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THE NATIVE ORCHID CONFERENCE JOURNAL

VOLUME 22, ISSUE 1 : TABLE OF CONTENTS

INVASIVE SPIDERS CAPTURE NEW POLLINATORS OF LARGE PURPLE FRINGED-ORCHID AT CHARTIERVILLE, QUÉBEC

By Paul M. Catling, Brenda Kostiuk, and Chris Schmidt

On 23 July 2023, south of Chartierville, in the eastern townships of Quebec, we had an opportunity to study both the Small and Large Purple Fringed-orchids. Although we were mostly interested in potential hybridization in this region where both species overlap in their habitat and flowering times, we made some interesting observations of pollinators as well.

The Large Purple Fringed-orchids were growing along a few km of a lumber road in a rugged area near the border with New Hampshire. They occurred on the road shoulders and ditches along edges of the surrounding, steeply sloping deciduous woodlands of Maple, Birch, and Poplar. We examined many plants closely to confirm their identity, which led to observations of pollinators.

Figure 1. **Candy Stripe Spider** (*Enoplognatha ovata* form *redmita*: Theridiidae) from an inflorescence of Large Purple Fringed-orchid (*Platanthera grandiflora*), Appalachian Mountains south of Chartierville, Québec. 23 July 2023. Photo by P.M. Catling.

An invasive predator

On approx. 50% of the inflorescences, we found a single Candy Stripe Spider (*Enoplognatha ovata* form *redmita*: Theridiidae) approximately 1.4 cm long. The spiders had found isolated inflorescences 50 m from others, and there were no other wildflowers in the vicinity. The roadside vegetation was mostly ferns and sedges, with non-flowering herbs. The colour and pattern of the spiders (Figure 1) was ideal for making them inconspicuous in the inflorescences of the Large Purple Fringed Orchids. It would have also provided protective coloration on Fireweed (*Chamaenerion angustifolium* (Linnaeus) Scopoli) blossoms which were frequent on the landscape but not on the well wooded hills where the relatively new lumber road was situated. The incidence of the spider predators seemed high, but as introduced species (from Europe), we realized that they may become abundant, as with many invasives.

Candy Stripe Spiders spin tangled and erratic webs in the inflorescences of the orchids to capture their prey. They often cover the prey with web strands to secure it for feeding. On two orchid inflorescences we found moths suspended in a tight mass of webs (Figure 2). It occurred to us that these were likely pollinators. There may have been many other cases where moths were dropped to the ground after being eaten, or survived but incapable of flight.

The dried-out moths were put in a moist container to "relax" them so that the webs could be partially removed to facilitate identification. They were examined for pollinia on the compound eyes or proboscis, the only places where pollinia can become attached due to the scaly surface of these Lepidoptera.

Figure 2**. Large Purple Fringed-orchid** (*Platanthera grandiflora*), from the Appalachian Mountains south of Chartierville, Québec. 23 July 2023. **a,** portion of an inflorescence with Candy Stripe Spider above the upper of the two facing flowers. **b**, Noctuid Moth (*Diachrysia balluca*) hanging on spider threads in lower right, and a Candy Stripe Spider is mostly concealed in the middle left. Photos by P.M. Catling.

Reports in the literature

Hawkmoths, Swallowtail butterflies and Noctuid moths have been reported as pollinators of *Platanthera grandiflora* (Argue 2012: 131). Noctuids, specifically *Autographa ampla,* were reported without locality information. The only comprehensive study remains that of Stoutamire (1974), a classic work which established the difference between *P. grandiflora* and *P. psycodes* based on pollinator-adaptation, and provided the basis for very clever future studies (e.g. Sheviak and Bowles 1986). However, Stoutamire did not observe pollinator visits in *P. grandiflora*. More recently Evans (2006) found *Bombus* spp. (Apidae) to be ineffective pollinators of *P. grandiflora.* However, there is a published photo of a European Skipper Butterfly (*Thymelicus lineola*) on flowers of *P. grandiflora* with three pollinia stuck on its eyes (Reddoch 1976: 134). With three pollinia, it must have visited two flowers and may be accepted as a pollinator. We know relatively little about pollination in *P. grandiflora*, and in *Platanthera* in general (see open access review article – Janes et al. 2024).

New Pollinators, - possibly important ones

The two Noctuid moths recovered from the webs on two different plants (near the border south of Chartierville on 23 July 2023) were new pollinator records (identified by Dr. Chris Schmidt, Agriculture Canada, Ottawa): ***Cucullia* cf. *convexipennis*** with a wingspan of 43 mm and proboscis 19 mm long, and ***Diachrysia balluca*** with a wingspan of 43 mm and proboscis 20 mm long (Figure 3). The *Cucullia* cf. *convexipennis* carried 4 pollinia, each 3 mm long, two attached by rounded-oval viscidia to the inner front of each compound eye. The *Diachrysia balluca* carried one 3 mm long pollinium attached by a rounded-oval viscidium to the inner front of a compound eye. Flowers from the first plant where a pollinator was found had spurs 22-23 mm long, and flowers from the second plant had spurs 20-22 mm long. Some flowers on both plants had pollinia that had not been withdrawn. These were 3 mm long, and had rounded-oval viscidia corresponding to those carried by the moths.

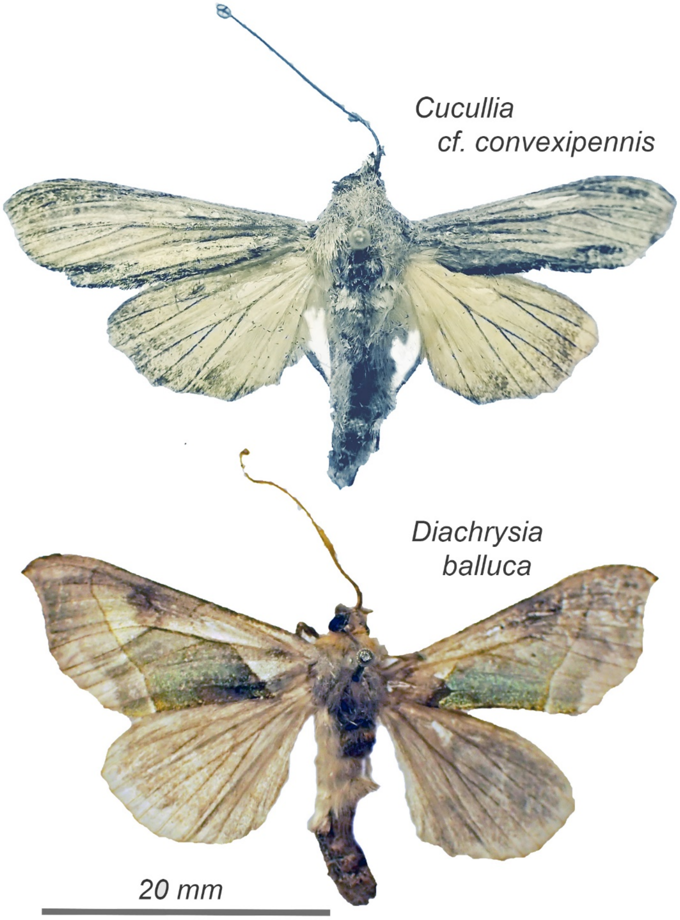

Figure 3. **Moth pollinators** of Large Purple Fringed-orchid (*Platanthera grandiflora*) at Chartierville, Québec, including *Cucullia cf. convexipennis* and *Diachrysia balluca,* both specimens captured by Candy Stripe Spiders. Photos by P.M. Catling.

The proboscis length of the two moths is well-suited to the length of the spurs in the orchid flowers (see above). The upcurved lip lobes of *P. grandiflora* may enable a moth to rest on a flower without falling off to the side. It may also discourage crawling over the inflorescence, thereby potentially increasing the number of visitors. Moths apparently force their heads into the front of the rostellum between the viscidia. The pollinia, projecting in front of the head encounter the stigmatic surface, and both pollen masses and scales from the head, are left on the stigmatic surface. Backing out of the narrow space, one or both pollinia are attached by the sticky viscidium to the inner front of the compound eye. The space between the two viscidia is 2-3 mm and the eyes of the moths are approx. 1.3 mm apart at their closest, and 2 mm apart at their greatest distance apart on the outer edges. Thus, the enclosed rostellum space at the tip of the column is also a good fit these noctuid moths. The fit is so good that one wonders if these noctuid moths are the main pollinators of the species. Since there is sometimes local adaptation to pollinators by variation in spur length (e.g. Robertson & Wyatt 1990), widespread importance of these and related Noctuid pollinators will require more research. A recent study has drawn attention to the potential importance of Noctuid moths in orchid pollination (Esposito *et al.* 2017).

Impact of the invasive spider on pollination of *Platanthera grandiflora*

Given the abundance of the spiders, one may expect that predation of pollinators may have a seriously negative effect on seed set. However, most flowers in inflorescences had been pollinated, and in some cases lower ovaries were expanding well. Thus, the impact of a Candy Stripe Spider on fecundity, at this site, appeared to be minor, this possibly explained by an abundance of the Noctuid pollinators.

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COELOGLOSSUM VIRIDE… ONE TAXON OR SOMETHING MORE?

By Tom Sampliner, tomgrouch716@gmail.com

When you think of a Long-bracted Orchid you think of the color green right? We all know it is so easy to pass right by these orchids since they blend in so well with other vegetation (Figure 1). I know I have certainly done it. How many of you know that this cryptic green orchid can show color variation?

Having just come back from my second trip to China and having seen Long-bracted Orchid specimens showing flower parts that were clearly other than green, I became curious. What does the literature as well as any other reference source say about this? It turns out, quite a few authors on this species have noticed color variants.

So, I first consulted North American orchid authors to see what they had to say about such sightings and how to treat them. I guess I should begin with the man who put modern orchidology classification into focus: Dr. Carlyle Luer.

The incomparable Dr. Carlyle Luer, in his monumental work of the "Orchids of United States and Canada, excluding Florida" (Luer 1975: 170) uses some species-descriptive phrases that are as much poetry as they are serving for scientific description. He references the roots with forked fleshy tuberoids (which are formed from the actual roots) are so very similar to those of *Dactylorhiza*. He described the sepals and petals as conniving to form a hood over the column, and the column having a pair of diverging anthers. For the lip he describes two blunt prongs at the apex with a small tooth between them (Figure 2). Finally, he mentions that the base of the lip has thickened margins that curve up.

Luer recognizes two varieties of this species; *C. viride* var. *viride* has stem bracts up to twice as long as the flower and reaches heights of less than 20 cm. In comparison to that variety, he recognized *C. viride* var. *virescens* where bracts exceed twice the flower length and the stem exceeds 20 cm (Luer 1975: 171). Luer provides an interesting taxonomic history when he referred to Linnaeus recognizing the plant in 1753 but assigning it to the genus *Satyrium*, which is now comprised by a group of orchids in Africa and Asia.

Fred Case (1987) in his highly respected work, "Orchids of the Western Great Lakes Region" comments that this orchid occurs in North America, Europe and Asia in habitats he describes as acid woodland and arctic heath. He also noticed the species exhibits clumping along offshoots. He further noticed that this species is rare in the southern Great Lakes. In my home state of Ohio we have only one depauperate site.

From Europe, Kew authors Phillip Cribb and Christopher Grey-Wilson describe *Coeloglossum viride* growing in north temperate and circumboreal regions, in damp grassy and stony habitats often in open shrub up to 3,300 meters in elevation.

Stanley L. Bentley, in his "Orchids of the Southern Appalachians" notes that *Coeloglossum viride* is ordinarily green, but the lip color can sometimes be yellowish or reddish in northern parts of its range (68). This is similar to what I was seeing in Sichuan Province of Southeastern China (Figure 3). He observed specimens distributed anywhere between 2,200-3,600 meters in alpine meadows.

Figure 1. In light alder forest at a site called Logslide in the Pictured Rocks in Michigan along the shore of Lake Superior, this is representative of the Long-braced orchids most of us know and expect.

Figure 2. This specimen shows that tiny tooth at the apex of the lip. The length of the floral bract certainly seems in line with those who agree with a variety named *virescens*.

Figure 3. This 2015 orchid is clearly red lipped with no hint of anything but green on the other flower parts.

Figure 4. Sure looks like Holger Perner's reddish-brown

This requires a reference back to Luer who at Page 172 observed that the flowers as well as the bracts and the leaves can be "tinged with red or purple."

Now I turn to Holger Perner whose domain was the fabulous World Heritage Site and Chinese national park called Huanglong, for which he wrote the "Orchids of Huanglong" (Perner 2007). His description is worth some scrutiny in our question of how to treat what is seen there. First, he distinguishes, as have others, between forma *virescens* and *viride*. He describes the latter as only 5-30 cm tall while *virescens* ranges from 14-85 cm at heights from 2,200-3,600 meters in alpine meadows. In lowest elevations he observes "red-brown flowers" in open to dense shrub (Figure 4).

So, we have authors in North America, Great Britain and China who all refer to specimens of this species which can show colors other than green. We also have authors giving different bract size descriptions and both habitat and elevation distributions vary according to whom you are consulting. It is fair then to ask how do you treat these two taxa? According to Sheviak and Catling (2002) and Bateman and Rudall (2018), the morphological and genetic variation within *C. viride* may warrant recognition at the varietal, or perhaps even species, level. Maybe there is also a lesson for me to not take differences I see in the field too lightly. I should consult all sources of information to see if anyone else has seen some difference in an orchid trait that I had taken for granted.

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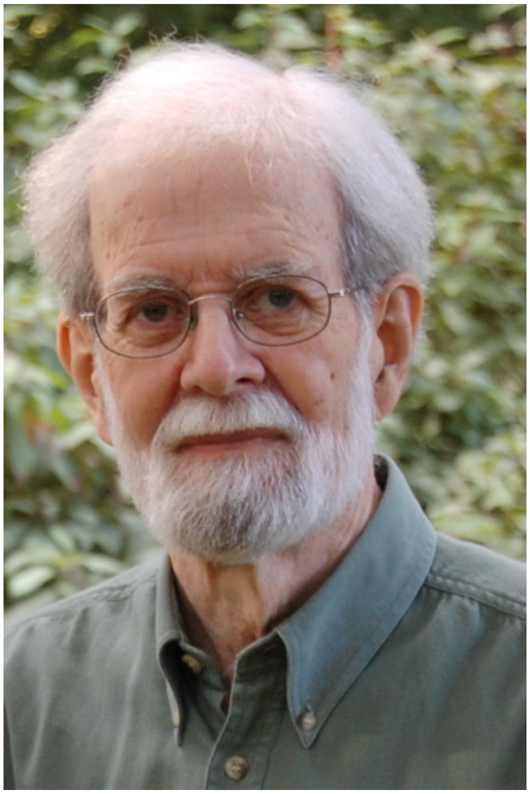
ALLAN HARVEY REDDOCH, AN OUTSTANDING ORCHIDOLOGIST

From Paul M. Catling



ALLAN HARVEY REDDOCH (1931-2023)
Canadian Orchidologist

Allan passed away in October 2023. He is well known for his work on North American orchids done with his wife Joyce M. Reddoch. Their long-term population studies of Ottawa District orchids began in the 1960s and spanned half a century, resulting in many publications, including their classic 1997 monograph “The Orchids in the Ottawa District: floristics, phytogeography, population studies and historical review”. They received Honorary Memberships in the Ottawa Field Naturalists’ Club and Certificates of Recognition from the Canadian Orchid Congress. They were key players in some of the most extensive and important work on the biology of North American orchids. Allan's interest, encouragement, and meticulous review of the work of others was unsurpassed. A list of their orchid publications is available in “Orchids in the Ottawa District” and in Reddoch (2024 in NOCJ 21(3): 33-36). It is anticipated that a detailed tribute will appear soon in The Canadian Field-Naturalist.

A NOTE ON THE REPUBLICATION OF ALLAN REDDOCH'S CLASSIC ARTICLE ON THE GREATER ROUND-LEAVED ORCHID

By Paul M. Catling

The American Orchid Society did a great service to orchid science in producing the top science journal, Lindleyana from 1986 to 2002. The journal content is available to members at the AOS website (Lindleyana Magazine - American Orchid Society). We are pleased to assist AOS, with their permission, in making some of their content available here. The present article entitled "The species pair *Platanthera orbiculata* and *P. macrophylla* (Orchidaceae): taxonomy, morphology, distributions and habitats" (details below), by Allan and Joyce Reddoch, is one of the most sought-after. The Lindleyana article is definitive. It was followed by a summary article in NOCJ (Reddoch and Reddoch 2009, below) that provides supplementary details. NOC considers the republication of this article as a fine way to honour Allan Reddoch and remember his commitment to education and conservation, at the same time assisting native orchid enthusiasts.

Reddoch, A. H., and J. M. Reddoch. 1993. The species pair *Platanthera orbiculata* and *P. macrophylla* (Orchidaceae): taxonomy, morphology, distributions and habitats. Lindleyana 8(4): 171–187.

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Allan Reddoch measuring a Ragged Fringed Orchid (*Platanthera lacera*) in the Larose Forest, Ottawa, 25 June 2007. Photo: Joyce M. Reddoch.

THE SPECIES PAIR *PLATANTHERA ORBICULATA* AND *P. MACROPHYLLA* (ORCHIDACEAE): TAXONOMY, MORPHOLOGY, DISTRIBUTIONS AND HABITATS[1]

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ABSTRACT

We report a numerical study aimed at clarifying the relationship and characteristics of a species pair in the orchid genus *Platanthera*. *Platanthera orbiculata* and *P. macrophylla* were found to be two well-defined species. The most reliable diagnostic character is a spur length less than 28 mm for *P. orbiculata* and 28 mm or greater for *P. macrophylla*. The only other good diagnostic character that we have found is the hemipollinarium length, less than 4.6 mm for *P. orbiculata* and 4.6 mm or greater for *P. macrophylla*. No other characters, including leaf size and plant size, were found to be useful in distinguishing these species, contrary to the suggestions of Ames and other authors. The two significant floral differences, spur length and column size, contribute to reproductive isolation through pollinator specificity and establish the taxa as biological species. *Platanthera orbiculata* is widespread in the forests of northern North America with some geographical variation in morphology, while *P. macrophylla* is restricted to the eastern mixed forest and is more homogeneous. *Platanthera orbiculata* is a plant of mesic and wet forest sites, including coniferous swamps, while *P. macrophylla* is essentially confined to mesic forest habitats. Information is provided on morphology and variation, distribution, tree associates and blooming dates.

THE ORCHID GENUS *Platanthera* was created by L. C. Richard (1818) to distinguish species with a concave, recessed stigmatic surface from those of *Habenaria* Willd. with convex, projecting stigmatic processes. Lindley (1835) transferred a number of species from *Habenaria* to *Platanthera,* but Ames (1910) and subsequent North American authors in the first half of this century retained *Habenaria sensu latu.* Most recent authors, such as Luer (1972, 1975) and Stoutamire (1974) in North America, Webb (1980) in Europe and Inoue (1983) in Japan, have recognized *Platanthera.* Senghas (1973) and Dressler (1981) placed *Platanthera* and *Habenaria* in different subtribes of the tribe Orchideae.

An interesting feature of *Platanthera* is the occurrence of several species pairs in which the constituent taxa differ primarily in their adaptation to different pollinators. At various times, the components of most of these species pairs have been regarded as species, varieties, forms or synonyms. Recent studies of species pairs include: *P. psycodes* (L.) Lindl. and *P. grandiflora* (Bigel.) Lindl. by Stoutamire (1974), *P. leucophaea* (Nutt.) Lindl. and *P. praeclara* by Sheviak and Bowles (1986), and the Eurasian *P. bifolia* (L.) Rich. and *P. chlorantha* (Custer) Rchb. by Nilsson (1983). A more complex situation in the *P. ciliaris* (L.) Lindl. complex has been discussed by Folsom (1984).

The subject of this work is the species pair *P. orbiculata* (Pursh) Lindl. and *P. macrophylla* (Goldie) P. M. Brown.

These taxa derive from Pursh's (1814, 1869) description of *Orchis orbiculata* from Pennsylvania and Virginia and from Goldie's (1822) description of *Habenaria macrophylla* from Montreal. Pursh's (1814) terse diagnosis includes the significant statement "cornu germine longiore," while Goldie's account contains the comment "cornu germine duplo

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[1] We are grateful to the Directors of the Canadian Museum of Nature, Ottawa, Ontario, for Research Associateships and to the curators and staff of the National Herbarium (CAN) for their help. We also thank the curators and staffs of the herbaria cited for the loan of specimens and other assistance; D. R. Gunn, E. W. and E. G. Skelton, P. E. Rothschild and L. P. Johnson for providing field locations, pickled flowers and photographs; J. D. Lafontaine for entomological assistance; and P. M. Catling, E. W. Greenwood and G. W. Argus for valuable discussions and encouragement. We appreciate the helpful comments made by C. J. Sheviak and a second, anonymous reviewer.

longiore." Goldie also stated that the leaves of his plant were four times as large as those of Pursh's plant. In a note attached to his type (K!), he wrote that the plant was three to four times larger than Pursh's.

As we will show, these comparisons of plant and leaf sizes are incorrect because Goldie mistook Pursh's plant for the then undescribed *P. hookeri* (Torr.) Lindl., but they have been the source of much confusion up to the present. Hooker (1825), presumably following Goldie, supported this error when he reported that *H. macrophylla* was twice as large as *O. orbiculata* which he illustrated with an excellent drawing of *P. hookeri.* Ames (1906) clarified the taxonomy, although he rejected Lindley's transfers from *Habenaria* to *Platanthera.* He also published measurements showing two distinct clusters of spur lengths, one from 16 to 27 mm and the other from 32 to 43 mm, and assigned these clusters species rank as *Habenaria orbiculata* (Pursh) Torr. and *H. macrophylla,* respectively, without discussion. However, he also accepted Goldie's and Hooker's erroneous comparisons of the sizes of the species and indicated that other, unspecified, characters were diagnostic.

Whether because of the novelty of his numerical approach, the terseness of his discussion or the problems resulting from the alleged size differences, subsequent authors in the first half of this century, except for Mousley (1934), Marie-Victorin (1935) and Fernald (1950a,b), reduced *macrophylla* to a synonym, form or variety. More recent writers (e.g. Luer, 1975; Hinds, 1986; Whiting and Catling, 1986) are again accepting the validity of the spur length as a distinguishing character, usually at varietal rank, although no new evidence has been published. Throughout the entire period, misconceptions about the relative plant sizes of the two taxa have persisted, although some recent authors recognize that there are difficulties.

In view of the problems surrounding the identity and description of Goldie's *H. macrophylla,* we undertook the present numerical study. We sought to check and extend Ames' measurements, to determine what characters might distinguish this plant from *P. orbiculata* and to establish its appropriate taxonomic rank. In addition, we planned to describe morphology, distribution, habitat, etc. for both taxa from a well-defined set of specimens.

MATERIALS AND METHODS—Approximately 1,100 herbarium sheets were examined from the following herbaria: ACAD, AMES, BLH, CAN, CM, DAO, F, HAM, K, MICH, MIN, MT, MTMG, NA, NCU, NY, PH, QK, SFS, TENN, TRT, VPI, WIS, WVA, UNB and US, as well as the private herbaria of R. E. Whiting, D. F. Brunton, and A. A. Resnicek and R. S. W. Bobbette. Photocopies of sheets were received from K, MO, QFA, QUE and TRT.

For three major herbaria (AMES, CAN, DAO), all specimens of *P. orbiculata* and *P. macrophylla* in anthesis on all sheets from east of about 92° W longitude were measured. This boundary was chosen to include the entire geographical range of the long-spurred plants, i.e., those plants with spurs longer than about 27 mm, following Ames (1906). These measurements from 108 short-spurred and 44 long-spurred plants are referred to as the unbiassed data set since the use of all plants from large herbaria covering much of the continent reduces the probability of a biassed sampling of the taxa. The resulting data set was used to determine the validity of the taxa and the criteria for identifying them. For the remaining herbaria, all long-spurred plants and a representative sample of the short-spurred ones were measured. This second set of data, together with the first set, a total of 275 short-spurred and 196 long-spurred plants, was used for general morphological description. This full data set will have some bias with regard to the relative abundance of the taxa as a result of the more extensive sampling of the long-spurred plants. The remaining sheets seen were checked for spur length and, where possible, pollinarium length to identify the taxa for preparing distribution maps.

The characters determined are shown in Fig. 1 and/or reported in the species descriptions. Smaller dimensions, e.g. hemipollinarium and seed sizes, were measured with a microscope. Averages of three, four, or occasionally, five measurements per plant were used where possible for floral parts. In addition to the ratios in Fig. 1, the ratios of plant height to raceme height and spur widths near the middle and the end were analyzed in the same manner as the direct measurements.

Living plants of *P. macrophylla,* necessary for measurements of column structure, were examined in Bruce, Haliburton and Lanark Counties, Ontario. Additional flowers in spirits were received from Peterborough County, Ontario. Scaled closeup photographs were also available from the Bruce County station from another year and from Gatineau Park, Quebec, near Ottawa, Ontario. Living plants of *P. orbiculata* from Haliburton County and various sta-

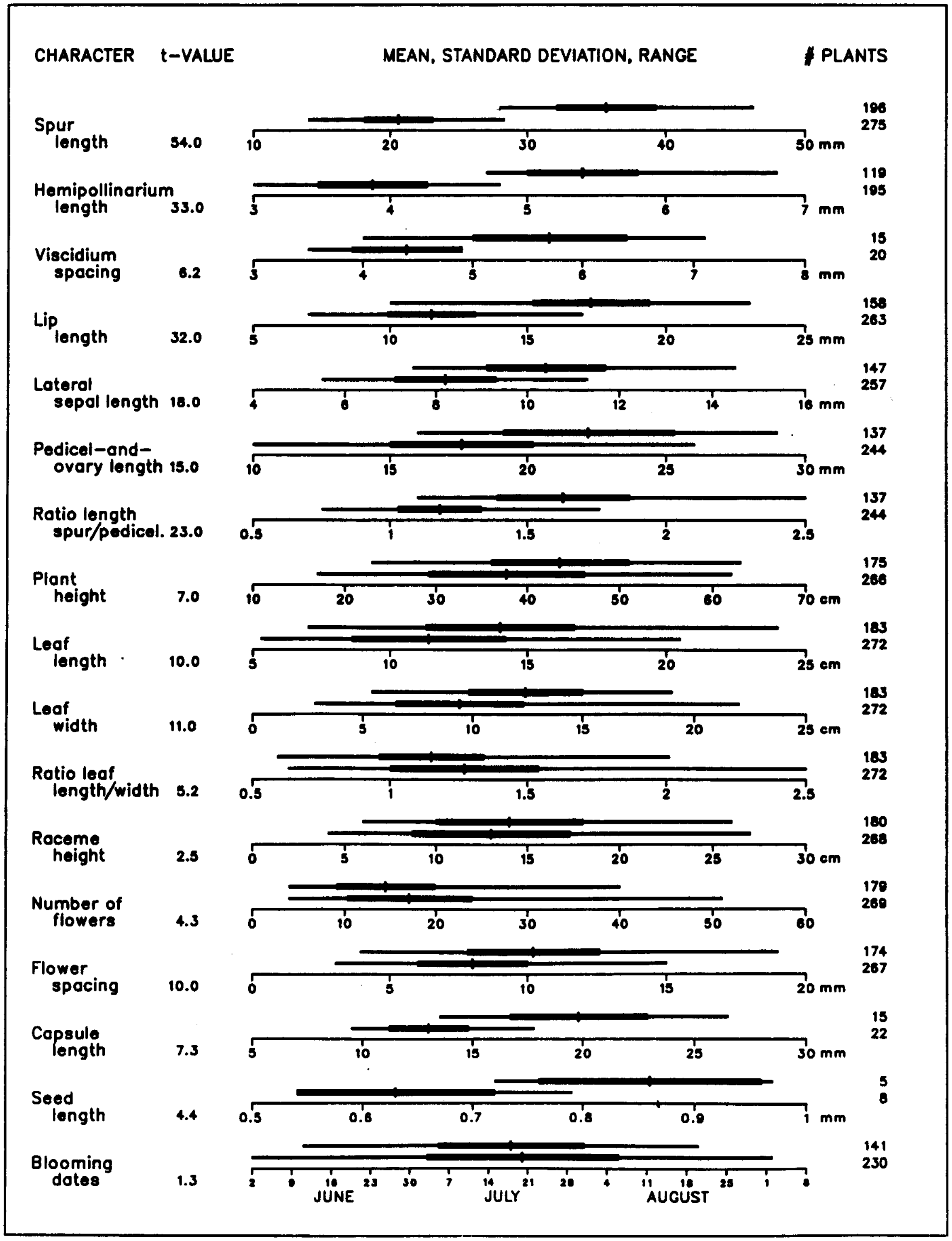


Fig. 1. Numerical summary of characters of *Platanthera macrophylla* (upper bar) and *P. orbiculata* (lower bar) for the full data set. The narrow bar shows the range of the character; the broad bar represents one standard deviation on each side of the mean.

tions near Ottawa were also examined.

The above measurements and ratios, together with latitudes and longitudes, were entered as a computer data set to obtain means, ranges, standard deviations of individuals and Student's *t*-statistic for differences of averages (Fig. 1), as well as histograms and correlation diagrams. Cluster, principal components and discriminant analyses were performed with programs written to utilize the Fortran subroutines from the IMSL® program library. The main programs permitted the analysis of any subset of characters and selected only those plants for which that subset of measurements was complete.

Geographical variation was analyzed by comparing means and standard deviations of characters for a set of regions. The size of the regions was a compromise between the greater resolution with numerous small regions and the greater statistical significance with few large ones. The eastern range was divided by a grid into eight equivalent zones between longitudes 50° W and 95° W and four equivalent zones between latitudes 35° N and 50° N. Data were available for 18 of these 32 regions, but only 11 had 10 or more records, the minimum considered necessary to make meaningful statistical comparisons. The sparsely represented area west of 95° W was treated as a single region.

RESULTS AND DISCUSSION—Histograms of the characters measured from the unbiassed sample show that the spur length (Fig. 2) is clearly bimodal. The crossover point of the two normal distributions is at 28 mm, which serves as the best statistical criterion for distinguishing the two taxa on the basis of their spur lengths. This result is in rough agreement with Ames (1906), whose small sample yielded no measurements between 28 and 31 mm. The somewhat less well-defined bimodality of the hemipollinarium length shows a crossover at 4.6 mm (Fig. 3). Lip length is less clearly bimodal, while the other characters, including those often mentioned as diagnostic features such as leaf size and plant height, show no significant separation.

Similar results for bimodality were obtained for the full data set, where the proportion of long-spurred plants is higher, as is suggested in Fig. 1.

The data from the unbiassed set were subjected to discriminant analysis. Membership in each group was decided by the spur length being greater or less than 28 mm. When the analysis was restricted to the two dominant characters, spur length (S) and hemipollinarium length (P) in mm, the linear discriminant functions with equal prior probabilities yielded the approximate boundary equation

$$S + 2P = 38,$$

which is represented by the line in Fig. 4. The evaluation of the discriminant function S + 2P for the full data set yields the histogram shown in Fig. 5.

The averages, standard deviations, ranges and *t*-statistics in Fig. 1 were obtained from the full data set, where the taxa were defined on the basis of the above boundary equation. The differences of the averages are significant at the 0.1 % level or better, except for the raceme height (2 %) and the blooming date (20 %). For some of the floral parts, i.e. the lengths of the spur, hemipollinarium and lip, the significance level is much better, although the test cannot properly be applied to the spur length because it was used to define the taxa.

Taxonomic Rank—The two well-defined clusters discussed above represent species in the morphological or phenetic sense (Davis and Heywood, 1963). Moreover, as the discussion below shows, the most significant differences between the taxa are those contributing to reproductive isolation and hence the taxa are species in the biological sense (Mayr, 1992).

Some orchid species are known to be highly pollinator-specific, usually as a result of a close mechanical fit between the floral and insect parts involved in pollen transfer (Darwin, 1877; van der Pijl and Dodson, 1966; Dressler, 1981). In particular, many of the long-spurred *Platanthera* species are adapted to pollination by lepidoptera (Darwin, 1877; Nilsson, 1983; Inoue, 1983). Some specific studies include the species pairs *P. chlorantha* and *P. bifolia* (Nilsson, 1983), *P. psycodes* and *P. grandiflora* (Stoutamire, 1974) and *P. leucophaea* and *P. praeclara* (Sheviak and Bowles, 1986).

Effective cross pollination within each species requires that the spur be short enough for the tongue of the insect to reach the nectar near the end of spur. Moreover, it must be long enough to bring the head of the insect into contact with the viscidia to ensure placement of the hemipollinaria on the eyes or the base of the proboscis, as the case may be. For eye placement, the spacing of the viscidia must be comparable to the eye separation of the insect. Finally, the length of the hemipollinaria must be such that their pollen will come into contact with the stigmatic surface of the next flower that the insect visits. Thus, marked differences in any of these three conditions between two plants will reduce cross pollination and contribute to reproductive isolation. In the present case, it is the spur and hemipollinarium lengths that show the most distinct bimodality, i.e., the smallest scatter relative to the differences between the two taxa. This is clearly a situation that favors different pollinators for the two taxa. Differences in the viscidium spacing will have a similar although smaller effect. Thus the distinguishing features of these two taxa are those that discriminate between pollinators and lead to reproductive isolation.

Hence, there are two sympatric taxa maintaining statistically significant differences in the average sizes of most of their parts, but showing the most rigorous distinction in those floral parts that would lead to reproductive isolation. These conditions indicate that these taxa are biological species.

It is consistent with the above interpretation of the taxonomic importance of the spur and the hemipollinaria that cluster analysis under various conditions and principal components analysis with standardized data both failed to reveal the bimodality defining these species. The reason appears to be that while these procedures seek the maximum contributions to the variance, the characters leading to reproductive isolation must meet very fine tolerances and make little contribution to the variance. Thus, within species, the spur and hemipollinarium lengths have small relative standard deviations of about 10 %, compared to 20 % to 30 % for other characters. The overall variances for both species combined are also smaller for these diagnostic characters, so that neither character dominates the total scatter.

Taxonomic History—From the data for Fig. 1, we found that the ratios of spur lengths, plant heights and leaf lengths of *P. macrophylla* to *P. orbiculata* are 1.7, 1.2 and 1.2. Thus, Pursh and Goldie were essentially correct in describing the spur lengths of their respective plants. Goldie, however, was in error in stating that his plant was three to four times larger with leaves four times larger that Pursh's. It is clear that this error resulted because Goldie was, in fact, comparing his plant to the then undescribed *P.*

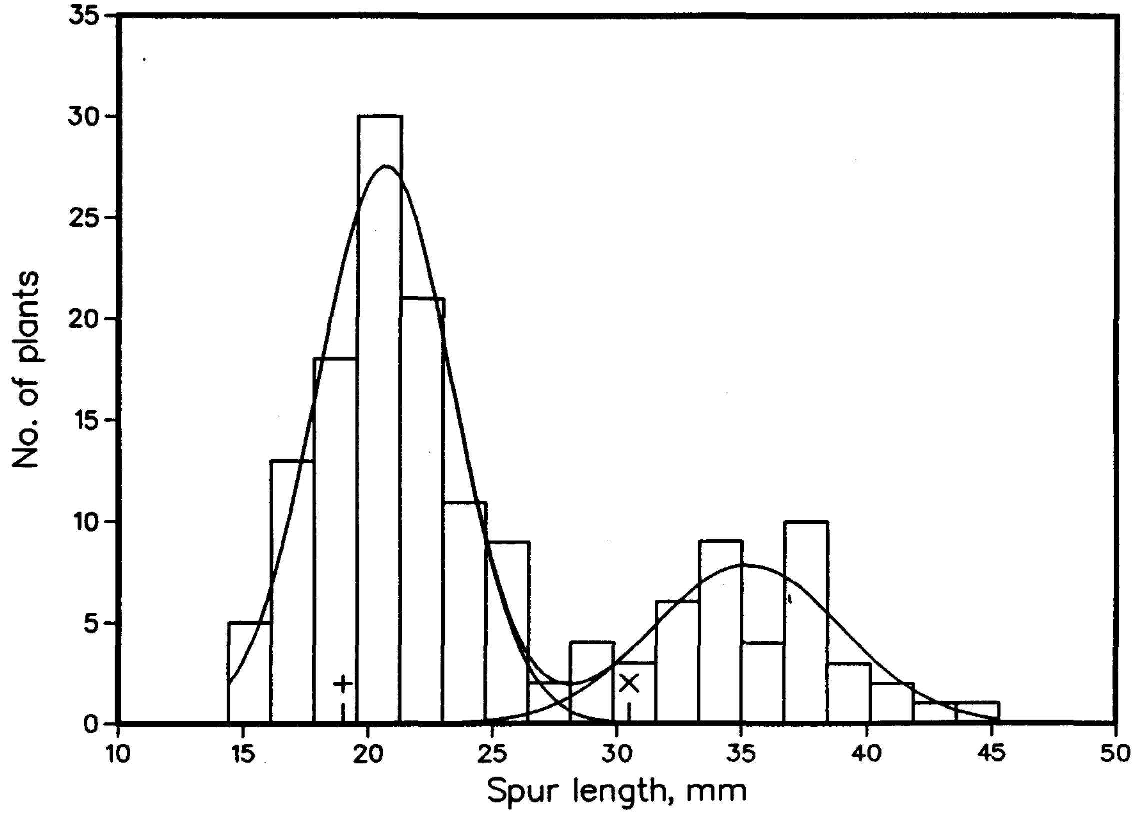


Fig. 2. Histogram of spur lengths of *Platanthera orbiculata* and *P. macrophylla* for the unbiassed data set. Component Gaussian distributions and their sum are also shown. Types are indicated: + = *P. orbiculata* and x = *P. macrophylla.*

hookeri. The evidence lies in two of his collections. His type bears a note (K!) apparently in his hand (G. Ll. Lucas, pers. comm.) presumably to Hooker referring to "O[rchis] orbiculata of Pursh, of which I have sent a specimen ..." (Ames (1906) quotes this note, making several mistakes, one being to transcribe this comment as " ... I have not sent ...") A specimen of *P. hookeri* in the Lindley Herbarium (K! as photocopy) annotated "Orchis orbiculata, Montreal" in the same hand as the note shows that Goldie had misinterpreted Pursh's description.

This misinterpretation, the inadequacy of the descriptions and the relative unavailability of the type specimens resulted in confusion of *P. macrophylla, P. orbiculata* and *P. hookeri* by Torrey (1826), Gray (1835), Lindley (1835) and subsequent authors. Descriptions of *P. orbiculata* often included the long spur of *P. macrophylla* and descriptions of *P. macrophylla* often claimed much larger plant size for it. Ames (1906) cleared up some of these problems (see introduction).

TAXONOMIC TREATMENT

KEY TO *PLATANTHERA MACROPHYLLA* AND *P. ORBICULATA*

a. Spur length 28 mm or longer, or in the absence of spur length, hemipollinarium length 4.6 mm or longer..1. *P. macrophylla*

b. Spur length less than 28 mm, or in the absence of spur length, hemipollinarium length less than 4.6 mm...2. *P. orbiculata.*

From the area of the overlap of the two normal components of the histograms in Fig. 2,3, the reliability of the diagnostic characters is estimated to be 99 % for the spur length (S) and 96 % for the hemipollinarium length (P).

A more accurate (99.7 %) key, based on the discriminant function (Fig. 5), is

a. $S + 2P \geq 38$ mm............................1. *P. macrophylla*

b. $S + 2P < 38$ mm............................2. *P. orbiculata.*

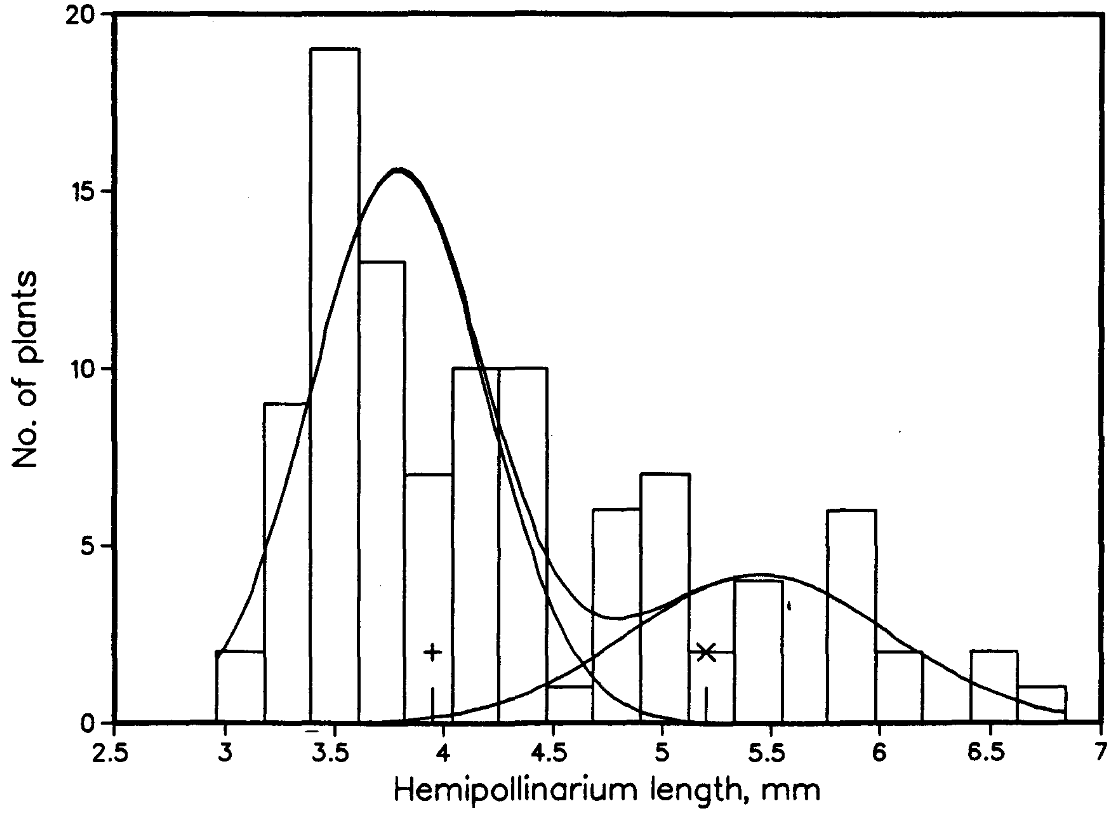


Fig. 3. Histogram of hemipollinarium lengths of *Platanthera orbiculata* and *P. macrophylla* for the unbiassed data set. Component Gaussian distributions and their sum are also shown. Types are indicated: + = *P. orbiculata* and x = *P. macrophylla.*

In the following descriptions, pairs of numbers in brackets represent upper and lower limits, and pairs of numbers not in brackets represent values two standard deviations above and below the mean.

1. ***Platanthera macrophylla*** (Goldie) P. M. Brown, Wild Fl. Notes New England Wild Fl. Soc. 3: 23. 1988.

BASIONYM: *Habenaria macrophylla* Goldie, Edinb. Philos. J. 6: 331. 1822. HOLOTYPE: CANADA: Quebec: moist shady woods Island of Montreal, K 1063/81-2 !. There are two other collections of *H. macrophylla* attributed to Goldie, one labelled "Canada Gouldie" (sic) in the Lindley Herbarium (K! as photocopy) and the other labelled "Canada Mr. Goldie" in PH!; they bear no dates.

SYNONYMS:

Habenaria orbiculata (Pursh) Torr., Comp. Fl. N. Middle Stat. 318. 1826, in part, not *Habenaria macrophylla sensu* Torr. *ibid.* (= *P. hookeri*).

Platanthera orbiculata (Pursh) Lindl., Gen. Sp. Orchid Pl. 286. 1835, in part.

Lysias orbiculata (Pursh) Rydb. *in* Britton, Man. Fl. N. States, 294. 1901, in part.

Lysias macrophylla (Goldie) House, Muhlenbergia 1: 127. 1906.

Habenaria orbiculata (Pursh) Torr. f. *macrophylla* (Goldie) Morris & Eames, Our Wild Orchids, 122. 1929, in part.

Habenaria orbiculata (Pursh) Torr. var. *macrophylla* (Goldie) B. Boivin, Naturaliste Canad. 94: 146. 1967.

Platanthera orbiculata (Pursh) Lindl. var. *macrophylla* (Goldie) Luer, Native Orchids U.S. & Can. 222. 1975.

COMMON NAME: Since *P. orbiculata* is commonly known as the Large Round-leaved Orchid, it would seem appropriate to refer to *P. macrophylla* as Goldie's Round-leaved Orchid. It is important that the common name not perpetuate the myth that *P. macrophylla* has notably greater plant height or leaf size than *P. orbiculata.*

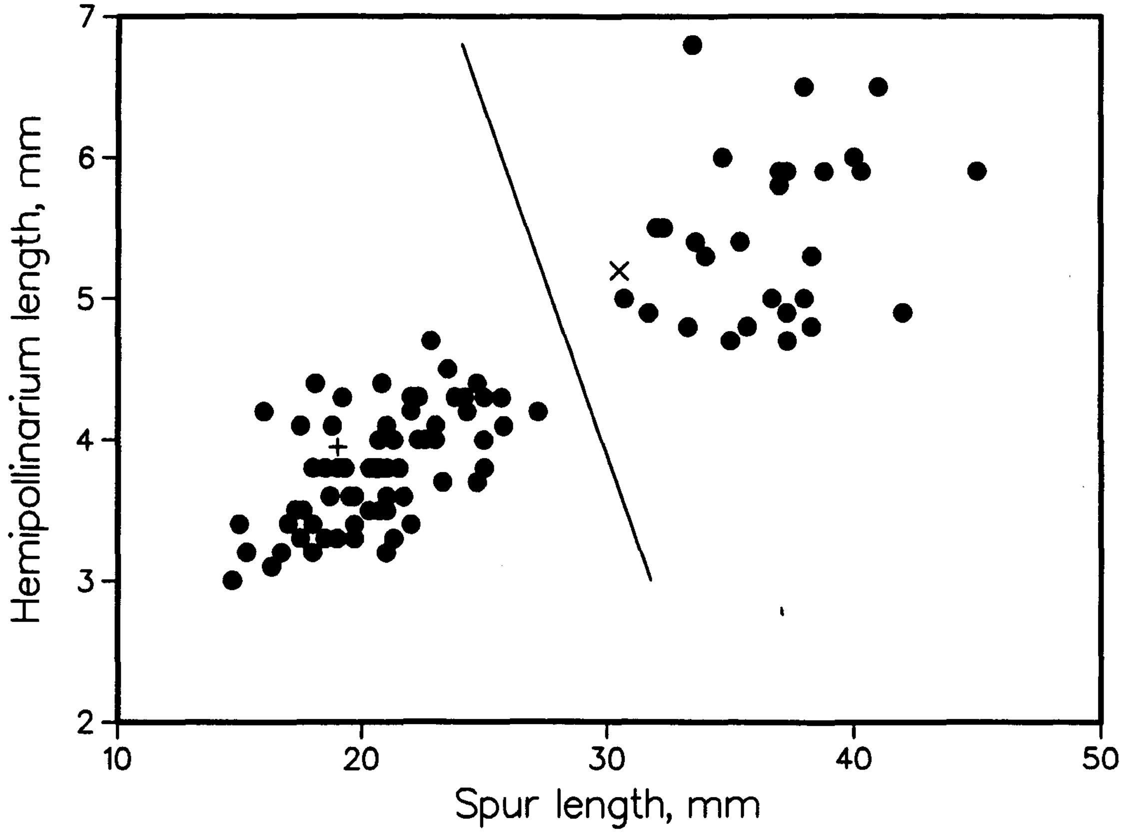


Fig. 4. Plot of hemipollinarium length *vs.* spur length for *Platanthera orbiculata* and *P. macrophylla* for the unbiassed data set. Discriminant function boundary is shown. Types are indicated: + = *P. orbiculata* and x = *P. macrophylla.*

Plant terrestrial herb, erect, scapose, glabrous, (23) 29-59 (63) cm tall. **Tuberous Root** 1, tapering, about 5 mm wide. **Roots** 4-6, cylindrical, up to 8 cm long, up to 2 mm wide. **Leaves** 2 (1-2 on non-flowering plants), basal, subtended by 2-3 sheaths, subopposite, conforming to ground, subequal, circular to oblate in larger plants, circular to elliptic in smaller ones, variously obtuse, acute, retuse or mucronulate, (7) 9-19 (24) cm long, (5) 7-18 (19) cm wide, smooth shiny deep green above, silvery below, conspicuous parallel veins with irregular cross veins. **Scape** ribbed, racemose, diameter (2.3) - (5.7) mm when flattened, with **bracts**, (0) 1-6 (8), sessile, narrowly triangular to narrowly lanceolate, (4) - (53) mm long, appressed to horizontal, evenly scattered to clustered on the upper part, rarely 1 close to leaves and half as large resembling a third leaf. **Inflorescence** regular to irregular, lax raceme of (4) 4-25 (40) flowers, (6) 6-22 (26) cm tall. **Floral bracts** narrowly lanceolate to lanceolate, (11) 11-18 (17) mm long, (1.8) - (4.0) mm wide. **Flowers** greenish-white, facing outward and often oriented irregularly, resupinate reverting to normal when capsule matures. **Pedicel and ovary** (16) 16-28 (29) mm long. **Dorsal sepal** erect, broadly ovate to depressed ovate, acute to obtuse, somewhat cordate, lower edges reflexed, (5) - (9) mm long, (6.0) - (8.5) mm wide, grayish-green with whitish margin. **Lateral sepals** obliquely ovate to broadly falcate, obtuse, reflexed, lightly short-papillose basally above, (8) 8-13 (15) mm long, (4) 3-6 (6) mm wide, grayish-green often with whitish margin, white basally. **Petals** obliquely lanceolate to falcate, obtuse to acute, ascending, (7) - (12) mm long, (1.7) - (4.6) mm wide, white sometimes tinged grayish-green distally. **Lip** narrowly lanceolate, obtuse, pendant, sometimes recurved, variously recurved or incurved apically, (10) 13-22 (23) mm long, (1) - (2.4) mm wide at middle (in dried material, wider in fresh material), occasionally lightly short-papillose on basal third above and also into spur entrance, white sometimes tinged grayish-green distally. **Spur** narrowly cylindrical, slightly flat-

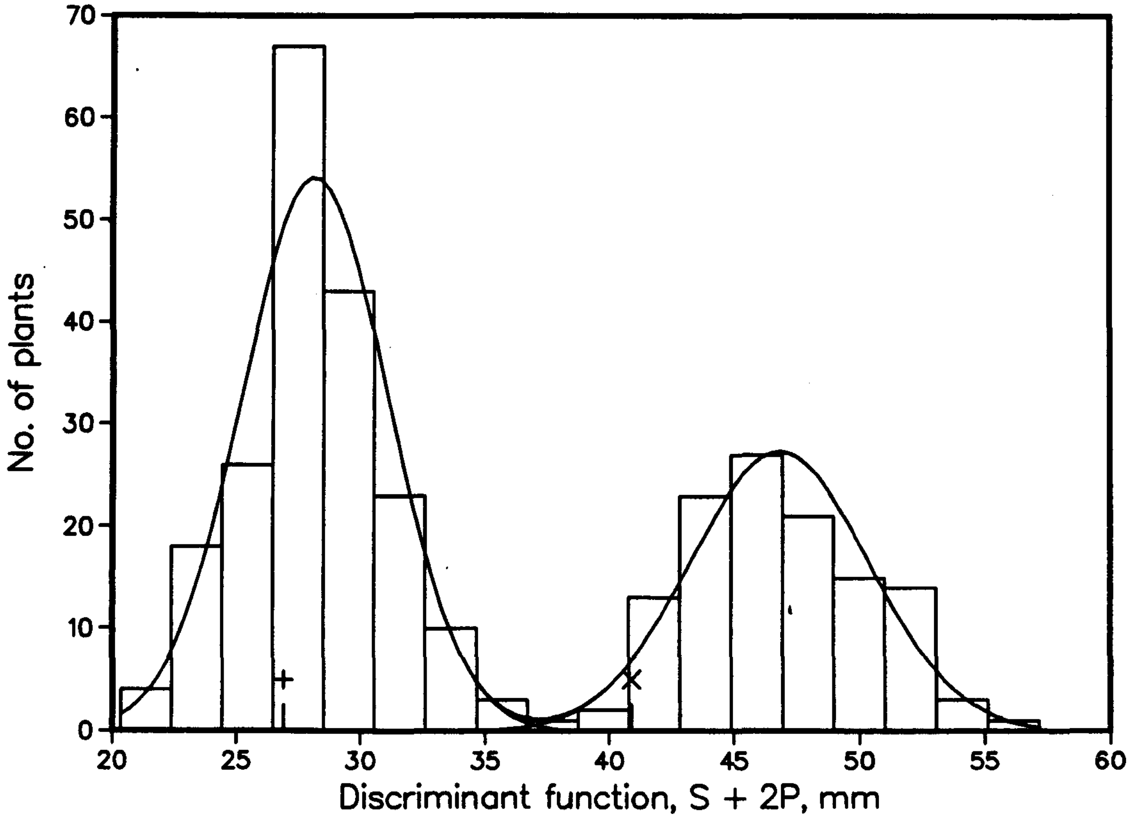


Fig. 5. Histogram of discriminant function values, S + 2P, of *Platanthera orbiculata* and *P. macrophylla* for the full data set. S = spur length; P = hemipollinarium length. Component Gaussian distributions and their sum are also shown. Types are indicated: + = *P. orbiculata* and x = *P. macrophylla.*

tened vertically, slightly clavate, horizontal or occasionally decurved, (28) 29-43 (46) mm long, (1.2) - (2.7) mm wide, translucent, white, grayish-green distally. **Column** averages 7.1 mm wide, 5.4 mm high, 5.7 mm deep at top, interviscidium spacing (4.0) - (7.1) mm, white. **Hemipollinaria** 2, (4.7) 4.6-6.2 (6.8) mm long, yellow pollinium (0.6) - (1.1) mm wide, on an elongated, faintly yellowish caudicle connected by an irregularly-shaped stipe to a translucent, colorless, discoid viscidium (0.5) - (1.0) mm diameter. **Capsule** ellipsoidal to oblong, vertical (even on sloping rachis), (14) - (27) mm long, (4) - (6) mm wide, light brown to brown. **Seeds** (0.7) - (1.0) mm long, (0.13) - (0.15) mm wide, brown to dark brown.

2. ***Platanthera orbiculata*** (Pursh) Lindl., Gen. Sp. Orchid Pl. 286. 1835, as to name not description or synonymy.

BASIONYM: *Orchis orbiculata* Pursh, Fl. Amer. Sept. 2: 588. 1814. LECTOTYPE: K 1063/81-1 ! designated by Ames, Rhodora 8: 1. 1906.

SYNONYMS:

Habenaria orbiculata (Pursh) Torr., Comp. Fl. N. Middle Stat. 318. 1826, in part.

Platanthera menziesii Lindl., Gen. Sp. Orchid Pl. 286. 1835. HOLOTYPE: N.W. America, Mr. Menzies. K, photo AMES 19194 !.

Habenaria menziesii (Lindl.) Macoun, Cat. Canad. Pl. 4: 17. 1888.

Lysias orbiculata (Pursh) Rydb., Mem. N.Y. Bot. Gard. 1: 103. 1900, in part.

Habenaria orbiculata (Pursh) Torr. var. *longifolia* Clute, Amer. Bot. (Binghamton) 7: 56. 1904.

Lysias menziesii (Lindl.) Rydb., Fl. Rocky Mts. 178. 1917.

Lysias orbiculata (Pursh) Rydb. var. *pauciflora* Jenn., J. Wash. Acad. Sci. 10: 453. 1920. HOLOTYPE: CANADA: Ontario: spruce-birch woods along Magnet Point inlet, Lake Superior, August 14, 1913, *O.E. & G.K. Jennings 4130* CM!.

Habenaria orbiculata (Pursh) Torr. f. *trifolia* Mousley, Orchid Rev. 42: 112. 1934, as to name not type (= *P. macrophylla*). HOLOTYPE: CANADA: Quebec: Lac Janveau [= Lac Janvier (*Répertoire géographique du Québec*, 1969)] near St. Hippolyte, July 8, 1929, *H. Mousley s.n.* MT!.

Habenaria orbiculata (Pursh) Torr. var. *menziesii* (Lindl.) Fernald, Rhodora 52: 63. 1950.

Habenaria orbiculata (Pursh) Torr. var. *lehorsii* Fernald, Rhodora 52: 60. 1950. HOLOTYPE: ST. PIERRE ET MIQUELON: bare spots among ericaceous shrubs on a denuded hill, Cap à l'Aigle, July 25, 1945, *M. Le Hors s.n.*, AMES!.

Platanthera orbiculata (Pursh) Lindl. var. *lehorsii* (Fernald) Catling, Naturaliste Canad. 109: 278. 1982.

COMMON NAME: Large Round-leaved Orchid.

Plant terrestrial herb, erect, scapose, glabrous, (17) 21-55 (62) cm tall. **Tuberous root** 1, tapering, up to 15 cm long, 8 mm wide. **Roots** 2-7, cylindrical, up to 7 cm long, 3.5 mm wide. [See Currah, Smreciu and Hambleton (1990) for illustrations of the roots.] **Leaves** 2 (1-2 on non-flowering plants), basal, subtended by 2-3 sheaths, subopposite, conforming to ground, subequal, circular to oblate in larger plants, circular to elliptic in smaller ones, variously obtuse, acute, retuse or mucronulate, (5) 6-17 (21) cm long, (3) 4-15 (22) cm wide, smooth shiny deep green above, silvery below, conspicuous parallel veins with irregular cross veins. **Scape** ribbed, racemose, diameter (2) - (5) mm when flattened, with **bracts**, (0) 0-6 (10), sessile, narrowly triangular to narrowly lanceolate, (10) - (27) mm long, (2) - (5) mm wide, appressed to horizontal, evenly scattered to clustered on the upper part, rarely 1 close to leaves and half as large resembling a third leaf. **Inflorescence** regular, lax to dense raceme of (4) 4-31 (51) flowers, (4) 4-21 (27) cm tall. **Floral bracts** narrowly lanceolate to lanceolate, (9) 7-17 (21) mm long, (1.6) - (3.7) mm wide. **Flowers** greenish-white, facing outward or slightly downward, resupinate reverting to normal when capsule matures. **Pedicel and ovary** (10) 12-23 (26) mm long. **Dorsal sepal** erect, broadly ovate to depressed ovate, acute to obtuse, often cordate, lower edges reflexed, (3.3) - (6.5) mm long, (3.5) - (7.0) mm wide, grayish-green with whitish margin. **Lateral sepals** obliquely ovate to broadly falcate, obtuse, reflexed, short-papillose above especially basally, (5.5) 6-10 (11) mm long, (2) 3-5 (6) mm wide, grayish-green often with whitish margin, white basally. **Petals** obliquely lanceolate to falcate, obtuse, ascending, (6) - (12) mm long, (1.5) - (3) mm wide, white sometimes tinged grayish-green distally. **Lip** narrowly lanceolate, obtuse, pendant, sometimes recurved, variously recurved or incurved apically, (7) 8-15 (17) mm long, (1) - (2.4) mm wide at middle (in dried material, wider in fresh material), lightly short-papillose on basal third above and also into spur entrance, white sometimes tinged grayish-green distally. **Spur** narrowly cylindrical, slightly flattened vertically, slightly clavate, horizontal or

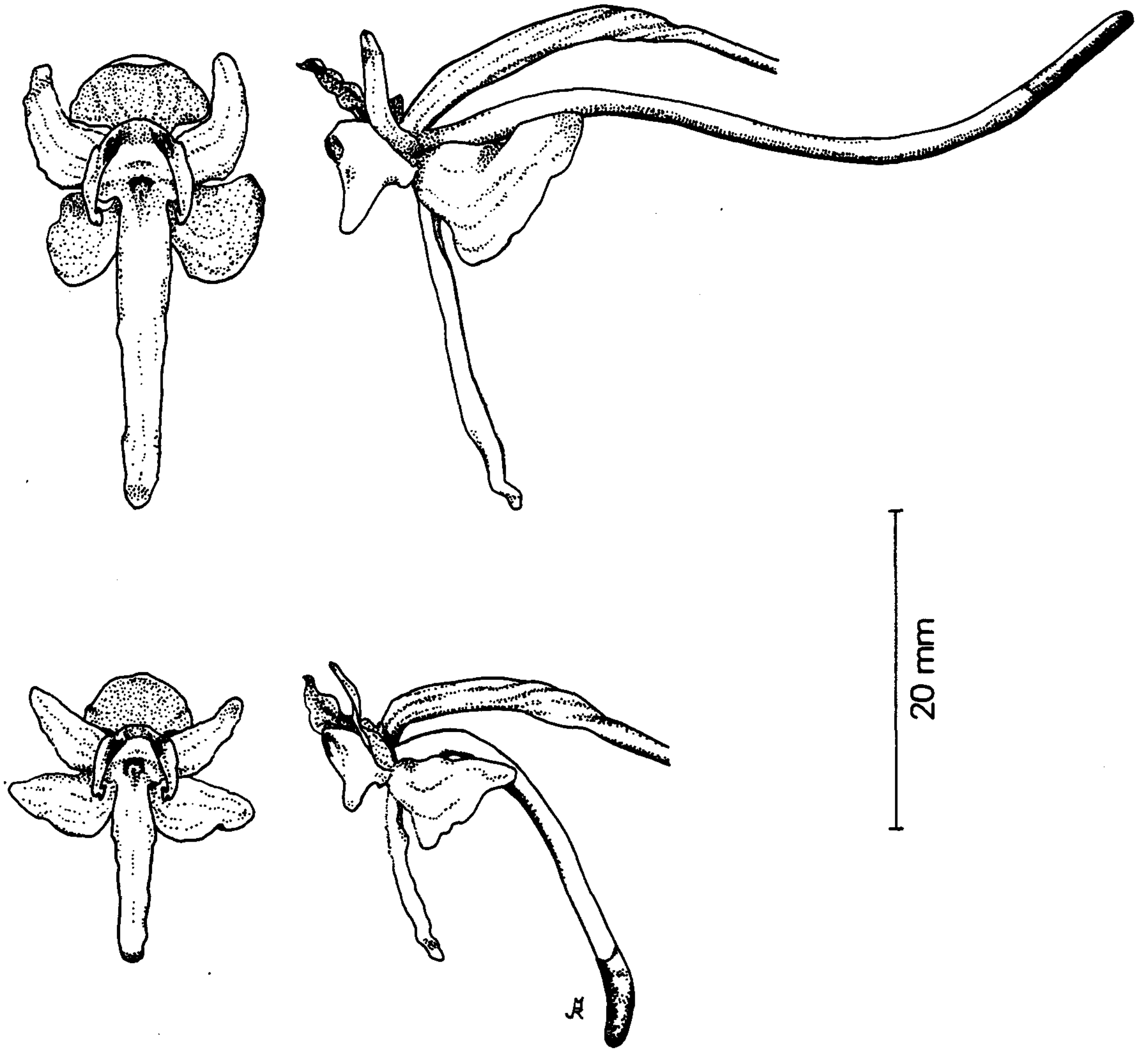


Fig. 6. Front and side views of typical flowers of *Platanthera macrophylla* (upper) and *P. orbiculata* (lower) based on fresh flowers and photographs of living plants in Ontario and Quebec.

decurved, (14) 16-26 (28) mm long, (0.8) - (2.0) mm wide, translucent, white, grayish-green distally. **Column** averages 5.5 mm wide, 4.5 mm high, 3.7 mm deep at top, interviscidium spacing (3.5) - (4.9) mm, white. **Hemipollinaria** 2, (3.0) 3.1-4.7 (4.8) mm long, yellow pollinium (0.5) - (1.1) mm wide, on an elongated, faintly yellowish caudicle connected by an irregularly-shaped stipe to a translucent, colorless, discoid viscidium, (0.5) - (0.8) mm diameter. **Capsule** ellipsoidal to oblong, erect, (9) - (18) mm long, (3.5) - (6) mm wide, light brown to brown. **Seeds** (0.6) - (0.8) mm long, (0.11) - (0.14) mm wide, brown to dark brown.

Morphology—Most of the morphological results are contained in Fig. 1 and the species descriptions; they are illustrated for the flowers in Fig. 6, 7. Our measurements of capsule sizes are in reasonable agreement with those of Fernald (1950a). The seed sizes of *P. orbiculata* agree with Stoutamire's measurements (1983).

In comparison with *P. orbiculata, P. macrophylla* is somewhat larger in most parts with slightly rounder leaves, wider spacing of flowers and, more commonly, straight spurs (90% vs. 60%). While *P. macrophylla* has somewhat larger seeds, it has appreciably larger capsules suggesting a greater number of seeds, although no count has been made.

Geographical Variation—The blooming date

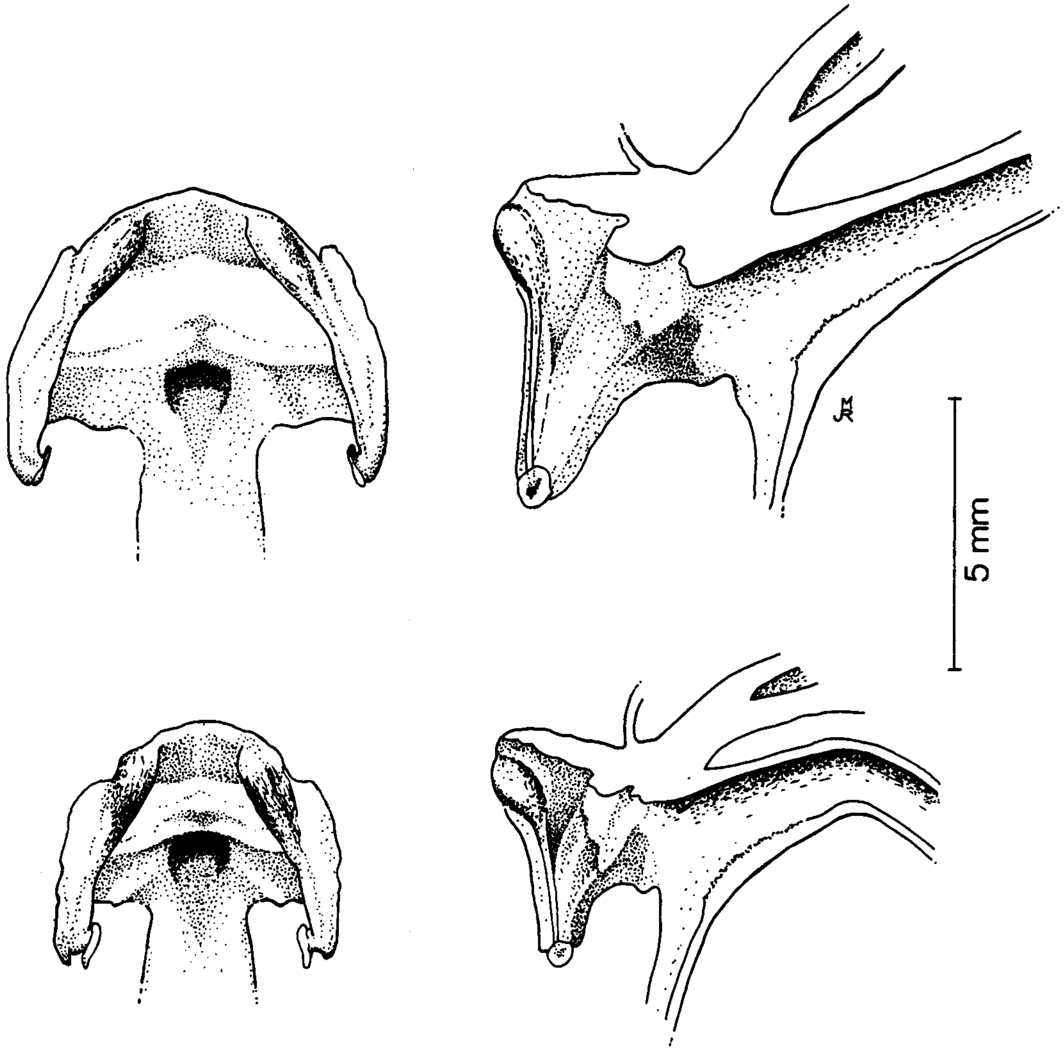


Fig. 7. Front view and median section of columns of *Platanthera macrophylla* (upper) and *P. orbiculata* (lower) based on fresh flowers and photographs of living plants in Ontario and Quebec.

shows a rough correlation with latitude for both species, with northern plants blooming later than southern plants, by about 12 days for *P. macrophylla* and 30 days for *P. orbiculata,* which has a somewhat greater geographical range. However, the earliest blooming *P. orbiculata* plants were in western Pennsylvania, while the more southern Appalachian plants bloomed 12 days later, suggesting that altitude also may be a factor.

Morphologically, *P. macrophylla* is a fairly homogeneous species, showing little significant geographical variation over its comparatively restricted range. Pedicel-and-ovary lengths and hemipollinarium lengths of plants from the eastern, southern and western margins of the range are about 7% smaller than those of plants from the core of the distribution.

Platanthera orbiculata shows more variation, with plants from Lake Superior to Maine and south along the Appalachians tending to be larger than those from the rest of the distribution. Plants from outside this core area have leaves 20% smaller than average and floral parts 10% to 15% smaller. In addition to these variations, the plants of Newfoundland are about 20% shorter and have racemes 35% shorter with 20% fewer flowers. Finally, southern plants have an average of 4.2 cauline bracts compared to 1.7 for western plants and 3.0 elsewhere.

Although the local population averages are statistically significant, the magnitudes of these geographical variations are generally only about one standard deviation. For individual plants, these geographical variations are not large enough compared to the intrinsic variation to permit taxonomic segregation (see Infraspecific Taxa below).

The spur shape of *P. orbiculata* shows a fairly marked variation in shape with at least 75% of the plants from the southern Appalachians and from Gaspé to Newfoundland having their spurs bent sharply downward. About 45% of plants from Lake Ontario to Maine are similar. In Pennsylvania and westward, fewer than 30% have the bent spur. The remainder have relatively straight, almost horizontal spurs.

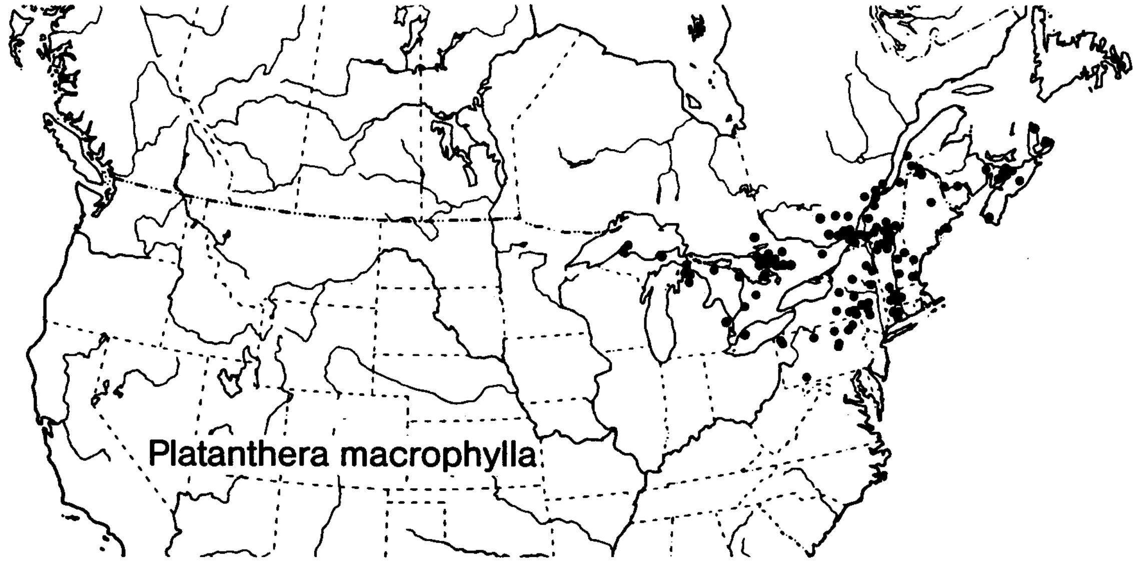
Leaf Venation—To describe leaf venation, which is similar for both species, we follow Hickey and Peterson (1978) and designate veins of decreasing width, as determined qualitatively, by the letters *A*, *B* and *C*. The basic pattern, starting with the first vein beyond the midvein, is *CBCA CBCA CBCA CBC*, which we write as 3(*CBCA*) *CBC*. With minor variations or imperfections, especially in the outermost veins, such as 3(*CBCA*) *CCC*, this pattern describes about half the plants. *Platanthera orbiculata* plants with leaves less than 6 cm wide have fewer veins, e.g. 2(*CBCA*) *CBC* or *CBCA CBC*. Leaves wider than 11 cm in *P. orbiculata* or wider than 13 cm in *P. macrophylla* have 4(*CBCA*) *CBC*, again with some variations.

Leaf venation can be helpful in separating nonflowering plants of *P. hookeri* from those of *P. orbiculata* and *P. macrophylla* since over half of the former have the patterns *CBCA CBCC* or *CBCA CBCB CC* and minor variations, and less than 5 % have patterns with over 11 lines on one side of the mid-vein. Differences in transverse venation between *P. hookeri* and the other two species can be recognized but are difficult to describe. In *P. orbiculata* and *P. macrophylla*, many of the transverse veins near the center of the leaf are roughly perpendicular to the longitudinal veins and are not branched. Near the edges of the leaf, the transverse veins branch more and run more forward as they go toward the edges. In contrast, *P. hookeri* has this latter, more irregular appearance at the center of the leaf as well as at the edges.

Geographical Distributions—Localities of collections seen by us are shown in Fig. 8. Since this study was undertaken mainly to understand *P. macrophylla*, an exhaustive search was not made for collections west of Ontario and the Mississippi River. Thus, the western range of *P. orbiculata* is underrepresented. Some additional western localities in published maps include central Saskatchewan (Maher et al., 1979), the Black Hills of South Dakota (Barkley, 1986), Victoria, B.C. (Szczawinski, 1959), and the southern Alaska panhandle (Hultén, 1968). Many local eastern floras have distribution maps, but they are not useful here because they do not clearly distinguish *P. macrophylla* from *P. orbiculata*. Comparison with Fernald's map (1933), which presumably includes both *P. orbiculata* and *P. macrophylla*, shows a considerable advance in knowledge of the range, especially of the northern limits in Canada.

The distributions were correlated with the biomes mapped by Rowe (1972) for Canada and *The Times Atlas of the World* (1975) for the United States. *Platanthera orbiculata* has a transcontinental distribution with a broad eastern portion and a smaller western section joined by a narrow band across the prairie provinces. It occurs in much of the Predominantly Forest section of the Boreal Forest Region, in parts of the Subalpine, Montane, Coast and Columbia Forest Regions of British Columbia and adjacent parts of Washington, Idaho and Montana, and in most of the Great Lakes-St. Lawrence and Acadian Forest Regions (= Mixed Forest) following the Appalachians south to North Carolina and Tennessee, and some nearby parts of the Deciduous Forest Region.

The species has not been recorded from Alaska except for the southern tip of the panhandle (Hultén, 1968; Scoggan, 1978) nor has it been located in the Yukon (Boivin, 1979; W. J. Cody, pers. comm.). In the east, we have seen no collections to support Luer (1975), whose map shows a northern limit running from the south end of James Bay to the central Labrador Coast, nor Porsild and Cody (1980), who show a point in Quebec just outside the southwest corner of Labrador. Ames (1910) included Labrador in the range of *P. orbiculata* on the basis of a collection, then at MO, annotated "Labrador Swamp, Ryegate, July 8, 1884, Dr. F. Blanchard." The present location of this sheet is unknown to us, but Ames' interpretation can be rejected since collections at HNH (R. M. Downs, pers. comm.) and elsewhere show that Blanchard was near his home at Peacham, Vermont, on July 8, as well as on June 30 and July 31 of that year. Also, there is a Ryegate about 15 km southeast of Peacham, but none is listed for Labrador



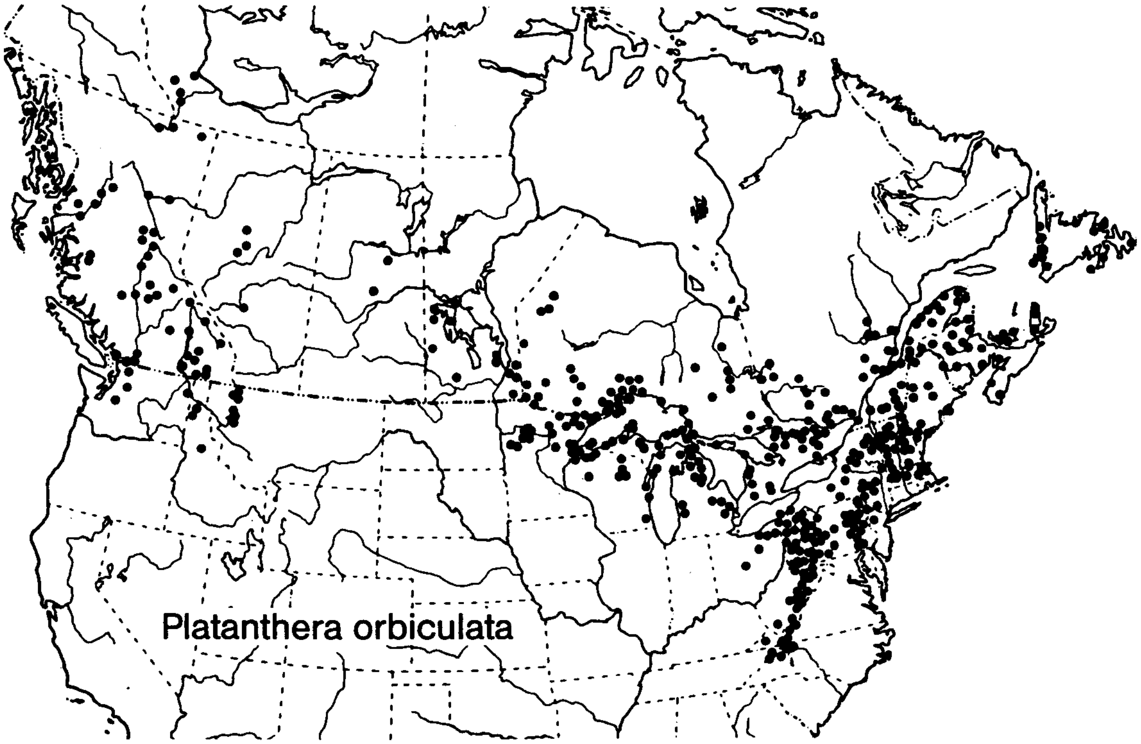


Fig. 8. Geographical distributions of ***Platanthera macrophylla*** (upper) and ***P. orbiculata*** (lower). The western range of ***P. orbiculata*** is underrepresented.

or Quebec (*Gazetteer of Canada/Newfoundland,* 1983; *Répertoire géographique du Québec,* 1969).

Platanthera macrophylla, by contrast, has a much smaller range within that of *P. orbiculata,* being restricted essentially to the Mixed Forest. Contrary to Luer (1975), we have found no collections from farther south than Pennsylvania. Fuller (1933) mentioned plants from northeastern Wisconsin with spurs 30-40 mm long that would have to be *P. macrophylla.* While collections from this area would not be surprising, we have not seen any ourselves.

Rarity—Local studies for rare plant protection are probably more intensive than the present work (and indicate some small extensions to the ranges shown in Fig. 8), although in the east there could be problems with the identity of the two species. *Platanthera orbiculata* has been designated as rare in Saskatchewan (Maher et al., 1979) and "of restricted range" in the Northwest Territories (Cody, 1979). It is listed in rare plant studies for Connecticut, Rhode Island, Tennessee, Ohio, Indiana and Washington (Gade, 1987) and may be extinct in Connecticut (Connecticut Geological & Natural History Survey, 1985), Illinois (Sheviak, 1974) and Oregon (Oregon Natural Heritage Data Base, 1985).

Platanthera macrophylla was described as rare by Goldie (1822), an assessment still valid in much of its range today. About 75 % of the collections mapped in Fig. 8 are over 50 years old (see also Reddoch et al., 1982; Connecticut Geological & Natural History Survey, 1985). *Platanthera macrophylla* has been designated as rare in Ontario (Reddoch et al., 1982), Quebec (Bouchard et al., 1983), New Brunswick (Hinds, 1983, 1986) and Newfoundland (Bouchard et al., 1991) and has been listed in studies for Connecticut and Rhode Island (Gade, 1987).

Habitats—Useful habitat citations were available from 247 sheets of *P. orbiculata* from the Boreal and Mixed Forests, and 61 sheets of *P. macrophylla* from the Mixed Forest. They provide some insight into the dominant habitats of the two species and the differences between them. The term "rich woods," appearing on about 60 other sheets, mainly older ones, was omitted as being too imprecise and possibly a cliché.

On 58 sheets of *P. orbiculata* from the Boreal Forest that listed tree associates, the dominants were white and black spruce (25), balsam fir (9) and poplar (11), the latter occurring mainly on clay soil in northern Ontario. Most sites were either mesic or wet; in the latter case they were often spruce swamps. On 107 sheets from the Mixed Forest, the tree associates in order of decreasing importance were white cedar (26), spruce (18), eastern hemlock (11), balsam fir (10), pine (10), maple (10), American beech (7) and tamarack (7). Again, most sites were either mesic or wet: mesic coniferous forest and swamp forest (cedar swamp).

Two curious results involve *P. orbiculata.* Tamarack was cited a moderate number of times in the Mixed Forest, but was not reported for the Boreal Forest, although it is common there (Rowe, 1972). Conversely, poplar or trembling aspen was noted a moderate number of times in the Boreal Forest, but only once in the Mixed Forest, although it occurs in both regions (Rowe, 1972).

For *P. macrophylla,* the dominant tree associates on 25 sheets from the Mixed Forest were maple (7), eastern hemlock (6) and American beech (6), a different selection from those of *P. orbiculata.* In contrast to *P. orbiculata,* sites of *P. macrophylla* were mainly mesic. There was little evidence for swamps or for association with white cedar, balsam fir or tamarack. For both species, references to slopes and nearby open water seem surprisingly abundant but are consistent with our own limited field experience.

Fernald (1950a) remarked that the two species "rarely, if ever, grow together" since he could find "only 7 cases in which both species have been collected in the same township or similar large area" out of 135 collections. We have seen five sheets bearing both species with a common cited location. For three other locations, the two species are represented on separate sheets. In the field, we have seen two sites where both species grew within 25 m. This situation is similar to that of *P. psycodes* and *P. grandiflora,* which are known to occur in four mixed colonies within 55 km of Ottawa (Reddoch, 1976; Reddoch and Reddoch, 1987). It is difficult to estimate the significance of this number of coincidences, but it does suggest that reproductive isolation is effective while there is a small overlap in habitat preferences.

Infraspecific Taxa—Fernald (1950a) segregated western plants as *Habenaria orbiculata* var. *menziesii*. Other authors, such as Ames (1906), Correll (1950), Luer (1975) and Scoggan (1978), have not agreed. Fernald, using only 12 sheets of western plants and 153 of others, noted the smaller leaves of the former and claimed that they had shorter scapes, racemes and spurs. As we have shown above, western plants exhibit some geographical variation, having, on average, smaller leaves, fewer bracts and slightly smaller flowers. Our range of plant heights for western plants, 21 to 62 cm for 34 plants, is not unusual for *P. orbiculata.* For the raceme and spur, we find no significant deviation of western plants from others. For these two characters, Fernald cited only the upper size limit. Unfortunately, such extremes cannot readily be compared between two samples. There seems to be little ground for recognizing the western plants as a distinct taxon.

Fernald (1950a) proposed *P. orbiculata* var. *lehorsii* for small plants from St. Pierre et Miquelon. He described plants from coastal barrens at several sites in southwestern Newfoundland, which are not quite as small, as "transitional," "somewhat approach[ing]" or "passing to" var. *lehorsii.*

Newfoundland woodland *P. orbiculata* plants are somewhat smaller in height and leaf size than mainland plants. We find that the barrens plants are 40 % shorter in height and raceme height, 25 % shorter in spur length and 15 % shorter in pedicel-and-ovary length than the woodland plants. No other statistically significant differences were noted, although the small sample size makes firm conclusions difficult. The number of flowers, leaf sizes, hemipollinarium lengths and blooming dates are the same for barrens and woodland plants. These latter similarities suggest that the barrens plants are not impoverished compared to the woodland plants. The major differences, the plant and raceme heights, then appear to be a response to the high winds (Eisikowitch, 1978) of the region.

While plants of St. Pierre et Miquelon are certainly small, these together with the plants of Newfoundland barrens are part of a continuum with the more normal woodland plants. As highly localized ecotypes, they do not justify varietal status. Perhaps the most interesting question about them is why they flourish in such a different habitat in such a small part of the range of the forest-dwelling *P. orbiculata.*

Clute's (1904) *Habenaria orbiculata* var. *longifolia* and Jennings' (1920) *Lysias orbiculata* var. *pauciflora* can also be rejected since the differences cited and our own measurements of the latter type show no significant deviations from the typical ranges for the species.

Mousley (1934) described *H. orbiculata* f. *trifolia* (his type is, in fact, referable to *P. macrophylla*). We have seen five sheets of *P. orbiculata* and three of *P. macrophylla* which might be described as three-leaved. The third leaf appears to be a cauline bract unusually low on the scape and roughly half the size of the leaves. Such behavior is not surprising since the bracts become longer and wider as they occur lower on the scape. Thus, the form, while visually distinctive, is probably not very significant and is somewhat arbitrary with regard to how large and how low the bract must be to qualify.

Pollination—There are few reports in the literature of the pollinators of *P. orbiculata* and *P. macrophylla* and these do not indicate clearly which of the pair is involved. Van der Pijl and Dodson (1966) listed the night-flying moth *Sphinx drupiferarum* as the pollinator of *Habenaria orbiculata,* citing Sargent as the observer in 1894. Luer (1975) attributed the same information to Sawyer in 1894 and suggested his var. *macrophylla* as the taxon involved. We have been unable to find the original 1894 reference. Luer also cited Stoutamire, without reference, for the information that two noctuid moths, *Autographa ampla* and *Diachrysia (Plusia) balluca,* pollinate *P. orbiculata.*

Inoue (1983) summarized the pollination syndrome of Japanese *Platanthera* species based on his extensive observations. He suggests that the dominant pollinators of green- (or white-) flowered *Platanthera* species with mainly curved spurs 10-20 mm long would be noctuid and geometrid moths, while those of white- (or green-) flowered plants with horizontal spurs 20-40 mm long would be sphingid moths. Other studies in Europe (Nilsson, 1978, 1983) and North America (Sheviak and Bowles, 1986) tend to confirm this syndrome. The syndrome is, of course, a rather broad generalization about the few dominant pollinators of a *Platanthera,* while it is recognized that there may be several other, minor pollinators of various types as well. Moreover, the dominants may well change over the range of a widespread orchid like *P. orbiculata.*

Thus, it is likely that the noctuids reported by Stoutamire would pollinate *P. orbiculata* rather than *P. macrophylla* and their structure is consistent with this view. Both moths are about 3 mm wide across the eyes and have tongue lengths in the 15-20 mm range (pers. obs.) and thus seem capable of pollinating this orchid. *Diachrysia balluca* covers most of the eastern half of the range of *P. orbiculata,* while *Autographa ampla* covers almost the entire range except for the northwest (Lafontaine and Poole, 1991).

Again, following Inoue (1983), the sphingid would be more likely to pollinate *P. macrophylla* than *P. orbiculata.* However, an examination of the moth suggests that it would be at best a rather inefficient pollinator and probably not a dominant one. The transcontinental range of *Sphinx drupiferarum* includes most of the range of *P. macrophylla* and its flying season includes the flowering season (Hodges, 1971). However, the reported tongue length, 44 mm in the eastern United States (Fleming, 1970) is quite long and the eye width is quite comparable to the interviscidium spacing of *P. macrophylla* (pers. obs.). (Outside the range of our orchids, tongue lengths of 60 mm have been reported from Colorado (Gregory, 1964) and in the range of 34-43 mm from the American prairies (Sheviak and Bowles, 1986)). These observations and the presence of dense tufts of hairs in front of the eyes suggest that this *Sphinx* would be an inefficient pollinator of *P. macrophylla.*

We have been unable to detect an odor from flowering plants of either species during the day or, in the case of *P. orbiculata,* shortly after sunset, but Brackley (1985) describes them as lightly fragrant at night. The papillae of the lip and lateral sepals could be osmophores (Dressler, 1981; Inoue, 1983). If so, their restricted occurrence near the entrance to the spur may indicate a very local function for any odor produced.

Both orchid species have the viscidia widely spaced in front of the circular nectary entrance and facing each other (Fig. 6,7), suggesting attachment of the hemipollinaria to the moths' eyes. Thus this species pair may interact with moths of two different sizes but by a similar mechanism. In contrast, the species pairs *P. psycodes* and *P. grandiflora* (Stoutamire, 1974), *P. leucophaea* and *P. praeclara* (Sheviak and Bowles, 1986) and *P. bifolia* and *P. chlorantha* (Nilsson, 1978, 1983) each interact with moths of comparable size, but in each pair the first-named species favors proboscis placement of the hemipollinarium, while the second is adapted to eye placement.

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WHAT IS *SPIRANTHES* ×*BOREALIS*?

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This question has come up because many have not heard of this plant before, or have never seen it, or both. It has not been featured in the recent taxonomic work on the genus. However, Pace and Freudenstein (2018) noted that: "There is no evidence to support the supposed hybrid status of *S.* ×*borealis*; it fits within the variability of *S. casei*." In fact, it is the other way around. The evidence for hybrid status is intermediacy which has been supported to some extent, but the evidence for it fitting within the variability of *S. casei* is incomplete.

A Google search does provide a little information, but details are lacking. Some basic sources ("Go Orchids") have information on this plant while others (such as the very helpful Kew's "Plants of the World online") do not, and sometimes information is incorrect (never mind the examples). Although I am not absolutely sure how this taxon originated, I can explain something about its history, and provide my own interpretation of its taxonomic status.

Spiranthes ×*borealis* P.M. Brown (Figure 1b) was described as a hybrid of *S. casei* var. *casei* (Figure 1c) and *S. ochroleuca* (Figure 1a) by Brown (1995: 290) in the first volume of the "North American Native Orchid Journal," which had a very limited distribution at the time. The type is a photo (Brown, 1995: 286), which was acceptable then (and until 1 January 2007 after which a specimen was required).

Brown (1995: 290) stated: "In Northern New Hampshire colonies of both species of *Spiranthes* occur and flower sympatrically. Plants which could be assumed to be small-flowered *S. ochroleuca* or large flowered *S. casei* occur in several of the colonies. These intermediate plants have characteristics of both parents and are occasionally found independent of both parents. The best colony of *S.* ×*borealis* occurs at the very southern limit of the range of *S. casei* in West Milan, New Hampshire. The majority of sites for *S. casei* in New Hampshire and Vermont are considerably north of this area where *S. ochroleuca* is less common. In each instance where the two parents are found together, the hybrid is always present."

Brown (1997: 155) devoted some effort to determining the validity of *S.* ×*borealis.* With measurements and analyses of 21 characters and flowering period, he showed that his concept of *S.* ×*borealis* was intermediate between *S. casei* var. *casei* and *S. ochroleuca*. Overlap between the three taxa was considered negligible for coloration of hairs, and position of dorsal sepal. *Spiranthes ochroleuca* flowered somewhat later than the other two taxa, and had the longest perianth parts. *Spiranthes casei* var. *casei* had the shortest perianth parts. A scatter diagram with regression lines was claimed to show a lack of genomic coadaptation characteristic of hybrid taxa. Some of this work may be flawed on the basis of small sample size and other considerations, but it does provide some evidence for discontinuity and intermediacy, which along with circumstantial evidence, makes a hybrid explanation plausible. There are other explanations as well (see below).

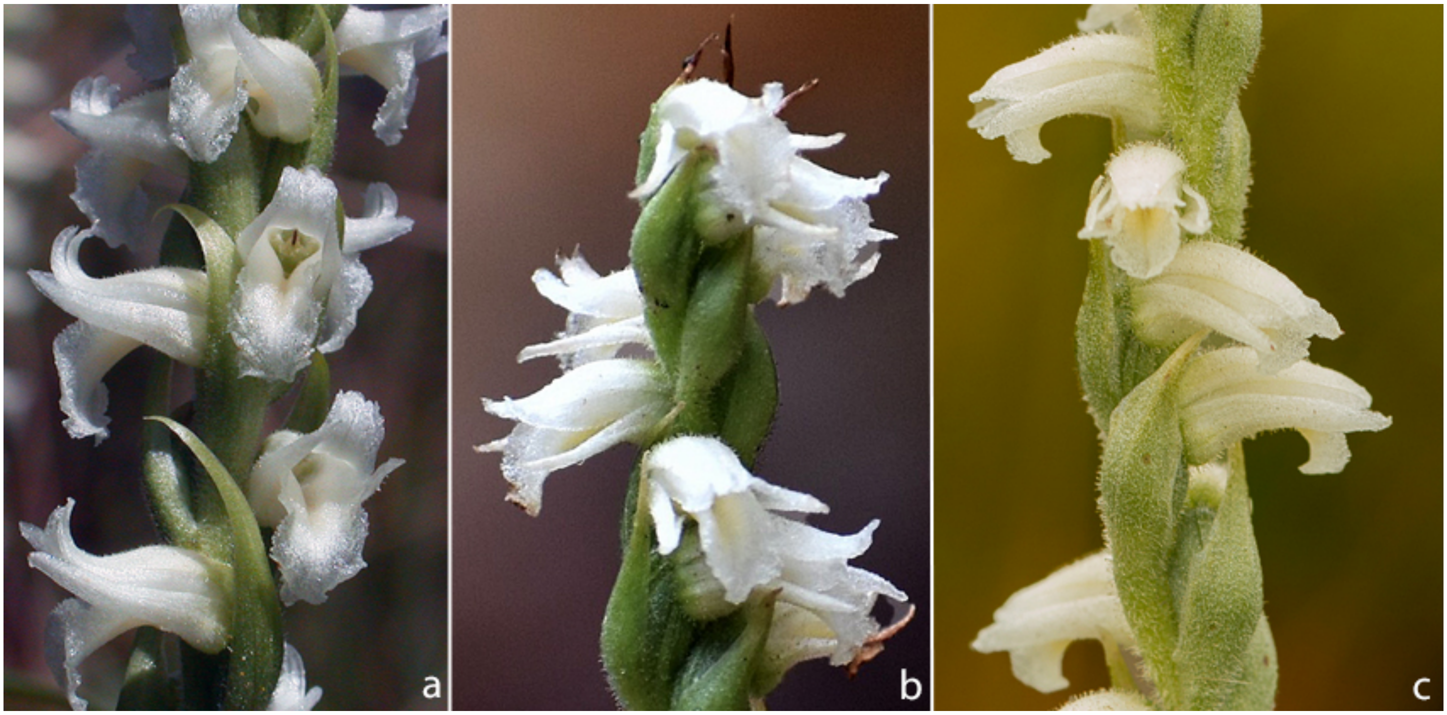

Figure 1. Portions of inflorescences of three *Spiranthes* taxa. **a, *Spiranthes ochroleuca***, New York, Syracuse area, September 2014, iNaturalist photo 61681753 by M. Hough, CC BY-NC 4.0. **b, *Spiranthes* ×*borealis*,** Ontario, Algonquin Park near Norway Lake, 22 Sept. 2022, iNaturalist photo 235092147 by Pinemartyn, CC BY_NC 4.0. **c, *Spiranthes casei* var. *casei*,** Québec, near Montebello, August 2021, iNaturalist photo 152834543 by Benoit Dorion, CC BY-NC 4.0. The flowers of *S. ochroleuca* have strongly upturned lateral petals and dorsal sepal. They are not upturned in *S. casei* var. *casei*, and weakly upturned in *S.* ×*borealis*. Petals, sepals and lip are shortest in *S. casei* var. *casei* and longest in *S. ochroleuca.* Lateral sepals in *S. ochroleuca* are usually directed upward but are horizontal or directed downward in S. *casei* var. *casei* and *S.* ×*borealis.*

The most interesting “aspect," is that it is a “thing.” A kind of *S. casei* with an upcurved dorsal sepal and longer perianth parts than hundreds of *S. casei* nearby, has been noticed rarely in Ontario, and an accompanying photo (Figure 1b) shows a plant from Algonquin Park in Nipissing District, Ontario. Although we may not know definitely how this "thing" originated, with the name “*borealis,*" it does have a convenient handle.

Brown (2006: 180) recognized it in his "Wild Orchids of the Canadian Maritimes and northern Great Lakes region" with a short text and a helpful photograph. Here Brown noted correctly that it was erroneously reported in Flora of North America as a hybrid of *S. casei* var. *novaescotiae* and *S. ochroleuca* (Sheviak and Brown 2002: 539, 541), which occurred as a result of publication of manuscripts not seen by the authors who had intended it to be accepted as a hybrid of *S. casei* var. *casei* and *S. ochroleuca*.

Brown (2007: 220) has the same photograph and note in his "Wild Orchids of the Northeast - New England, New York, Pennsylvania and New Jersey.” In both of these references he notes that this hybrid is known primarily from northern New England.

The next useful publication in the understanding of *S.* ×*borealis* was Brown's summary and update (Brown 2008) of work on *S. casei* and the hybrid that was published in his M.Sc. thesis (Brown 1997). Here Brown notes that the hybrid was known to P.M. Catling and C.J. Sheviak, and that it also occurred in regions of sympatry of the parents in New York State and northern Pennsylvania. Although he suggested that "the following data demonstrate that these plants are the resulting hybrids …", there is no summary of supporting data that appeared in his thesis, only a reference to the reddish color of the gland-tipped hairs, - a character shared with *S. casei*.

Most recently *S.* ×*borealis* was overlooked by Pace & Cameron (2017) when they tightened the Gordian knot as part of their work on the *S. cernua* complex. In 2024 it was noted that (1) *S.* ×*borealis* was found in Ontario near Melon Creek south of Kaladar in Lennox and Addington, as well as in Muskoka; (2) it is also known from New England and Québec on the southern range limits of *S. casei*; (3) it is possibly a rare transitional form in the evolution of *S. casei* by a change from sexual reproduction to adventitious embryony, rather than a hybrid (Catling 2024: 38).

Hybrid or not?

An unusual expression of *S. casei* (Figure 1b) that is similar to *S. ochroleuca* (Figure 1a), and apparently referable to the concept of *S.* ×*borealis* does occur outside the range of *S. ochroleuca* in parts of Ontario, including Muskoka, Lennox and Addington (both personal observation) and Nipissing, Ontario, and in New York State, and New England. These occurrences are north of the range of the *S. ochroleuca* putative parent (Catling 1980: 466). Hybrids may occur in the absence of one, or both, putative parents, but are less likely to do so. Hybrid presence in the absence of a parent does raise the question of alternative explanations for an intermediate morphology, i.e. alternative to hybrid origin. Origin as a rare transitional form in the direct evolution of *S. casei* (Figure 1c) associated with change from sexual reproduction to adventitious embryony is another possibility (Catling 2024: 38, see also below). The question of origin is best considered along with additional information, and a hybrid explanation seems satisfactory at present.

Taxonomic future and details

A recent molecular study has indicated a close relationship between *S. ochroleuca* and *S. casei* var. *casei* (Pace and Cameron 2017). This has been suggested in the past on the basis of ecology, morphology and distribution. Change from outbreeding to agamospermy (vegetative reproduction using seeds) would enable efficient spread and colonization without a disadvantage due to decreasing flower size. The latter may become less important when pollinators become less important.

Such derivation might lead to the idea of making *S. casei* var. *casei* a synonym of *S. ochroleuca,* or an "ecologically specific subspecies of *S. ochroleuca"* (Pace and Cameron 2017: 663). However, the two have different distributions, different flower morphology and there is substantial phenological discontinuity between the early flowering *S. casei* var. *casei*, blooming from early August to early September, and the late flowering *Spiranthes ochroleuca*, blooming in September and early October. People have not had much trouble distinguishing *S. casei* var. *casei* and *S. ochroleuca,* which have been thought to have had mostly discrete distributions in the past (Catling 1980: 431, Figure 139, and 466, Figure 144) and at present based on the iNaturalist maps (https://inaturalist.ca/taxa/243056-Spiranthes-casei-casei, https://inaturalist.ca/taxa/169271-Spiranthes-ochroleuca).

If *S.* ×*borealis* is an unbalanced, sterile, triploid hybrid (possibly 2n=*ca*. 45) of *S. casei* var. *casei* (2n=60-75, Catling 1980: 265) and *S. ochroleuca* (2n=30, Catling 1980: 265, and Sheviak 1982: 28), this could explain its rarity. Although "sterile," it may be capable of some seed production by agamospermy, this acquired from either, or both, putative parents. It would also explain the fact that it is largely restricted to northern New England, an unusual area of overlap for *S. casei* var. *casei* and *S. ochroleuca.*

Northern Hybrid Ladies'-tresses

Spiranthes ×*borealis* P.M. Brown appears to be a hybrid of *S. casei* var. *casei* and *S. ochroleuca* that differs from the former in its longer and more divergent perianth parts, and from the latter by its smaller flowers. It can be called Northern Hybrid Ladies'-tresses. *Spiranthes casei* var. *casei* is easy to propagate and can bloom in its third year of growth from seeds (Webber 1996: 61), suggesting that it may not be difficult to produce the hybrid with *S. ochroleuca,* not just to confirm the natural hybrid, but to answer a number of other interesting questions, such as how some populations of the mostly outbreeding *S. ochroleuca* became agamospermic.

Key to taxa

1a. Flowers with dorsal sepal and lateral petals not upcurved at the tip (Figure 1c); sepals 5-8 mm long; lip 6-7 mm long

S. casei var. casei

1b. Flowers with dorsal sepal and lateral petals upcurved at the tip (Figure 1a, b); sepals 6-10 mm long; lip 7-10 mm long

2

2a. Flowers with dorsal sepal and lateral petals slightly upcurved at the tip (Figure 1b); lateral sepals directed horizontally (Figure 1b); sepals 6-9 mm long; lip 7-8.5 mm long

S. ×borealis

2b. Flowers with dorsal sepal and lateral petals prominently upcurved at the tip (Figure 1a); lateral sepals often directed upwards (Figure 1a); sepals 7-10 mm long; lip 9-10 mm long

S. ochroleuca

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