



The Native Orchid Conference Journal



Volume 10(2) April-June 2013

Volume 10, Issue 2

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A Cytogeographic Survey of *Spiranthes romanzoffiana* Cham. and Its Taxonomic Implications

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Cytology has proven to be a key to understanding the evolution of much of the genus *Spiranthes* (Sheviak 1976, 1982, 1984, 1990, 1991, 2008, 2012; Sheviak and Catling 1980; Sun 1996). From mere determination of chromosome numbers to more complex cytogenetic analysis, species status has been demonstrated and the nature of variation elucidated. Lula Pace's pioneering efforts established a base number of $n=15$ and also disclosed the presence of tetraploids (Pace, 1914). For many years afterward, little additional information was obtained, and some that was later proved to be erroneous. Chromosome analysis is not easy, and people tend to get the numbers that they expect. Hence initial counts of *S. romanzoffiana* Cham. reflected the existing knowledge of the group, rather than the actual condition in the species. Counts of $2n=60$ (Heslop-Harrison in Löve and Löve 1961) and $2n=30$ (Taylor and Mulligan 1968) were in keeping with expectations and stood without question for a number of years. It was only with Paul Catling's critical determination of $2n=44$ (Catling 1980) that the picture began to change.

In the course of my studies of the genus, I collected cytological material from *Spiranthes romanzoffiana* across a broad geographic area. Initially these samples were obtained as peripheral to a study of the *S. cernua* (L.) L.C. Rich. complex, but later the effort was expanded greatly as the data proved to be critical for analysis of various western problems, including the determination of species status for *S. diluvialis* Sheviak and *S. delitescens* Sheviak. Although the focus of these more recent efforts was resolution of certain problems in the far West, a general pattern began to emerge that in itself is significant to interpretation of the species' variation, evolution, and proper taxonomic treatment. This paper presents certain aspects of the cytogeography of *S. romanzoffiana* and its taxonomic implications.

The genus *Spiranthes* is comprised of two principal cytological lineages (Sheviak 1984, 2008). The larger group, including most of the eastern North American and Old World species, is based on $n=15$. A number of these species

have broad geographic ranges. The other group, with $n=22$, includes relatively few species, primarily of the cordilleran region of North America. The only wide-ranging member of the group is *S. romanzoffiana*. This mostly boreal and montane species is transcontinental in the North and ranges along the cordillera from the Arctic to Chihuahua. Further east, it occurs south through the Great Lakes region. Disjunct, probably introduced populations are known from Ireland and Great Britain.

THE ROLE OF POLYPLOIDY IN *SPIRANTHES* SPECIES AND SPECIATION

Most *Spiranthes* species are diploids, with either $2n=30$ or $2n=44$. A few polyploids are known. Polyploidy commonly confers genetic isolation from diploid relatives due to the sterility of hybrids with odd-numbered or unbalanced chromosome complements. Hence allotetraploids are typically isolated from their diploid parents and backcrosses are not conduits for gene flow. Furthermore, the mathematics of tetrasomic inheritance greatly restricts recombination of parental characteristics in tetraploids, while simultaneously variation in the percentages of parental chromosomes in subsequent generations can give rise to a multi-character, nodal variation pattern quite different from that seen in diploids.

Two classic examples of allotetraploids are known among North American *Spiranthes*: *S. diluvialis* and *S. delitescens*. Each of these species was derived through hybridization of members of the $n=15$ and $n=22$ series. The distinctive cytology of these species, with $2n=74$ and the regular formation of 37 bivalents in meiosis, unequivocally established their allotetraploid origins (Sheviak 1984, 1990). The morphology of *S. diluvialis* furthermore unambiguously indicated *S. magnicamporum* Sheviak [$2n=30$] and *S. romanzoffiana* [$2n=44$] to be its progenitor species (Sheviak 1984). Subsequent allozyme analysis further demonstrated this evident origin (Arft and Ranker 1998). Although the origin of *S. delitescens* through hybridization between members of the two cytological lineages is similarly clearly established, the parental species are less obvious. Through a combination of morphological analyses and artificial hybridization, it was suggested that one parent was *S. vernalis* Engelm. & Gray [$2n=30$]; the other parent was less satisfactorily proposed as *S. porrifolia* Lindl. [$2n=44$] (Sheviak 1990). The cytology of both *S. diluvialis* and *S. delitescens* precludes hybridization and gene flow with other species, and both are recognizable within limited ranges of morphological variability that express combinations of parental characteristics. The more diverse genetic origin of *S. diluvialis* (Arft & Ranker 1998) and its broad, highly discontinuous range support greater variation in that species than in the very local endemic *S. delitescens* with its small total population. In *S. diluvialis*, occasional plants may appear markedly more like *S. romanzoffiana*; such plants may be chromosomal segregates with unbalanced chromosome sets, as one such plant [*Sheviak 2300b*, Garfield Co., Utah.

(NYS)] variously displayed in meiosis a trivalent and corresponding univalent, six univalents, or regular bivalent formation.

The situation in *Spiranthes cernua* is more complex and has bearing on the interpretation of *S. romanzoffiana*. This species is part of a small polyploid complex occurring across the eastern half of the United States and southern-most Canada. In its most limited sense it includes four species. Three are diploids ($2n = 30$): *S. ochroleuca* (Rydb.) Rydb., *S. odorata* (Nutt.) Lindl., and *S. magnicamporum*. The fourth, *S. cernua*, is a polyploid (for the most part tetraploid, $2n = 60$, but including some triploids) noted for extraordinary morphological variability. This species is a facultatively apomictic compilospecies: It acquires genes from its diploid relatives via unreduced diploid gametes and then utilizes these adaptively, preserving unique combinations through apomixis while nonetheless undergoing limited recombination that generates still more variation. In part, this variation involves the variable expression of parental characteristics, but a salient feature of the variation of *S. cernua* is the appearance of novel forms that are not predictable from the features of the parents. In different portions of the species' range, and under the influence of different diploids, distinct suites of forms may be present; these are at once unique, and yet merely local expressions of an underlying theme. The species, then, is intrinsically hybrid in nature, yet forms a coherent conceptual unit due to certain patterns of variability and the universal presence of apomixis. The diploids remain isolated from the polyploids by asexual, obligately apomictic triploids that are reasonably viewed as part of the variability of the facultative agamospecies *S. cernua* (Sheviak, 1982; 1991). The gene flow that underlies the diversity that characterizes *S. cernua* is thus unidirectional, and the diploids are maintained as distinct species.

METHODS

Initial study of herbarium material in collections across the West was conducted as basic to elucidation of *Spiranthes diluvialis*. This survey disclosed other patterns that warranted investigation, leading to the recognition of *S. delitescens* and *S. infernalis* Sheviak, and highlighting a number of other patterns that guided field work. Standard herbarium collections were made in the field over a period of decades. Often these were supplemented by representative live plants that were subsequently cultivated, permitting continued study for a number of years. Phenotypic stability or plasticity could then be assessed and serve to aid interpretation of herbarium specimens collected by others across a wide geographic area. In morphologically variable populations a range of collections was made to sample the perceived range of variants. Samples for cytological study were obtained in the field and sometimes from collected plants in cultivation. All counts are from ovarian tissue as outlined in Sheviak (1982). This provides an abundance of mitotic divisions and, in appropriate buds, meiotic

figures as well. All counts are vouchered by pressed specimens deposited at NYS. In most cases the actual specimen counted is preserved, but in a few cases the count is represented only by other members of the population; this status is recorded on the sheet.

SYNOPSIS OF THE SPECIES

Spiranthes romanzoffiana

Spiranthes romanzoffiana is a particularly distinctive species (Figure 1, page 18). Although considerable variation occurs in the size and proportions of flowers, the relative density of inflorescences, and the number, dimensions, and persistence of leaves, the species is remarkably constant in a few floral characters (Figure 2, page 18). The sepals are basally connate to form a short calyx tube, and the lateral sepals are connivent with the dorsal and petals, sweeping upward and together forming a hood above the lip. The lip is strongly constricted subapically, with a pronounced isthmus separating a broad base from a usually abruptly expanded apex. Glabrous above, the apex is reflexed just beyond the point at which the lip extends from the calyx tube. This combination of upswept hood and reflexed lip, when repeated along the length of an inflorescence, imparts a precise geometry that is immediately distinctive. Most significantly, the lip bears only three veins; the lateral bear a few branches that depart and branch again at nearly right angles (Figure 2, page 18). Lip venation is perhaps the key diagnostic feature, as lip shape and lateral sepal orientation vary.

Spiranthes porrifolia

A related species, *Spiranthes porrifolia* Lindl., has in the past caused considerable confusion. It is widespread in California, ranging into extreme southwestern Oregon, and is disjunct at a few sites in Washington and Idaho. Plants variously intermediate between *S. romanzoffiana* and *S. porrifolia* have been well known from the West, and led Ames and Correll (1943) to reduce *S. porrifolia* to varietal status under *S. romanzoffiana*. In their discussion of *S. romanzoffiana* var. *porrifolia* (Lindl.) Ames & Correll, they emphasized lip shape and the size of basal calli, attributing to var. *porrifolia* an essentially lanceolate lip without apical dilation, and large basal calli. Plants with these characteristics were said to be common in California, and found less frequently elsewhere in the far West. Such plants furthermore commonly bore slender, even secund inflorescences. Intermediate plants obscured the distinctions, however, and led these workers to conclude that *S. porrifolia* was merely a local, variable race of the wide-ranging *S. romanzoffiana*. In fact, true *S. porrifolia* bears little resemblance to *S. romanzoffiana*, and consideration of a number of

characters beyond the two treated in their work serve to discriminate it. (Figure 3, page 19). The yellowish ivory flowers are slender, rather tubular, with the sepals and petals curving outward apically. Lips are scarcely or not at all dilated apically, and the subapical upper surface bears a dense cushion of stout trichomes (Figure 4, page 19). Venation of the lip is variable, often with a number of veins with parallel branches. Problematically, throughout the region these features can be found in various combinations and to various degrees in plants otherwise typical of *S. romanzoffiana*.

Spiranthes stellata

Spiranthes stellata P.M.Br., Dueck, & K.M.Cameron comprises two subspecies, with the diploid subsp. *perexilis* Sheviak the presumed progenitor of the tetraploid subsp. *stellata*. The former is a rare plant known from only a few sites in the Sierra Nevada (Sheviak 2012). This is an exceedingly slender, tall plant with long inflorescences of very small flowers. The spike is only slightly spiraled, with many flowers per cycle; some are virtually secund. Flowers are for the most part typical of *S. romanzoffiana*. However, lateral sepals tend to project forward, or spread to a varying degree, but may be connivent with the petals and dorsal sepal to form a hood as in typical *S. romanzoffiana*. Lip shape is typical of that species, and the venation may also duplicate its three nerves with branches at right angles. The subapical adaxial surface, however, bears a cushion of peg-shaped trichomes as in *S. porrifolia*. I have earlier accommodated these plants in a key to western and Central American *Spiranthes* (Sheviak, 1990), where I treated them as a local race of *S. romanzoffiana* and commented that they might constitute a distinct taxon.

Much more widespread, tetraploid subsp. *stellata* occurs throughout much of montane California and scattered sites in the Central Valley and southwestern Oregon. Plants are in general similar to subsp. *perexilis*, but larger and more robust, with yellower flowers that are highly variable in individual characters, in contrast to the more uniform, white flowers of the diploid. (Figure 5, page 19-20). In particular, lateral sepal position and the shape of the flowers varies greatly. Lip characters range well beyond those of subsp. *perexilis*. The apical dilation of the lip is often suppressed, and the overall lip shape varies from pandurate to lanceolate. Lip pubescence varies from a well-developed cushion to sparse and unorganized or completely lacking. Whether the variability of the subspecies results directly from the increased ploidy level or reflects ancestral or recent gene flow is unknown. The variability of these rather well-defined plants is only part, however, of a much more complex pattern of variation that obscures distinctions and furthermore involves still other distinctive forms in the region.

MORPHOLOGICAL VARIATION

Although a hood formed by the connivent sepals and petals is characteristic of *Spiranthes romanzoffiana*, it is not an invariable feature. Lateral sepals may curve outward to varying degrees. This is evidently not a simple phenomenon. In some plants arching sepals are constant features, appearing annually. In others, however, they occur sporadically, sometimes in only a single season, while in subsequent years the flowers are normal. In the West, they sometimes occur in yellowish flowers with sparse pubescence on the lip, suggesting gene flow from *S. porrifolia*. Spreading sepals by themselves, however, are not reliable indicators of introgression, because plants with this habit occur widely, even to the East Coast, where they are unlikely to be products of hybridization (Figure 2, page 18). Furthermore, the usually pubescent lip of *S. stellata* and the variable sepal position in that species renders these characters of limited utility as markers. Plants referable to *S. romanzoffiana* in general appearance but with irregular hood development, sparse lip pubescence, or yellowish color appear intermediate with *S. porrifolia*; others with more openly spiraled, often smaller flowers seem to intergrade with *S. stellata*.

An entirely distinct pattern occurs along the Pacific Coast from central California to British Columbia. Here, coastal bluffs and dune lags support unusually stout plants of *Spiranthes romanzoffiana* with very large flowers in dense inflorescences. The flowers are particularly broad-based, with the basal half of the dorsal sepal arching very high above the lower lateral sepal margins and lip (Figure 6, pages 21-22). On steep bluffs and adjacent dunes plants are leafless at anthesis; in moist dune lags and more generally toward the north plants are leafy, and the leaves may be very broad and the plants particularly foliose. These large-flowered plants seem to be limited to the coastal environment, although the leafless morphotype can be found some hundreds of meters inland on dry banks. Furthermore, when representative coastal plants were cultivated under moderate conditions in pots, both outdoors and indoors under high-intensity lamps, they developed in subsequent years floral morphology that was typical of the species and inseparable from other plants from diverse localities. Vegetative characteristics, however, were less plastic, with the leafless habit maintained in cultivation.

Elsewhere, in the course of field work in 1982, an unusually variable population of *Spiranthes romanzoffiana* was found in San Miguel County, Colorado (*Sheviak 2465* [NYS]). Although most of the plants bore inflorescences and flowers typical of the species, many were aberrant (Figure 7, pages 21-22). The unusual features of these plants included recurved lateral sepals free to the base, lips without an apical dilation, lips green and lanceolate, flowers greenish, and flowers rather ringent and the inflorescence without the usual precise geometry typical of the species. In some respects some plants with more open inflorescences of ringent flowers and with lanceolate lips suggested plants in

the *S. cernua* complex. This population was encountered during the initial field work that led to the recognition of *S. diluvialis*, and these characteristics dictated careful analysis. The results of this work, however, have not been reported.

CYTOLOGY

The samples analyzed for this study show *Spiranthes romanzoffiana* as morphologically delimited to include both diploid and tetraploid individuals (Table 1, pages 8-10). Moreover, a marked geographical component is evident in the occurrence of the different ploidy levels (Figures 8 and 9, pages 7 and 12, respectively). Across most of its transcontinental range, the species appears to be strictly diploid. Tetraploids, however, are significant along portions of its southern and western range limits, perhaps corresponding to drier habitats and warmer regions. Across the Great Lakes region and eastward, tetraploids are

(Continued on page 11)

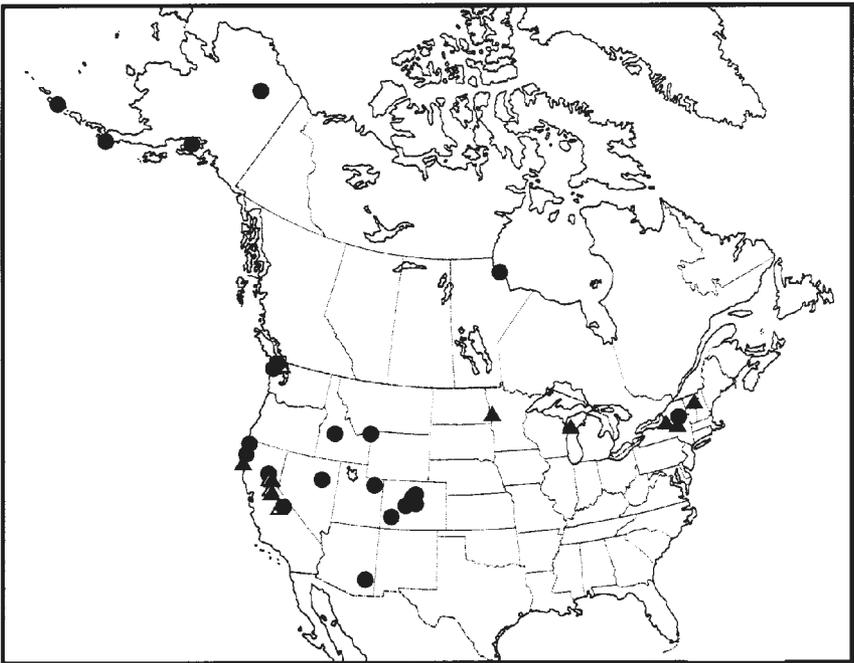


Figure 8. The geographic distribution of diploid (circles) and tetraploid (triangles) plants of *Spiranthes romanzoffiana* determined in this study.

Table 1. Chromosome numbers and meiotic characteristics of specimens employed in this study.

Locality	Collection	mitotic	meiotic
<i>Spiranthes romanzoffiana</i>			
Alaska			
Kenai Peninsula	<i>Sheviak & Sheviak</i> 5513	2n=44	
Haul Road, Lost Creek	<i>Sheviak & Sheviak</i> 5478a	2n=ca. 44	
Shumigan Islands, Popof Island	<i>Sheviak & Sheviak</i> 6453	2n=44	n=22
Amaknak Island (Unalaska)	<i>Sheviak & Sheviak</i> 6424a	2n=44	
Arizona			
Graham Co.: Mt. Graham	<i>Sheviak & Burling</i> 2642b	2n=44	22 _{II}
California			
Del Norte Co.: Crescent Beach	<i>Sheviak</i> 2524a		22 _{II}
El Dorado Co.: Union Valley Reservoir, FR3/Ice House	<i>Sheviak</i> 2933b	2n=88	
Humbolt Co.: Trinidad	<i>Sheviak</i> 2520a <i>Sheviak</i> 2520c	2n=66 2n=44	1 _I 19 _{II} 9 _{III}
Humbolt Co.: Table Bluff	<i>Sheviak</i> 2518b <i>Sheviak</i> 2518c	2n=ca. 88 2n=88	38 _{II} 3 _{IV} 40 _{II} 2 _{IV}
Mono Co.: Rock Creek	<i>Sheviak</i> 5979	2n=44	22 _{II}
Sierra Co.: Yuba Pass	<i>Sheviak</i> 2493b <i>Sheviak</i> 2493c	2n=88	44 _{II} 44 _{II}
Sierra Co.: vic. Yuba Pass	<i>Sheviak</i> 2494a	2n=88	38 _{II} 3 _{IV} 2 _I 34 _{II} 2 _{III} 3 _{IV}
Colorado			
Boulder Co.: Mitchell Lake Trailhead	<i>Pyrzynski s.n.</i> "a" [<i>Sheviak</i> 2061] <i>Pyrzynski s.n.</i> "1" [<i>Sheviak</i> 2061] <i>Pyrzynski s.n.</i> "3" [<i>Sheviak</i> 2061] <i>Pyrzynski s.n.</i> "h" [<i>Sheviak</i> 2061]	2n=44 2n=44 2n=44 2n=44	22 _{II}
Boulder Co.: Eldora	<i>Sheviak</i> 2433	2n=44	
Clear Creek Co.: vic. Squaw Pass	<i>Sheviak et al.</i> 2429b	2n=44	
Clear Creek Co.: South Chicago Ck.	<i>Sheviak et al.</i> 2431	2n=44	22 _{II}
San Miguel Co.: Lime	<i>Sheviak</i> 2465b	2n=44	6 _I 19 _{II} [consistent]
	<i>Sheviak</i> 2465c	2n=ca. 44	
	<i>Sheviak</i> 2465h	2n=44	
Summit Co.: Blue River CG	<i>Sheviak</i> 2302	2n=ca. 44	

Locality	Collection	mitotic	meiotic
Idaho			
Elmore Co.: Sawtooth National Forest	<i>Sheviak 6346</i>	2n=ca. 44	
Minnesota			
Clay Co.: Buffalo River	<i>McCabe s.n. "a"</i>	2n=ca. 88	
Montana			
Gallatin Co.: vic. West Yellowstone	<i>Sheviak 2530</i>	2n=44	
Missoula Co.: vic. Lolo Hot Springs	<i>Shelly s.n.</i> [<i>Sheviak 3178</i>]	2n=44	
Nevada			
Elko Co.: Ruby Range	<i>Sheviak 2474a</i>		22 _{II}
	<i>Sheviak 2474b</i>	2n=44	22 _{II}
	<i>Sheviak 2474c</i>	2n=ca. 44	
	<i>Sheviak 2474</i>	2n=44	
	<i>misc.</i>		
New York			
Hamilton Co.: Indian Lake	<i>Sheviak 1878a</i>	2n=44	
	<i>Sheviak 1878/3</i>	2n=ca. 44	
	<i>Sheviak 1878/5</i>	2n=44	22 _{II}
Herkimer Co.: Grant.	<i>Sheviak 4025</i>	2n=88	44 _{II}
Oswego Co.: Sandy Creek	<i>Sheviak & Mitchell</i> <i>1552</i>	2n=ca. 88	
Utah			
Uintah Co.: Whiterocks Canyon	<i>Sheviak 5925</i>	2n=44	
Vermont			
Caledonia Co.: Walden	<i>Sheviak & Sheviak</i> <i>906/1</i>	2n=ca. 88	
	<i>Sheviak & Sheviak</i> <i>906/3</i>		44 _{II}
Washington			
Thurston Co.: vic. Olympia	<i>Alverson s.n.</i> [<i>Sheviak 2972</i>]	2n=44	
Wisconsin			
Door Co.: Baileys Harbor	<i>Sheviak 716</i>	2n=ca. 88	
British Columbia			
Victoria, Dallas Road	<i>Ceska 20383</i>	2n=44	
Victoria, Golf Hill	<i>Ceska 20384</i>	2n=ca. 88	
Manitoba			
Churchill	<i>Sheviak, Sheviak, Heshka & Heshka 6947</i>	2n=44	

Locality	Collection	mitotic	meiotic
<i>Spiranthes stellata</i> subsp. <i>stellata</i>			
California			
El Dorado Co.: Union Valley Res., vic. Yellow Jacket CG	Sheviak 2512a	2n=88	
	Sheviak 2512b	2n=88	32 _{II} 6 _{IV} 33 _{II} 2 _{III} 4 _{IV} 1 _I 20 _{II} 2 _{III} 9 _{IV} 1 _V
	Sheviak 2924a	2n=ca. 88	
El Dorado Co.: Union Valley Reservoir, above east shore	Sheviak 2513	2n=88	2 _I 16 _{II} 4 _{III} 8 _{IV} 2 _V 2 _I 28 _{II} 2 _{III} 13 _{IV}
El Dorado Co.: Union Valley Reservoir, Wench Creek	Sheviak 6994b		44 _{II}
El Dorado Co.: Loon Lake	Sheviak 6995a	2n=ca. 88	
Inyo Co: Rock Creek	Sheviak 5980	2n=88	
	Sheviak 5980/1	2n=ca. 88	
	Sheviak 5980/2	2n=ca. 88	
	Sheviak 5980/3	2n=88	
<i>Spiranthes stellata</i> subsp. <i>perexilis</i>			
California			
Plumas Co.: vic. Butterfly Valley	Sheviak 2500a	2n=44	
	Sheviak 2500b	2n=66	5 _I 11 _{II} 13 _{III}
	Sheviak 2500c	2n=44	22 _{II}
	Sheviak 2500d	2n=44	22 _{II}
	Sheviak 2500e	2n=44	22 _{II}
<i>Spiranthes porrifolia</i>			
California			
El Dorado Co.: Loon Lake	Sheviak 2510	2n=66	
	Sheviak 2510b	2n=66	
	Sheviak 2510c	2n=66	
	Sheviak 2510d	2n=66	
Mono Co.: Fish Slough	Sheviak 5969b	2n=44	
Trinity Co.: Burnt Ranch	Sheviak & Sheviak 2911a		22 _{II}
	Sheviak & Sheviak 2911b		22 _{II}
	Sheviak & Sheviak 2911c	2n=44	22 _{II}
Unknown			
California			
El Dorado Co.: Union Valley Res., vic. Yellow Jacket CG	Sheviak 2925a	2n=66	

(Continued from page 7)

frequent and perhaps the dominant ploidy level. If the single prairie collection from the Red River valley of northwestern Minnesota is representative, they may similarly predominate across the Northern Plains. The sample shows the Rocky Mountains to support exclusively diploids, but this pattern might be an artifact of the sampling itself: the collections were from montane stations and none were made on the Plains or the base of the mountain front. In the East, for example, diploids were found at moderate elevations in the Adirondacks, but tetraploids were more generally distributed at lower elevations. In the West, then, tetraploids might be more widely distributed at lower elevations and latitudes than disclosed by the present sample. Tetraploids again become frequent on the West Coast and throughout the range of the species in California.

Typical *Spiranthes romanzoffiana*, as defined by normal expression of floral characters, comprises both diploid and tetraploid individuals within California. Significantly, the large-flowered, leafless plants of coastal bluffs and dunes have been found to be tetraploid, whereas the similarly large flowered but leafy plants sampled from wet dune lags are diploid. This pattern continues up the coast to British Columbia, where the sample includes leafy diploids and leafless tetraploids. Further north in coastal Alaska, only diploids have been found, even in severely exposed coastal settings. Significantly, at one site in northern California, a population of diploids merely some hundreds of meters inland from a coastal bluff appeared entirely comparable to the leafless bluff plants; among the diploids was found a triploid.

In contrast, the complex of variable plants with loose lateral sepals, yellowish color, pubescent lips, etc., have been found to be universally polyploid, in almost all cases tetraploid. At one site, morphologically unique triploids were found.

The aberrant population of *Spiranthes romanzoffiana* in San Miguel County, Colorado was sampled, including a range of morphological forms (*Sheviak 2465* [NYS]). Unfortunately some samples dried in storage, but others showed $2n=44$. One plant with flowers typical of *S. romanzoffiana*, furthermore, in meiosis consistently formed 19 bivalents and 6 univalents, suggesting that the chromosome complement was abnormal and unbalanced. The morphological abnormalities exhibited by plants in this population, then, may have been due to cytogenetic peculiarities; there was no evidence of hybridization with species in the $n=30$ lineage.

A few populations of *Spiranthes porrifolia* were also sampled. Although the sample was too small to allow any conclusions, one curious result was obtained. In contrast to the diploids found elsewhere, the four plants representing one population were uniformly triploid. This unlikely situation has bearing on one of the specific problems discussed below.

illustrates the complexity of the situation. The area was visited repeatedly during a period of over 20 years. This permitted the assessment of population structure, and to a limited extent, changes in it.

Spiranthes are abundant on roadside banks, in ditches, on moist open flats, and about seeps. Most abundant and generally distributed were the yellowish, slender plants referable to *S. stellata* subsp. *stellata*. The sampled plants were tetraploid. One group of plants typical of *S. romanzoffiana* occurred without other variants on a moist bank. These were also tetraploid. One year only, in one roadside ditch population of *S. stellata*, were a few small triploids with white flowers and recurved sepals (Figure 10, page 22). Scattered about were a variety of plants that were more or less variable and through which typical *S. romanzoffiana* seemed to merge morphologically with the slender yellowish *S. stellata* forms. These included plants with dense inflorescences of slender flowers with loose sepals. The samples of these have also all proven to be tetraploid. Finally, at one site only, in 1983 a population of *S. porrifolia* was found in a moist spot below a seeping cliff. All plants appeared typical of the species. Four plants were collected for cultivation and cytological study. All four proved to be triploid. Under cultivation their floral morphology was consistent and continued to be a good representation of *S. porrifolia*. In subsequent years when the site was revisited, no *Spiranthes* could be found. Finally, in 2004, the site was found to be completely overgrown with shrubs that had eliminated *Spiranthes* habitat. However, at the edge were found a number of plants that were variably intermediate in nature, with a slender scapose habit and white flowers that varied from slender with spreading sepals to others nearly typical of *S. romanzoffiana*. (Figure 5e and f, page 20). These plants also proved to be tetraploid. Presumably they represent a subsequent colonization of the site. However, they illustrate the fluidity of population structure resulting from the broader-scale genetics of the area. In general, then, the area supports a range of forms that correspond morphologically to typical *S. romanzoffiana*, *S. stellata*, and *S. porrifolia*, and includes other diverse forms as well. All sampled morphological forms were tetraploid, except for the triploid *S. porrifolia* and small white-flowered triploids. No diploids were found in the area, and the origins of these triploids is unknown.

DISCUSSION

Polyploidy often isolates and delineates species. Tetraploidy is often viewed as a one-step speciation event, because it may provide a genetic barrier to gene flow between the tetraploid and its diploid progenitor. However, if the diploid repeatedly generates tetraploids, these may interbreed, and thus the barrier is only one-way. The tetraploid level continues to receive genes from the diploid. Furthermore, whereas an allotetraploid is a new genetic combination isolated from its diploid progenitors, an autotetraploid individual is genetically identi-

cal to its diploid parent. How then is the tetraploid immediately a member of a different species? It is not. This is not necessarily, then, a speciation event. Such is the case of *Spiranthes romanzoffiana*. This species repeatedly generates tetraploids. Perhaps this occurs throughout the species' range, but the tetraploids are successful and important only at the periphery, where the normal diploids are at the limits of their tolerance and polyploidy confers greater vigor in a stressful environment (Stebbins, 1950). It is in the nature of *S. romanzoffiana* to produce tetraploids. In a sense, it is an adaptive mechanism that aids survival under adverse conditions.

This penchant for tetraploidy then leaves *Spiranthes romanzoffiana* open to accommodating allotetraploids within it. An existing tetraploid can produce allotetraploid offspring via pollination by unreduced gametes from a diploid, or normal gametes from another tetraploid. Perhaps these are more likely occurrences than the doubling of chromosomes resulting from the failure of the first mitotic division of the zygote, which is the most likely mode of origin of allotetraploid derivatives of diploid species. The evolutionary and taxonomic status of resulting allotetraploids then becomes a question of population biology and the degree of isolation or interbreeding between allo- and autopolyploids and the differentiation of allopolyploids into discrete morphotypes and their interactions.

The populations along the immediate Pacific Coast illustrate the flexibility of the species' cytology as well as the potential independence of some phenotypic variation. Evidently the coastal environment induces the large-flowered form independently of the plants' cytology, as both leafless diploids and tetraploids and leafy diploids bear large flowers in dense inflorescences. However, the leafless habit of the bluff plants appears to be a fixed trait associated with drier coastal habitats and may therefore delimit a localized race. Tetraploidy may, however, convey an advantage in extreme coastal bluff sites. The presence of morphologically similar diploids a short distance inland and the occurrence of a triploid there suggests the potential for repeated generation of polyploids in that environmental setting.

In contrast, the San Miguel County, Colorado population shows clear cytogenetic influence in its aberrant morphology. The diploid numbers of these plants evidently mask cytological irregularities that underlie their meiotic pairing characteristics. Similarly profound effects are seen in aneuploids of *Spiranthes cernua*, where duplications have been linked to peloria and other floral abnormalities (Sheviak 1982, 1991). In a sense, the morphology of the Colorado plants, with ringent flowers with lanceolate lips, is less distinctive than normal *S. romanzoffiana*, and more typical of the genus as a whole. It appears, then, that the upset of cytogenetic control has promoted a reversion to atavistic morphology in this population. This suggests that some variation at the

tetraploid level may be cytogenetically based, rather than derived from parental characteristics.

The complexity of forms illustrated by the plants described above from El Dorado County, California is at once both informative and intractable. The cytological data accumulated over 20 years of study and the transient appearance of various morphotypes as populations waxed and waned during that period provide a framework for interpretation. These phenomena permit a basic understanding, yet simultaneously a definitive taxonomic judgment remains elusive.

From the available sample, it is apparent that all intermediates are polyploid, mostly tetraploid. The tetraploids furthermore include a range of forms exhibiting not only variously intermediate features, but also plants entirely referable to *Spiranthes romanzoffiana*. Other plants similar to *S. romanzoffiana* but with variably loose sepals, poor hood development, some incidence of trichomes on the lip, or a slightly yellower color occur throughout the geographic range of the complex. Even as far as Idaho, where *S. porrifolia* occurs as a disjunct, characteristics suggesting introgression can be detected. Plants such as the tetraploids collected on and near Yuba Pass, Sierra County, California (Figure 11, page 22) are typical. This variably expressed range of hybrid characteristics at the tetraploid level and field study of sites like the El Dorado County station described above suggest that these plants are effectively interbreeding

A major component of the complex is *Spiranthes stellata*: intrinsically variable subsp. *stellata* merges with the background tetraploid variation and through it with *S. romanzoffiana*. Might it also provide a conduit for genes of subsp. *perexilis* into the tetraploid complex such that the lip pubescence that suggests gene flow from *S. porrifolia* might in fact derive from *S. stellata*? It is tempting to view the variably spiraled inflorescence of subsp. *stellata* and of some other tetraploids to be expressions of this characteristic of subsp. *perexilis*, but it may be a result of hybridization itself, rather than a reflection of parental characteristics. Openly spiraled inflorescences are sometimes seen in *S. diluvialis*, despite that species' derivation from densely-flowered parental species. In *S. cernua*, too, allotriploids are often openly spiraled, even when the diploid parent is the densely-ranked *S. magnicamporum*. The characteristics of the intermediate plants and of *S. stellata* subsp. *stellata* itself, including lack of a perianth hood, variably lanceolate lip, variable lip pubescence, and yellowish color, suggest hybridization with *S. porrifolia*. Lip pubescence and variable sepal position, however, are also features of subsp. *perexilis*. Similarly, the floral shape of subsp. *perexilis* and its uniformly pandurate lip suggest *S. romanzoffiana*. So, if hybridization underlies the variability, what are the contributing species? Parental species may vary across the region and under different local settings. Conversely, variability in the tetraploids may derive not from

hybridization, but from ancestral characteristics expressed as a result of complex tetraploid genetics.

The triploids detected in this area consequently are more than mere curiosities, because they provide an identifiable proxy for tetraploid products of gene flow between diploids and tetraploids involving unreduced gametes. While the plants referable to *Spiranthes porrifolia* might be simply autotriploids, their prevalence in the colony indicates an origin in a cross of diploid and tetraploid parents. The simplest origin, then, would involve diploid and autotetraploid *S. porrifolia*. More complex, and less likely, scenarios are possible, including the frequent generation by allotetraploids of diploid gametes comprising homologous sets of *S. porrifolia* chromosomes and backcrossing to diploid *S. porrifolia*. Regardless of their precise origin, these triploids demonstrate the presence of *S. porrifolia* chromosomes at the tetraploid level, providing opportunities for introgression and diversification of tetraploid populations. Similarly, the origin of the other triploids in this area, the ones with white flowers with spreading sepals in an open spiral, is obscure. In particular, the identity of the diploid parent is unknown. But again, their very presence establishes the occurrence of hybridization between the ploidy levels and verifies the opportunity for gene flow via unreduced gametes.

Where, then, does one draw the line around *Spiranthes stellata* subsp. *stellata*? To delimit it narrowly, restricting the name to those plants exhibiting the typical suite of characteristics, is artificial and ignores the other segregates of a common gene pool. If delimited broadly, including all morphotypes, how is it to be isolated from the mélange of variable tetraploids? How best to delineate *S. stellata* will depend on intensive population study and a better understanding of the extent and consequences of gene flow in the group's tetraploids. This cannot reasonably be done from the East Coast, as I learned years ago. The DNA sequence data of Dueck and Cameron (2008) provide an added dimension to the study, and their report of different sequences in Oregon and California plants suggests a focus for further investigation.

The limited data that I have accumulated and with which I have struggled for 30 years have led me to view *Spiranthes romanzoffiana* as an abstraction. The situation is somewhat akin to that of *S. cernua*, where gene flow from diploid relatives has progressively modified an archetypical form and led to ever-increasing variability and complexity, yet permits recognition of *S. cernua* as a polyglot species maintained by common reproductive mechanisms supporting a basic pattern of variation. In the case of *S. romanzoffiana*, however, the diploids include the bulk of *S. romanzoffiana* itself, which continually contributes genes to its tetraploid domain. Both *S. cernua* and *S. romanzoffiana* display similar variation patterns resulting from introgression, but under fundamentally different reproductive regimes. *Spiranthes romanzoffiana* is maintained as largely discrete primarily because across most of its vast

range there are no opportunities for hybridization with other members of its cytological lineage. Consistency of treatment, then, suggests that *S. romanzoffiana* be treated taxonomically as is *S. cernua*, i.e., as a variable unit of diverse genetic makeup and evolutionary potential.

ACKNOWLEDGEMENTS

I have devoted nearly 50 years toward an understanding of North American *Spiranthes*, and it is simply not possible to discriminate the contributions of the many people that have helped me to gain whatever level of understanding I have of the present problem as distinct from the more remote portions of the genus; the total forms an integrated whole not subject to division. Obviously, however, this work would not have been possible without the support of the curators and staffs of the herbaria who loaned material or accommodated my visits specifically for study of western material, including ARIZ, ASU, BRY, CAS/DS, COLO, CS, DAV, FSC, ID, JEPS, K, LA, MICH, MO, MONTU, MSC, NEB, NY, OGD, OSC (including WILLU), RENO, RM, RSA/POM (including LAM), SD, UBC, UC, UCR, UNLV, US (including NTS), UT, V, WANF, WS, WTU. Frequent discussions with Richard Mitchell, my colleague at The New York State Museum, routinely provided new insight and viewpoints. As always, William Jennings contributed in ways too diverse to enumerate. Ronald Coleman generously shared field and herbarium knowledge of critical localities. Cytological material or live plants were laboriously collected and provided by Ed Alverson, Adolf Ceska, Timothy McCabe, James Pyszynski, and J. Stephen Shelly; their contributions significantly extended and deepened the cytological foundation of this work. Early field work was funded by grants from the Denver Botanic Gardens.

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(Continued on page 31)

Figures to accompany “A Cytogeographic Survey of *Spiranthes romanoffiana* Cham. and Its Taxonomic Implications” by Charles J. Sheviak, page 1. Photos by author.



(above) Figure 1. *Spiranthes romanoffiana* in the North. Left: At the type locality, Unalaska Island, Aleutian Islands, Alaska. Note venation of lip, with three primary veins, the lateral branching at wide angles. Sheviak & Sheviak 6424 [NYS] $2n=44$. Right: Typical plant in habitat, Churchill, Manitoba. Sheviak et al. 6947 [NYS]. $2n=44$.



(left) Figure 2. *Spiranthes romanoffiana*. Left: Inflorescence of typical flowers showing sepal connation, typical hood development, and broad apical expansion of the lip. Hamilton County, New York. Sheviak 1878a [NYS] $2n=44$; Right top: Flowers with lateral sepals loose and spreading. Grafton Co., New Hampshire. Sheviak & Sheviak 1020 [NYS]. Right bottom: Typical flower showing lip with abruptly expanded apex and three nerves. San Miguel County, Colorado. Sheviak 2465b [NYS]. $2n=44$.

(right) Figure 3. *Spiranthes porrifolia*. a: Typical plant in the field, Trinity County, California. *Sheviak & Sheviak 2911c* [NYS] $2n=44$. b: Inflorescence showing tubular flowers with prominent basal sepal connation, recurving perianth apices, and reduced apical lip expansion typical of the species. Collected plant in cultivation. El Dorado Co., California. *Sheviak 2510b* [NYS] $2n=66$.

(below) Figure 4. *Spiranthes porrifolia*. Flower showing lip apex densely covered with stout trichomes. In this plant, the lip is more broadly expanded and generally pubescent than is typical. Mono County, California. *Sheviak 7001c* [NYS] $2n=44$ (from population sample)



(following page) Figure 5: Within-population variation in two populations of tetraploids referable to *Spiranthes stellata* subsp. *stellata*. a-c: Inyo County, California. a: *Sheviak 7000b* [NYS]. b: *Sheviak 7000a* [NYS]. c: *Sheviak 7000d* [NYS] ($2n=88$; from population sample, 5 plants). d-g: Eldorado County, California. d: *Sheviak 6994b* [NYS]. e: *Sheviak 6995c* [NYS]. f: *Sheviak 6995a* [NYS] $2n=88$. g: *Sheviak 2513d* [NYS]. ($2n=88$, from population sample, 5 additional plants).

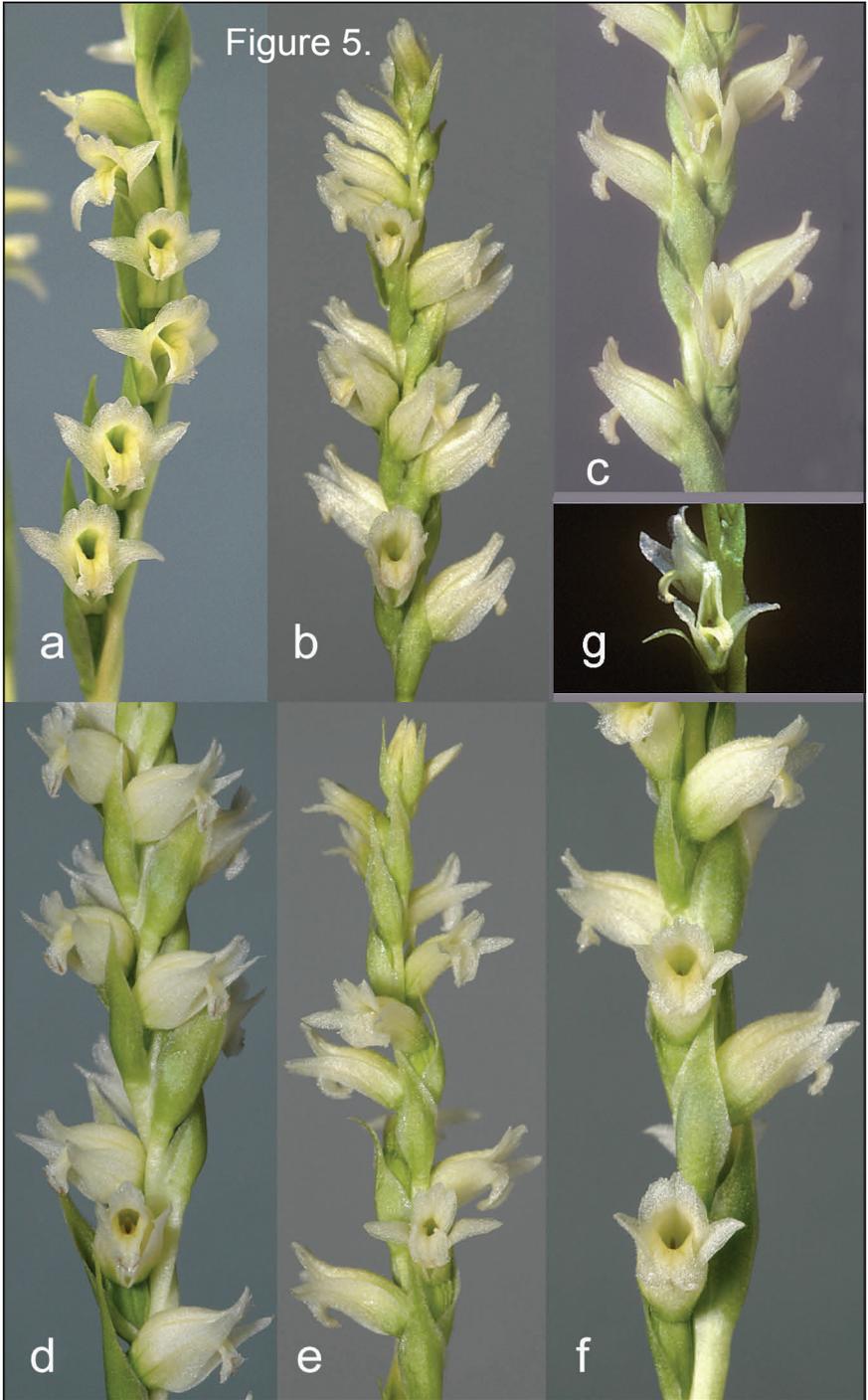




Figure 7.



(previous top right) Figure 6. *Spiranthes romanzoffiana*. Left: Inflorescence of a leafy plant from wet coastal beach sand, showing large flowers in dense inflorescence. Note the weathering damage to freshly opened flowers. Del Norte County, California. *Sheviak* 2524 [NYS]. $2n=44$; Right: Leafless plant with large flowers in dense inflorescence, in habitat on coastal bluff face. Humboldt County, California *Sheviak* 2518a [NYS]. $2n=88$. (from population sample)



Figure 10

(previous top left and bottom) Figure 7. *Spiranthes romanzoffiana*. Sample from population supporting aberrant plants, San Miguel County, Colorado. a: Plant with typical flowers, but with irregular meiosis (see Table 1). *Sheviak* 2465b [NYS]. $2n=44$. b: Plant with poor hood development and irregular lateral sepal position. *Sheviak* 2465d [NYS]. c: Plant with ringent flowers and lanceolate lip. *Sheviak* 2465g [NYS]. d: Inflorescence of same plant as “c,” showing slender, centrally green lips and ringent flowers.

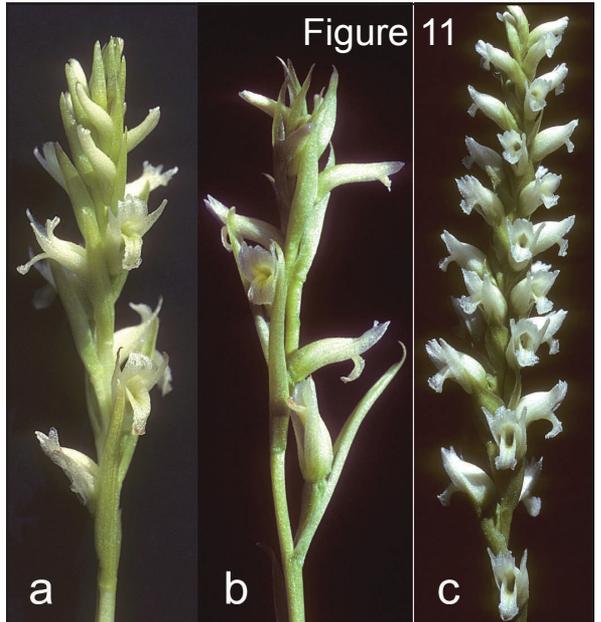


Figure 11

(top) Figure 10. Evident hybrid of uncertain parentage, perhaps *Spiranthes romanzoffiana* × *S. stellata* subsp. *stellata*: small white-flowered plants with recurved lateral sepals. left: Plant in habitat. right: inflorescence. El Dorado County, California. *Sheviak* 2925a [NYS] $2n=66$.

(right) Figure 11. *Spiranthes romanzoffiana*. Population displaying variable expression of characteristics of *S. porrifolia*, Sierra County, California. a: Flowers with slightly spreading lateral sepals and scarcely expanded lip apex. *Sheviak* 2493b [NYS] $2n=88$. b: Very slender, tubular flowers with moderate apical lip expansion. *Sheviak* 2493c [NYS] $2n=88$. c: Flowers with typical lip shape, but with poor hood development, the lateral sepals straight and not connate. *Sheviak* 2494a [NYS].

Figures to accompany “Life History of *Goodyera pubescens* Rosettes in Southwestern Quebec” by Joyce M. Reddoch and Allan H. Reddoch, page 32. Photos by Joyce M. Reddoch.

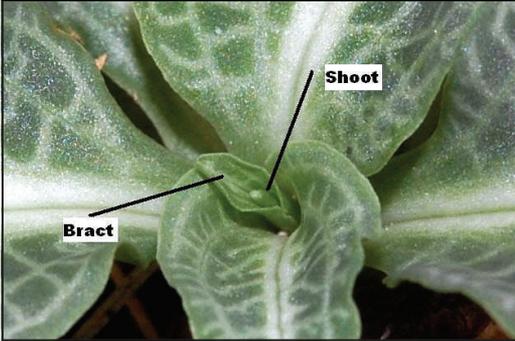


Figure 1. The central portion of a rosette on 4 October 2010 showing the emerging inflorescence shoot subtended by a leaf-like bract.

Figure 2. The same rosette on 21 June 2011 showing the expanding inflorescence.



Figure 3 a (left) and Figures 3 b and c (next page). The same rosette in flower on 9 August 2011 and in seed on 5 October 2011.



Figure 3b



Figure 3c



Figure 4. The two offshoots from the same rosette on 27 Sept 2012, the 2011 inflorescence leaning to the right, the remains of the rhizome and one root on the top. Development was delayed by the 2012 severe summer drought.

Figures to accompany “The Pollination Biology of *Liparis loeselii* (L.) Richard (loesel’s twayblade or fen orchid)” by Charles L. Argue, page 36.



Figure 1. Inflorescence of *Liparis loeselii*. Photograph by Eleanor Saulys. Used with permission.

Figure 2. Flower of *Liparis loeselii*. Photograph by Rogier van Vugt. Used with permission.



Figures to accompany “The Cedars” by Raymond Prothero, Jr., page 43. All photos by author.



Figure 1. *Piperia leptopetala* (lace orchid, thin wood rein-orchid).

Figure 2. *Hesperocyparis sargentii* (sargent cypress).





(above) Figure 3. Serpentine landscape. Note the red oxidation of the iron in the rocks and soil.



Figure 4. Calcium carbonate mineral springs.

(below) Figure 5. *Epipactis gigantea* f. *rubrifolia* (purple leaf stream orchid).





Figure 6. *Cypripedium californicum* (California lady's slipper).



(above) Figure 7. *Piperia transversa* (flat-spurred piperia).



Figure 8. *Piperia elongata* (chaparral orchid, wood rein-orchid).



(top) Figure 9. *Calochortus raichei* (The Cedars fairy lantern).

(above) Figure 10. *Rhododendron occidentale* (western azalea).

(right) Figure 11. *Streptanthus morrisonii* (ssp. *morrisonii*) Morrison's jewelflower.



Figure 12. *Aquilegia eximia*,
(serpentine columbine).

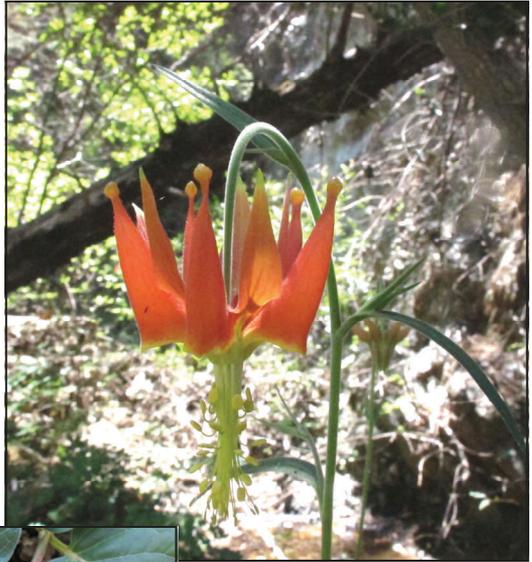


Figure 13. *Asclepias solanoana*
(serpentine milkweed).

(below) Figure 14. *Eriogonum
cedrorum* (The Cedars buck-
wheat).



(Continued from page 17)

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Life History of *Goodyera pubescens* Rosettes in Southwestern Quebec

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In 2007 we published the results of our 31-year (1976-2006) study of two *Goodyera pubescens* populations in Gatineau Park in southwestern Quebec near Ottawa (Reddoch and Reddoch 2007). Here we summarize some life history observations from that study and give a six-year update on the progeny of a rosette that flowered in 1992.

In Gatineau Park, near the northern edge of its distribution (Kallunki 2002), *Goodyera pubescens* is an orchid of mature forests that flourishes in undisturbed sites away from trails and other human disturbances. It is a clonal species that consists of unbranched, leafy rhizomes that extend along the soil surface. By the time they flowered, the rhizomes in our study generally were 12-17 cm long and had produced 16-30 leaves. Leaves lived for a maximum of four years both in New Hampshire (Keenan 1990) and in Quebec (Reddoch and Reddoch 1997); they were not replaced after they died. (Each leaf has a different pattern and so can be identified uniquely.) The leaves along the rhizome and around the growing tip have the appearance of an elongated rosette.

- Each rosette **flowers only once**, after developing for 4-8 years, rarely longer.
- Flowering of mature rosettes is initiated by a warmer and drier than average period in May lasting 19 days or more, perhaps combined with other conditions, **in the year (t-1) before the rosette will flower**.
- **In the late summer of that year (t-1)**, a small bract (rarely 2-4) appears at the growing tip of the rhizome subtending an inflorescence shoot (Figure 1, page 23). One can look for the bract(s) and shoot to discover whether a rosette will flower the next year.
- **The following summer (t)**, the inflorescence emerges from within the bract(s) (Figure 2, page 23), flowers in August and releases seed in October (Figures 3a, b, c; pages 23-24). As can be seen by comparing Figures 3b and 3c, most flowers produce seeds, as is typical in this area.

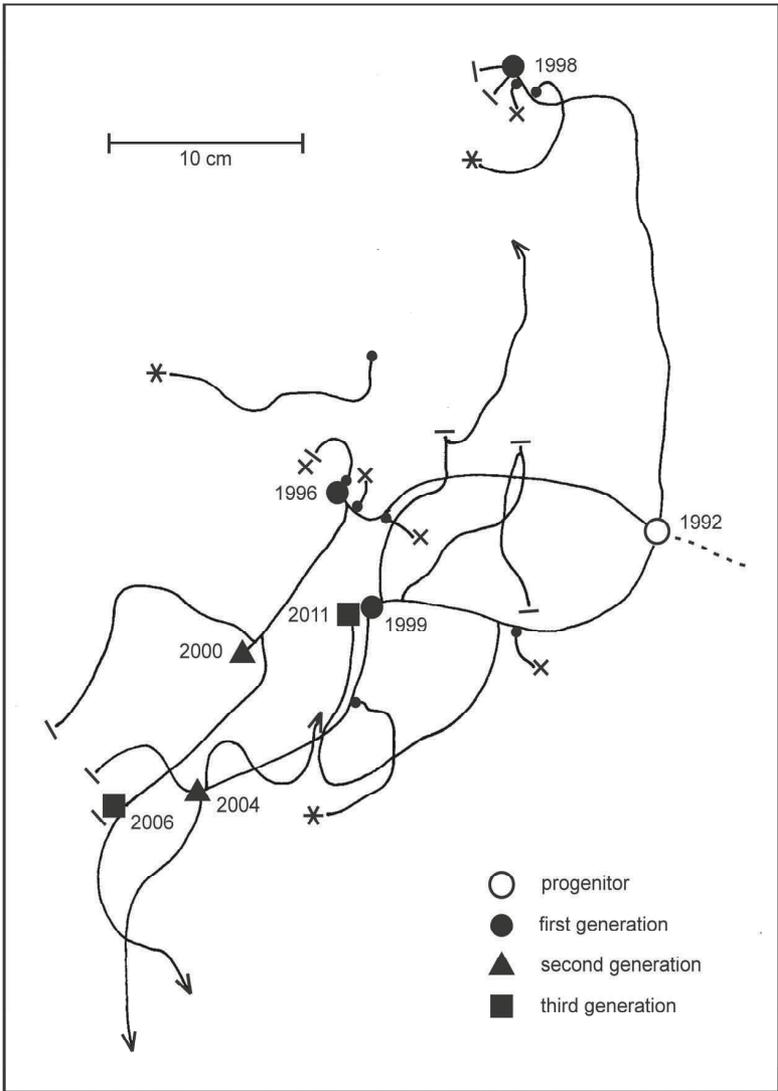


Figure 5. Diagram of the 21-year cumulative record of rhizome locations of the progeny of a rosette that flowered in 1992 and seedlings in the same area. Arrows show growing tips of rosettes not yet flowered in 2012; bars denote where rosettes and seedlings were bitten off by deer between 1999 and 2008. Seedlings extant in 2012 are represented by asterisks; Xs show seedlings that have died. Small dots mark the origins of the seedlings. The flowering year of each rosette is adjacent to the flowering stem location.

- **At the end of the summer (t) or early the following year (t+1)**, 1-3 offshoots emerge near the base of the flowering stem (Figure 4, page 24), and the parent rhizome slowly dies.
- These **offshoots**, which are the next generation of rosettes, follow the same pattern of growth as the parent. During their development, the rhizomes extend along the ground at a rate of 3-5 cm a year and generate 3-5 leaves each year until they flower. Rhizomes grow in various directions away from the parent rhizome. They may cross over other rhizomes and, in some places, may turn abruptly (Figure 5, page 33).
- Because flowering is initiated by an extensive warm and dry period in the May preceding flowering, there are **synchronous large flowerings** in the *Goodyera pubescens* populations in Gati-neau Park and area every several years. A large flowering means that 8% to 30% of the rosettes are in flower.
- **Seedlings** require many years to achieve maturity and have a high mortality rate. The longest surviving seedling that we have followed, which appeared in 1998, still has not flowered after 14 years; the two that appeared in 2004 similarly have not yet flowered (Figure 5, page 33). Establishing a patch must be a lengthy and chancy procedure, and patch growth is strongly dependent on vegetative reproduction. Seedlings often originate close to rhizomes, both in Massachusetts (Ames 1921, 1922) and in our study (see Figure 5, page 33). When young, seedlings can readily be distinguished from offshoots by their small, delicate appearance, but, as they develop, they come to resemble offshoots, which are more robust from inception (Figure 4, page 24). Thus, anyone looking at a patch for the first time will not be able to distinguish maturing seedlings from offshoots and might mistakenly conclude that there are branched rhizomes.

Figure 5, page 33, shows the 21-year history of the progeny of a rosette that flowered in 1992 at the left edge of a large patch. Since 1992, eight rosettes have flowered, including the parent rhizome, and these flowering rosettes generated an average of 2.3 offshoots each. There have been eight seedlings, three of which remained in 2012 (see above).

Between 1999 and 2008, herbivory by White-tailed Deer made a considerable impact on the growth of the clone in Figure 5. Seven rosettes and one seedling were browsed; four of the rosettes and the seedling were killed. Two other rosettes initiated new offshoots such as would have happened if they had flowered; two years later, one of the new offshoots was eaten and killed. In our

experience, rhizomes browsed by deer generally die the same season and do not generate offshoots. The rosette that flowered in 2006 was bitten off while in flower, but one offshoot emerged the next year from the end of the remaining section of rhizome. In 2009 we placed a large tree branch over the patch to deter deer browsing. No further rosettes have been eaten (Reddoch and Reddoch 2012).

Goodyera pubescens populations expand mainly through vegetative reproduction by offshoots that are initiated after flowering has occurred. Flowering takes place only on mature rosettes following certain climate conditions. In addition, flowering rosettes must produce at least two offshoots, one to replace the parent rosette, which dies after flowering and reproduction, and at least one additional offshoot to contribute to the growth of the population. Seedlings also contribute to population growth but on a longer time scale.

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The Pollination Biology of *Liparis loeselii* (L.) Richard (Loesel's twayblade or fen orchid)¹

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¹ Modified from the author's book *The Pollination Biology of North American Orchids*, vol. 2, Springer, New York (2012).

HABITAT AND DISTRIBUTION

Liparis loeselii (Figure 1, page 25) is a small, often overlooked orchid found on both alkaline and acidic substrates in a wide range of habitats (McLain 1968, Luer 1975, Catling 1980, Correll 1978, Thompson and MacGregor 1986). These can include moist ravines, bogs, fens, stream banks, wet meadows, forested wetlands, seeps, and dune slacks as well as occasional dryer upland sites. It frequently occurs on peat or sand with high organic content and shows a preference for early successional stages and disturbed areas. Also found in Europe, this orchid is distributed throughout northeastern North America from eastern Nova Scotia to Saskatchewan and south to Iowa, Tennessee and North Carolina. A number of more westerly and southerly disjunct populations are spread from Alabama to Washington and the Northwest Territories (Scoggan 1978, McMaster 2001, Magrath 2002).

FLORAL MORPHOLOGY

Up to 19 very small, white to greenish, resupinate flowers are borne in a single loose raceme (Table 1, page 37) (Magrath 2002). The sepals are spreading or directed forward, while the petals are spreading to pendant. Both have rolled margins and can be more or less tubular to filiform in outline (Figure 2, page 25; 3a; page 38) (Luer 1975, Magrath 2002). The lip is obovate or suborbiculate to oblong and arching-recurved with an obtuse to apiculate apex and crenulate-wavy margins. It is translucent to opaque, green to yellowish, and thickened down the center (Luer 1975, Magrath 2002). An incurved column bears wing-like projections on its upper part and stigmatic surfaces on the underside (Figure 3e, f; page 38). Two pairs of waxy, yellow pollen masses

Table 1. Data on *Liparis* (Magrath 2002)

Character	<i>Liparis loeselii</i>
Plant height (cm)	6-26
Raceme length (cm)	2-10
Flower number	2-15(19) ¹
Dorsal sepal (mm)	4.5-6 x 1-2
Lateral sepals (mm)	4.5-5.5 x 1-2.2
Lateral petals (mm)	4.5-5.5 x 0.5-1
Lip (mm)	4-5.5 x 2.2-3.5
Column (mm)	2-3 x 0.5-1

¹McMaster (2001) reported up to 30 flowers.

(pollinia) are contained within a 2-celled terminal anther with a hinged cap (Figure 3f, page 38) (Kirchner 1922, Luer 1975). The pollinia lack a well developed stalk (caudicle/stipe) and an adhesive pad (viscidium) for attachment to a pollinator. The flowers produce no nectar and lack a perceptible odor (Kirchner 1922).

COMPATIBILITY AND BREEDING SYSTEM

Liparis loeselii is self-compatible and its flowers can self pollinate in the absence of a pollinator (i.e., they are autogamous) (Kirchner 1922, Hagerup 1941, Catling 1980). In a study of plants from York County, Ontario, Catling (1980) established seven treatment groups. All were held in a large insect-proof cage in the greenhouse while in flower. Flowers in the first group were maintained as a control. In the second they were emasculated, in the third they were vigorously agitated by “wind” from a strong fan, in the fourth they were watered from above with a rain-like spray for five minutes once every two days over the course of the three-week flowering period. In the fifth, sixth, and seventh groups the flowers were artificially fertilized by self-pollination, geitonogamous pollination (i.e., the transfer of pollen between flowers on the same plant), and cross-pollination, respectively.

No seed developed in emasculated flowers suggesting the absence of apogamy (the development of seeds and embryos without fertilization). Artificial intrafloral-, geitonogamous-, and cross-pollinations produced seed in 94% to 100% of the ovaries tested compared to 17% in undisturbed (control) plants. Flowers agitated by “wind” did not differ from undisturbed plants in their levels of autogamous pollination. However, flowers receiving the simulated rain treatment (group 4) had quadruple the level of autogamy (viz. 70%) found in undisturbed plants.

In addition to seed production, *L. loeselii* reproduces vegetatively. The pseudobulb of the current year routinely produces a new rhizome each autumn with a daughter pseudobulb primordium at its tip. This primordium matures into a new pseudobulb with roots the following spring. Sometimes two rhizomes may elongate, giving rise to two daughter pseudobulbs at a distance of 1 to 3 cm from the parent (e.g., Jones 1998). Further studies are needed to assess the development of clones in *L. loeselii*; some accounts describe such development as rare to absent (e.g., McMaster 2001), others as common (e.g., Jones 1998, Pillon et al. 2007). Dormancy has been reported but is thought to be negligible in this species (Jones 1998; Wheeler, Lambley, and Geeson 1998).

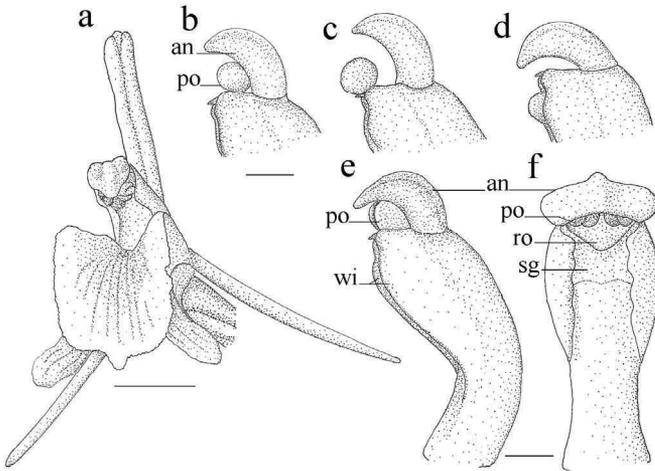


Figure 3. *Liparis loeselii*. a. Flower, slightly oblique view, scale bar = 2 mm; b-d. Movements leading to autogamy, scale bar = 0.5 mm; b. Elevation of the anther cap (cf. “e”); c. Pollen masses (represented diagrammatically as a single unit) rotate out of the anther; d. Quick downward movement of the anther cap pushes pollinia onto the stigmatic surface; e. Column, side view; f. Column, front view, scale bar = 0.5 mm. an, anther; po, pollinium; ro, rostellum; sg, stigma; wi, wing.

POLLINATION MECHANISM

Catling (1980) saw no insects visiting the flowers in York County despite 30 hours of observation during the period of peak flowering. One to four days after the flower opened the anther cap tissue began to degenerate and turn brown. Browning was accompanied by an elevation of the cap at its point of attachment on the top of the column, probably due to a contraction of dead tissue (Figure 3b, compare with Figure 3e; page 38). Its elevation released the pollen masses, permitting them to rotate or slide out of the anther compartments to a small ridge separating the upper surface of the column from the stigma (Figure 3c, page 38). A deposit of adhesive material usually held the pollinia in this position, but in 17% of the flowers rotation onto the stigmatic surface occurred directly. If water droplets from an eyedropper were made to fall on the anther cap, the cap was forced quickly downward, pushing the pollinia around the edge of the margin onto the stigmatic surface (Figure 3d, page 38). The pollinia may be guided during this movement by the wing-like projections on the upper part of the column. The pollen masses were also pulled onto the stigma by cohesive forces as the water droplets were slowly reduced in size by evaporation or as they ran rapidly over the flower surface. In most cases, however, the rapid depression of the anther cap was sufficient to explain the movement of the pollinia onto the stigmatic surface.

Catling (1980) observed a similar mechanism in additional plants from York and Simcoe Counties, Ontario, and from Cattaraugus County, New York, and Adams County, Wisconsin. Here again elevation of the anther cap led to a descent and rotation of the pollen masses. Placed in insect-proof cages and watered from below these orchids showed levels of autogamy varying from 15% to 50%. Higher levels were once more observed in a small sample treated with a simulated rain spray.

Catling's (1980) results are consistent with earlier observations by Kirchner (1922) and Hagerup (1941) on European plants of *L. loeselii*. Kirchner noted that the pollen masses slipped out of the anther onto the stigmatic surface without the participation of a pollinator, but failed to note the role played by the elevation of the hinged anther cap. Hagerup, on the other hand, reported that the downward movement of the anther cap expelled the pollen directly onto the stigmatic surface, but considered that this movement occurred without outside influence. Neither Kirchner nor Hagerup associated the movement of the anther cap or pollen masses with rain. In other European studies, Reinhard et al. (1991) considered autogamy to be obligatory, but Zeigenspeck and Kirchner (in Fuller 1966) mentioned mosquito pollination as a possible supplement to regular self-fertilization. In North America, McMaster (2001), like Catling, saw no pollinators visiting the flowers over a seven-year interval in Massachusetts.

Factors that may have favored selection for autogamy in this orchid remain to be established, but it is perhaps not surprising to find such a breeding system associated with short-lived plants that appear to be heavily dependent on prolific seed production for survival (see below). Moreover, the tendency of this orchid to occur on disturbed sites and its frequent association with early successional stages suggests a capacity for colonization, a circumstance where autogamy can be advantageous.

REPRODUCTIVE SUCCESS AND LIMITING FACTORS

McMaster (2001) reported that well-watered and fertilized, cultivated transplants in partially shaded beds were significantly larger and produced many more flowers than the wild populations, suggesting that drought, temperature, herbivory, competition, and/or resources might be critical under natural conditions. Possible effects of herbivory, hydrology, and other factors on the population dynamics of this orchid are reviewed by Rolfsmeier (2007). Resources, however, may not be limiting. In a five year investigation, through as many as four transpositions, McMaster found that fruit-bearing plants in wild populations were more likely to survive, bear flowers, and produce fruit the following year than non-fruiting plants. Although more extended studies are needed to further assess the cost of repeated flowering and fruiting (e.g., Primack and Stacy 1998), the quantity of stored resources required might be reduced in orchids such as *L. loeselii* that can have partially exposed, green pseudobulbs and that produce green, long-lived flowers potentially capable of making a photosynthetic contribution to the plant (Jones 1998, McMaster 2001). Moreover, the small, nectarless flowers are probably relatively inexpensive to produce (Hagerup 1952, Neiland and Wilcock 1998).

McMaster (2001) recorded herbivore damage on 10% to nearly 60% of the plants over six years at a study site in Franklin County, Massachusetts. Predators were thought to include invertebrates such as insects that damaged leaves and other organs and vertebrates such as deer and rabbits that removed most or all of the plant. Beyond the immediate effects of predation, grazed plants showed significant overall reductions in survival, flowering, fruiting, and size in subsequent years, suggesting that the long-term energy budget of *L. loeselii* may be more significantly affected by herbivory than by flowering and fruiting. Similarly, Wheeler, Lambley, and Geeson (1998) reported that only 3% of plants in eastern England damaged by grazing produced flowers the following year compared to 22% for the entire population. Although mollusks fed on young shoots, predators of the adult plants were not identified.

Jones (1998), in Wales; Wheeler, Lambley, and Geeson (1998), in East Anglia (UK); and McMaster (2001), in Massachusetts, reported high mortality rates in populations of *L. loeselii*. The plants were short-lived, with mortality

levels that exceeded the rates of population depletion. In Massachusetts, for example, 97% of the plants in one population died over a five-year interval, whereas the size of the population declined by only 52% during the same period. Since McMaster found dormancy was absent at this site and pseudobulbs did not produce multiple ramets, the population was apparently maintained primarily by seedling recruitment. Increased competition, especially from tall herbs and grasses, and herbivory were considered the most likely explanation for the decline in the total number of individuals. In the United Kingdom studies, populations were also believed to be largely dependent on recruitment to offset the mortality of individual plants, which ranged from 18 to 60% over a period of seven years. The level of seed production is therefore clearly a matter of interest.

Kirchner (1922) reported self-pollination and capsule development in 72 of 102 (ca. 71%) flowers on 20 plants, and McMaster found fruiting success varied from 51-77% among 49 plants that flowered over three successive seasons. Seed count per capsule averaged 4270 and ranged from 1601 to 11748 for five capsules examined at McMaster's site. Extrapolation to the 551 capsules counted one year gives a total estimate of over two million seeds produced in a 7 x 3 meter area. Seed dormancy and seed bank longevity are poorly studied, but most recruitment is probably derived chiefly from the previous season's crop (Mrkvicka 1990). Ramsey (in McMaster 2001) determined that about 81% of the seeds were viable in one natural population in England, whereas Henrich, Stimart, and Ascher (1981) reported 25% germination in culture. Provided, then, that suitable conditions are available for the establishment and development of new individuals, prolific seed production, abundantly augmented by rain-assisted autogamy, may account for the survival of many populations despite short life spans for individual plants. Although this species appears to be generally secure in much of North America (NatureServe 2004), "suitable conditions" are apparently becoming increasingly rare in some areas, and faced with habitat destruction and natural succession, this seral orchid is now said to be in decline in more than 50% of the states and six provinces within its historic range (McMaster 2001, Rolfsmeier 2007). Management strategies to halt or reverse this decline along with ideas for further research on the conservation biology of this species are discussed in a number of recent works (e.g., Jones 1998; Wheeler, Lambley, and Geeson 1998; McMaster 2001; and Rolfsmeier 2007).

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The Cedars

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I first visited The Cedars, a canyon in Sonoma County's northwestern corner near the town of Cazadero CA, in the early spring of 2009 with a California Native Plant Society field trip. I knew little about the place other than it was very remote and several orchid species grew there. After a seven or so mile drive in the back of a pickup truck on windy dirt roads with seven creek crossings and through several locked gates, I found myself in a vast canyon floor with strange looking red soil. I soon found a native orchid, *Pipera leptopetala*, (Figure 1, page 26) just off the side of the road as I got out of the truck. I met Roger Raiche, the guide for our field trip and the owner, at the time, of The Cedars. Roger has been visiting The Cedars since 1981, and in 1999 he purchased the land with his partner David McCrory at which time he started the trails and cleaning up of the property. In 2011 he sold most of the land to the Bureau of Land Management and kept two ten-acres plots in holding. He is still the go to person for tours of the area. The name "The Cedars" is misleading because no true cedars (genus *Cedrus*) are in the valley, but there are Sargent cypress trees (*Hesperocyparis sargentii*) (Figure 2, page 26) that look much like cedars.

Soon Roger gathered our group together and explained a little about The Cedars, the size of the area is about 5,700 acres of mostly Harzburgite, an "igneous rock", and serpentinite, "the metamorphosed form of Harzburgite". Both have iron as a part of their composition, and the red soils and rocks around the canyon are due to the oxidation of the iron in the rocks. (Figure 3, page 27). However, for conversational purposes, the word "serpentine" is typically used to describe the rocks, soil, vegetation, or other aspects related to this geology.

As Roger lead us up the canyon floor along one of the headwater branches of Austin Creek, I discovered the vast beauty of the amazing landscape with lovely waterfalls, calcium carbonate mineral springs (Figure 4, page 27), old chrome mines, and the many botanical rarities. We soon came up to the orchid I really wanted to see — the purple form of *Epipactis gigantea*, purple leaf stream orchid, (Figure 5, page 27) and the normal green form too. Both were just beginning to come into bloom. It was a very easy hike with Roger stopping often to point out the many native plants along the way. As we walked

further up the canyon we soon came up to the last orchid of the day, *Cypripedium californicum*, California lady's slipper (Figure 6, page 28) also just coming into flower. I went home with a new respect for the area and the many rare plants that only grow in this truly amazing environment.

Over the years Roger and I have developed a friendship, and I have made many trips to The Cedars. I have seen other orchids there like *Piperia transversa*, flat-spurred Piperia (Figure 7, page 28) and *Piperia elongata*, chaparral orchid or wood rein-orchid (Figure 8, page 28) both of which I've seen flowering in late June and early July.¹

Plants there that should be in flower when the conference field trip happens in mid-June include the following. Some are shown in the figures on pages 29 and 30.

- *Calochortus raichei* (The Cedars globe lily) is a beautiful species of *Calochortus* named for Roger in the mid 1980s.
- Many color forms of *Rhododendron occidentale* (western azalea).
- *Cypripedium californicum* (California lady slipper).
- *Epipactis gigantea* f. *rubrifolia* (purple leaf stream orchid).
- Several species of *Streptanthus* (jewelflower).
- *Aquilegia eximia* (serpentine columbine).
- *Asclepias solanoana* (serpentine milkweed).
- *Eriogonum cedrorum* (The Cedars buckwheat).
- *Piperia leptopetala* (lace orchid, thin wood rein-orchid).

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(1) Some should be in bloom during the 2013 Conference. Our group size will be limited to around 25 people because of the difficulty accessing The Cedars.

2013 Fred Case Grant

David McAdoo
Grant Committee Chairman
ncorchid@yahoo.com

I am pleased to report that we had five great applications for the Fred Case Grant this year. Submissions came from students working on degrees at:

- Florida International University in conjunction with Fairchild Tropical Botanic Garden
- Northwestern University in conjunction with The Chicago Botanic Garden
- Texas Tech University
- The University of North Carolina at Chapel Hill
- The University of Wisconsin at Madison

The judges who volunteered to evaluate the projects had a tough time. The team is comprised of:

- Dr. Katharine Gregg, WV
- Hal Horwitz, VA
- Eleanor “Sam” Saulys, MA
- Dr. Chuck Sheviak, NY
- David McAdoo, NC

When the committee voting was done and approved by the board, Ms. Anne Nies was chosen as this year’s winner. She is a Masters student at Northwestern University working on a degree in Plant Biology and Conservation. Her proposal is to study “Nutrient assimilation and management practice in communities of *Cypripedium candidum* in the Chicago Region.” Dr. Pati Vitt, who is a long time member of our organization, is Anne’s advisor and wrote a letter of recommendation for her.

We wish Anne the best of luck on her research and look forward to reading and hearing about the results in a future Journal issue and at a conference.

The deadline for 2014 submittals is the end of next January. Application requirements are on line in the “Files” section of our Yahoo web site or available from me at ncorchid@yahoo.com. Time has a way of racing by so it is not too early to start thinking about preparing a proposal for next year or encouraging a student whom you know. The reward for the winner is a grant of up to \$1,000.

In addition to deciding on a winner this year there had been a concerted effort to increase money to endow future research. You may be aware that we have added \$25 per person donation requirement to the conference registration fee to help build the fund. In addition we added a line on the membership form for people to indicate a donation. Since we are a registered, non-profit organization, these donations are tax-deductible. People have been extremely generous since the increased solicitation, and we have grown our fund from inception to over \$5,500. Thank you to everyone who has supported this. I believe this is a valuable project that will increase our knowledge of native orchids, and almost as important it may entice more young people to get involved with them and our organization.

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11th Annual Native Orchid Conference

June 10 - 13, 2013

FEATHER FALLS CASINO
OROVILLE, CALIFORNIA

Feather Falls Casino in Oroville — meet, eat, sleep and play all in one location. Field trips will be around Quincy area of Plumas County (North Central CA). There are twenty-one species of native orchids in the county.

Speakers expected include:

- Jyotsna Sharma – *Current Orchid Research*
- Tom Miranda, Smithsonian Institution – *An Update on the North American Orchid Conservation Center*
- Christina and Eric Holenda – *China's Cypripediums*
- Matt Richards, Atlanta Botanical Garden – *Recovery efforts for *Cyrtopodium punctatum**
- Ken Cameron, Botany Professor University of Wisconsin
- Bob Laurie – *Platanthera Research*
- Ron Parsons – *Coastal Orchids of California*
- Barry Rice, University of California, Davis – *Carnivorous Plants*
- James Belsher-Howe – *Butterfly Valley Botanical Area*
- Dick Hilton, Sierra College – *Geology of Feather River Region*

The cost will be \$150 for a single or \$275 for a couple. \$25 per person of either registration will be a tax deductible donation to the Fred Case Grant Fund. Lunch will be provided on the two days of meetings. The registration form is in the NOC website “Files” folder”.

Information on the hotel/casino can be found on their web site located at:

Feather Falls Casino & Lodge

www.featherfallscasino.com

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Reservation Code: NOC13

Rooms start at \$65.77 per night

Meetings are in the Silver Moccasin Ballroom on Monday 6/10 and Wednesday 6/12. Field trips are on Tuesday 6/11 and Thursday 6/13.

For any questions, please contact Raymond Prothero, Conference Chair, raypro64@aol.com, or David McAdoo, ncorchid@yahoo.com and (336) 996-2324.

AND

The Conference Committee is open to adding presentations from the membership. Talks can be either 25 or 55 minutes. Interested members should submit abstracts to the Conference Committee at ronorchid@cox.net.

11th Annual Native Orchid Conference

June 10 - 13, 2013

**FEATHER FALLS CASINO
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