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Reasons to Recognize The Newfoundland var. *abbreviata'* of *Platanthera hookeri*

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When Fernald described var. *abbreviata* from Newfoundland (Fernald 1933), it was the only variety of *P. hookeri* occurring on the island (**Fig. 1**) and was confined to limestone barrens along less than 30 miles of coastline in the vicinity of Port au Choix. Various authors treating both North American orchids and the Newfoundland flora have not recognized var. *abbreviata* (Luer 1975, Bouchard et al. 1991, Voitk & Voitk 2006. Maunder 2012, Meades et al. 2015). Fernald (1933) emphasized plant size in differentiating var. *abbreviata* partly because he noticed that plants from other parts of the northeast also have small spurs. A belief that plant size was influenced by environment and difficulty in drawing a line of demarcation between var. *abbreviata* and var. *hookeri* due to the transition that Fernald described were probably among the reasons why it was not accepted.

Fig. 1. Hookers Orchid (*Platanthera hookeri*), Newfoundland limestone barrens. Image: Bob Gibbons. Used with permission.

However, there has never been a review of its putative distinctive features. Here I consider three questions that bear on recognition: (1) does it <u>have a distinctive and restricted distribution and habitat on Newfoundland? (2) </u>are the measurements given by Fernald to distinguish it supported by a larger sample from a wider area of Newfoundland? (3) Do measurements from a sample of northeastern plants from outside Newfoundland support the recognition of var. *abbreviata*?

Methods

(1) Distribution and habitat

There is a question of whether or not more populations of *P. hookeri* have been found in Newfoundland, (42,030 square miles, 108,900 km^2) or whether it has remained a very restricted taxon only in limestone areas of the west coast since its description in 1933. There are other limestone areas on the island (Tucker's Head at Bonne Bay, Raglan Head in the Bay of Islands, Humber Gorge, Cow Head Peninsula, North Twillingate Island, Grand Falls, etc., see *http://www.limestonebarrens.ca/Overview.htm* . The current distribution and habitat (**Fig. 2**) was explored through discussion with Newfoundland botanists and survey of specimens in collections (CAN, CDFN, DAO, GH, GMNP, MT, NFLD, NFM, and SWGC, - acronyms from Index Herbariorum - http://sweetgum.nybg.org/science/ih/).

(2) Local measurements

Since this is a rare plant in NFLD, no whole plants were collected but individual flowers were collected from all specimens measured and are deposited in DAO (the Agriculture Canada Collection in Ottawa). Measurements of height, inflorescence length and leaf length were made in the field while the floral measurements were made on detached flowers using a microscope. A total of 71 plants from 6 locations were measured with a maximum of 22 per location (**Fig. 3**). The measurements were compared with those provided by Fernald (1933).

Fig. 2. Open barrens habitat with *Juniperus horizontalis, Juniperis communis, Betula sp, Arctostaphylos uva-ursi,* and *Empetrum nigrum*, with scattered and dwarfed White Spruce, near the Bateaux Barren north of Bellburns, west coast of Newfoundland.
Photo by P.M. Catling. 15 July 2002.

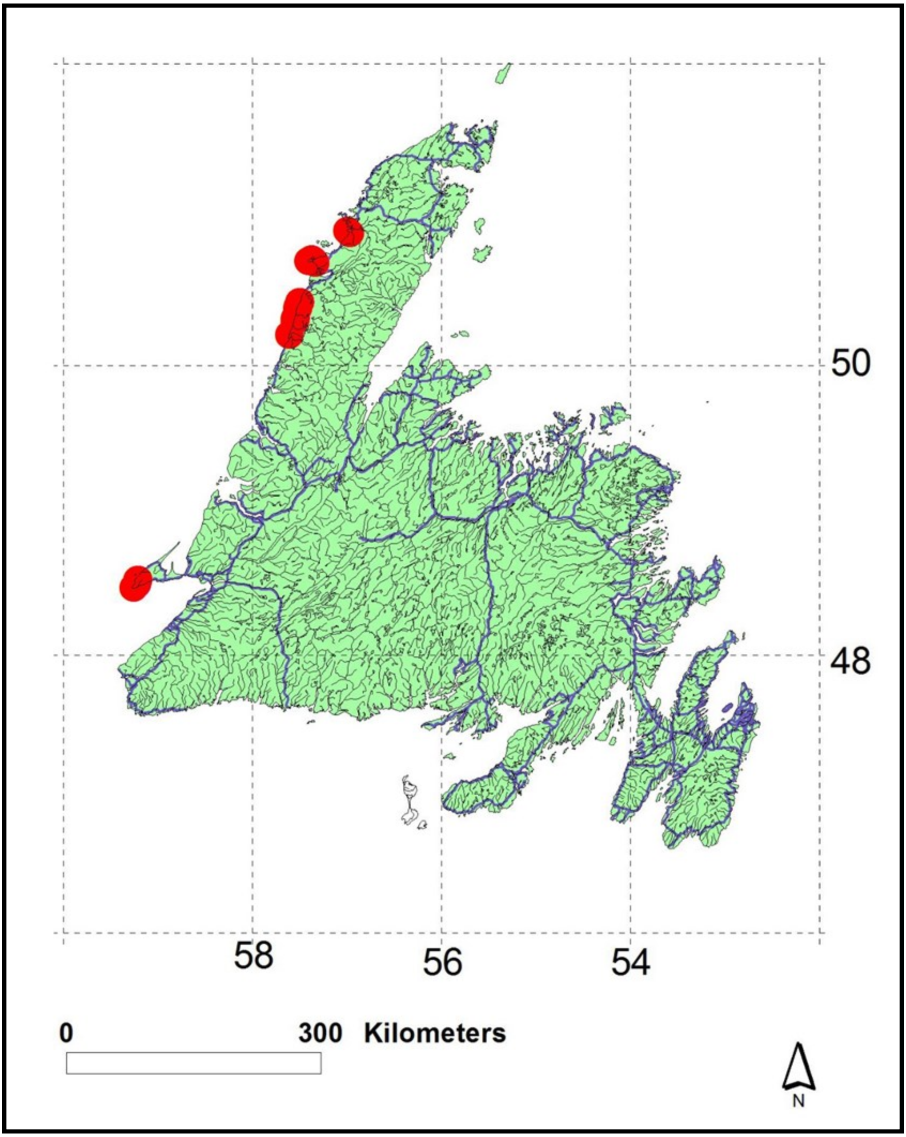

Fig. 3. Distribution of Hookers Orchid in Newfoundland based on personal observations of Paul Catling, John Maunder, Claudia Hanel, and specimens examined at CAN, DAO, GH, and MT.

(3) Outside Newfoundland

The 71 measurements of spur length and plant height from Newfoundland plants were compared with measurements of the same characters in 71 specimens from throughout the Canadian northeast in the DAO (Agriculture Canada) collection.

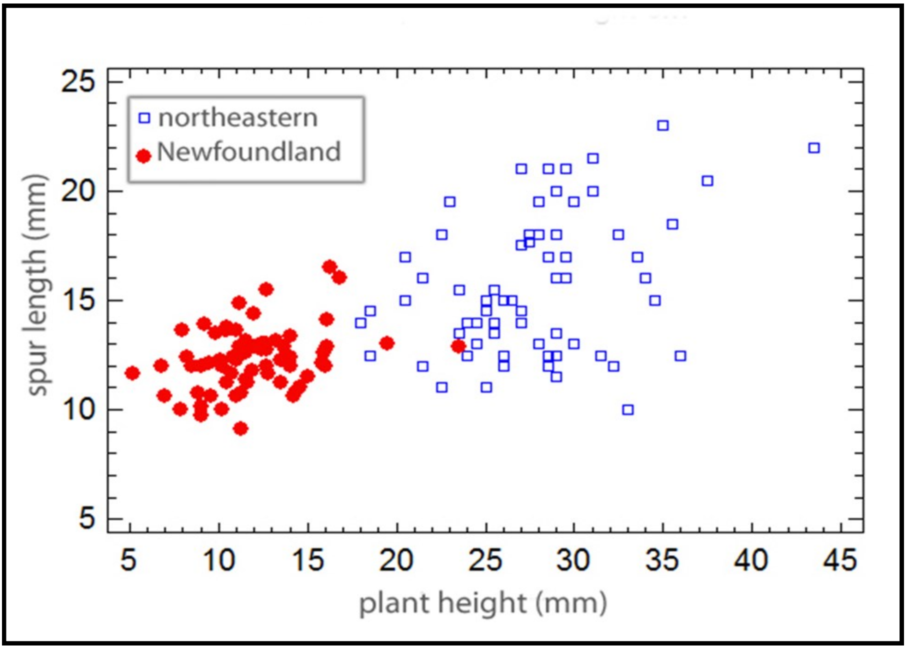

Fig. 4. Scatterplot of plant height versus spur length in a sample of 71 plants from the west coast of Newfoundland (red dots, Table 1) and a sample of plants at DAO from the mainland northeast (including specimens from north of New York State) open blue squares) (Table 2).

The position of the two groups was evaluated in a scatter diagram (**Fig. 4**).

Results

(1) Distribution and habitat

Three mapped localities (Bouchard et al. 1991, Rouleau and Lamoureux 1992) must be rejected. Firstly, specimens from St. Pierre and Miquelon have been revised to *Platanthera orbiculata* as described in detail by Etcheberry et al. (2010). Secondly, a location apparently in Barachois Pond Provincial Park, approx. 15 miles East of Stephenville (Rouleau & Lamoureaux 1992, map 848) is based on a collection by Black in 1977, but it has not been possible to trace it to confirm the identity of the collected plant. Lastly, there is a mapping of a site on the west coast, East of Corner Brook and South of the Bay of Islands. The location of the justifying specimen is again unknown.

In Newfoundland *Platanthera hookeri* is known only from two restricted limestone areas on the west coast (Voitk and Voitk 2006 and personal communications with John Maunder and Claudia Hanel), corresponding to two distinctive ecoregions recognized by Damman (1983), and is considered rare In Newfoundland (Bouchard et al. 1991). These two areas are: (1) mostly flat open limestone areas along the coast between St. Johns Bay - Port au Choix and Portland Creek, extending for a distance of 40 miles, and (2) the Port au Port Peninsula, a rugged hilly area, with steep open slopes and limestone talus. The latter area is the only substantial addition to Fernald's area of initial discovery.

(2) Local measurements

Compared to Fernald's (1933) sample of 64, the recent sample of 71 averaged larger (**Table 1**) in upper extremes except for leaf length. The differences however, are not substantial and indicate the recent Newfoundland sample as a group of small plants.

Table 1. Lengths of various floral parts for var. *hookeri,* var. *abbreviata*, transitional forms and Newfoundland plants in a recent study. Sample size for lip lengths was 54.

Character	**Var. *hookeri* (Fernald 1933)**	**Var. *abbreviata* (Fernald 1933) n=64**	**Transitional northeastern plants (Fernald 1933)**	**Newfoundland plants in recent study (Catling 2012) n=71***
Height (cm)	***17-45***	***7-18***	-	***5.2-23.5 (11.8)***
Inflorescence length (cm)	***5-25***	***2.5-9***	***6-22***	***3.2-11.8 (5.9)***
Leaf length (cm)	***5-16***	***2.5-9***	***6-12***	***3.3-8.1 (4.8)***
Spur length (mm)	***14-26***	***9-13***	***9-14***	***9.0-16.5 (12.3)***
Lateral sepal length (mm)	***8.5-11.5***	***6-8.5***	-	***6.3-10.3 (8.6)***
Lip length (mm)	***9-13***	***6-10***	***7.5-10***	***6.9-10.3 (8.5)***

(3) Outside Newfoundland

In the plot of plant height versus spur length, there was extensive overlap in the former but much less overlap in the latter. Two plants from Newfoundland were in the mainland group.

Discussion

(1) Distribution and habitat

Despite extensive botanical survey in Newfoundland since Fernald's work in 1929, the very restricted range and habitat of *Platanthera hookeri* has not changed. It occurs in one very unusual habitat on the island and only small plants are present. Fernald noted that "Its habitat, with arctic alpine xerophytes on limestone gravel, is so unlike the conventional habitat, in acid woodland humus on the continent, that one would at first feel compelled to consider it a distinct species." The immediate habitat of *P. hookeri* in Newfoundland is not dominated by arctic-alpine species, but by boreal species including Juniper (*Juniperus horizontalis* and *J. communis*) and Bearberry (*Arctostaphylos uva-ursi*) and it is not in open gravel but in vegetation mats over thin soil over limestone. However, Fernald is correct that rock and open gravel with arctic-alpine species are closely associated with plants of *P. hookeri* and that does require some more consideration (see below).

If it was widespread on Newfoundland and the small plants of barrens merged with larger plants of more wooded habitats, then varietal rank would be less well supported, but in the actual situation as reported here, its recognition is well supported. It appears to be a specialized local endemic.

(2) Local Measurements

The fact that the recent Newfoundland sample is a little larger (**Table 2**) than Fernald (1933) suggested is contrary to varietal recognition, but the difference is small, and the recent sample does not challenge varietal rank. If much more variation and much larger plants had been found, the challenge would have been more relevant.

Table 2. Location, latitude, longitude and number of plants for measurement of spur length and height in *Platanthera hookeri* from Newfoundland.

Location	Latitude	Longitude	Number of plants
Port au Port Peninsula about 5 km from Cape George	48.49439	-59.22171	4
Port au Port Peninsula about 10 km from Cape St. George	48.5227	-59.21272	3
N of Daniel's Harbour	50.3002	-57.5527	3
N of Bellbruns	50.39146	-57.51846	22
N of Daniel's Harbour	50.3002	-57.5527	9
far N of Bellburns	50.42582	-57.49632	14
1.3 km S of Bellburns turnoff S & 2.5 km S of Bound Brook	50.31629	-57.54451	15

Table 3. Locations, number of plants and DAO accession numbers for the mainland sample used in the scatter diagram of plant height versus spur length.

Location	Number of plants	DAO accession numbers
Manitoba	**3**	**125472, 768191, 169189**
New Brunswick	**5**	**15483, 158485. 769164. 769165.\, 769166**
Nova Scotia	**2**	**769169, 769162**
Ontario	**17**	**17097, 17098, 17101, 17103, 17104, 17106, 17237, 304280, 452061, 620308, 620308, 623866, 657143, 691110, 761669, 768188, 769187**
Prince Edward Island	**1**	**769163**
Quebec	**26**	**307059, 357434, 462256, 577151, 769167, 769167, 769168, 769169, 769170, 769171, 769172, 769173, 769174, 769174, 769175, 769176, 769178, 769179, 769179, 769180, 769181, 769182, 769183, 2011219, 6366265**
Quebec-Ottawa	**17**	**267282, 267283, 267284, 267285, 267286, 267287, 267287, 267289, 267292, 267293, 26729426294, 267294, 267296, 267296, 267298, 611058**

(3) Outside Newfoundland

The separation of mainland and Newfoundland plants in plant height is near to complete with colour coding. Discontinuity is only partial and the two Newfoundland plants in the mainland group suggest that genetic differentiation may not be complete. While most of the Newfoundland plants may be small due to environmental stress, a small percentage (3.55%) can find an uncommon open habitat where stress is less and where they can grow taller than usual. This observation makes it possible to interpret the scatter diagram as either supportive or not.

Considerations

Despite some support for the recognition of var. *abbreviata* in all areas of evaluation there are three reasons why it is rejected: (1) Fernald's comparison is inappropriate, (2) two Newfoundland plants are tall, (3) there is no clear discontinuity in plant height.

(1) Fernald's comparison. Fernald (1933) suggested that var. *abbreviata* "differs ... in its shorter dimensions in every part, ... but it exhibits no definite morphological characters by which it can be specifically separated, although it is as clearly separated from *H. hookeri* as is *H. macrophylla* from *H. orbiculata* ...". The differences between these latter two species had not been thoroughly elaborated when Fernald made this comparison. Based on what we know today about the differences between *H. macrophylla* and *H. orbiculate*, the comparison would inspire the immediate acceptance of var. *abbreviata*. However, *H. macrophylla* and *H. orbiculata* differ discontinuously in spur length, and thus in their pollination system (Reddoch and Reddoch 1993), whereas var. *abbreviata* was not shown to differ in spur length from mainland plants (**Fig. 4**).

(2) Some Newfoundland plants tall. If height was a consequence of climate, some plants of *P. hookeri* in the coastal barrens should occasionally be found in more shaded places and should be larger. This appeared to be the case since some Newfoundland plants were equivalent in size to mainland plants suggesting that either the dwarfing in Newfoundland is climate-induced or at least genetically variable. Either way var. *abbreviata* is not supported as distinct.

(3) Lack of discontinuity. The lack of complete discontinuity in plant height, which is the only potentially significant differentiating character, does not support recognition of var. *abbreviata*. The diagram is probably promoting discontinuity because there are relatively few specimens (**Table 3**) from the mainland transition areas (noted by Fernald), so the partial discontinuity is not considered sufficient for acceptance of var. *abbreviata*.

Regardless of whether or not var. *abbreviata* is worthy of formal recognition, the situation with *P. hookeri* in Newfoundland is of great interest. The plants may be an indicator of a rare postglacial relict habitat. This habitat with a mixture of boreal and arctic species may be a postglacial relict from the tundra bounding the *Picea* Parkland that existed in front of the Wisconsin Glacier 10,000 years ago. Plants from there would have needed an open and cool, but not cold, place to survive into modern times. The new boreal forest would have been a cold and dark barrier and the arctic tundra to the north would have been too cold, but a partial analogue may exist on particular parts of the west coast of Newfoundland.

Acknowledgements

John Maunder of St. John's provided a wealth of valuable information (as usual). Dr. Luc Brouillet and Geoffrey Hall of the Montreal Botanicial Garden herbarium provided images of 9 specimens in their collection. Jennifer Doubt and Kim Madge provided information on three specimens from the Canadian Museum of Nature. Nathalie Djan-Chékar of the the Rooms Provincial Museum kindly made information available on three specimens in their collection. Julissa Roncol of the Ayre Herbarium at Memorial University advised that the collection is temporarily closed so that information on the single collection there was not available. Claudia Hanel, Provincial Ecosystem Management Ecologist, and Carson Wentzell of Parks Canada, and Michael Burzynski of Rocky Harbour, assisted with the location of plant occurrences. Patricia Baines reported that there are no specimens of *P. hookeri* in the Newfoundland Federal Forestry Herbarium in Corner Brook.

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Corallorhiza trifida Châtelain - A Pictorial Monograph

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Introduction: *Corallorhiza trifida* is a tiny orchid that departs from the norm for other *Corallorhiza* species in that all aboveground parts of the plant, except for the lip are green; indicating that significant quantities of chlorophyll are present. Substantial quantities of chlorophyll are also present in its close relatives, *C. odontorhiza* and *C. wisteriana*, but in those species, it is often masked by highly colored anthocyanin pigments. The species epithet *trifida*, is derived from Latin, meaning divided into three parts, in reference to the three lobed lip. Common names applied to this species include: Northern Coralroot, Early Coralroot, and Yellow Coralroot.

Fig. 1. The slender green stem rises from a basal sheath and bears 4 to 15 flowers.

Taxonomy and Phylogenetics: The taxonomic history of *Corallorhiza trifida* (**Fig. 1**) is long, tortured, and highly convoluted. Summaries detailing the history of *Corallorhiza* have been compiled by both Fernald and Freudenstein (Fernald 1946, Freudenstein 1996, 1997). The reader is referred to these works for a detailed history of both the generic name *Corallorhiza*, and the species name *C. trifida*. The following is an abbreviated synopsis, which begins in northern Europe, where *C. trifida* is widely distributed. The use of *Corallorhiza* as a botanical descriptor predates the Linnean classification system, having been used by Albrecht von Haller in 1742 to describe plants we now know as *C. trifida* (Haller 1742). A decade later, Linneaus applied the name *Ophrys corallorhiza* in Species Plantarum, his seminal work creating the binomial nomenclature system (Linneaus 1753). It is at this point confusion reigns; In 1755 Gangebin validly described the genus *Corallorrhiza*, a fact that was long overlooked (Gangebin 1755). To complicate matters further, he inserted an extra ‘r”, thus introducing the spelling “*Corallorrhiza*” into the botanical literature. Gangebin only published the generic name, not assigning a species epithet. This was remedied five years later by Chatelain, who validly published the name *Corallorhiza trifida* in a short monograph (Chatelain 1760). At this point it should have all been over, except for a bit of shouting, unfortunately the work of Chatelain was not widely known, and in 1813 Robert Brown published the name *Corallorrhiza innata*, which was widely used throughout the nineteenth century and into the twentieth (Brown 1813). Further confusion was introduced by American botanists, such as Nuttall, who applied the name *Corallorhiza verna* to plants having an unspotted lip, observed in the northeastern United States (Nuttall 1823). Later in the nineteenth century the invalid name *Corallorrhiza corallorrhiza*, proposed by Karsten, came into common use for several decades (Karsten 1881). The first attempt to bring order to the situation was Oakes Ames, who in 1909, and again in 1924, recognized the work of Chatelain, proposing that *Corallorrhiza trifida* (note extra "r") be accepted (Ames 1909 1924).

As the twentieth century advanced, botanists gradually dropped the extra "r", with prominent botanists such as Fernald arguing for "*Corallorhiza* not *Corallorrhiza*" (Fernald 1946). Freudenstein in 1996 brought closure by proposing that "*Corallorhiza*" be conserved. At the same time proposing that the genus be attributed to Gangebin (Freudenstein 1996).

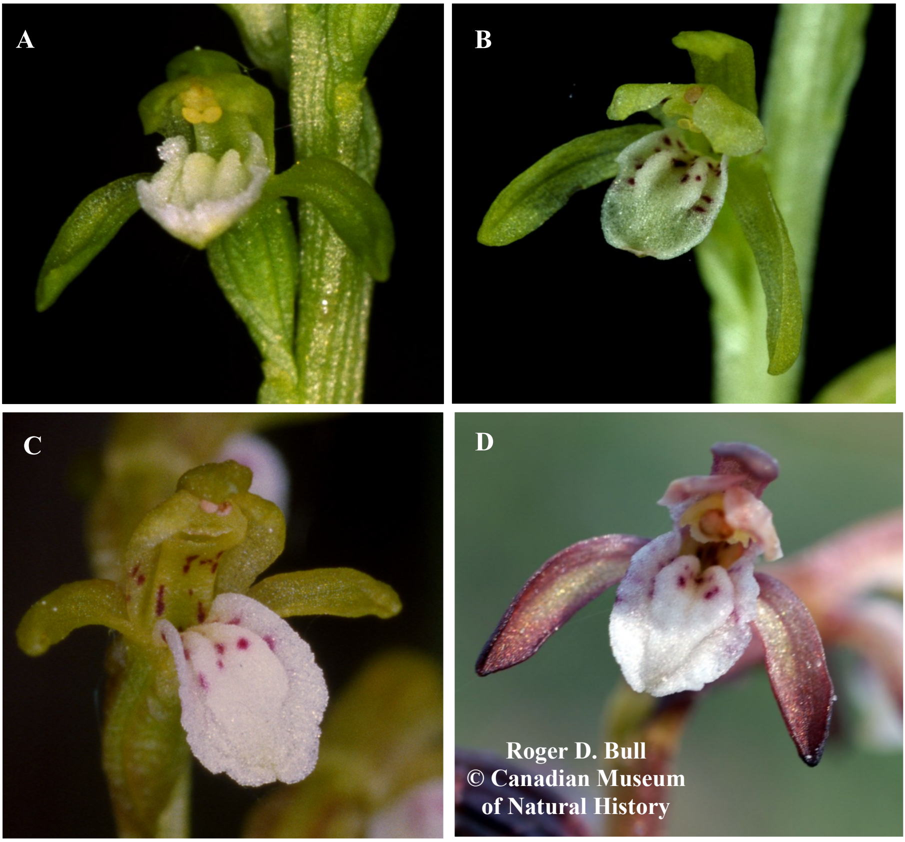

Fig. 2. Variation in *C. trifida* flower coloration and spotting. A) forma *verna* showing a bright green flower with pure white lip. B) forma *trifida* showing a bright green plant with purple spotted lip. C) forma *trifida* showing a yellowish-green flower with a purple spotted lip with spotting on column and sepals. D) forma *trifida* from the Canadian arctic showing intense brown coloration (photo from http://arcticplants.myspecies.info/taxonomy/term/1814/media?type=All&page=1 (original image cropped to emphasize single flower).

Description: The slender flowering stem of *Corallorhiza trifida* rises from a basal sheath and typically ranges from 4 to 20 cm in height; with 8-15 cm being typical. The stem bears 4 to 15 tiny flowers in a raceme that may be lax or densely flowered. The stems and floral parts except for the lip are bright green or yellowish green, sometimes tinged with brown. Some plants, particularly in the high arctic, can be intensely brown, showing minimal green (**Fig. 2D**). In forma *trifida* the lip is white spotted with purple; the sepals, petals, and column may also be spotted with purple. In forma *verna* the lip is pure white with no spotting; the sepals, petals and column likewise lack spotting. The petals and dorsal sepal form a hood that arches over the column, the lateral sepals are linear-oblong and spread wide, often drooping downward. The lip is typically 5 mm long, oblong to ovate, sometimes rectangular, with two small tooth-like basal lobes. The margin is slightly irregular, but untoothed; the edges may be slightly to strongly upcurved to give a concave or even boat-like appearance. The upper surface bears two prominent ridges (calli). The column is 4-5 mm long and curves upward over the lip, bearing two bright yellow pollinia at its tip., behind an anther cap that decays shortly after the flowers open. The flowers often appear sessile or nearly so, the pedicel being indistinct, short, and commonly merging smoothly with the ovary base. (**Fig. 7**). The flowers initially stand erect, but as the ovary swells, and the fruit capsules begin to mature, sag as the now noticeable pedicel bends downward until the fully developed capsules point downward along the stem (**Fig. 5**).

Fig. 3. Newly opened flower of *Corallorhiza trifida* with an intact anther cap and pollinia at the end of the column. The anther cap has not yet decayed to allow the pollinia to rotate downward onto the stigma. The flower shows purple spotting on the column and a mostly white lip with minor spotting, which technically places it under forma *trifida*. The difficulty of making generalizations about the range of the two varieties is illustrated by this plant which was found growing at the extreme southern end of the species range, eighty miles north of Milwaukee, Wisconsin, along the Lake Michigan shoreline, where one expects to find forma *verna*.

Pollination: Although the flowers appear to be adapted to visitation by small insects, pollination in *C. trifida* has been shown to be autogamous by studies carried out in both North America and Europe (Freudenstein 1997, Claessens 1998, Catling 1983). These authors all report that fruit set is high with values ranging from 50 to 100%, even when the plants are protected from insect visitation. Small insects such as empid flies have been observed as visitors, but none have ever been observed to remove pollinia (Evans 1917). The process of self-pollination is however readily observed. Four pollinia are attached to the end of the column by a short stipe, behind an anther cap. Shortly after the flowers open, or sometimes as the flowers open, the anther cap decays and the pollinia are free to rotate downward from the end of the column onto the stigmatic surface immediately below (**Fig. 4**). Reports by several authors indicate that the possibility for outcrossing is further minimized by the fact that the viscidia are poorly developed, and are functional only for a short time; quickly loosing their adhesive properties shortly after the flowers open, resulting in minimal opportunity for outcrossing (Claessens, 2011). Nevertheless one does encounter occasional flowers where the pollinia have been removed without being deposited on the stigma (**Fig. 4F**). The ovaries typically begin to swell within a few days.

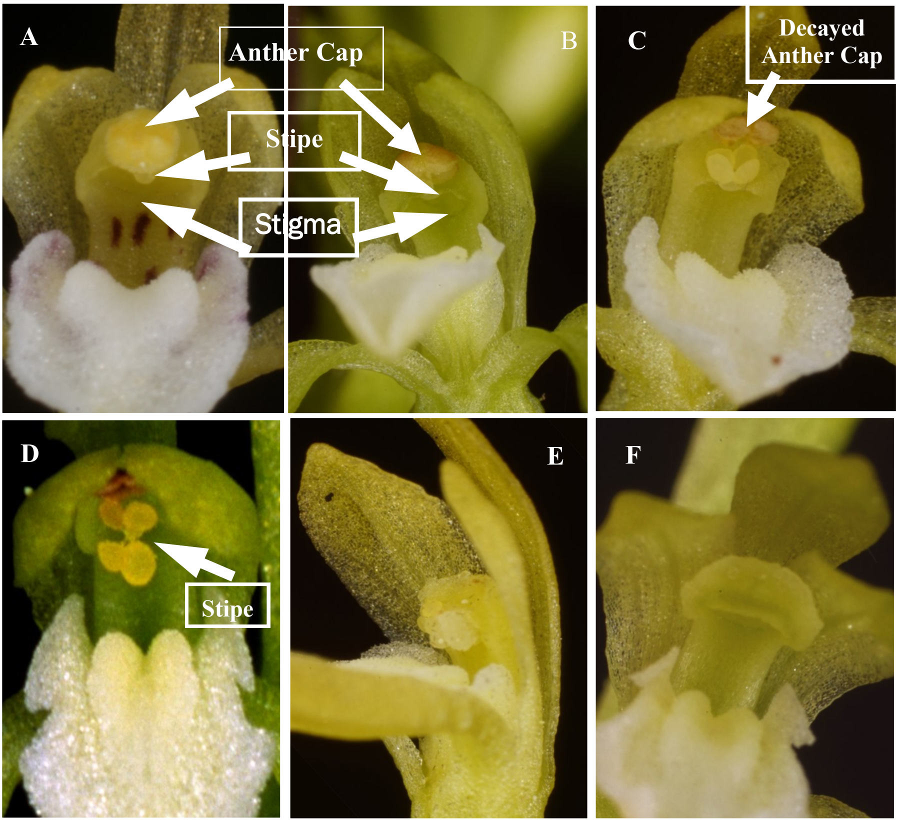

Fig. 4. Self-pollination in *C. trifida* **A, B**) Newly opened flowers with pollinia and anther cap in place, showing the pollinia with pollinia and anther cap resting on the rostellum at the column tip. The rostellum serves to separate the pollinia from the stigmatic surface on the underside of the column **C**) Flower with decayed anther cap with pollinia still resting on the rostellum. **D**) Flower with pollinia attached to stipe rotating downward toward the stigmatic surface. **E**) Flower with pollinia attached to stigmatic surface. **F**) Failed autopollination, the pollinia have been removed by unknown agent.

The initially green seed capsules (**Fig. 5A**) turn brown by fall, and commonly persist through the winter. In the author's experience, dehiscence is often delayed, and intact seed capsules can be found a year after blooming, even as new plants emerge and begin to bloom. Cursory observation of the contents of a small number of seed capsules in Great Lakes populations indicate that seed set is generally high, (**Fig. 5B**). Please note that this is a qualitative observation, based on the author pinching open a few mature capsules and observing the numerous seeds inside.

Fig. 5. The fruiting capsules and seeds of *C. trifida*. **A**) The capsules are visible for several months and often persist through the winter. **B**) The capsules are filled with numerous seeds (0.6mm to 0.7 mm long and 0.15 to 0.2 mm wide).

Photosynthesis and Fungal relationships: All tissues of *C. trifida* except for the labellum still contain significant quantities of chlorophyll, as evidenced by the simple fact that the plants are green. On this basis one might suspect that *C. trifida* might still be an autotroph in good standing, despite being in a genus that is primarily mycoheterotrophic. As a reminder, mycoheterotrophs are plants that obtain nutrients through a parasitic relationship with soil fungi, that first invade the plants rhizome, are taken inside cells within the rhizome, and are subsequently digested. With few exceptions this appears to be a true parasitic relationship, in that the fungal mycelia derive little or no benefit from this interaction. These fungal partners have been identified by DNA analysis as members of the closely related genera *Theleophora* and *Tomentella* (McKendrick 2009)

The position of *C. trifida* on the continuum between pure autotroph and pure mycoheterotroph was for a period of time a matter of contention. An initial study in 2008, compared the natural abundance isotopic ratios of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ of *C. trifida* with those of nearby autotrophic and mycoheterotrophic species (Zimmer 2008). This study was based on the observation that $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios differ significantly between autotrophic plants and soil fungi. Thus the isotopic ratios observed for mycoheterotrophic plants which digest soil fungi should resemble those of the fungi as opposed to neighboring autotrophic plants. The results indicated that *C. trifida* was mostly mycoheterotrophic, but still derived some nutrition through photosynthesis. A more conclusive study reported a year later, using isotropic tracer methodology, determined that there was minimal fixation of carbon dioxide (Cameron 2009). The authors of that study exposed *C. trifida* plants, along with known autotrophic and mycoheterotrophic control species, to ^{13}C labeled carbon dioxide, and subsequently determined the quantity of ^{13}C incorporated into plant tissues. The results indicated that CO_2 uptake by *C. trifida* closely resembled that of the fully mycoheterotrophic (and achlrophyllous) orchid *Neottia nudas-avis.* Uptake in both species was roughly 2% of that observed for fully autotrophic plants. The conclusion reached was that *C. trifida* is a true mycoheterotroph, despite producing chlorophyll and having an intact photosystem capable of harvesting light energy. The light energy absorbed is apparently dissipated unproductively and is never used to drive carbon fixation.

The epiparasitic relationship of *C. trifida* to adjacent autotrophic woody plants was demonstrated by exposing birch (*Betula*) and willow (*Salix*) seedlings to ^{14}C labeled carbon dioxide, and finding that carbon fixed by photosynthesis in the seedlings was transferred to *C. trifida* via an ectomycorrhizal network (McKendrick 2000a). The fungal mycelia acted as a conduit for nutrients between nearby trees and the orchid. Even as *C. trifida* derives nutrition from fungal mycelia that invade the rhizome from the surrounding soil, the fungal mycelia form an extensive network that extends many feet outward from the orchid. As these mycelia come into contact with the roots of nearby trees, they surround the root, encase it, and hold it in a symbiotic embrace. This interaction of the fungal mycelia with the tree roots is completely different from the interaction with the orchid rhizome a few feet away. Rather than being taken up and consumed by the cells of the tree root, the mycelia merely invade the root cortex without entering the cells. The relationship is described as ectomycorrhizal, in that the mycelia do not enter the individual cells of root, but rather surround the root cells, and form a structure known as a Hartig net (named after Robert Hartig, a 19th century German plant pathologist, who first described it). The fungal cells and root cells are in direct physical contact and hence are able to easily exchange nutrients through their cell membranes. Sugars produced originally in aboveground leaves by photosynthesis are transferred to the fungal mycelia. In return the fungus provides the tree root with inorganic nutrients such as phosphate, nitrogen, and metal ions, which it is able to take up from the soil much more readily than the root cells alone (Bücking 2012).

Habitat: As a mycoheterotroph that is dependent on fungi, that are in turn, in an ectomycorhizzal relationship with the roots of nearby trees (Zelmer 1995), one would expect *C. trifida* to be confined to forested areas, and in much of its range this is indeed true. However in the extreme north of its range, *C. trifida* is at home on open tundra, where the boreal forests, found further south, have given way to a landscape of stunted shrubby willows (*Salix*), birches (*Betula*), and alders (*Alnus*). Further south in less brutally harsh environments, it is found in varied habitat; being found in both coniferous and hardwood forests, in both upland and low lying wet areas. In the Great Lakes region of North America *C. trifida* (**Figs. 6, 7**) can grow in sunny open forest or in areas of deep shade; in habitats as varied as *Sphagnum* hummocks in Balsam-Cedar swamps or on forested sand dunes, within a few hundred meters of the Lake Superior or Lake Michigan shorelines. At the southern end of its range in New Mexico, it can be found at high elevations growing in dry pine and fir duff (Coleman 2002).

Fig. 6. Typical flowering raceme with scale. Typical plants in the Great Lakes region are 12 to 15cm tall with a 3cm long raceme, 1.5cm in diameter.

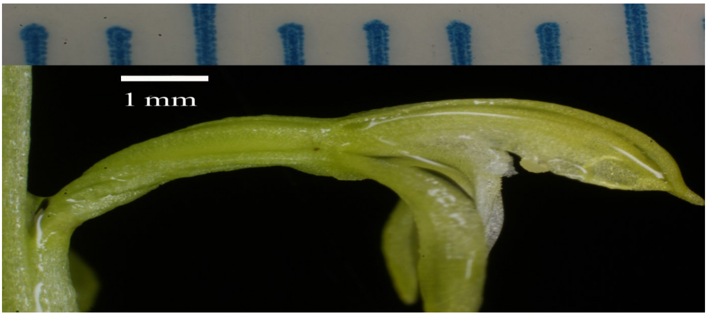

Fig. 7. Side view of *C. trifida* flower. Note striations on the ovary resulting from twisting during resupination and the absence of a distinct pedicel. The overall flower length ranges from 7-9 mm, with a slender ovary 3-4 mm in length.

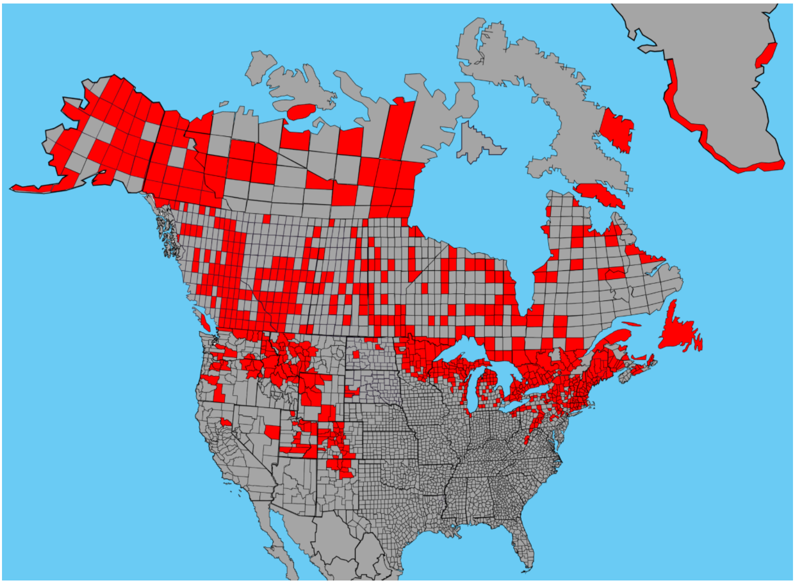

Fig. 8. Distribution map of *Corallorhiza trifida* in North America. Alaska and most of Canada are divided into one degree or four degree latitude-longitude grids. The lower 48 states are divided by county.

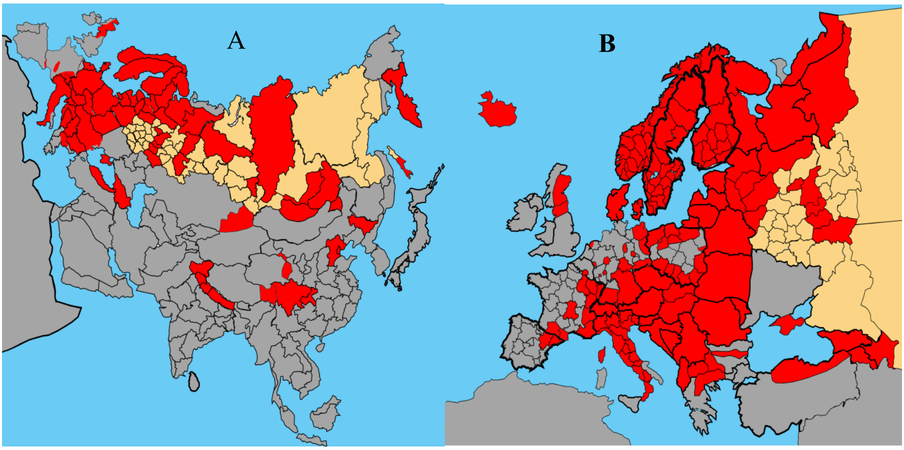

Fig. 9. Maps showing the distribution of *C. trifida* in Eurasia **A**) Distribution in Eurasia, with emphasis on Asia. **B**) Expansion of European area. Regions colored yellow indicate where *C. trifida* should be present according to Vakhrameeva (Vakhrameeva, 2008), while areas in red mark areas where *C. trifida* is confirmed either by online herbarium reports, or botanical literature listing its presence in a specific province or geographic area.

Distribution: *Corallorhiza trifida* is the most widely distributed of all the species of Coralroot; its distribution is circumpolar; being at home in alpine and arctic regions of North America, Europe, and Asia (**Figs. 8, 9**). Forma *trifida* is the only form found in Eurasia, while both forma *trifida* and forma *verna* occur in North America. Forma *trifida* occurs primarily in the arctic and subarctic regions of Canada and Alaska, while forma *verna* is found typically further south in southern Canada and the United States. The goal of this distribution analysis is to provide an analysis of places where *C. trifida* is found, based first on primary botanical sources such as online herbarium records and journal articles. The second source of information came from state, provincial, and regional monographs, books, and online floras where the author(s) clearly took the time to examine herbarium specimens from their region. The third source of information came from state or provincial status reports often prepared for the general public, commonly prepared by trained botanists, but not necessarily botanists specializing in the Orchidaceae. Finally the author in several cases consulted online photographic sources, containing photos posted by the general public.

In arctic North America C. *trifida* is found from Alaska to Newfoundland, its northern limits extending well above the Arctic Circle into the Canadian Arctic Archipelago; where it reaches its northern limits on Baffin Island, off the northern coast of Quebec, and on Victoria Island off the northern coast of the Northwest Territories (Gould 1997, Gillespie 2015). The range extends eastward from Newfoundland to coastal Greenland (Kliim-Nielsen 1971), and southward through Quebec (Houle 2013, Beausejour 2008), into the northeastern United States, where it reaches its southeastern limit in the Appalachian Mountains of West Virginia (Bentley 2000). In 2015 it was discovered for the first time in Virginia (Nelson County) (Digital Atlas of the Virginia Flora, http://vaplantatlas.org/). Previous reports from Virginia are in error (*vide infra*).

Along the east coast it extends as far south as northern New Jersey, where it is still extant (Lamont 2011). In the Great Lakes region, the range extends south from Canada into northern Michigan, northern Wisconsin, and northeastern Minnesota (Case 1987, Smith 2012). In the western Great Lakes region it once reached its southern limit at the southern tip of Lake Michigan, in Indiana and Illinois. It likely occurred in southern Cook county in what is now the far southside of Chicago. (Higley 1891). Based on this late nineteenth century report, Sheviak accepted it as part of the Illinois flora, but was unable to locate any surviving herbarium specimens (Sheviak 1974a, 1974b). It also occurred in nearby northern Indiana, near what is today Indiana Dunes National Lakeshore (Peatie 1930). These Illinois and Indiana sites were almost certainly destroyed as a result extensive industrial development in the nineteenth and early twentieth centuries (Homoya 1993). Further to the east it is still found along the southern shore of Lake Erie in northern Ohio, where it is considered endangered. This statement is based on post 1980 reports of its occurrence in three northern Ohio counties, and the existence of an herbarium specimen from northern Ohio (Summit county), dating from 2002. [The Ohio State University Herbarium Online Database search, and Ohio DNR Rare Plant List (https://naturepreserves.ohiodnr.gov/portals/dnap/pdf/Rare_Plant_Abstracts/Corallorhiza_trifida.pdf)].

In the northern Great Plains area it is known from a few locations in North Dakota and the Black Hills of South Dakota (McGregor 1977, Stewart 1973). In the western United States its range extends south in the Rocky Mountains through Montana and Wyoming to Colorado, Utah, and northern New Mexico (Coleman 2002). The species is rare in Washington, Oregon, California, and Nevada; reaching its southwestern limit in Plumas county California, the only known station for the species in California (Coleman 1995). Its presence in Nevada is based on a single herbarium specimen collected from White Pine County in 1941 (Sorrie 1978). No further botanical reports, photos (Flickr), or herbarium specimens (online) could be located for Nevada. Reports of this orchid from Missouri (Lawrence and Warren counties) and Virginia (Albermarle County) have proven to be incorrect; the plants were shown to be misidentified yellow color forms of *Corallorhiza wisteriana* and *Corallorhiza maculata*, respectively (Summers 1996, Bentley 2000). Similarly, a herbarium specimen collected in 1974 in southern New Mexico (disjunct from other New Mexico locations by 200 Miles), and now at Brigham Young University, is a misidentified *C. wisteriana* (Ron Coleman, personal communication).

C. trifida is widely distributed in cold regions of Europe and Asia, being found from Iceland to India, and from the Pyrenees of Spain to the Kamchatka Peninsula of northwest Siberia. *C. trifida* has two primary centers of distribution in western Europe, the first area is centered on the Baltic Sea, the second in the Alps and other high elevation regions of southern Europe and Asia Minor. In extreme northern Europe, from Iceland, to Scandinavia, and northwest Russia, it is widespread and in some locations common (Johnsen 1997, Blinova 2008, Bournerias 1998, Efimov 2012, Vakhrameeva 2008). As one moves southward from Scandinavia, it becomes rarer and is found only in scattered locations in northern Poland, northern Germany, and Denmark (Kretschmar 2008 Szlachetko, 2001). In the Netherlands it was known from a single small site on the Dutch coast; having been discovered there in 1902. The plants were observed up to 1942, but after the Second World War, the plants at this site could not be relocated, and *C. trifida* is now considered extirpated in the Netherlands (Hiemans 1902, Bijleveld 1962, Kreutz, 2000). It is known from the Ardennes Forest region of southern Belgium and adjacent areas of northern France (Bournerias 1998). It is not known from Ireland, but is widespread in eastern and central Scotland, becoming less common in northern England (Northumberland, Cumbria, and Yorkshire)(Allen 1993, Harrap 2005). *C. trifida* is widespread in the Alps and other mountain ranges of central Europe from eastern France, through Switzerland, northern Italy, and Austria to Bulgaria, Romania, and Ukraine (Reinhard 1991, Bujoczek 2002, Griebel 2013, Dusak 2010, Perraza 2013, Assyov 2012, Flaviu-Crisan 2014). It reaches its southwestern limit in the Pyrenees of southern France and northeastern Spain; being found along the French-Spanish border in the French provinces of Languedoc-Roussillon and Midi-Pyrenees, and in the adjacent Spanish provinces of Catalonia and Aragon (Bournerias 1998, Otango 2004, Gonzales-Prat 2001-2002, Casals 2012-2013, Canal 2016).

It has not been found on the Mediterranean Islands of Sicily or Sardinia, but is known from a single location on the island of Corsica (San Petrone Massif)

(Schatz, 2013). It is found in all provinces of mainland Italy, except for Puglia, which forms the "heel" of the Italian boot on the Adriatic coast. It is found throughout the Balkans from Slovenia and Croatia southward through Serbia and Albania, reaching its southern limit in Northern Greece (Raus 1996). In the Black Sea region it is found in mountainous areas of northern Turkey and the Crimean Peninsula (Kreutz 1995). Just to the east of Black Sea it is found in the Caucasus Mountains of Armenia, Georgia, and Azerbaijan (Fateryga 2014, Gabrielian 1981, Akhalkatsi 2003). The yellow area on the accompanying Eurasian distribution maps (Figs. 9A,B) indicate areas where *C. trifida* is possibly or likely present based on general distribution information for Russia and adjacent areas (Vakhrameeva 2008), but for which no specific corroborating province level information could be located in the botanical lireature.

The details of the distribution of *Coralloriza trifida* in Asia are sketchy at best. Due to political instability, and, or closure to outsiders, minimal information is available for several countries in this region; in particular, North Korea, Pakistan, and Afghanistan come to mind. The most detailed information for *C. trifida* is available for India, China, and parts of Russia. In the north, its range extends from Scandinavia, across European and asiatic Russia to the Pacific Coast (Vakhrameeva 2008). Reports in Russian botanical literature indicate its presence in the following areas; Penza, Bashkortostan, Komi Republic, Perm Krai, Kermovo, Nizhni-Novogorod, Vologda, Mordovia, Tyumen, Ivanovo, Sverdlovsk, Transbaikalia, and the Kamchatka Penninsula (Andrievska 2010, Biryukova 2014, Borisova 2014, Borisovich 2014, Glazunov 2012, Gorchakovskii 2003, Krestov 2008, Muldashev 2010, Ovesnov 2010, Shepeleva 2009, Sheremetova 2012, Sherbina 2009, Tereyuk 2011, Vasjukov 2012). From Siberia the range extends southward across China, finally reaching its southern limit in the western Himalaya Mountains of Nepal, and the adjacent northern Indian provinces of Utarakhand, and Jammu and Kashmir (Rai 2010, Jalal 2012). Here at only 30 degrees north latitude, the same latitude as central Florida, the cold environment *C. trifida* requires is made possible by high elevation; being found at an elevation of 3800 meters (11000 feet).

C. trifida is widely distributed in the mountainous regions of China (Perner 2007, Ke 2009) The treatment in the Flora of China attributes *C. trifida* to the following provinces; Gansu, N Guizhou, Hebei, Jilin, Nei Mongol, Qinghai, Sichuan, Xinjiang (Ke 2009). Specimens corresponding to these provinces were found in a search of the Chinese National Virtual Herbarium.

Its status in Korea and Japan is questionable. Many references, both online and written, list *C. trifida* as occurring in both countries, without citing either herbarium specimens, or primary botanical sources. No reliable references could be found documenting its current existence in either of these countries. With respect to Korea two recent publications dealing with Korean orchids provide little insight. The first reference, which documents the distribution of orchids in Korea, could find no herbarium specimens supporting its presence, and thus listed the status of *C. trifida* as data deficient (Lee 2006). The second, a genetic study dealing with barcoding of Korean Orchids, used a specimen taken from Mt. Changbai, in Jilin Province of China, located on the border of North Korea (Kim 2014). It should be noted that Mt Changbai was traditionally part of Korea, but came under Chinese control in the 1950's.

In addition to references cited in the accompanying text, the following online herbarium databases were searched. 1) Museum of Biological Diversity Herbarium, The Ohio State University, Online Specimen Access; https://herbarium.osu.edu/online-data-access. 2) Consortium of Northern Great Plains Herbaria, http://ngpherbaria.org/portal/collections/index.php. 3) SEINet, http://swbiodiversity.org/seinet/index.php. 4) Intermountain Region Herbarium Network, http://intermountainbiota.org/portal/ 5) Consortium of Pacific Northwest Herbaria, http://www.pnwherbaria.org/ 6) Consortium of Midwest Herbaria, http://midwestherbaria.org/portal/ 7) Consortium of Northeast Herbaria, http://neherbaria.org/ 8) University of Colorado Boulder, Museum of Natural History, Specimen Database of Vascular Plants, http://cumuseum-archive.colorado.edu/Research/Botany/Databases/search.php 9) Chinese Virtual Herbarium, http://www.cvh.org.cn/cnpc 10) Virtual Guide to the Flora of Mongolia, http://greif.uni-greifswald.de/floragreif/

Several references consulted in the preparation of this manuscript were originally written in foreign languages (French, Dutch, Spanish, Catalan, Italian, and Russian) that the author is unable to read. Relevant portions of these documents were translated using Google Translate. The author also thanks Elisabeth C. Creutz for translating portions of several French documents.

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Calypso bulbosa xkostiukiae with Other Varietal Forms Observed.

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I play badminton with John Whittall who is a nature photographer so we often talk about wild orchids. I mentioned to him that one of my favourite spots for *Calypso bulbosa* had disappeared due to beetle kill and the resultant cleanup. He told me of a campsite near Merritt. BC that had these orchids. I went to visit the site. Unfortunately the campsite was so full, I couldn't even park. I told John this and he asked if I would like to meet him at the campsite on the next Friday and he would show me three orchid sites. I jumped at the opportunity. So, on May 13 2016 I met John and his wife Anne at the campsite and along with another couple, we went to look at the sites. We found *Calypso bulbosa* var. *americana* (**Fig. a**) at the first two sites, including some forma *rosea.* (**Fig. b**) which have the pink lips.

On our way to the third site, I spotted a different site and called John back because I saw some *Calypso bulbosa* var. *occidentalis* (**Fig. c**). Closer inspection showed crosses of the two varieties, *Calypso bulbosa xkostiukiae* (**Fig. d**).

I had no idea that the western fairy-slippers were so far east. So to find them and crosses between the eastern and western fairy-slippers within an hour of my home was really exciting! We all took pictures and had spent so much time at the three spots we never did go on to John's third site.

I was disappointed in my shots of the *Calypso bulbosa* var. *occidentalis* so I went back to the campsite on May 16th to take more pictures. Unfortunately over six orchids had been picked and thrown on the ground, including the one I most wanted to photograph.

So, how do you tell the difference between these varieties and the cross?

Fig. a shows the *Calypso bulbosa* var. *americana*. It features a plain white lip and has a yellow beard (or a pink lip if it is the *Calypso bulbosa* var. *americana* forma *rosea,* **Fig. b**). *Calypso bulbosa* var. *occidentalis* (**Fig. c**) has a spotted lip and a white beard. *Calypso bulbosa xkostiukiae* has the spotted lip but a yellow beard (**Fig. d**). The pictures below show the variations in beards I observed.

Fig. e shows the white beard and the spotted lip of the *Calypso bulbosa* var. *occidentalis.* **Fig. f** shows the yellow beard and the plain coloured (white or pink) lip of the *Calypso bulbosa* var. a*mericana.* Note that the spots in the var. *americana* are in the beard, not on the lip.

I don't see the *Calypso bulbosa* var. *occidentalis* much in my area so I am not sure if the following observations are the norm or not:

Older blooms have darker lips than young blooms and the beard hairs get to be thicker and more like a rope. See the examples in **Figs. g & h**, and compare to **e**.

The site for the orchids was beside a path that went by a very swampy area. I had five pictures with mosquitoes on or in the orchids. **Figs. i & j** show two orchids that were beside each other in a group of eight *Calypso bulbosa* var. a*mericana* blooms, so it is possible that the mosquitoes are the pollinators.

Figs. i & j. *Calypso bulbosa* var. *americana* with a mosquito on each.

Fig. k. *Calypso bulbosa* var. *occidentalis*
with Fig. l. a *Calypso bulbosa xkostiukiae* just behind it

Last in this display of variations in this brief summary of *Calypso bulbosa* flowers observed, is one of *Calypso bulbosa xkostiukiae* (**Fig. m, upper image**) and

one of a lateral view of *Calypso bulbosa* var. *occidentalis*. (**Fig. n, lower image**).

...and this display closes without further comment.

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