimen of *N. banksiana*, CAN 363199, Glacier National Park, BC, showing an unhatched clutch of eggs.

Figure 13. A detailed view of the clutch of seven eggs seen in Figure 12.

Figure 14. Part of a herbarium specimen of *N. cordata*, CAN 287299, Kenora District, ON, showing two unhatched eggs on a leaf undersurface.

Figures 12, 13), *N. borealis* (3/167 specimens, AB, NWT), and *N. cordata* (12/308 specimens, BC, NF, ON, QC; Figure 14) including an infested specimen with a larva *in situ*, DAO 691482, collected by Joyce and Allan Reddoch on June 11, 1978, approximately 35 km from our study site in Gatineau Park (Reddoch and Reddoch 1997). No eggs or mines were found with specimens of *N. bifolia* (0/32), or with *N. convallarioides* (0/247) but absence of infestation should not be taken as proof that these taxa are never infested by the leafminer.

Can we use a variety of data sources to establish host use by an insect herbivore? Reared specimen data in the Canadian National Collection (Ottawa) led to the confirmation of *Neottia cordata* as a host of *P. vittatum* in North America, while examination of *Neottia* specimens in three herbaria has revealed a further three species of *Neottia* as hosts in Canada. Funk (2004) noted that herbaria "provide insect collections that have been incidentally collected along with the plant". Herbarium and entomological records together can provide biological and historical evidence of leafminer incidence and range. Herbaria are an emerging tool to study biogeographical patterns (Lavoie 2013). Larvae within pressed herbarium specimens are available for further examination including molecular analysis (Lees *et al.* 2011), but rarely do we see mention or even images of insects associated with living orchids except if they are flower visitors/pollinators or pests of economic importance (Light and MacConaill 2011). The leafminer that is the subject of this article is heavily controlled by parasites, but host use and infestation dynamics are providing us with insight to yet another aspect of orchid-related biodiversity and ultimately, conservation. Those observing wild orchids are encouraged to photograph, record, and share their discoveries of easilydetected insect herbivores such as the leafminer discussed in this paper.

Acknowledgments

We thank the National Capital Commission and Gatineau Park for permission to conduct research; Stéphanie Boucher, Jeff Cumming, Richard Vockeroth, and Robert Wharton for their assistance with the identification of insects; Jennifer Doubt (CAN), Jacques Cayouette (DAO), and Geoffrey Hall (MT) for access to herbaria; Stéphanie Boucher (LEMQ), Steve Paiero (OAC), and Jeff Cumming (CNC Ottawa) for access to insect collections; Brian Pitkin (NHM London) for his useful comments on orchid leafminers in Britain, and Joyce Reddoch for her helpful comments.

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Edge of Appalachia: A String of Botanically Rich Nature Preserves, Adams County, Ohio

Tom Sampliner

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tomsam265l@hotmail.com

Getting up at 4 AM is never my idea of fun. I can always count on numerous overnight wakeups due to pre-trip anxiety, aggravated in this instance by knowing I faced the prospect of a four and one-half hour journey each way. I also was not looking forward to sauna like weather conditions with temperatures in the nineties and humidity to match. Just the prospect of carrying a backpack loaded with heavy camera gear, a tripod, a long PVC canister filled with metal stakes and artificial black background, and a shade umbrella is enough to make me start to sweat.

My botanical exploration friend Phil Schieve arrived at my house early as usual for these adventures. So I rushed through some coffee and breakfast and finished loading up my car and placed his safely parked in my drive. We drove toward the rendezvous for our immediate area, the Marriott on Harvard just off I-271 early and parked awaiting the arrival of our third member, Wayne Mazorow, professional photographer. Events went smoothly so by 4:45 AM we were all loaded up and drove off to begin the day's adventure. It was then I discovered my first error of the day; my water bottle would do me no good still chilling in the refrigerator at home.

As we proceeded downstate we ran into areas that had obviously just been drenched in heavy downpours. We even experienced a few heavy downpours to the point that they taxed the windshield wipers to their highest capacity.

We arrived at Lynx Prairie, the designated first preserve we were to visit in Adams County, Ohio, by about 9:30 AM almost one half-hour prior to our scheduled local rendezvous. Our head guide would be arborist and plant-man extraordinaire, Dan Boone. Dan was bringing friends. He had as passenger, Ray Cranfill, another expert plant-man, botanical professor and author of the well-respected work, "The Ferns of Kentucky". By separate car, came Andrew Lane Gibson, one of the state DNR botanists, who is also a professional photographer and blogger.

Slightly after 10 AM all were assembled, so we began our walk into Lynx Prairie. We quickly noticed at a wooden fence near the trailhead an extensive

patch of invasive alien vinca. Upon further inspection, to our surprise was our first orchid of the day, *Tipularia discolor*, the so-called cranefly orchid. This seemed like an unusual companionship, the aggressive invader vinca acting as the host for at least a dozen or two flowering orchid scapes, many in nice condition. We would photograph them on our way back out, as they were not to be the prime attraction targeted for the day.

We used a trail that passed through savanna, forest, glades and streamside parcels. At various places excellent specimens of prairie plants were present and blooming. Composites, grasses, and some of the specialty forbs that inhabit the glade type of openings with calcareous substrates were present. We saw American bluehearts (*Buchnera americana*) which I made mental note of to photograph on our walk back out. If time permitted I made a similar note regarding the spiked blazing star (*Liatris spicata)*. The composites were quite showy at this time; one such example, the gray-headed coneflower (*Ratibida pinnata*) was particularly impressive. For those whose taste runs more toward patterns and textures, then the leaves as exhibited by the upright rough-textured gray-greenish Prairie dock (*Silphium terebinthinaceum*) are hard to beat.

We walked very slowly, especially those of us laboring under the weight of heavy equipment. We were experiencing enough exertion that figuratively rivers of sweat ran inside our clothes. In about one half hour or less we got to the lightly wooded area where our prime target, the Crested Coralroot Orchids (*Hexalectris spicata*) were (Figures 1 and 2). Possibly two dozen blooming stalks were scattered about in this one location. Many were still in prime condition. They ranged from very pale colored specimens to those with deep rich colors. There was also considerable variance in their heights and posture. We had caught them at an excellent time of bloom thanks to the much appreciated advance scouting the previous

Figure 1. *Hexalectris spicata.* Photos by author.

Sunday by our leader, Dan Boone (you've heard of his legendary forbearer). We took a while taking our pictures; after all, this was the primary target.

Not too far away we encountered a glacial erratic boulder with a plaque dedicating the area to famous southern Ohio botanist Lucy Braun and her sister. We got to see and photograph the smooth cliffbrake fern (*Pellaea glabella* var. *glabella*) growing upon it. The dark stipes (stem) contrasted dramatically with the dark green pinnae.

It is a strange phenomenon that a walk out always seems so much shorter than the journey in to a site. Certainly by this time, the heat and humidity were sapping my strength. Dehydration was yet another issue, yet I was filled with a sense of accomplishment and satisfaction with what I saw and had the chance to photograph. Though tired, uncomfortable and dehydrated, I mustered up the strength to take a few parting shots at the purple- blue five part oversized flowers of the Carolina Wild Petunia (*Ruellia caroliniensis*) and we were on our way.

We could hardly wait to get into our vehicles and crank up the A/C as we drove to our second and final destination for the day. Stop 2 was the nearby Edge of Appalachia preserve they call the Wilderness. What they didn't tell us was that this walk, though not as lengthy, would be more demanding. It would require fording a stream, crossing some slippery wooden bridges, then off trail for the modest ascent. Even before starting, all the other photographers had shed their tripods and as much heavy gear as they possibly could. Your senile author didn't even consider doing this to his later chagrin. Building humidity, if that was even possible, foretold of a soon coming hard rain. Somehow, with the aid of a drink from Phil's water canteen, I made it. We passed more *Hexalectris*, though not in as fresh or good a condition as had been the case at Lynx.

The overview of the valley from the escarpment ridge top was spectacular. The vegetation was even more impressive. This place was one of only two sites in Ohio for Canby's Mountain Lover (*Paxistema canbyi*). This woody creeper with needle leaves of dark green may not be real showy, but it was a life plant for me and it is extremely rare throughout its six state central Appalachian range. For comparison purposes, Kentucky has but one site. Ohio is the northern terminus for the range.

Also up on top of this overlook was the endangered Georgia or Dwarf Hackberry Tree (*Celtis tenufolia*). The leaf margin is toothed along the upper half of each leaf and it is said to be more apically acuminate; otherwise, it just looks like another hackberry.

Also up here but very dried up was the Texas Sandwort, formerly *Arenaria stricta texana*, but recently made a synonym of *Minuartia michauxii*.

We had noticed the spent stalks from spring-blooming lady slipper orchids, both yellow and pink. We saw in prime bloom rattlesnake plantain orchids: the downy (*Goodyera pubescens*) and the lesser or dwarf (*Goodyera repens*). I was too exhausted to bother with them. Even back in the parking lot there was a surprise when Dan showed us the native vine passionflower.

We said our goodbyes and promised to share more joint field experiences as our Cleveland group took off. Just in time too, because we would run into some steady prolific downpours very shortly on our drive back. Lightning strikes and peals of thunder accentuated the need by Mother Nature for a drenching release. We went to the nearest convenient store for much needed liquid to replenish all that had been lost. Somehow, the return drive seemed to literally fly by after the wonderful sights, memories and hopefully successfully captured orchid images of this day.

Figure 2. *Hexalectris spicata* close-up.

Greetings folks,

Those who attended the 2011 Native Orchid Conference conference in Delaware will recall Dennis Whigham's presentation about the **'Go Orchids'** project being undertaken by the Smithsonian Institution and the U.S. Botanic Garden. The project is well underway and progress to date may be viewed at: http://goorchids.northamericanorchidcenter.org/

Many of the images posted are the generous contributions of NOC members. Jay O'Neill, who coordinates the acquisition of photos, has reached out to us with specific requests for the following:

Accepted by Kew	synonym
Cypripedium yatabeanum	*(Cypripedium guttatum* subsp. *guttatum)*
Platanthera ephemerantha	*(Piperia candida)*
Platanthera unalascensis	*(Piperia unalascensis)*
Platanthera convallariifolia	*(Habenaria convallariifolia)*
Platanthera tipuloides	*(Gymnadenia keiskei)*

(Not sure anyone's been to Adak for *P. tipuloides* ... maybe our 2015 conference.)

If you can help, please contact Jay directly at: oneillj@si.edu

When the Alaskan section is completed, Jay will be moving on to the Southeast (including Florida). If you would like to participate in this project by contributing images from your collection, contact Jay and he will provide you his wish list. In addition to individual flowers, there is a need for leaves, seed capsules, habitat shots, racemes etc.

Thanks,
Bob Sprague

Pollination, Rapid Caudicle Rotation and High Fecundity of the Southern Marsh Orchid (*Dactylorhiza majalis* subsp. *praetermissa*) at Tilt Cove, Newfoundland

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Abstract

At Tilt Cove in northern Newfoundland, six observations were made of bumble bees (*Bombus* spp.) visiting flowers of the introduced Southern Marsh Orchid (*Dactylorhiza majalis* subsp. *praetermissa*), including *Bombus borealis*, *Bombus frigidus* and *Bombus vagans bolsteri*. One observation, involving a female of the latter, likely involved pollen transfer. Three bumble bees (two *B. vagans bolsteri* and one *B. borealis*) had pollinia attached to the base of the mandible or to the space between the base of the mandible and the compound eye. Bumble bees were the only insects seen on the orchid flowers. Removal of six pollinia suggested that rotation of the caudicle may be sufficiently rapid in this population to allow geitonogamous pollination, which would be advantageous to a colonizing species in ensuring pollination if the bee did not visit a second plant. Spikes from the previous year had ripened 90–95 % of the fruit, which is unusual for the group of orchids to which Southern Marsh Orchid belongs. A high diversity of nectar-producing introduced species in the vicinity, leading to a high bumble bee population, as well as rapid caudicle rotation, may contribute to the high fecundity.

Introduction

The introduced Southern Marsh Orchid (*Dactylorhiza majalis* subsp. *praetermissa*, Figure 1) was first found naturalized at Tilt Cove, Newfoundland in 1988 (Hay et al. 1990, *sub D. incarnata*). This remains its only North American locality. It is now well established here in a variety of mostly moist, open habi-

Figure 1. Southern Marsh Orchid (*Dactylorhiza majalis* subsp. *praetermissa*), also known in Canada as the Tilt Cove Orchid. Above, Tilt Cove, Newfoundland with a part of the habitat of the Southern Marsh Orchid in the foreground. Lower left, a flowering inflorescence. Lower right, Paul Catling watches for pollinators with the orchids flowering nearby. Photos by Brenda Kostiuk.

tats (Meades 1994, 1995, Clase and Meades 1997, personal observation 2012) and over 1000 plants occur at several sites within a km of the old copper mining community. Although there has been some concern about the correct name for these introduced plants (Sheviak et al. 2002), it has been verified by experts in Europe (R.M. Bateman pers. comm.) and matches very well what is generally referred to as *D. majalis* subsp. *praetermissa* (= *D. praetermissa*) in various European literature and on-line illustrations (Soó 1980), with the lateral petals erect and then bent downward as in the *D. incarnata* group, instead of more or less flat and spreading as in the *D. maculata* group. Within the *D. incarnata* group, *Dactylorhiza majalis* subsp. *praetermissa* belongs to the tetraploid marsh orchids, whereas *D. incarnata* belongs to the diploid marsh orchids,

within which its distinctive characters include the obscurely 3-lobed lip, 4–8 unspotted leaves less than 4 times as long as wide, and stems 20–60 cm tall (Bateman and Denholm 1983,1985, Soó 1980).

The largely Eurasian orchid genus *Dactylorhiza* and some allied genera have non-rewarding blossoms and generally low levels of capsule ripening because of low levels of pollinator visitation (reviewed by Catling and Kostiuk 2011). Consequently we were surprised to find high fecundity and to make several observations of insect visitation and pollination during three hours of photographing *Dactylorhiza majalis* subsp. *praetermissa* at Tilt Cove, Newfoundland. Here we report on those and other observations that relate to the successful establishment of this introduced orchid in Canada.

Methods

Observations and collections of visiting insects were made at Tilt Cove (Figure 1), located at 49.8854°N, -55.6293°W, on 24 July 2012, over a period of three hours around noon. The visiting bumble bees (*Bombus* spp.) were identified using Laverty and Harder (1988).

Results and Discussion

Visitation and Pollination Observations

We made six observations of bumble bees visiting flowers: (1) bee visited three flowers on the same plant as it crawled up the inflorescence probing the flowers; (2) bee collected and later identified as *Bombus frigidus* Smith visited two flowers near top of an inflorescence and then two near the top of another inflorescence of a plant 2 m away probing all flowers; (3) bee leaving an inflorescence and visiting a flower on another inflorescence when captured while probing a flower. It carried three pollinia, one attached to the base of the mandible and two attached to the space between the base of the mandible and the compound eye. The possession of three pollinia and visit to only one flower on the second plant suggests pollen transfer (pollination). This bumble bee was collected and later identified as *Bombus vagans bolsteri* Franklin; (4) bee collected and later identified as *Bombus borealis* Kirby, on an inflorescence when captured had a pollinium attached to the base of the mandible; (5) bee visited two plants approx. 10 m apart probing a few flowers of each and spending about 10 seconds on each inflorescence; (6) bee visited two plants approx. 7 m apart probing a few flowers of each and spending 5–10 seconds on each inflorescence. In addition, one *B. vagans bolsteri* of 10 bumble bees (*B. vagans bolsteri* and *B. borealis*) visiting Black Knapweed (*Centaurea nigra* L.) flowers in the vicinity carried a pollinium of Southern Marsh Orchid attached at the

base of the mandible. These bumble bees were the only insects seen on the orchid flowers over the three hour period of observation.

Rapid caudicle rotation and its significance

The pollinia rotated (from the base) 90º to a forward position (Figure 2) so that they would encounter the stigma of a visited flower within 6–10 seconds of removal (based on 2 flowers from each of three plants). It appears that the pollinator would push the bursicle back liberating fluid that allows the viscidium to attach. Since the bees only spent 5–10 seconds on an inflorescence, and visited only 2–3 flowers on an inflorescence in that time, the likelihood of geitonogamous pollination is increased by this rapid rotation. Since the bees may not visit additional flowers as a result of lack of reward, this rapid rotation may be beneficial in ensuring pollination. In some other related species it requires 60 seconds or more so that the bee has moved on to other plants by the time pollination is possible. Although slower bending of the caudicle prevents pollination of consecutive flowers on the same spike, it does favour cross-pollination. This may be generally advantageous, but less so to a colonizing species where fertility insurance is important. For rapid rotation to have a benefit, the plants would have to be self-compatible, but even if they were not, the amount of pollination at this site may be sufficient to achieve the high capsule set.

High Fecundity

Species of *Dactylorhiza* and species in allied genera have been reported to have 0–60% of the flowers on a plant or in a colony produce fruit (references

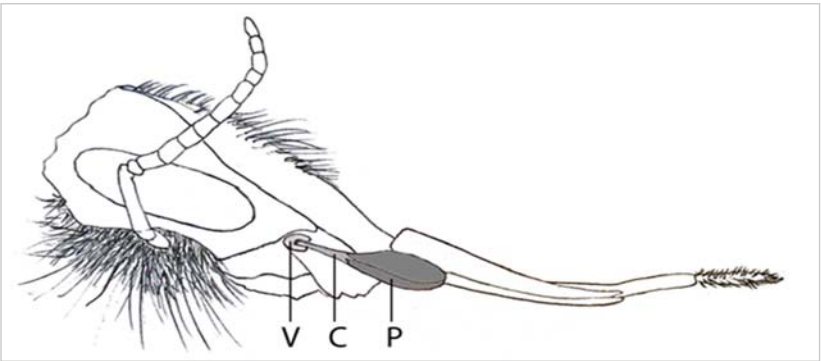

Figure 2. Camera lucida drawing of a head of a female *Bombus* vagans ssp. *bolsteri* showing attachment of pollinarium (grey) including the viscidium (v), caudicle (C) and pollen mass (P).

summarized by Catling and Kostiuk 2011). In the case of the Southern Marsh Orchids at Tilt Cove, the fruit ripening noted on 12 stems from the previous year was 90–95%. These stems were scattered over an extensive area approximately 100 x 50 m. They were the only persistent stems found, but nevertheless they suggest an unusually high fecundity for this group of orchids, which lacks reward and is reported generally to have relatively little fruit ripen.

Significance of a diversity of introduced plants

In the vicinity of the orchids, which occur mostly (but not exclusively) in moist seeps, there is a patchy distribution of orchids and nectar-providing food plants for bees. Since bees are so abundant they are frequently passing over patches where only orchids occur, and they stop to visit these patches where choice is limited. The orchids observed (10% of those present) occurred mostly in moist or periodically moist places on slopes with Scouring Rush (*Equisetum arvense* L.), Baltic Rush (*Juncus balticus* Willd.), Vernal Grass (*Anthoxanthum odoratum* L.) and Timothy (*Phleum pretense* L.), Also frequent were Canadian Burnet (*Sanguisorba canadensis* L.), Wild Strawberry (*Fragaria virginiana* Duchesne), Canada Goldenrod (*Solidago canadensis* L.), Hawkweeds (*Hieracium* spp.), Red Clover (*Trifolium pratense* L.), and Black Sedge (*Carex nigra* (L.) Reichard). The orchids occurred in places dominated by any of these species. Nearby on gravelly substrate were extensive patches of Black Knapweed (*Centaurea nigra* L.). Also in the vicinity was Butterwort (*Pinguicula vulgaris L.*) suggesting calcareous substrate. The measured pH was 6.4–7.0 and the substrate in most places was 3–8 cm of dark soil over gravel. In the immediate vicinity were 300 flowering orchid plants, but at least that many more occurred elsewhere below steep cliffs that surrounded a central lagoon in this remarkable place that looked like a volcanic crater. The only other orchid present in the area was a few plants of *Spiranthes romanzoffiana* Cham., but see also Meades (1994, 1995).

The pollen and nectar available at Tilt Cove was substantially augmented by an abundance of introduced species during the mid-July flowering period of Southern Marsh Orchid to support a large bee population. The abundantly blooming Back Knapweed has flowers of similar colour, and there is evidence (see above) that the bumble bees pollinating it were also pollinating the Southern Marsh Orchids.

A Colonization Advantage

For plants requiring pollination to reproduce, that of a flower by itself (selfing), or by another flower in the same inflorescence (geitonogamous pollination), is an advantage in colonization because a single individual can give rise to more plants. In the case of the Southern Marsh Orchid at Tilt Cove, geit-

onogamous pollination is enabled by rapid caudicle rotation. That chance is further improved by an abundance of bumble bee pollinators as a result of a diversity and abundance of mostly introduced plants, particularly *Centaurea nigra*, the flowers of which resemble the orchid in some respects.

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Presentations Scheduled for NOC 2014

Lake Itasca, MN July 14-17

Hal Horwitz

We have a terrific lineup of speakers this year. As you can see, they cover a variety of topics and represent the highest level of expertise. Come, learn and enjoy.

Dr. Ken Cameron, Professor of Botany and Director of the Wisconsin State Herbarium, will speak on "When it comes to orchid conservation, it's not enough to be rich: phylogenetic diversity is important, too!" Dr. Cameron is an NOC all-star and always informative and entertaining.

Melissa Curran, environmental scientist and botanist with Stantec Corporation, will explain the decision-making process concerning the orchid restoration project at the Ridges Sanctuary. A wonderful insight for all of us interested in conservation.

Dr. Marion Harris, Professor, Department of Entomology at North Dakota State University, will talk on "Rescued by Aliens: Pollinators of a Rare Orchid (*Platanthera praeclara*) of the Tallgrass Prairie."

Matthew Pace, PhD student at University of Wisconsin, has studied the genus Spiranthes for years and will present his findings in a talk entitled "Untangling Gordian's knot: Reevaluating species status and the biogeographic origins of *Spiranthes*," which includes some surprises.

Dr. Robert Pemberton, an expert in Slipper orchids, will give a presentation entitled, "Pollination of Slipper Orchids – Worldwide."

Nancy Sather, a botanist/ecologist at the Minnesota DNR, has followed populations of the Western Prairie Fringed Orchid for three decades and will share her findings. Her talk will be, "Phenological observations enhance understanding of *Platanthera praeclara.*"

Jean Stefanik, a long time member of NOC, spent months in New Zealand this summer (our winter) and will talk on "The Orchids of New Zealand."

Scott Weber, owner of Bluestem Farm Native Plants, will discuss, "Native Orchids, Propagation, Cultivation, Conservation" and his work providing plants for the Ridges Sanctuary orchid restoration project.

Ron Weinhold, Owner of River Glen Gardens in Long Prairie, MN, and intrepid explorer, will present on, "From Glacial Ice to Wild Orchids of Today."

North American Orchid Conservation Center will have a representative give an update and further reports.

Dr. Larry Zettler, Professor of Botany at Illinois College, will give two talks; one on "Fungus-assisted Orchid Conservation in South Florida, Cuba and Hawaii." The second talk is entitled, "Madagascar – an Update."

Kim Risen, author of Orchids of the North Woods, will talk on that subject.

Lorne Heshka, a founding member and past president of NOC, will present a newly released movie, "The Wild Orchid Man in the Land of the White Bear."

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https://groups.yahoo.com/neo/groups/NativeOrchidConference/files/2014%20Conference%20Information/

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