Biosystematic Study of the Spiranthes cernua Complex

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CHARLES J. SHEVIAK
Curator of Botany
New York State Museum

1982

Bulletin No. 448
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The University of the State of New York
THE STATE EDUCATION DEPARTMENT
Albany, New York, 12230
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Spiranthes is the most perplexing orchid genus in our flora. It is the least understood and the one that furnishes to authors who grow impatient under the restraints imposed by cautious progress, the best opportunities for the multiplication of species. It is a genus that repays intensive observation in the field and prolonged contemplation in the herbarium.

Oakes Ames, 1921
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INTRODUCTION

The genus *Spiranthes* has gained considerable notoriety as a taxonomically perplexing group. The history of its study includes alternating periods of splitting and lumping, and a general lack of acceptance of any one treatment has been apparent. In large part this situation seems to reflect the northeastern viewpoint from which much of this work was done. Some of the most confusing species are wide-ranging; treatments which appeared appropriate in a limited geographic context often were inadequate and misleading elsewhere. This has been particularly true of the *S. cernua* complex, a group harboring some of the most intractable problems in the genus. The present study has benefited from an initial focus on the largely neglected western portions of the complex, where a combination of unique character states and striking habitat differences provided some early insight; subsequent work in the East has been guided by the Midwestern findings and has shown the complex to behave similarly in both areas, and, ultimately, has revealed its intrinsic nature.

In 1870, E. L. Greene, in his paper on the vegetation of central Illinois, reported from the prairies of the region “a *Spiranthes* of doubtful species.” He was thus the first worker to recognize the systematic intricacies of the *Spiranthes cernua* complex in the prairies. It was not until very recently, however, that anyone seriously began to study the problem. Over one hundred years elapsed between Greene’s publication and the description of *S. magnicamporum*, the first Midwestern member of the complex to be separated from *S. cernua*.

This lack of treatment of the group stems in part from the difficulty encountered in the use of herbarium material. *Spiranthes* does not provide many characters of suitable quality for systematic work, and many that are present in living material, including some of the most important, are lost when preserved as dried specimens. The situation was made more difficult by the poor representation of midwestern material in the major eastern herbaria. The pioneering work that was conducted in the East thus suffered from a paucity of quality midwestern specimens; the material that was available was often collected on early expeditions or by early settlers and was very poorly preserved. Under these conditions, eastern workers failed to recognize the distinct nature of much of the variation in the Midwest and attempted for a century to accommodate these western plants within an eastern framework. The result of this situation is a major disparity of treatment of the same plants by different regional floras, due to their authors’ inability to similarly treat western populations within an eastern system that did not in fact recognize their existence.

It was under such conditions that I began a study of the complex in the Midwest. In 1968, I began to attempt to determine specimens of *Spiranthes cernua* from the region, both in the herbarium and the field. It eventually became evident that two of the taxa reported by various workers did not occur there, although it was clear that the populations referred to *S. cernua* were not uniform to any reasonable degree, and that taxonomically distinct entities were present. It was also clear that some were not members of any currently recognized taxa, and in 1973 I described the new species, *S. magnicamporum*.

The recognition of a new species in the complex was significant beyond the addition of another taxon, for the emphasis during this century had been on a reduction of taxa from specific rank to varietal status under *S. cernua*. The publication of *S. magnicamporum* was thus contrary to established precedent. Significantly, it was in part the lack of understanding of the situation in the Midwest that had led eastern workers to abandon specific status for some of the eastern taxa; Midwestern specimens were viewed as serving to obscure the distinctions between eastern species. This situation suggested that a reassessment of the entire complex was in order.

Another important factor contributing to the confusion in the group has been the lack of information on the reproductive biology of the plants. Although polyploidy has long been known in some members of the complex and its correlation with apogamy has been established, the presence or absence of apomixis, although frequently cited in the literature, has not been utilized nearly to its potential for elucidation of the evolution and relationships of the various members of the complex and of the intrinsic nature of the complex as a whole. This failure on the part of earlier workers no doubt arose through the almost complete lack of cytological study, although the evidence for polyploidy in the genus should have stimulated this line of investigation. The present study has shown the significance of cytological study to an understanding of the reproductive biology of the complex and allowed assessment of morphological variation from an evolutionary standpoint.

This paper is intended to introduce the problem, to summarize the principal findings of the study, and to present the resulting taxonomic treatment. More detailed analyses of the nature and origins of the variation patterns and the evolution and biogeography of the complex will appear in subsequent papers.
For convenience, reference is made throughout this work to S. cernua, S. odorata, S. ochroleuca, and S. magnicamporum as distinct at the specific level. Great variation is recognized in S. cernua, whereas the other species are delimited more strictly. These interpretations are based on the findings of this study presented below and in subsequent papers.

These four species were chosen for study because of their morphological similarity, overlapping ranges, and apparent interrelationship. Variation in the complex is primarily between these species. Additionally, S. romanzoffiana appears to be involved in the Great Lakes region and eastward, but its vast subarctic and cordilleran distribution prohibited its study. The nearly allopatric distributions of S. romanzoffiana and the S. cernua complex furthermore suggests only local interaction between them. Spiranthes romanzoffiana is thus only dealt with peripherally. Closely related to S. romanzoffiana is S. portifolia, a far-western species which is geographically isolated and morphologically distinct; it does not appear to be involved in the complex.

Three additional species must be mentioned. Spiranthes ovalis is structurally very similar to S. cernua and may be closely related; S. casei is similar to S. ochroleuca in certain floral and foliar characters, which similarly may reflect a relationship. Both S. ovalis and S. casei, however, are entirely distinct from members of the complex, and any involvement in it is apparently of a different order than that of the other species mentioned here. These two species are consequently not treated in this work. The last species of interest here is S. parksi. This morphologically unusual plant is linked to the complex by its reproductive mode and some morphological characters, and indeed it is likely related. Its extremely narrow range and certain peculiar morphological features suggest, however, that it is a product of the complex rather than a contributor to the variability in the group; since essential live material was not available, the species was not included in this study.

The species discussed here, with the exception of S. casei and S. parksi, are characterized by dense inflorescences in which the flowers often appear in three or four ranks. The only other North American member of the genus to share this characteristic is the spring-blooming and apparently not closely related S. lucida; all other species characteristically exhibit more open inflorescences with the flowers spiraled about the rachis or secund. Hence, the species considered here form a natural group which provides meaningful limits to the study.

**TAXONOMIC REVIEW**

Spiranthes L. C. Richard, antedated by Gyrostachys Persoon, Ibdium Salisbury, and others, has been designated a *nomen conservandum*. The genus has been variously delimited, and in the broadest sense over three hundred species may be included within it. Schlechter (1920) proposed the recognition of a number of comparatively smaller genera. If his approach is adopted, Spiranthes is seen to contain only a few dozen species, with a center of diversity in eastern North America. Few species occur in the Old World, although the actual count may vary depending on how one interprets the extraordinarily wide ranging *S. sinensis*. Schlechter’s treatment has resulted in a proliferation of small, often poorly differentiated genera which has led a number of workers to return to a broad concept of *Spiranthes*. With regard to the present work, taxonomic decisions at the generic level are of no direct importance, for the nomenclature of the taxa considered in this work does not vary as different generic concepts are adopted. For philosophical and rhetorical convenience, *Spiranthes* is here used in the strictest sense.

The focus of this study is a species complex centering on *S. cernua* (L.) L. C. Rich. This species is based on the Linnaean *Ophrys cernua* (1753), described from “Virginia, Canada.” This northeastern plant was concisely described as bearing a few thick, fibrous roots and long, basal, linear leaves. Flowers were nodding, with an oblong, acute, lip. Later, Torrey (1826) proposed *S. cernua* var. *latifolia*, now recognized as a synonym of *S. lucida* (Eaton) Ames, and not part of the *S. cernua* complex. Similarly, Chapman (1897) described *S. cernua* var. *parviflora*, a synonym of *S. ovalis* Lindl. and not part of the *S. cernua* complex. Eaton (1829) included in his treatment of *Neottia cernua* a brief description of var. *major*. The plant was described as tall, with a somewhat leafy stem and very large flowers. Although mentioned by Ames (1905b), it has not been otherwise treated.

Other taxa referable to the *S. cernua* complex have been described intermittently since *Species Plantarum*. Walter (1788) described *Limodorum autumnale* from the Southeast. It was described as bearing large flowers, the stem bracted and pubescent, leafy, and with the spike doubly spiraled. Ames (1905b) and later workers have treated this taxon as synonymous with *S. cernua*. Rafinesque (1833) next described *S. petiolaris* from Illinois. This was reported as bearing
long-petiolate, cuneate, lanceolate basal leaves and lanceolate-acuminate leaves on the base of the stem. The spike was densely spiralled, with large, curved, white flowers. The lip was described as “obl. acut.” This taxon has not been treated elsewhere.

Nuttall (1834) described, as Neottia odorata, a plant from swampy sites in North Carolina. Without mention of earlier taxa, he described this species, “the largest and finest Spiranthes in the United States,” as exhibiting a leafy stem with long basal leaves. The white to greenish, fragrant flowers were recurved; the lip was ovate. The “root runs considerably,” according to Nuttall.Beginning early in this century, the proper rank of this plant has been a subject of controversy. Small (1913) placed it in synonymy under S. cernua. Ames (1921) stated, “It would seem that S. odorata owes its success in escaping synonymy to the fact that it was born under authority and subsequently sustained because efforts to recognize it have persisted. I am convinced that S. odorata is conspecific with S. cernua.” Correll (1940) published the combination S. cernua var. odorata. These treatments have not been universally accepted, however. Fernald (1950) maintained the specific status of S. odorata, a position recently adopted by Luer (1975) and popular with southern workers familiar with the plant. This debate has generated some confusion, for Gleason (1952) treated S. cernua var. odorata as distinct from S. odorata, an impossible situation since both names refer to the same plant.

Two additional taxa of interest here are Gyrostachys constricta and G. triloba, described by Small (1898). The first, from marshes in Louisiana, was described as a tall, stout plant with linear to linear-spatulate leaves mainly on the lower portion of the stem. The flowers, born in a dense spike, possessed lips deltoid-ovate in outline, truncate at the base and constricted above the middle. The second, from southern Florida, was described as bearing oblong to elliptic-oblong leaves mainly near the base of the stem. The lip was three-lobed, with a cordate base. Small considered G. constricta to be related to G. vernalis, but Ames (1905b) reported that the specimens with which Small compared G. constricta were in actuality S. odorata, and he reduced Small’s taxon to synonymy under this earlier species. Small (1913) later treated G. constricta as a synonym of Ibidium cernuum, along with G. odorata. Small (1898) originally reported G. triloba as without close relatives and later (Small, 1913) maintained it (as Ibidium trilobum) as distinct. Ames (1905b), however, had treated it as synonymous with S. odorata, stating that lips of the type were not three-lobed as described by Small, but rather more characteristic of S. odorata. More recently, Correll (1950) was noncommittal and referred all synonyms to S. cernua while maintaining S. cernua var. odorata. Luer (1972, 1975), however, placed G. constricta under S. cernua but followed Ames in the treatment of G. triloba.

In Britton’s Manual (Britton, 1901), Rydberg described G. ochroleuca. This plant bore linear, petiolate basal leaves and similar, but often sessile, leaves on the base of the stem. The spike was dense, with ochroleucous to greenish yellow, strongly fragrant flowers. The lower floral bracts were noted as longer than the flowers. The description ended, “type from Mt. Washington, Mass.” No other taxon in the S. cernua complex has caused so much confusion. Ames (1905b) early reduced G. ochroleuca to varietal status under S. cernua. Later (Ames, 1921), he commented on the near impossibility of separating the two taxa and stated that the only reliable difference known to him was the presence of polyembryonic seeds in S. cernua and of monoembryonic seeds in var. ochroleuca. Correll (1950) did not treat this taxon separately, but rather merely mentioned it as impractical to separate in his treatment of var. odorata. Recently, however, Luer (1975) recognized S. ochroleuca as distinct at the specific level.

Questions regarding the proper rank of this taxon, however, have not been responsible for the confusion surrounding it. Rather, the identity of the plant has been of primary importance. Different workers have variously limited the species’ range to the East Coast or expanded it to include the entire range of S. cernua. Sheviak (1973) explained this disparity of treatments largely on the basis of confusion with other members of the S. cernua complex. Most recently, Sheviak and Catling (1980) have established the identity of S. ochroleuca and shown it to be distinct at the specific level.

Another taxon in the complex is Ibidium incurvum, described in 1906 by Jennings from an island in Lake Erie. This plant was very thoroughly described. It possessed linear-oblong to ovate, petiolate basal leaves and linear-oblancoleate leaves on the lower portion of the stem. The dense inflorescence supported white to rarely somewhat yellowish flowers recurved on the spike. The lip was more or less contracted at the middle with a truncate or cordate-orbicular base. The feature which Jennings used to separate this plant from others in the complex was the elongated, incurved nature of the basal callosities of the lip, a situation indicated by Jennings to be atypical of I. cernuum. He further suggested that the closest relative of I. incurvum was I. odoratum, but stated that “the differences are . . . quite marked between the species.” Later (Jennings, 1953), however, he commented on the oc-
currence of long, incurved callosities in both typical *S. cernua* and var. *ochroleuca* and indicated that *I. incurvum* consequently could not be recognized. This taxon has been overlooked in the past, and until recently only Britton and Brown (1913) and Winter (1936) had treated it. Sheviak and Catling (1980) have shown it to be synonymous with *S. cernua*.

The last taxon proposed in the *S. cernua* complex to date is *S. magnicamporum* (Sheviak, 1973), a prairie species described from Illinois. This species was described as possessing tuberously thickened roots and lacking leaves at anthesis. The strongly fragrant white to ivory flowers, born in a dense inflorescence, were rather narrowly ringent with spreading or ascending lateral sepals and an ovate to oblong lip. It was suggested that this species was most closely related to *S. odorata*, from which it differed in the nature of the roots, the lack of cauline leaves, and the loss of leaves before anthesis. Similarly, it differed in these features from *S. cernua*, from which it also was distinct in floral configuration and lip shape.

Most significantly, it was found (Sheviak, 1973) that much of the confusion surrounding both *S. odorata* and *S. ochroleuca* stemmed from attempts to accommodate *S. magnicamporum* within these taxa. Rootless specimens of *S. magnicamporum* were found annotated *S. cernua* var. *odorata* by Correll, whereas ones bearing roots were determined as *S. cernua* by him. Catling and Cruise (1974) report a similar confusion of *S. odorata* and *S. casei* by Correll. Reports of *S. ochroleuca* from the Midwest were also found to be largely based on *S. magnicamporum*. Correll’s confusion regarding the identity of *S. odorata* suggested that his concept of the taxon was faulty, and hence his conclusions regarding the proper status of the plant were subject to doubt. A need for a critical reevaluation of *S. odorata* was thus evident (Sheviak, 1973).

The specific status of *S. magnicamporum* was originally determined largely on ecological grounds (Sheviak, 1973). Although *S. magnicamporum* was very distinct from *S. cernua* in well developed, live material, it was early apparent that under stressed conditions individuals of the two species often became very similar, and it was only through cultivation that their potential phenotypes became evident. Furthermore, many characters that served to distinguish the two species were lost with preservation, so that determination of herbarium specimens was sometimes exceedingly difficult. Consequently, it was only through the study of cultivated material and extensive field experience that determination of the specific status of *S. magnicamporum* was possible. This was based on the parapatric distributions of the two species which resulted from their different habitat requirements. Furthermore, the few stations that could be found at which the species occurred together disclosed very little evidence of hybridization.

It was apparent, however, that hybridization was not impossible, although experimental crosses produced no seed. Because of the difficulties encountered with herbarium work, I was very reluctant to accept as evidence for hybridization solely intermediate herbarium specimens. If a hybrid origin of such a plant was reasonable in light of locality and ecology, then more weight was given to its intermediate condition. In this fashion, I hypothesized a remote hybrid origin for what I termed (Sheviak, 1973, 1974b) the “low prairie race.” The hypothetical ancestry of this race and limited familiarity with it dictated that it not be treated definitively, and it consequently was treated merely as a vague, ill-defined race of possibly hybrid origin.

A major factor preventing the definitive treatment of the low prairie race was the occurrence of occasional specimens from the prairie region which were variously intermediate between *S. cernua* and *S. magnicamporum* and yet quite distinct from the low prairie race. During the initial phase of this study only a few such specimens were known to me, and they served more to obscure the identity of the low prairie race than to cast doubt on the distinctness of *S. magnicamporum*. Subsequent work has shown these intermediates to be widespread and important members of the complex in much of the prairie region and even in portions of the forested regions to the east. This diverse assemblage of variably intermediate forms has been the focus of much of this study and is referred to below as the “prairie complex.”

A salient feature of the prairie complex is a series of teratologies which occur in varying degrees and combinations over much of the area occupied by the complex. Significantly, similar conditions occur in north-eastern populations supporting specimens intermediate between *S. cernua* and *S. ochroleuca*.

Clearly, then, the publication of *S. magnicamporum* was merely a first step toward an understanding of the *S. cernua* complex, even in the prairies, and work continued on it, focusing on the natures of “intermediate” specimens and certain monstrous individuals. Eventually it became possible to characterize the various taxa in the complex and to identify a number of morphological types that did not appear referable to any presently known taxa but were often to some extent intermediate between *S. cernua* and other species. The salient features of the variation pattern in the complex are presented graphically in Figure 12.
SYNOPSIS OF CHARACTERS

Spiranthes are difficult taxonomic subjects. Size of individual plants varies greatly depending on the vigor of the plant and its habitat; individual organs also show considerable variation, and floral characters are often more unstable than vegetative ones. Root systems, frequently of some use as sources of characters, are only occasionally collected. Leaf characters are useful in a few cases, but often leaves are lacking at anthesis or are not collected. Inflorescences are all spicate, although variation in the presentation of the flowers occurs. The flowers themselves are discouragingly uniform, with the majority of species exhibiting an essentially identical size range; except for the pink-flowered S. sinensis of Eurasia, color is characteristically white, frequently with various shadings of yellow and green. Seeds can be very important but frequently are not present in herbarium material. This situation is made even more difficult by the loss of some characters with preservation, and the alteration of qualitative ones from one condition to another.

It is thus not surprising that the genus has gained a reputation of being exceedingly difficult systematically, and virtually all of the principal works dealing with the eastern North American species have been prefaced with comments regarding the complexities of the group and the poor state of our knowledge of it (Ames, 1903, 1904, 1906, 1921, 1947; Correll, 1940, 1950; Fernald, 1946a, 1946b; Case, 1964; Luer, 1972, 1975; Sheviak, 1973; Catling and Cruise, 1974; Sheviak and Catling, 1950). Characters utilized in the past and others investigated during the present study are reviewed below.

Roots

Spiranthes odorata, S. ochroleuca, and S. cernua are characterized by slender, usually wide-spreading roots. In contrast, S. magnicamporum bears roots that are tuberously thickened and abruptly descending; the roots of S. romanzoffiana are also commonly tuberous, often bulbously so. Virtually the entire prairie complex exhibits tuberous roots; in some forms they are extraordinarily thickened. Since the last two species are the only likely contributors of root tuberosity in the complex, this character can be an aid in assessing the origins of variation in S. cernua.

Spiranthes odorata is characterized by stoloniferous roots, and this characteristic has been used by various authors to aid in distinguishing this taxon from S. cernua and S. magnicamporum (Correll, 1950; Sheviak, 1973; Luer, 1975). Correll (1950) and Catling (1980), however, indicated the occasional occurrence of the stoloniferous condition in S. cernua, and this behavior has been observed in some cultivated material of this species during the present study. Root apices have produced shoots when pot-grown plants were maintained at summer temperatures for several weeks following blooming; the delay in the onset of normal autumn and winter temperatures seems to promote stoloniferous reproduction in S. cernua.

Leaves

Spiranthes cernua and S. magnicamporum bear leaves typical of most of the genus, varying from linear-lanceolate to oblanceolate, and exhibiting distinct petioles. Leaves of S. odorata are broader, elliptical to oblong-oblanceolate, and petiolar development is often reduced or lacking. In S. ochroleuca, the linear-oblanceolate to narrowly elliptical leaves commonly lack petioles. The leaves of S. cernua and S. magnicamporum are thin and submembranaceous, whereas both S. odorata and S. ochroleuca produce flesher leaves. Those of S. odorata have been described as succulent (Correll 1940, 1950), but are actually aerenchymatous, a condition probably reflecting the swampy habitat of the species. The leaves of well-grown specimens of S. ochroleuca are slightly fleshy and highly flexible, which, together with a vaguely rough surface, contribute a sensation to touch very similar to that of crepe rubber. In depauperate or etiolated specimens, however, leaves are merely subcoriaceous or membranaceous. The distinctive leaf characters are obscure in depauperate or stressed specimens of all taxa.

Leaves of S. magnicamporum are wholly basal and ascending. Those of S. cernua are similar, but in some plants one or two leaves may be born on the very base of the stem. The similarly basal to subbasal leaves of S. ochroleuca curve generally throughout the length of the blade, and a lack or abbreviation of petioles and relative abundance of leaves in this species produce a compact rosette at the base of the plant. These leaves are strongly canaliculate, contributing to the distinct vegetative appearance of the plant. In S. odorata the leaves are not wholly basal but may extend partially up the stem, often merging gradually with the bracts below the inflorescence.

Leaf persistence, the presence or absence of leaves at anthesis, frequently is a useful character and has been utilized rather widely (Ames, 1905b; Fernald, 1946a; Correll, 1950; Case, 1964; Luer, 1972, 1975; Sheviak, 1973). Within the S. cernua complex, S. magnicamporum and members of the prairie complex are distinct in the fugaceous nature of their leaves. Plants with a truly fugaceous habit lose their leaves sometime before the inflorescence appears above.
ground. In *S. magnicamporum*, frequently three or more weeks elapse between the loss of leaves and the appearance of the spike. In *S. ochroleuca*, *S. odorata*, and typical *S. cernua*, leaves persist during and after flowering if conditions are favorable. Under comparatively xeric conditions, however, leaves may be lost before blooming, although even then this usually occurs as the inflorescence develops rather than before. Conversely, at the northern limit of its range in North Dakota, *S. magnicamporum* blooms much earlier than elsewhere, sometimes in mid-August, and then occasionally retains its leaves into anthesis. This situation is the result of the shorter growing season and the independent control of leaf loss and flowering.

Cultivation is very useful in determining the inherent natures of the plants in question. With adequate moisture and freedom from competition, *S. magnicamporum* and the fugaceous prairie plants continue to lose their leaves well in advance of anthesis, whereas specimens of the rest of the *S. cernua* complex maintain their leaves in good condition.

**Inflorescence**

The spiral arrangement of flowers in the inflorescence has long been recognized as the most striking morphological feature of the genus and has contributed two of the names proposed for it, *Gyrostachys* and *Spiranthes*. The degree to which the coil of flowers is spiralled around the rachis varies greatly from second to so densely coiled that the spiral aspect is lost. Ames, in his pioneering works on the North American species, utilized this character extensively. It has become standard practice to introduce keys to the species with a couplet separating "single-ranked" from "multi-ranked" species. The single-ranked plants are those with obvious coils laxly extended along the rachis, or, in extreme cases, with a second arrangement of flowers. The multiranked plants produce a dense inflorescence in which usually three or four rather variably coiled ranks ascend the rachis. These plants frequently produce inflorescences with no obvious ranking at all, thus complicating the situation.

The emphasis placed on this character in keys has caused considerable confusion in determination of some plants, especially in the *S. cernua* complex. This problem has arisen not so much through difficulties intrinsic to the character itself as to a lack of understanding of the nature of the "multiranked" inflorescence. In reality, the inflorescence types divided into two categories in the past represent the extremes of a continuous range of variation. This is easily demonstrated in terms of phyllotaxy. In "single-ranked" plants, the parastichy is clearly recognizable as the coil of flowers around the rachis. The higher the angle of the parastichy, the lower the phyllotaxy, until the second condition is reached, at which time phyllotaxy jumps to 1/1 (it is philosophically more satisfactory to consider this state as $1/\infty$). Hence, as the angle of the parastichy decreases, the phyllotaxy increases until, between 1/5 and 1/4, the superposed flowers are brought into such vertical proximity that orthostichies become evident, and the "multiranked" condition is reached. "Multiranked" plants thus exhibit a phyllotaxy of 1/4 or 1/3. The orthostichies may be either vertical or themselves exhibit varying degrees of spiralling; in some cases this becomes great enough that ranking of any sort is not evident.

Since the *Spiranthes cernua* complex can be characterized as comprised of those plants with multiranked inflorescences of rather large flowers, some further comments on the behavior of the inflorescence in multiranked species are necessary. The division of single-ranked and multiranked configurations at the 1/5–1/4 boundary is not due merely to the ease with which the eye perceives geometric configurations. In multiranked plants, the number of flowers per cycle is not usually a product of the angle of the parastichy as it is in single ranked types. Hence, the presence of three or four orthostichies is not necessarily affected by the "openness" nor "laxness" of the spike. This is an important point, for only very rarely do even the most densely coiled spikes of single-ranked species exceed a phyllotaxy of 1/5; indeed, I have seen this situation only twice, in *S. grayi*. Thus specimens and races of the *S. cernua* complex with high angled parastichies are readily separable from similar single-ranked species. For example, some specimens of *S. cernua* are occasionally determined as *S. cernalis*, because they exhibit a high-angled parastichy and hence are run through the single-ranked portions of standard keys (Sheviak, 1974a, 1974b); the phyllotaxy of such plants, however, shows them to be *S. cernua*.

Phyllotaxies lower than 1/4 do occasionally occur in normally multiranked taxa, however, and complicate the situation. Ames (1921) indicated that much of the variability of *S. cernua* was due to changes in the vigor of the plants. He traced the development of large specimens from seed and pointed out that the aspect of the inflorescence varied more or less continuously from year to year "until the limit of vigor of the vegetative system is attained." My horticultural experience with these plants confirms this. Particularly small plants, probably almost always very young ones, may occasionally produce truly single-ranked inflorescences with phyllotaxies lower than 1/4. These inflorescences
are small and few-flowered; they are occasional in S. cernua and somewhat more common in S. ochroleuca.

Changes in vigor are not solely responsible for single-ranked specimens, however. In the Northeast, two races of S. cernua are characterized by truly single-ranked inflorescences. These plants can confound determination by the uninitiated.

**Floral Bracts**

The original description of *Gyrostachys ochroleuca* (Rydberg, 1901) attributed unusually long bracts to this species, the lower exceeding the flowers in length, a condition supposedly not occurring in S. cernua. This character was initially adopted by Ames (1905b), but later abandoned (Ames, 1921). The bracts of *S. ochroleuca* do tend to be longer than those of *S. cernua*, but the relationship is not constant (Sheviak and Catling, 1980). The longest floral bracts occur in robust specimens of *S. magnicamporum* and in some members of the prairie complex.

**Flowers**

A number of floral characters are of significance in the genus, but their use is often difficult or ambiguous due to phenotypic plasticity and modifications introduced during preservation. Recent statistically-based work (Simpson and Catling, 1978; Sheviak and Catling, 1980; Catling, 1980, 1981), however, has demonstrated their reliability and utility in the great majority of specimens.

Floral shape varies significantly in the complex but is difficult to assess consistently and has been little used. It has been mentioned by Ames (1905b), Femald (1946a), Correll (1950), Luer (1972, 1975), Sheviak (1973), Catling and Cruise (1974), and Sheviak and Catling (1980), often rather in passing.

*Spiranthes cernua*, *S. ochroleuca*, and many *S. odorata* bear flowers with a general dorsi-ventral curvature. The lip matches the curve of the rest of the flower for about one-half to two-thirds of its length and then rather abruptly diverges downward apically. In contrast, *S. magnicamporum* possesses narrowly ringent flowers (Sheviak, 1973). Curvature is restricted to the base, and the lip curves rather generally throughout its length, although the apex may be abruptly reflexed. Similar, but usually less slender flowers commonly occur also in *S. odorata*. In this species, either generally curved or ringent flowers may be produced by individual plants in different years.

The position of the lateral sepals varies significantly between species. The hooded nature of flowers of *S. romanzzoffiana* is one of the two characteristics typically used to separate this species from *S. cernua*. Except for this one case, few workers have used lateral sepal orientation as a taxonomic character (Ames, 1921; Sheviak, 1973; Catling and Cruise, 1974; Luer, 1975).

In the *S. cernua* complex, lateral sepal orientation is significant. In *S. cernua*, the lateral sepals occupy the same plane as the rest of the flower; they spread very slightly at the base, parallel the flower for most of their lengths, and then abruptly curve inward apically. For the most part, *S. ochroleuca* and *S. odorata* duplicate this pattern, although in the former, the sepals are frequently appressed to the petals, and the latter frequently approaches the behavior of *S. magnicamporum*. In the last species, the sepals spread more or less widely from the base of the flowers, often also ascending above the rest of the flower.

In preserved material, it is often possible to assess the lateral shape of the flower, but sepal position is only rarely determinable, and the ease with which it may be altered during pressing dictates that it be used with extreme caution. Even in the field, where these characters are of considerable use, caution is needed due to the frequently great phenotypic plasticity exhibited by individual plants. As I learned early in this study (Sheviak, 1973), depauperate and stunted individuals of different taxa may appear essentially identical in floral configuration but diverge greatly in phenotype when provided with conditions more favorable for growth, then exhibiting the characteristics typical of their taxa.

The labellum, or lip, is of considerable interest to taxonomists working in the Orchidaceae, for it very frequently exhibits species-specific variation of great usefulness in determination. It is due probably more to the established precedent in the family, however, than to any value intrinsic in the character itself that lip features have been so emphasized in *Spiranthes*. In his original description of *Ophrys cernua*, Linnaeus (1753) described the lip as "labio inferiore oblongo, acuto, integro." Since that time, lip shape has been one of the principal characters stressed by workers in the genus. Yet, early in this century Ames (1905b), in a discussion of the difficulties encountered in the group, wrote, "Another circumstance which leads to confusion is the interpretation, often faulty, of the lip characters in species which exhibit little or no consistency in the outline or measurements of this important organ." His later emphasis on lip configuration is thus remarkable. Lip variation is minor and often nearly as great within species as between them. Lip shape may be altered during pressing. It is also particularly susceptible to modification by the environment and endogenous physiological fluctuations. Hence, the frequently smaller flowers at the apex of a spike usually
possess lips very different from those of the large basal flowers. In robust specimens of some taxa, it is often possible to find lips characteristic of three species along a single inflorescence. Consequently, some recent work (Catling, 1980) has emphasized comparisons of flowers on the basal portion of the spikes. Difficulty in application of this character led to the reduction to varietal status of *S. odorata* by Correll (1940) and, apparently, of *S. ochroleuca* by Ames (1905b).

Three of the species in the complex, *S. odorata, S. magnicamporum*, and *S. ochroleuca*, possess very similar lips. They vary from rhombic-ovate or ovate in *S. odorata* to ovate or oblong in *S. magnicamporum* and *S. ochroleuca*. The margins are nearly to quite entire. In contrast, the distinctly lacerate lip of *S. cernua* is characterized by a distinct orbicular or suborbicular dilated base, the lip then appearing somewhat constricted at the center. This distinction has been recognized in varying degrees in the past (Ames, 1921; Correll, 1950; Luer, 1972, 1975; Sheviak, 1973). Except for the lack of a secondary apical dilation, the lip of *S. cernua* suggests the pandurate form seen in *S. romanzoﬀiana* and can be viewed as intermediate between this species and the three other members of the *S. cernua* complex. Lip shape of *S. cernua* is highly variable, and some of the variation can be used in conjunction with other characters to deduce gene flow in the complex.

Lip texture is of considerable significance in the genus but has been little used (Ames, 1904; Sheviak, 1973; Luer, 1975; Sheviak and Catling, 1980). *Spiranthes odorata, S. ochroleuca*, and *S. magnicamporum* are characterized in the herbarium by lips that are thick and rather fleshy, especially centrally, and which are rather opaque to transmitted light. In contrast, typical *S. cernua* and *S. romanzoﬀiana* possess membranaceous lips in which the venation is readily apparent. Segregates of *S. cernua* show varying degrees of development of this central thickening. This character can be used in interpreting gene flow in the complex, but it must be used with care, because the fleshy nature of the lip is lost as the flowers senesce on the plant, and occasionally during drying in the press the fleshy condition (especially in older flowers) is altered to the membranaceous. This problem is compounded by the occasional development of basal dilations with senescence or poor preservation in plants normally lacking them. Hence, it is essential that only well preserved material be used, and, if possible, only flowers showing no discoloration should be selected.

At the base of the lip, adjacent to the claw, are located two more or less marginal, conical protuberences. They have been variously termed "callosities" (Ames, 1903, 1904; Correll, 1950); "tubercles" (Case, 1964); "tuberosities" (Luer, 1972; 1975); "calli" (Sheviak, 1973; Sheviak and Catling, 1980); and "nectar glands" (Ames, 1921). Of these possibilities, "tubercles" is perhaps the best. Tubercle variation has been used as a character with varying degrees of emphasis, the extreme case being *Ibidium incurvum* (Jennings, 1906), which was proposed solely on the basis of supposed differences in these structures. Ames (1921) stated that the tubercles of *S. ochroleuca* tended to be longer and more curved than those of *S. cernua*. This is frequently the case, but in some material of *S. ochroleuca* they may be distinctly shortened. In *S. cernua* tubercles vary greatly from the long, curved structures which served as the basis for *Ibidium incurvum* to short, conical nobs. The latter condition is typical of *S. magnicamporum*; *S. odorata* typically bears moderately long, somewhat curved tubercles. In *S. cernua* and *S. magnicamporum*, and probably other species as well, short tubercles elongate greatly as the flower ages, making this already variable character even more difficult to assess.

Variation in floral color can be significant and has been employed by most workers. In typical form, *S. cernua* is characterized by pure white flowers. In contrast, those of *S. ochroleuca* are distinctly yellowish or at least ivory-colored. In *S. odorata* a range of white to ivory is common, with the thickened center of the lip frequently suffused with green or yellow, the latter sometimes quite intensely. *Spiranthes magnicamporum* exhibits a similar range of white to ivory, with the center of the lip usually more or less yellow. Great variation is found in the prairie complex and in Northeastern populations of *S. cernua*.

The use of floral color is complicated by a tendency for the ivory or yellowish condition to be accentuated under more xeric conditions. Specimens of *S. magnicamporum*, for example, when found on dry, exposed prairie, characteristically bear yellowish or ivory flowers, but when they are transferred to the greenhouse produce whiter flowers in subsequent years. Similar results are obtained with some of the races of *S. cernua*. This character is particularly variable in some abnormal material; one cultivated plant (Sheviak 388b), for example, in various years has produced pure white, yellow, and green and yellow flowers.

Fragrance varies somewhat in the genus but has been used only rarely. In the *S. cernua* complex, flowers of *S. cernua* are often scentless or very nearly so. Fragrance, when present, is variable, but is generally pervaded by a distinct earthy quality. The characteristically fragrant flowers of *S. ochroleuca* are rather more pungent in the terminology of Fernald (1950). In *S. odorata*, flowers are distinctly fragrant, with a scent varying from like that of fragrant *S. cernua* to a condi-
tation suggesting *S. magnicamporum*. Correll (1950) described it as a mixture of vanilla, coumarin, and jasmine. The flowers of *S. magnicamporum* are the most fragrant in the complex, producing a strong scent of coumarin (Sheviak, 1973; Luer, 1975); this scent is also present in *S. romanoffiana*. Consequently, this character is of interest as a possible indicator of gene flow in the complex, especially in the prairies where the intensely fragrant *S. magnicamporum* contributes its singular scent to its hybrids with *S. cernua*. Such a subjective character (definitive chemical analysis has not yet been technically possible) is, of course, difficult to utilize precisely and uniformly.

**Seeds**

Leavitt (1900) early determined the presence of polyembryony in *S. cernua*. Curtis (1893), however, had previously reported normal seeds in this species. This discrepancy stimulated further work, and Leavitt (1907) reported the more general occurrence of polyembryony. Ames (1921) first used this character taxonomically to separate the polyembryonic "wet meadow and bog form of *S. cernua" from the monoembryonic *S. ochroleuca* stating that it was the only character by which this separation could be reliably achieved. This character is of extreme importance.

Since Ames first recognized the monoembryonic nature of the seed of *S. ochroleuca*, the characteristic has been stressed as the principal difference between this species and *S. cernua* (Correll, 1950; Fernald, 1950; Case, 1964; Luer, 1975). The monoembryonic condition in *S. odorata* seems to have largely escaped notice, as only Fernald (1950) mentioned it. One of the principal differences utilized in distinguishing *S. magnicamporum* from *S. cernua* similarly lies in the presence of the monoembryonic condition in the former (Sheviak, 1973; Luer, 1975). Since this variation reflects the cytological condition of the plant (see below), it is of great importance.

The shape of the seed rarely has been used. Ames (1921) described the seeds of *S. cernua* as "balloon-shaped" and those of *S. ochroleuca* as slenderly elliptical. Sheviak (1973) noted the oblong-quadrate seeds typical of *S. magnicamporum* and compared them with the fusiform seeds of *S. cernua*. It is now clear that comparatively short and broad seeds are characteristic of *S. ochroleuca*, *S. odorata*, and *S. magnicamporum*, whereas *S. cernua* produces slender, fusiform seeds. Although variation occurs within taxa and individuals, this character can be of use particularly in cases involving peculiar specimens of uncertain affinities.

Representative seeds are illustrated in Figure 6 and Figure 7.

**CYTOLOGY**

Polyploidy in natural orchid populations was reported first in *Spiranthes* (Pace, 1914). By study of serial sections, Pace found *Spiranthes lacerca* to be diploid and *S. cernua* to be tetraploid, although in the latter case, "no count was entirely satisfactory."

It is thus remarkable, considering the taxonomic complexities of the genus and the controversy which has surrounded it, that until the present study no one had conducted cytological studies in an effort to clarify relationships. The available literature reports are presented in Table I.

In the present study, the majority of counts have been obtained from root tips. Root tips are collected during the morning. Some evidence for mitotic periodicity has been noticed, for root tips obtained before 8:00 a.m. tend to exhibit abundant prophase nuclei and few or no metaphase figures. Root tips are treated with a saturated aqueous solution of monobromonaphthalene at room temperature for four hours. During hot weather temperatures must be maintained below 25°C for best chromosome condensation. Alternatively, roots may be treated at about 4°C for periods of twelve to eighteen hours, but results are not so consistently satisfactory. Initially, 8-hydroxyquinoline was used, at both .002M. and .004M., but the results were not satisfactory.

Following this treatment the root is fixed for twenty to thirty minutes in Carnoy’s solution. Longer periods retard chromosome spreading. Farmer’s solution was originally used, but Carnoy’s promotes better spreading.

Following fixing, the root is stored in 70% ethanol in a freezer or prepared for immediate squashing. For this it is hydrolyzed in 1N. HCl at 55° to 60°C. for eight to fifteen minutes. Although the longer periods allow significantly better squashing, hydrolyzing in excess of nine minutes sometimes prevents staining.

For staining, aceto-lacmoid prepared as indicated by Darlington & LaCour (1969) and Melquist and Clovis (1957) is used. Aceto-carmine and orcein, both after and during hydrolysis, proved unsatisfactory, as did the Fuelgen method.

I have not had success with anther preparations. No meiotic figures have been seen, and the only count obtained from anthers was from a mitotic tapetal division in *S. odorata*.
For field use, immature ovaries are used. Suitable buds include all sizes from those near anthesis to the smallest which have a distinguishable ovary. The buds are treated with monobromonaphthalene solution and fixed in Carnoy’s solution for 20 to 30 minutes. Buds are hydrolyzed for 15 minutes, and the ovaries then dissected to remove the immature ovules; the ovules are stained and squashed in the same manner as root tips.

Ovaries were selected as likely sources of mitotic figures due to the great abundance of developing ovules. The quality of the figures is in general somewhat lower than in root tip preparations, but this is often made up for by the comparative abundance of material. Meiotic figures are also commonly present, and these preparations have been the sole source of meiotic information obtained in this study.

The interpretation of cytological data has been straightforward. Endopolyploidy has not been found in Spiranthes. Counts obtained from root tips and flowers agree in chromosome number and correlate with meiotic counts. Although endopolyploid cells may occur in tissues not studied, they do not contribute difficulties to cytological work on the tissues utilized in this study.

Hydroploid cells, however, are consistently present in the root tips of tetraploids. They generally exhibit chromosome counts somewhat above the triploid level, with a frequent range of about 47 to 52 chromosomes. The cells are unusually large and unstaining and increase in importance in the root tip as the root nears cessation of growth in the summer. One division figure was found which provides a possible explanation of the origin of hydroploid cells. This was a late anaphase figure in which one daughter complement was organizing into two groups, one with approximately two-thirds of the chromosomes. Possibly this larger hydroploid aggregation organizes a normal nucleus and undergoes later mitotic division.

True B-chromosomes have not been clearly demonstrated in orchids. Vij and Vohra (1974) reported B-chromosomes in some specimens of S. autumnalis, but correlated these with morphological variation, suggesting that this designation might be inappropriate. In the present study, no evidence of B-chromosomes was found.

The chromosome counts obtained in this study and some meiotic information are presented in Table II. As can be seen from this table, the S. cernua complex has been found to consist of three diploid species, S. odorata, S. ochroleuca, and S. magnicamporum, with 2n=30. A large tetraploid complex, with 2n=60, includes S. cernua. The putative hybrid “low prairie race,” the two single-ranked northeastern forms, and some other northeastern plants have been found to be triploids. A few aneuploids (hypertetraploids) have also been found.

Photographs documenting the chromosome counts of the species dealt with in this work and other squashes of interest are assembled in Figures 1–5.

From these findings it is evident that Paces’ (1914) material was, indeed, referable to S. cernua, but that Tanaka’s (1965, 1969) was not and probably was a member of one of the diploid species in the complex. The report by Smith (1964) of a count of 2n=ca. 50 for S. cernua is inaccurate. The voucher for this collection is a typical member of the prairie complex, and many other typical collections have been made at the locality. I have collected there and found the plants to be identical with Sheviak 962 which was collected only a few miles away. Unfortunately, the cytological specimens I collected at Smith’s locality proved unusable. It is clear, however, that Smith’s count is in error. It is possible that his preparation was not adequate, but most likely he based his report on hydroploid cells. These are more easily counted than normal cells because of their lower chromosome number and larger size and hence are more apt to be chosen for counts than normal tetraploid cells.

The meiotic information obtained in this study is limited but highly significant. Diploids show regular meiosis with perfect bivalent formation. In contrast, tetraploids generally display varying degrees of meiotic irregularity (Figure 4). Quadrivalents are common. Chromatin bridges indicate the presence of inversions in some plants. Lagging chromosomes are occasionally seen. The presence of translocations is indicated by complex pairing including branched chains and multivalents above the quadivalent level. Considering the complex pairing in the tetraploids examined in this study, it seems likely that they are segmental allotetraploids.

Some of the tetraploid races studied, however, frequently exhibit exceptionally good pairing. Figure 5 shows first meiotic metaphase and anaphase of Sheviak B325, an aneuploid (2n=61) derivative of one of these races. The metaphase shows 30 bivalents, with a few secondary associations, and one very small univalent. Similarly, in the anaphase, one daughter complement shows 30 chromosomes plus one out of the plane of the others and lagging slightly.

These cytological data have provided the basis for an understanding of the S. cernua complex as discussed below. The presence of translocations and irregular pairing has been of major importance in the deduction of the origin of some members of the complex. These phenomena will be treated in detail in a subsequent paper.
GUARD CELL MEASUREMENTS

Guard cell measurements were undertaken in an effort to extend cytological data to herbarium material and to aid in the determination of problem specimens. Measurements were obtained from abaxial surfaces of floral bracts; usually a single bract was chosen from each specimen. Usually ten, but occasionally up to fifty cells were measured and the mean determined. Measurements were made on over 300 specimens; these included plants for which chromosome numbers were known and others which had been determined on the basis of morphological characters. The ranges in mean measurements were:

- S. magnicamporum & S. ochroleuca 29.8-38.4 microns
- S. odorata 35.9-40.8 microns
- 3n low prairie race 31.2-43.9 microns
- known and apparent tetraploids 34.6-47.4 microns

Although exhibiting a continuous range of variation, these measurements do have a certain applicability. The ranges exhibited by diploids and tetraploids overlap widely, but the smaller measurements for S. magnicamporum and S. ochroleuca and the larger tetraploid figures are distinct. This situation permits the use of guard cell measurements as a character.

Significantly, a tendency was noticed for the largest cells to occur in specimens which are difficult to determine on morphological grounds, and a distinct correlation between hybrid-like morphology and large guard cells is evident. This situation is often helpful in determination. Conversely, very small cells typical of diploids have been found in some hypertetraploid, morphologically abnormal material; these specimens are readily determined by consideration of gross morphology, and hence guard cell size is not likely to contribute to misidentification of these plants. This apparent cytogenetic influence on guard cell size is a significant phenomenon and will be dealt with in a subsequent paper.

APOMIXIS

Leavitt (1900, 1901) was the first to recognize the presence of polyembryony in S. cernua. His observations further indicated the development of seed without pollination, and he reported the abortion of pollen tubes in experimentally pollinated flowers. Schnarf (1929) reported S. cernua to be an apomict. Stebbins (1941), however, questioned this conclusion. To clarify the situation, Swamy (1948) studied embryogenesis in S. cernua. He found that the polyembryonic condition was due to the adventive development of two to six embryos through mitotic division of the inner integument.

Swamy based his work largely on material from the northeastern United States, with greatest emphasis on populations in eastern Massachusetts. He concluded that S. cernua was comprised of three races. Members of the first reproduce sexually. Seeds were monoembryonic, the embryo always developing from a fertilized egg. The second race was wholly apomictic. Adventitious embryony resulted in seeds containing two to six embryos of nucellar origin. Occasionally nucellar mitotic division began before the completion of meiosis in the adjacent megaspore mother cell. Embryo sac development usually was arrested at the four cell stage. Microsporogenesis, in contrast, proceeded normally, but the mature pollen degenerated and became infested with "a saprophytic fungus" by the time of anthesis. The third race was "intermediate" in its behavior. Capsules normally contained a mixture of seeds of sexual and apomictic origin. The apomictically produced seed of this race, however, contained not more than three embryos. Pollen was normal and functioned in the fertilization of sexual ovules. Significantly, in this race adventitious embryos did not develop in ovules containing a functional embryo sac, and they developed in sexually sterile ovules only following fertilization of the normal ovules. The relative proportion of apomictically produced seed varied from 25% to 65% in various individuals.

Using embryo number as the critical character, Swamy then attempted to determine ranges and relative importance of the three races. From examination of herbarium specimens he concluded that by far the greatest proportion of specimens were wholly apomictic, and that sexual and "intermediate" plants were considerably less important (520 and 412 plants, respectively, out of a total of 5,000) and essentially restricted to the northeastern United States.

My own experience with cultivated material early confirmed the apomictic nature of S. cernua. Not only did plants of this species characteristically produce seed without pollination, the pollinia removed and pollinators excluded, but buds from which the entire column had been excised continued to develop and formed normal capsules with abundant seeds. In contrast, plants of what was later described as S. magnicamporum were found to require pollination for seed production. Seeds in these plants were monoembry-
onomic. Subsequent studies showed the presence of monoembryony and the absence of apomixis in *S. ochroleuca* and *S. odorata*.

Cytological study has been of great importance to an understanding of the significance of reproductive mode in the complex. Study of numerous specimens from throughout the range of the complex has shown diploids to be uniformly sexual and to produce strictly monoembryonic seed (Figure 6). Conversely, polyploids exhibit varying degrees of apomixis and correspondingly variable percentages of polyembryonic seed (Figure 7). The earlier report (Sheviak, 1973) of polyembryony in specimens of *S. magnicamporum* from some portions of its range has been found to be based on polyploid members of the prairie complex. Very recently, Catling, (1980, 1981, 1982) has reported polyembryonic seed and adventitious embryo in *S. magnicamporum, S. ochroleuca*, and *S. odorata* toward the northeastern range limits of the species. These reports would appear to be based on polyploids, a conclusion supported by examination of some of Catling’s material. He has reported (Catling, 1980), however, a diploid chromosome number for a single apomictic specimen of *S. magnicamporum*; this count supports his conclusions and indicates that the correlation between ploidy level and reproductive mode is not absolute. Cytological study of these plants is needed. It is apparent, however, that apomixis in diploids is very restricted.

Although Swamy’s work is basically sound, some error in interpretation is apparent now that I have made protracted observations on cultivated material and have been able to study the plants over much of their ranges. The most obvious flaw is in his establishment of three races based on reproductive mode. The actual situation is much more complex. It is now apparent that sexuality is a characteristic of more than one taxon within the *S. cernua* complex. Furthermore, Swamy’s utilization of relative number of embryos in polyembryonic seeds as a means to distinguish obligate and facultative apomicts is of very dubious reliability when one considers the great diversity of genotypes and habitat requirements as well as the wide range of *S. cernua*. Indeed, some allotriploids apomictically produce abundant seed in cultivation, but a large proportion of such seed is monoembryonic, indicating a more complicated situation than that proposed by Swamy. There is also some question as to the absolutely obligate nature of apomixis indicated by Swamy for his “asexual race.” My observations indicate that, although some obligate apomicts do occur, most notably certain teratological plants, the majority of plants within *S. cernua* are capable of some sexual reproduction.

An indication of variation within *S. cernua* has been obtained from comparison of flowering behavior between clones and of the same clone over several years of cultivation. With the exclusion of pollinators a striking difference is seen. In some plants enlargement of the ovary is precocious, and flowers open on developing capsules. In such plants, flowers are open often for only a day or two. Such behavior is to be expected as an extreme development in Swamy’s “asexual race,” in which adventitious embryo development begins at the time of first meiotic prophase. It is doubtless significant that such races frequently are stable over wide areas. In contrast, in the majority of plants of *S. cernua* which I have examined, flowers remain open and functional for a protracted period. Thus, in the absence of pollination, an entire inflorescence may remain in good condition for two weeks before swelling of the ovaries is seen, followed shortly by collapse of the perianth. This would be the expected behavior of the “intermediate race” of Swamy, although he makes no mention of it. In my experience, races exhibiting such floral behavior are morphologically variable.

Swamy’s report of pollen abortion and fungal infestation in his asexual race appears to be unrelated to reproductive mode. Pollen abortion appears to be influenced by the environment; greenhouse studies have suggested that this phenomenon and irregularities of stipe and disc formation are associated with high ambient temperatures. *Spiranthes ochroleuca* and various other species exhibit the same anomalies as *S. cernua*.

The correlation of apomixis and polyploidy, and hence of polyploidy and polyembryony, has been most useful, for it has aided the recognition of polyploids in the herbarium. Care must be taken with seed characters, however. It should be noted that embryo number merely provides an indirect means of assessing the underlying character, reproductive mode. Hence, observation is directed at irregularities in seed development associated with adventitious embryo (Figure 7). Monoembryonic seeds with extruding or externally developed embryos (as figured by Swamy) and disassociated embryos lacking testae are as indicative of apomixis as is polyembryony. Great variation is seen in the expression of seed and embryo characters in apomicts, and only in part does this reflect differing percentages of sexual and apomictic processes. Apparently normal, monoembryonic seeds are characteristically produced by some obligate apomicts; irregularities in such plants must be sought carefully. No evidence, however, for the occurrence of polyembryony in obligately sexual individuals has been found. Polyembryony and other irregularities are good indicators of apomixis; their apparent absence is somewhat less significant. In either case, such characters are best used in conjunction with other characters for determination.
A significant percentage, in some areas the majority, of the variation in floral characteristics in the S. cernua complex involves varying degrees of expression of two abnormal conditions.

One of these, peloria, reaches its extreme development in the prairie complex, where plants bearing truly peloric flowers are frequent and often characteristic components of some populations. In these plants the lip is scarcely if at all differentiated from the petals. Some of the most significant variation in the prairie complex involves the partial suppression of the lip, and similar semipeloria is seen elsewhere in the range of the complex, especially in the Northeast. In this region an opposing peloric tendency, the elaboration of petals toward characteristics of the lip, is also sometimes seen.

The second abnormality of interest here is the failure of floral buds to open. This condition suggests cleistogamy and has been noted as such on some herbarium sheets. Such use of the term is not appropriate, however, as pollination does not occur, and seed production is wholly apomictic; I will refer to this phenomenon as "cleistapogamy." Cleistapogamy is best developed and most important in the prairie complex, where it occurs in two basic forms here referred to as obligate and facultative cleistapogamy. Plants exhibiting the former condition are always cleistapogamous and produce no pollen. They are, additionally, wholly peloric and the perianth retains a uniform green color. The behavior of facultatively cleistapogamous individuals, however, varies from year to year and even between flowers on the same inflorescence. Often flowers are normal, but in some years they may be totally cleistapogamous. Often a mixture of conditions and degrees of intermediacy occurs.

Floral form in facultatively cleistapogamous individuals may be influenced by the environment, much as cleistogamy often is. In cultivated plants I have noticed a more frequent production of cleistapogamous flowers during hot weather. This has been particularly true of Sheviak 388b which has been in cultivation for a number of years. This plant has produced either normal or cleistapogamous flowers in various years, or occasionally a mixture of the two. During one hot August, the plant produced an inflorescence which had developed a number of cleistapogamous flowers but was still largely in bud when cooler weather arrived. Under the cooler temperature the remaining buds developed into normal flowers. Most remarkably, the perianth segments of some of the previously formed cleistapogamous flowers elongated apically and diverged, such that the essentially closed flowers were open at the apices. The remaining cleistapogamous flowers and the cleistapogamous portions of the newly modified ones were uniformly green; the elongated apical segments of the latter varied through yellow to white. The normal flowers higher on the spike were wholly white. The apparent correlation of cleistapogamy in facultative individuals with environmental variables, most likely including air temperatures, parallels abnormalities in pollen and pollinaria formation reported earlier (Sheviak & Catling, 1980).

Facultative cleistapogamy occurs not only in the prairie complex but is occasionally found elsewhere in the S. cernua complex, especially in the Northeast. The partial expression of cleistapogamy also appears to be reflected in the floral shapes of certain members of the S. cernua complex. These plants are characterized by variously cylindrical or urn-shaped flowers which open partially but never assume the gaping form typical of their relatives. Such plants are important components of the complex in the northeast and the prairies, and often contribute strikingly to the variation exhibited by a given population.

Both peloria and cleistapogamy have proven to be correlated with, and doubtless resultant from, aneuploid conditions. The origins and relationships of these phenomena will be treated in detail in a subsequent paper.

### Pollination Biology and Hybridization

In the original work on S. magnicamporum (Sheviak, 1973), experimental crosses between this species and S. cernua were found to be unsuccessful. Additional crosses more recently were made utilizing these species and S. odorata and S. ochroleuca. These experiments were conducted primarily to determine compatibility of the diploids, but supplemental S. cernua crosses also were made. The results are presented in Table III. These results indicate that the species are partially isolated genetically, although occasional crosses are successful. This isolation is particularly significant in the Orchidaceae, which is noted for ease of hybridization. All crosses involving S. cernua, however, employed the diploids as pistillate parents; reciprocal crosses utilizing S. cernua as the pistillate parent were not attempted due to the apomictic nature of this
species. If the observed isolation results from a lack of stimulation of fruit development, such crosses would provide a ready means of bypassing this mechanism and would allow unidirectional gene flow into S. cernua. The poor seed production of even the larger capsules obtained in the present crosses indicates, however, that other factors are operative as well.

Further isolation due to possible pollinator recognition of S. cernua and S. magnicamporum was earlier hypothesized (Sheviak, 1973). This suggestion was based on the very different aspects of the inflorescences of these plants and also the singular, intense fragrance of S. magnicamporum. Observations of pollination of Spiranthes in the field are rare and do not clarify the situation. Table IV presents the available reports.

Robertson (1983) reported pollinia of S. lacera to be born on the mandibles of Calliptosis andreniformis and Megachile brevis. I have found similar placement of S. cernua pollinia on Bombus species. Van der Pijl and Dodson (1966) suggested that the reports of Bombus on the small-flowered S. spiralis (Darwin, 1877) and S. lacera (Robertson, 1893, 1928) were due to misidentifications or casual visits. Robertson, however, specifically reported these as pollinating, and Van der Pijl and Dodson have accepted his determinations elsewhere. They have further stated that Godfrey's (1931, 1933) reports of Bombus on S. romanzzoffiana clearly arose from a chance visit. I have found Bombus to be the characteristic pollinators in the S. cernua complex.

Some significant observations were made in the greenhouse during the present study, when in one year the cultivated collection was actively visited by specimens of Bombus impatiens. Because of the arrangement of the collection, the bees most easily passed among members of the same species, but they were seen to move between S. cernua and S. odorata and between S. cernua and S. ochroleuca. Pollination was affected. Only one specimen of S. magnicamporum bloomed at this time and it was bagged for hybridization experiments, so no observations were made on this species. The available observations, however, suggest a lack of pollinator discrimination. Additionally, it should be noted that in Spiranthes the granular nature of the pollinia allows several flowers to be pollinated by the pollinia of a single flower, pollen being progressively removed by several flowers. This, then, would increase the effectiveness of even rare interspecific visits by individual bees.

ECOLOGY

The wide range of the S. cernua complex, extending approximately 2,700 kilometers north from southern Florida and 3,800 kilometers west from the Atlantic coast, presents a great array of environmental conditions and encompasses a number of major biomes. The ecological requirements of the different members of the complex vary accordingly. In common, however, they all exhibit an intrinsic colonizing habit and heliophbic tendency. They are predominately plants of open ground and typically colonize disturbed sites. They may appear within a few years of excavation or similar major disturbance, rapidly increase in abundance, persist for an indefinite period, and then decline and disappear as successional changes alter the site. Other forms of disturbance which serve to arrest succession, such as mowing, grazing, or burning, often promote the indefinite persistence of the species in areas previously disturbed or originally in a natural condition. Upon this fundamental nature are imposed the limiting edaphic and climatic requirements of the various members of the complex, yielding a considerable range of habitats utilized.

The most southeasterly range is occupied by S. odorata, an essentially coastal species occurring from eastern Texas to Florida and Delaware (Figure 8). Within the S. cernua complex the ecology of this species is in two respects unique. Spiranthes odorata characteristically occupies swampy situations subject to at least periodic inundation and occasionally occurs as an emergent aquatic in permanently flooded sites. Such behavior is unknown in the rest of the complex. Spiranthes odorata is also unusual in its frequent occurrence in forested sites, and the species is a characteristic plant of swamp forests. Frequency of anthesis is low in such sites, however, and in the deepest shade few plants bloom. Typical of the rest of the complex, S. odorata commonly also occurs in open situations in clearings and ditches and along trails and roadsides. Under such conditions it blooms abundantly.

This species also occurs in natural marshes, often under tidal influence, in fresh or brackish water. Soils are unusually diverse, varying from peat and muck to rather low-organic sands, usually of subacid reactions. In the Florida Everglades, and perhaps elsewhere, soils are highly calcareous, structureless, and high in clay.

Spiranthes ochroleuca is more characteristic of the S. cernua complex. Essentially northeastern in distribution (Figure 9) it is a plant of rather xeric open communities under natural or disturbed conditions. It is
commonly found in sterile openings in scrubby pine and oak woodland, on rock out-croppings, in old fields, and on the upper portions of roadcuts. It commonly occurs in coastal sites exposed to occasional salt spray, which may promote the occurrence of the species by maintaining open conditions. Soils are characteristically acidic and vary in texture from sand to clay loams. Organic matter is commonly very low, but locally may be high.

*Spiranthes magnicamporum* is a prairie plant with an essentially Midwestern distribution (Figure 10). Its range corresponds in large part to the distribution of tallgrass prairie, with disjunct populations in prairie relics to the east. To the west, it is also known from disjunct stations in the upper Rio Grande valley and the mountains of northern New Mexico. This species occurs in xeric to mesic grassland. The most acutely drained, exposed sites on loess and dolomite bluffs and sand ridges are occupied in the eastern portion of its range; the further west the species occurs, the progressively more mesic are the sites occupied until, at its western limits, it is dependent on relatively constant groundwater supplies and occurs in marshes and fens.

Reaching a peak of abundance in open communities, *S. magnicamporum* is comparatively rare in dense, undisturbed grassland. The species is most prevalent in the low open prairie communities developed on sand and dry bluffs, and it responds favorably to a variety of forms of disturbance which serve to produce similar conditions; it is often particularly abundant under light mowing or grazing regimes. Soils supporting *S. magnicamporum* are uniformly calcareous and minimally subalkaline. Textures range from sands to clay loams, with organic matter ranging from essentially absent to high; rarely the species occurs in mucks.

The range of the remainder of the complex nearly includes the ranges of the three diploids, apparently avoiding only Florida, New Mexico, and the Dakotas (Figure 11). Its ecology is correspondingly varied.

In the Northeast, the Great Lakes region, and along the Appalachians and Atlantic Coast, *S. cernua* occurs in a variety of moist to rather wet open sites. Under natural conditions the species occurs in open meadows, marsh borders, and bogs and fens. It is very commonly found in roadside ditches, abandoned borrow pits, moist roadcut banks, and in pastures and lawns. Populations of many thousands of plants may develop in small disturbed sites.

These eastern populations characteristically occupy sandy soils exhibiting a range of development and organic matter content from raw sand to sandy peats and mucks; infrequently true peats and mucks and finer textured soils are utilized. Reactions are most commonly medi-or subacid, but vary to minimalkaline.

The sand-inhabiting *S. cernua* populations are replaced very quickly along the northeastern margin of the prairie and are rarely encountered within the prairie region proper, where they are replaced by various members of the prairie complex. Members of the prairie complex occur usually in open prairie and prairie-like communities. Natural communities often support only scattered individuals, but under light mowing or grazing regimes the plants may become very abundant. Excavated sites, shallow roadside borrow ditches, and railroad rights-of-way are often colonized, especially if prairie-like communities develop and are occasionally mowed or burned.

Soils range widely from gravelly sands through clay loams and mucks; various loams are most important. Reactions vary from subacid and occasionally mediacid to minimalkaline.

In the forested region to the southeast of the prairies, a member of the complex occupies habitats similar to those of *S. ochroleuca* in the Northeast. Under natural conditions it occurs in dry open woodland on bluff crowns and ravine rims. It is very rare under such conditions and is more common about the margins of openings, such as prairie borders. This plant is characteristically a colonizer of old fields undergoing succession to oak-hickory and mixed hardwood-pine forests; consequently, it has been referred to as the "old field ecotype" (Sheviak, 1974b).

Soils are loams and silt- and clay loams of mediacid to very highly subacid reaction.

**DISCUSSION**

Once morphological variation is analyzed in terms of ploidy level, the *S. cernua* complex is seen to be composed of three distinct, sexual diploids and a highly variable, apomictic polyploid complex. The three diploids, *S. odorata*, *S. ochroleuca*, and *S. magnicamporum*, present a reticulum of character combinations, suggesting that they are closely related. Additionally, no other species are known in which occur an essentially ovate, fleshy lip and dense, "multiranked" inflorescence, suggesting that they are more closely related to each other than they are to any other species. Considering the great differences in ecological requirements of these plants and their allopatric distributions together with their morphological distinctions, it is
clearly best to treat them as distinct species. This conclusion is further supported by breeding experiments discussed previously.

Once these three diploid species have been recognized, the problems of determination and interpretation are seen to be largely at the tetraploid level. Tetraploids exhibit a great range of morphological combinations and include what has classically been treated as *S. cernua* (Figure 12). They characteristically exhibit a lip bearing a strong basal dilation. This feature is present in the great majority of polyploids and is nearly always present in plants characteristic of *S. cernua* in other respects; hence, it is considered to be a very important, unifying characteristic of the complex. The variation exhibited by the tetraploids includes character combinations seen in the diploids (Figures 12 and 13a). Occasional extreme plants may very strongly resemble one of the diploids, but I have not encountered any that was entirely characteristic of a diploid species.

The inclusion in a variable tetraploid assemblage of characteristics of related diploids suggests the possibility of unidirectional gene flow from the diploids to the tetraploids. The necessary input of genes might occur in any of several ways. Autotetraploid individuals could provide a means of bridging the differences in ploidy level, and autopolyploidy is well-known in the Orchidaceae. The morphologically extreme tetraploids mentioned above suggest autotetraploids, but these and all other tetraploids studied have always shown at least some morphological features of *S. cernua* and meiotic characteristics of segmental allotetraploids. Although the effects of polyploidy itself on the genomes are unknown, the available evidence indicates that all tetraploids are members of a single tetraploid complex, and autotetraploids are not known to occur.

Gene flow might be by way of allotetraploids. Vardi (1971) has shown that such triploids frequently possess a limited fertility. In the present study, the triploid low prairie race exhibits characteristics of *S. magnicamporum* and *S. cernua* and hence is apparently of hybrid origin. This race, however, occupies a habitat not utilized by tetraploids (and only rarely by *S. magnicamporum*) and is not a likely triploid bridge for such gene flow. In the Northeast, mixed populations of *S. ochroleuca* and *S. cernua* are known to support occasional triploids (Sheviak and Catling, 1980); these plants might be involved in unidirectional gene flow in such populations.

Gene flow may also occur directly from diploids into tetraploids, for allotetraploids are possible products of crosses involving unreduced gametes. The prodigious quantity of seed produced by orchids makes such occurrences likely, and they are frequently found in commercial orchid breeding. Additionally, Hagerup (1947) found in several European orchids that eggs were sometimes fertilized by two nuclei from one pollen tube, or by nuclei from more than one tube. Such unusual occurrences were found to be present in most ovaries studied. This behavior would permit direct gene flow from diploids into tetraploid populations.

Whether such gene flow accounts for the variation seen in tetraploids is another matter, however. Attempts at verification have met with varying degrees of success. Breeding experiments, as discussed earlier, have not satisfactorily indicated its likelihood. Pollen sterility determination has been ambiguous due to technical problems involving the breakup of pollinia and due to fundamental questions relating to the apomictic process and polyploidy. Chemical characterization of fragrance components has met with technical problems and flavonoids have been found to be in such low concentrations that samples cannot be obtained from single individuals as is necessary in the complex populations under study.

Cytogenetic data have been more revealing. The presence of translocation heterozygotes in the intermediate prairie complex could indicate hybrid ancestry. More significant is the presence of cytologically based teratological forms in the prairie complex, in the zone of contact of *S. cernua* and *S. magnicamporum* (Figure 13b), and in mixed populations of *S. cernua* and *S. ochroleuca*; the occurrence of these forms, and hence the presence of the meiotic irregularities producing them, in populations of morphologically intermediate plants and in situations permitting hybridization is strong evidence for the presence of gene flow.

Analyses of morphological variation further indicate the occurrence of widespread gene flow. Multivariate statistical analyses performed on populations of *S. ochroleuca* and *S. cernua* in the Northeast (Sheviak & Catling, 1980) have suggested the possibility of unidirectional gene flow between these species. In these analyses known triploids and one aneuploid teratological specimen were determined to be well within the variation pattern of the tetraploids, suggesting regressive dilution of the tetraploid gene pool.

Another analysis, employing a relatively large sample but rather qualitative characters, has yielded particularly suggestive results. It employed populations of *S. cernua* from the western Great Lakes region, where the species exhibits, to varying degrees, characteristics of *S. magnicamporum*. Three characters were chosen: the shape and texture of the lip and the presence or absence of leaves at anthesis. These characters were useable on most specimens of reasonable quality and were readily assessed. Figure 14 presents the findings of this analysis. These graphs are based on 189 speci-
mens from principally northern and western Illinois, northern Indiana, Wisconsin, and Michigan; a few were included from Minnesota and the Lake Erie regions of Ohio, Pennsylvania, and Ontario. Specimens were chosen from every sheet of appropriate locality in my own collection and the herbaria of the Milwaukee Public Museum, the University of Illinois, and the Illinois Natural History Survey. One specimen per sheet was chosen except in variable populations in which a range of morphotypes was utilized. Lips were rated for shape and texture on arbitrary scales of one to five. An ideally ovate, non-dilated and strongly fleshy lip of S. magnicamporum was assigned a value of (1, 1). Extreme development of S. cernua was considered to be strongly dilated basally and wholly membranaceous; this was ranked (5, 5). Intermediate conditions were rated accordingly.

The scatter diagram in Figure 14a shows these characters plotted as leafy or leafless. Chromosome counts for individuals exhibiting particular combinations are given where determined. The leafless conditions ranked from (1, 1) to (2, 2) are within the range of variation of S. magnicamporum. The leafy S. cernua is more difficult to characterize, but (5, 5) to (4, 4) is a likely range. All other combinations suggest hybridization. Even if S. cernua is allowed a greater range in lip morphology, apparent recombinations are evident.

Complicating interpretation is the inclusion of triploids in the sample. These cannot be reliably determined, and hence any attempt to exclude them would invite the introduction of error. Present information, however, indicates that the majority of the leafless plants in the range (5, 5) to (4, 3) and probably others are triploid. Such plants as the leafless (1, 4) appear from guard cell measurements and gross morphology to be tetraploid.

When the two lip characters are combined in a hybrid index by multiplying them together, a striking pattern is disclosed (Figure 14b). In the left-hand graph, the line plots two-point sliding means for the total population; to the right these means are plotted separately for the leafy and leafless members. From these plots the influence of the leafless triploids is clearly seen in the secondary hump in the leafless plot. Most significantly, a very rapid drop with departure from characteristics typical of S. magnicamporum is seen. A much more gradual climb into typical S. cernua is evident. This is precisely what is to be expected in unidirectional introgression involving establishment of allotetraploids and subsequent backcrossing to the tetraploid parent.

The results of these analyses indicate, first, that much of the variation of S. cernua in the western Great Lakes region may be due to introgression from S. magnicamporum, and in the northeast from S. ochroleuca. Secondly, this suggests that the variation of S. cernua as a whole might be due to introgression. These findings indicate that the hybrid-like morphologies seen in the prairie complex are indeed due to hybridization. Since the much more subtle infusion of genes from S. magnicamporum to S. cernua in the lakes region appears to be a classic case of unidirectional introgression, there is little reason to suspect that the apparent hybrids in the prairies are not also of hybrid origin. Certainly the intermediate morphology of the triploid low prairie race supports this conclusion. It thus appears to be an allotriploid agamic race, as was originally proposed on morphological and ecological grounds before cytological data were available in the complex (Sheviak, 1973). Recent work on pollen characters by Balogh (1979) provides additional support to these conclusions. Her studies have included one prairie complex member (Palmer 3263); its pollen is reported (personal communication) to approach that of S. magnicamporum, a condition which again suggests hybridization.

Evidence for gene flow from S. odorata to S. cernua is, at the present time, limited. The clearest example is in one collection from, significantly, outside the known range of S. odorata on Long Island (F.A. Mulford s.n.; NY). Another collection, from southern Mississippi (J.T Stewart s.n.; F#115658), may be referable to the prairie complex, as the sheet bears two very dissimilar specimens, one very similar to S. magnicamporum but bearing polyploidy seeds. The second suggests S. cernua florally and S. odorata vegetatively. It could, however, have attained its robust condition as a segregate of a prairie complex population. Additionally, the report of apomixis in S. odorata by Catling (1982) may indicate the occurrence of alloploidy, these plants warrant further study.

It would appear that S. cernua hybridizes with related diploids, and that this hybridization is responsible for much of the variation seen in the species. Since autoploidy has not been found, all tetraploids must be treated as S. cernua. Through hybridization and recombination a great range of forms has developed; some of these very closely resemble the diploid species which contributed genes to the complex. The evolutionary nature of the complex and the adaptive significance of this hybridization will be the topic of a subsequent paper. It can be concluded here, however, that the incorporation of genes of related species is a fundamental characteristic of S. cernua; it is, consequently, a complospecies (DeWet and Harlan, 1966). This conclusion is basic to the taxonomic treatment which follows.
TAXONOMIC TREATMENT

The difficulty encountered with morphological characters in the *S. cernua* complex is not unique. Stebbins (1971) has stated, “The morphological criteria used by taxonomists . . . are obviously inadequate guides to the evolutionary origin of many plant populations.” It is the polyploid complex, like the one centering on *S. cernua*, that frequently presents the greatest problems for the taxonomist. Significantly, segmental allopolyploids are characteristically most difficult taxonomically, and small complexes, with two or three diploids, are usually classified as a single species by conservative taxonomists (Stebbins, 1950). Tetraploids are often placed with the diploid species which, through gene flow, they most closely resemble, rather than with the rest of the tetraploid complex of which reproductively they are a part (Grant, 1971). The history of classification of the *S. cernua* complex clearly reflects these problems.

The almost complete isolation of the diploids in the *S. cernua* complex and their morphological divergence dictates that they be treated as distinct species. An entirely satisfactory treatment of the polyploids is more elusive, however. This difficulty is a direct result of the combination of hybridization and apomixis present above the diploid level. Although apomixis preserves distinct hybrid lines, the hybrid nature of much of the tetraploid complex dictates that hybrid ancestry not be the basis for formal recognition, and even allopolyploids cannot be accorded special status. Although taxonomic recognition of ecotypes and similar segregates is often desirable for greater precision, in the present case such a treatment does not appear reasonable. Considering the difficulty in determination even at the specific level, recognition of infraspecific segregates is impractical. *Spiranthes cernua* is best treated as a polymorphic complex species without formal recognition of infraspecific taxa.


*Ibidium trilobum* Small, Fl. SE U.S. ed. 2. 320. 1913.


TYPE: ['“along the borders of the Neuse River . . . on the wet and muddy shores” (Nuttall, 1834)], Newburn, N.C.! (PH).

Typification of synonyms:

*Gyrostachys constricta* Small: Marshes, Louisiana (Small, 1898), Oct., Dr. Hale 444! (NY).


Erect herb, 15–100 cm. tall; pubescent above, at least some trichomes capitate. Roots few, fasciculate, fleshy, slender, 10–30 cm. or more in length, horizontally spreading, stoloniferous. Leaves persistent, few to several, basal and extending partially up the stem, the basal short-petiolate or sessile, cauleine sessile, elliptical to oblong-oblancoelate, fleshy and aerenchymatous, lucid to rather dull, the longest up to 4 x 40 cm. Inflorescence densely flowered, orthostichies usually obvious, sometimes obscure, vertical to commonly spiraled. Flowers white to ivory, the lip often yellow or greenish centrally. Perianth ringent to urceolate, 4–15 mm. long, the stout, sessile ovary somewhat shorter. Sepals lanceolate, the lateral usually spreading or sometimes inward-arcuate, the dorsal with the apex recurved. Petals lanceolate, adherent to the dorsal sepal, apices recurved. Lip fleshy, rhombic-ovate to ovate, the margin tapering to a subacute apex, crenulate, recurved, basal tuberules prominent and inward curving. Seeds monoembryonic.

Plants of very wet, usually submerged sites. Chromosome number: 2n = 30.

Figure 15.

Small (1933) cited a specimen at NY as the type of this species without explanation of the reasons for his decision. This specimen bears appropriate locality data and also cites “Dr. Loomis.” Nuttall’s description does not attribute the collection to Loomis, although he is cited as the collector of various other specimens cited in the same publication. Significantly, an additional specimen from this locality housed at AMES (originally at GH) has been annotated by Correll as “doubtless a cotype.” This specimen bears the notation “legit H.B.
KEY TO NORTH AMERICAN MULTIRANKED SPIRANTHES*

1: Sepals connate toward base (sometimes only slightly so in S. lucida).**
2: Lip pandurate, strongly constricted near the middle and dilated toward the base and apex; sepal and petals connivent throughout their lengths and forming a hood (rarely their apices or the lateral sepals free and spreading) ................................................................. S. romanzoffiana
2: Lip ovate to oblong-quadrat, not pandurate; sepals and petals not connivent throughout their lengths, their apices or the lateral sepals free and spreading.
3: Lip ovate to ovate-lanceolate, tapering toward the apex; flowers yellowish or greenish throughout; far western................................................................. S. porrifolia
3: Lip oblong-quadrat; flowers white with lip bright yellow centrally; northeastern and, rarely, central ................................................................. S. lucida

1: Sepals not connate, free to base.
4: Spike slender, less than 12 mm. in diameter; lip 3–6 mm. long.
5: Lower cauline leaves with well-developed, spreading blades; inflorescence very dense; eastern and central U.S. ................................................................. S. ovalis
5: Lower cauline leaves reduced to sheathing bracts; inflorescence often an open spiral; Mexico ................................................................. S. graminea
4: Spike usually stout, 12–35 mm. in diameter; lip more than 6 mm. long.
6: Lip ovate-oblong, fleshy; seeds monoembryonic, the embryo enclosed within the testa.
7: Leaves absent at anthesis; roots tuberous; tubercles of the lip short, conical nob; lateral sepals spreading and/or ascending .............................................. S. magnicamporum
7: Leaves present at anthesis; roots slender; tubercles of the lip relatively long, usually somewhat inward-curving.
8: Lateral sepals usually straight, rather appressed, often connivent with the petals; flowers usually ascending, urceolate; leaves flexible, thin, linear-oblancoceolate to narrowly elliptical, basal or a few on the base of the stem; dry or mesic sites in the Northeast (southward along the mountains). ................................................................. S. ochroleuca
8: Lateral sepals usually curved, loose, spreading and/or ascending, not connivent with the petals; flowers usually nodding, urceolate or often ringent; leaves stiff, thick and aerenchymatous, elliptical to oblong-oblancoceolate, extending partially up the stem; swamps and marshes in the Southeast (primarily on the Coastal Plain) ................................................................. S. odorata
6: Lip usually dilated basally, membranaceous to fleshy, or occasionally undifferentiated from the petals; seeds polyembryonic (at least in part), monoembryonic seeds commonly with extruding embryos................................................................. S. cernua

* phyllotaxy of inflorescence 1/3 or 1/4 (see text).
** Very rare specimens of S. cernua from the southern prairie region bear sepals connate at the base. These plants would key to the far-western S. porrifolia, from which they differ in their whitish, nodding flowers.
Crown.” Although it is possible that all of these specimens were indeed utilized by Nuttall, such a conclusion is purely conjectural. The lack of collector citation on the PH specimen, its place of deposition, and aspects of Nuttall’s description which suggest that he had experience with live material, suggest that this specimen is correctly considered as the type.

_Gyrostachys triloba_ and _G. constricta_ Small have been variously treated. Ames (1905b) treated both as synonyms of _S. odorata_, stating that the three-lobed nature of the lip of _G. triloba_ cited by Small was merely apparent, due to improper spreading of the moistened material. Recently Luers (1975) has treated _G. constricta_ as a synonym of _S. cernua_, apparently due to the membranaceous, basally dilated lip of Small’s type. Examination of the types of both _G. constricta_ and _G. triloba_ has shown them to be clearly referable to _S. odorata_. These specimens are poorly preserved, doubtless accounting for their membranaceous and rather dilated lips; vegetatively they are characteristic of _S. odorata_ and are, I think, reliably treated as such.


_Basionym:_ _Gyrostachys ochroleuca_ Rydberg in Britton; Man. 300. 1901.


Erect herb, 10–60 cm. tall, pubescent above, at least some trichomes capitate. Roots 1–3, rarely more, fasciculate, stout, fleshy, descending, to 8 mm. in diameter and about 10 cm. long. Leaves fugalce, few, wholly basal, linear-lanceolate to oblanceolate, long-petiolate, membranaceous to rarely somewhat fleshy, lucid, to 1.5 x 16 cm. Inflorescence densely flowered, with the orthostichies prominent, vertical to slightly spiraled. Flowers white to ivory, the lip commonly yellow centrally. Perianth ringent, 5–14 mm. long, the stout, sessile ovary somewhat shorter. Sepals linear-lanceolate, the dorsal appressed to the petals, the lateral spreading and/or ascending, the apex of the dorsal slightly arcuate, the lateral more nearly straight. Petals linear, associated with the dorsal sepal, their apices slightly arcuate. Lip fleshy, ovate to oblong, obtuse to acute, crenulate, arcuate, the apex occasionally reflexed, basal tubercles conical. Seeds monoembryonic.

Plants of calcareous grassland.

Chromosome number: 2n=30.

Figure 16e-h.

_Rydb. (1901) failed to designate the type of _S. ochroleuca_, and the basis for his description has been unknown. Recently, a comparison of his description with a drawing at NY has indicated that this illustration is Rydberg’s type (Sheviak and Catling, 1980).


_TYPE:_ Hill prairie, 3.5 mi., S., of Eldred, Greene Co., Illinois, October 10, 1968, R. A. Evers 98153! (ILLS).

Erect herb, 10–60 cm. tall, pubescent above, at least some trichomes capitate. Roots 1–3, rarely more, fasciculate, stout, fleshy, descending, to 8 mm. in diameter and about 10 cm. long. Leaves fugalce, few, wholly basal, linear-lanceolate to oblanceolate, long-petiolate, membranaceous to rarely somewhat fleshy, lucid, to 1.5 x 16 cm. Inflorescence densely flowered, with the orthostichies prominent, vertical to slightly spiraled. Flowers white to ivory, the lip commonly yellow centrally. Perianth ringent, 5–14 mm. long, the stout, sessile ovary somewhat shorter. Sepals linear-lanceolate, the dorsal appressed to the petals, the lateral spreading and/or ascending, the apex of the dorsal slightly arcuate, the lateral more nearly straight. Petals linear, associated with the dorsal sepal, their apices slightly arcuate. Lip fleshy, ovate to oblong, obtuse to acute, crenulate, arcuate, the apex occasionally reflexed, basal tubercles conical. Seeds monoembryonic.

Plants of calcareous grassland.

Chromosome number: 2n=30.

Figure 16e-h.


_Limodorum autumnale_ Walter, Fl. Car. 221. 1788.


_Neottia cernua_ (Linnaeus) Swartz var. _major_ Eaton, Man. 303. 1829.
Spiranthes petiolaris Rafinesque, Herb. Raf. 45. 1833.


TYPE: [Virginia, Canada. (Linnaeus, 1753)] Linnaean Herbarium no. 1056.9 (LINN), (photograph).

Typification of synonyms:

Limodorum autumnale Walter: Walter Herbarium no. 722 (BM), (photograph).

Neottia cernua var. major Eaton: unknown.

Spiranthes petiolaris Rafinesque: apparently destroyed.

Ibidium incurvum Jennings: Pennsylvania, Erie County, in zone around lagoons in eastern part of Presque Isle, sand soil, August 26, 1905, Otto Jennings 18! (CM, NY, NYS).

Erect herb, 10–50 cm. tall, pubescent above, with at least some trichomes capitate. Roots few, fascicate, fleshy, slender, horizontally spreading to stout and descending. Leaves persistent to fugaceous, few, wholly basal or with a few on the lower portion of the stem, linear-lanceolate to linear-ob lanceolate or oblanceolate or occasionally obovate or elliptical, membranaceous to rarely slightly fleshy, dull to highly lucid, long- to short-petiolate or occasionally sessile, to 2.0 x 26 cm. Inflorescence densely flowered, with the parastichy low- to rarely very high-angled, the orthostichies obvious to seemingly absent, vertical to spiraled. Flowers white to ivory or rarely yellowish or green, the lip sometimes yellow centrally. Perianth urceolate to ringent or occasionally unopening, 5–12 mm. long, the stout, sessile ovary somewhat shorter. Sepals lanceolate to linear-lanceolate, the dorsal appended to the petals, the lateral appended to spreading, the dorsal straight or with the apex recurved, the lateral straight or most commonly with the apices incurved. Petals linear-lanceolate, associated with the dorsal sepal, straight or with the apices recurved; occasionally broad and lip-like, then the apices strongly wide-spreading. Lip membranaceous to fleshy, ovate to oblong in general outline, usually constricted at the middle and with a more or less prominently dilated suborbicular to orbicular base, crenulate, lacerate or sometimes entire, genulate to arcuate or sometimes straight, basal tubercles prominent and incurved to small and conical; or occasionally lip scarcely or not at all differentiated from petals. Seeds at least in part polyembryonic. Plants of wet to dry situations.

Chromosome number: 2n=(45) 60 (-62).

Figures 17–23.

Although Linnaeus' brief description of Ophrys cernua could apply to S. ochroleuca as well as S. cernua and in some respects more closely fits the former species, examination of his type clearly has demonstrated that his epithet has been properly applied (Sheviak and Catling, 1980).

Walter's Limodorum autumnale is less easily placed. This taxon has typically been treated as a synonym of S. cernua (e.g. Ames, 1905b; Luer, 1975). Walter's description, however, with "caule foliis obsito" would appear more characteristic of S. odorata. Examination of number 722 in Walter's herbarium, the apparent type, does not support such a conclusion. This specimen bears a single leaf, either basal or borne on the base of the stem. In this respect, then, it is more characteristic of S. cernua than S. odorata, and, indeed, the general aspect of the specimen is that of the former species. Walter's reference to a leafy stem may have been meant in contrast to his L. praecox, the specimen of which bears only withered leaves. It thus seems proper to include L. autumnale in the synonymy of S. cernua.

Eaton's Neottia cernua var. major cannot be placed with absolute certainty from his scanty description. Very likely, however, it is referable to a particularly robust, large-flowered race of S. cernua which is abundant in the northeast (Figure 19a-d). Certainly S. cernua is among the largest species in the area and it would appear unlikely that Eaton's name is based on another species.

Rafinesque's description of S. petiolaris is clearly referable to S. cernua. The description closely fits an important race of S. cernua from the prairie margin and Southeast [the "old field ecotype" of Sheviak, (1974b); Figure 20e-h] and considering the Illinois origin of Rafinesque's plant, such an identity is a distinct possibility.

Ibidium incurvum Jennings was separated from S. cernua primarily on the basis of the long, incurved tubercles of Jennings' type material. Later, Jennings (1953) recognized the variable nature of this character in S. cernua and stated that I. incurvum is characteristic of northeastern, arenicolous S. cernua. Furthermore, live material from the type locality has proven to be typical S. cernua and also identical with Jennings' material of I. incurvum (Sheviak and Catling, 1980).
Nomina Obscura

*Spiranthes brevicaulis* Rafinesque, Herb. Raf. 45. 1833.

This taxon would appear to be part of the *S. cernua* complex on the basis of, "fl. magnis curvis," and the origin having been Kentucky. Rafinesque’s description is difficult to interpret, however. This is particularly true of, "fol. rad. conica longissima lineari cuneati acuta." I cannot with certainty ascribe such leaves to any plant known to me. However, in some members of the prairie complex, commonly the very base of the stem immediately above the withering leaves bears a number of bracts with elongated, divergent apices. These structures have the blade rolled to form a tube that might be described as conical. This is typical of one important form (Figure 21a-d), small plants of which sometimes produce open, rather obviously spiralled inflorescences. It is thus significant that Rafinesque described the spike of this “semipedal” plant as "spicis flexuosis obl. laxis paucifl." Such analysis is purely conjectural, however, and the name cannot be placed.


These two taxa are included here on the basis of "spicis densis spir." The flowers of both are described as "mediocris." These features suggest one of the smaller flowered forms of *S. cernua*. Fernald (1946a) referred *S. montana* to *S. ovalis*, but this is purely conjectural; it is doubtful that the very small flowers of *S. ovalis* would warrant the use of "mediocris." These names cannot be placed.

22
LITERATURE CITED


Linnaeus, Carl. 1753. Species Plantarum. Vol. II.


### TABLE I

Literature Reports of Chromosome Numbers of North American *Spiranthes* (Numbers reported for *S. cernua* complex members by Sheviak (1976) and Sheviak & Catling (1980) are included in Table II).

<table>
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<th>reference</th>
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<td><strong>KENTUCKY</strong></td>
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<td>LaSalle Co. (<em>Sheviak 363</em>)</td>
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<tr>
<td><strong>IOWA</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Boone Co. (<em>Sheviak 869a</em>)</td>
<td>60</td>
<td></td>
</tr>
<tr>
<td>Boone Co. (<em>Sheviak 869b</em>)</td>
<td>ca. 60</td>
<td></td>
</tr>
<tr>
<td>Decatur Co. (<em>Sheviak &amp; Niemann 929</em>)</td>
<td>45</td>
<td></td>
</tr>
</tbody>
</table>
### TABLE II: Chromosome Number Determinations (cont’d)

<table>
<thead>
<tr>
<th>species/locality/collection</th>
<th>somatic</th>
<th>sporogenous</th>
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<tbody>
<tr>
<td><strong>S. cernua</strong> (cont’d)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>KANSAS</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bourbon Co. (Sheviak &amp; Sheviak 975a)</td>
<td>ca. 60</td>
<td></td>
</tr>
<tr>
<td>Franklin Co. (Sheviak &amp; Sheviak 962)</td>
<td>60</td>
<td></td>
</tr>
<tr>
<td>Osage Co. (Sheviak &amp; Niemann 954)</td>
<td>60</td>
<td></td>
</tr>
<tr>
<td><strong>MAINE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>York Co. (Sheviak &amp; Sheviak 1113)</td>
<td>45</td>
<td></td>
</tr>
<tr>
<td><strong>MASSACHUSETTS</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Berkshire Co. (Catling 83a)</td>
<td>ca. 60*</td>
<td></td>
</tr>
<tr>
<td>Middlesex Co. (Sheviak 821)</td>
<td>ca. 60</td>
<td></td>
</tr>
<tr>
<td>Worcester Co. (Sheviak 891)</td>
<td>60</td>
<td></td>
</tr>
<tr>
<td>Worcester Co. (Sheviak 922)</td>
<td>60</td>
<td></td>
</tr>
<tr>
<td><strong>NEBRASKA</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sarpy Co. (Sheviak &amp; Niemann 939a)</td>
<td>60</td>
<td></td>
</tr>
<tr>
<td><strong>NEW HAMPSHIRE</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Merrimack Co. (Sheviak 875)</td>
<td>60</td>
<td></td>
</tr>
<tr>
<td>Sullivan Co. (Sheviak 1063)</td>
<td>45</td>
<td></td>
</tr>
<tr>
<td>Sullivan Co. (Sheviak &amp; Sheviak 1036b)</td>
<td>61</td>
<td></td>
</tr>
<tr>
<td>Sullivan Co. (Sheviak &amp; Sheviak 1034)</td>
<td>45</td>
<td></td>
</tr>
<tr>
<td><strong>NEW YORK</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hamilton Co. (Sheviak 1654)</td>
<td>ca. 60</td>
<td></td>
</tr>
<tr>
<td>Hamilton Co. (Sheviak 1926)</td>
<td>45</td>
<td></td>
</tr>
</tbody>
</table>

* Counted by P.M. Catling
### TABLE III

**Results of Experimental Crosses**

Parental plants are indicated by the author’s collection number (or other collector) and the collection locality. Capsule development for each flower is indicated as an approximate percentage of the volume of normal capsules resulting from intraspecific crosses; in some early crosses capsule development was not noted. Fertility of the total sample of each cross is indicated as a percentage of normal seed set resulting from intraspecific crosses, based on an average figure of 10,000 seeds per capsule. *In one cross, capsules did not dehisce.*

<table>
<thead>
<tr>
<th>cross</th>
<th>no. flowers used</th>
<th>capsule development</th>
<th>seeds</th>
<th>% fertility</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>S. odorata</strong> (814; Manatee Co., Florida)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X S. ochroleuca (715; Cheshire Co., N.H.)</td>
<td>3</td>
<td>1 abort, 2–50%</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>X S. ochroleuca (915; Sagadahoc Co., Maine)</td>
<td>3</td>
<td>3–50%</td>
<td>8</td>
<td>0.0003</td>
</tr>
<tr>
<td>X S. magnicamporum (362b; Lake Co., Illinois)</td>
<td>4</td>
<td>2 abort, 1–75%, 1–100%</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>S. ochroleuca</strong> (715; Cheshire Co., N.H.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X S. odorata (814; Manatee Co., Florida)</td>
<td>3</td>
<td>2 abort, 1–50%</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>X S. magnicamporum (362b; Lake Co., Illinois)</td>
<td>3</td>
<td>1 abort, 2–100%</td>
<td>25</td>
<td>0.0008</td>
</tr>
<tr>
<td>X S. cernua (891; Worcester Co., Mass.)</td>
<td>3</td>
<td>3 abort</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>S. ochroleuca</strong> (877; Sullivan Co., N.H.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X S. odorata (814; Manatee Co., Florida)</td>
<td>2</td>
<td>1 abort, 1–25%</td>
<td>4</td>
<td>0.0002</td>
</tr>
<tr>
<td>X S. magnicamporum (362b; Lake Co., Illinois)</td>
<td>3</td>
<td>3–25%</td>
<td>ca. 300</td>
<td>0.01</td>
</tr>
<tr>
<td><strong>S. ochroleuca</strong> (915; Sagadahoc Co., Maine)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X S. magnicamporum (362b; Lake Co., Illinois)</td>
<td>5</td>
<td>1 abort, 4–25%</td>
<td>4</td>
<td>0.0008</td>
</tr>
<tr>
<td><strong>S. magnicamporum</strong> (362b; Lake Co., Illinois)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X S. odorata (814; Manatee Co., Florida)</td>
<td>4</td>
<td>1 abort, 3–75%</td>
<td>ca. 20,000</td>
<td>50</td>
</tr>
<tr>
<td>X S. ochroleuca (915; Sagadahoc Co., Maine)</td>
<td>4</td>
<td>1 abort, 3–30%</td>
<td>10</td>
<td>0.0003</td>
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<tr>
<td>X S. cernua (470; Will Co., Illinois)</td>
<td>3</td>
<td>3–25% *</td>
<td>22</td>
<td>0.0007</td>
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<tr>
<td>X S. cernua (256; Will Co., Illinois)</td>
<td>3</td>
<td>n.d.</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>X S. cernua (275; Pope Co., Illinois)</td>
<td>2</td>
<td>n.d.</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>X S. cernua (276; Fountain Co., Indiana)</td>
<td>2</td>
<td>n.d.</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>S. magnicamporum</strong> (350; Greene Co., Illinois-3 plants)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X S. cernua (256; Will Co., Illinois)</td>
<td>5</td>
<td>n.d.</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>X S. cernua (275; Pope Co., Illinois)</td>
<td>4</td>
<td>n.d.</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>X S. cernua (276; Fountain Co., Indiana)</td>
<td>4</td>
<td>n.d.</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>S. magnicamporum</strong> (McCabe s.n.; Clay Co., Minnesota)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X S. odorata (814; Manatee Co., Florida)</td>
<td>5</td>
<td>3 abort, 2–33%</td>
<td>38</td>
<td>0.0008</td>
</tr>
</tbody>
</table>

---

* *In one cross, capsules did not dehisce.*
### TABLE IV

**Spiranthes** pollinator records

<table>
<thead>
<tr>
<th>species/pollinator</th>
<th>locality</th>
<th><em>Spiranthes</em> coll. #/notes/reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>S. odorata</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bombus americanorum</td>
<td>Florida</td>
<td>Dodson (pers. comm.)</td>
</tr>
<tr>
<td>B. impatiens</td>
<td>Massachusetts</td>
<td><em>Sheviak</em> 814, 816/ greenhouse</td>
</tr>
<tr>
<td><strong>S. ochroleuca</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bombus impatiens</td>
<td>Massachusetts</td>
<td><em>Sheviak</em> 712/ greenhouse</td>
</tr>
<tr>
<td>B. vagans</td>
<td>Vermont</td>
<td><em>Sheviak</em> 1057</td>
</tr>
<tr>
<td><strong>S. magnicamporum</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bombus fervidus</td>
<td>North Dakota</td>
<td><em>Sheviak</em> &amp; <em>Sheviak</em> 1302</td>
</tr>
<tr>
<td><strong>S. cernua</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bombus fervidus</td>
<td>New Hampshire</td>
<td>Luer (1975)</td>
</tr>
<tr>
<td>B. fervidus</td>
<td>Vermont</td>
<td><em>Sheviak</em> 1059</td>
</tr>
<tr>
<td>B. fervidus</td>
<td>New York</td>
<td><em>Sheviak</em> 1928</td>
</tr>
<tr>
<td>B. fervidus</td>
<td>New York</td>
<td><em>Sheviak</em> 1958</td>
</tr>
<tr>
<td>B. impatiens</td>
<td>Massachusetts</td>
<td><em>Sheviak</em> 256, 276, 702, 821, 891/ greenhouse</td>
</tr>
<tr>
<td>B. terricola</td>
<td>New York</td>
<td><em>Sheviak</em> 1644</td>
</tr>
<tr>
<td>B. terricola</td>
<td>Kansas</td>
<td><em>Sheviak</em> &amp; <em>Sheviak</em> 972</td>
</tr>
<tr>
<td>Bombus sp.</td>
<td>New York</td>
<td><em>Sheviak</em> &amp; Paulson 1667</td>
</tr>
<tr>
<td>Bombus sp.</td>
<td>Nebraska</td>
<td><em>Sheviak</em> &amp; Niemann 939</td>
</tr>
<tr>
<td><strong>S. romanzoffiana</strong></td>
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<td></td>
</tr>
<tr>
<td>Bombus sp.</td>
<td>Northern Ireland</td>
<td>Godfery (1931, 1933)</td>
</tr>
<tr>
<td>Halictus sp.</td>
<td>Northern Ireland</td>
<td>Godfery (1933)</td>
</tr>
<tr>
<td>Chlorhalictus sp.</td>
<td>Northern Ireland</td>
<td>Godfery (1933)</td>
</tr>
<tr>
<td><strong>S. casei</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bombus terricola</td>
<td>New York</td>
<td><em>Sheviak</em> &amp; <em>Sheviak</em> 1954</td>
</tr>
<tr>
<td><strong>S. lacera</strong></td>
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</tr>
<tr>
<td>Bombus americanorum</td>
<td>Illinois</td>
<td>Robertson (1893, 1893)</td>
</tr>
<tr>
<td>Calliopsis andreniformis</td>
<td>Illinois</td>
<td>Robertson (1893, 1893)</td>
</tr>
<tr>
<td>Anthidium notatum</td>
<td>Florida</td>
<td>Robertson (1893)</td>
</tr>
<tr>
<td>Megachile brevis</td>
<td>Florida</td>
<td>Robertson (1893)</td>
</tr>
<tr>
<td><strong>S. spiralis</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>“humble bees”</td>
<td>England</td>
<td>Darwin (1877)</td>
</tr>
<tr>
<td><strong>S. sinensis</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coelioxys albolineata</td>
<td>Australia</td>
<td>Coleman (1934)</td>
</tr>
<tr>
<td>Halictus sp.</td>
<td>Australia</td>
<td>Coleman (1934)</td>
</tr>
<tr>
<td>Apis mellifera</td>
<td>Australia</td>
<td>Coleman (1934)</td>
</tr>
</tbody>
</table>

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FIGURE 1: Mitotic Metaphase: Diploids
a: *Spiranthes odorata*: Sheviak 810, Sarasota County, Florida. 2n=30.
b: *Spiranthes ochroleuca*: Sheviak & Hart 1076a', Berkshire County, Massachusetts. 2n=30.
FIGURE 2: Mitotic Metaphase: Polyploids

a: Sheviak 891, Worcester County, Massachusetts. 2n=60.
b: Sheviak 691, Macon County, Illinois. 2n=60.
c: Sheviak 703, Vermilion County, Illinois. 2n=60.
FIGURE 3: Mitotic Metaphase: Polyploids

a: Sheviak & Niemann 954, Osage County, Kansas. 2n=60.
b: Sheviak 388b, Coles County, Illinois. 2n=61.
c: Sheviak 1926, Hamilton County, New York. 2n=45.
d: Sheviak et al. 1314, Dekalb County, Illinois. 2n=45.
FIGURE 4: Meiosis
a-b: Complex pairing at Metaphase I in *Spiranthes cernua* (2n=60): Sheviak & Sheviak 962, Franklin County, Kansas.

c-d: Bridges and lagging chromosomes at Anaphase I in *Spiranthes cernua* (2n=60): Shildneck C-7823/8, Bond County, Illinois.
FIGURE 5: Meiosis

a: Perfect pairing (30n 1) at Metaphase I.
b: Perfect segregation at Anaphase I, with 30 chromosomes to the right, plus one lagging slightly and out of the plane of focus.
FIGURE 6: Seeds: Diploids

a: *Spiranthes odorata*: Sheviak 810, Sarasota County, Florida.
b: *Spiranthes ochroleuca*: Sheviak 712, Sagadahoc County, Maine.
c: *Spiranthes magnicamporum*: Sheviak 352, Greene County, Illinois.
FIGURE 7: Seeds: Polyploids

a: Sheviak 1051, Addison County, Vermont. Seed with two embryos, one wholly internal, the other partially extruding.

b: Sheviak 707, Pope County, Illinois. Three monoembryonic seeds, two with wholly internal embryos (appearing "normal"), and the third with the embryo partially extruding.

c: Sheviak 707, Pope County, Illinois. Two seeds, one without embryo and sterile, and the other with two internally developed embryos.

d: Sheviak 707, Pope County, Illinois. Seed with three internally developed embryos.

e: Sheviak 363, La Salle County, Illinois. Two monoembryonic seeds with internally developed embryos and appearing "normal."

f: Sheviak 363, La Salle County, Illinois. Three seeds, two without embryos and sterile, and the other with one large and possibly two small embryos developed externally.

g: Sheviak 363, La Salle County, Illinois. Seed with two externally developed embryos and a small, necrotic, internal one.

h: Sheviak 363, La Salle County, Illinois. Seed with laterally extruding embryo, and an apparently distinct, second, internal embryo.

i: Sheviak 363, La Salle County, Illinois. Two seeds, one with small, probably necrotic embryo, the other with two internal embryos.

j: Sheviak 363, La Salle County, Illinois. Seed with two embryos, one internal, the other partially extruding.

k: Sheviak 363, La Salle County, Illinois. Two seeds, one with small, necrotic, internal embryo, and four embryos developed externally, and the other with ill-defined internal development and a single externally developed embryo.

l: Sheviak 892, Middlesex County, Massachusetts. Two seeds with narrow embryonic masses filling much of the interior of the seed; embryo number is unclear, but note the extruding portion in the left-hand seed.
FIGURE 8: Distribution of *S. odorata*.

FIGURE 9: Distribution of *S. ochroleuca*. [A few collections plotted in Sheviak & Catling (1980), but not seen by the present author, are omitted from this map.]
FIGURE 10: Distribution of *S. magnicamporum*.

FIGURE 11: Distribution of *S. cernua*. 
FIGURE 12: The pattern of combinations of character states in important members of the *S. cernua* complex in the Northeast and Midwest. Three lip characters are plotted as functions of leaf persistence, petiole development, root orientation, and tuberosity. The positions of *S. ochroleuca*, *S. magnicamporum*, and "typical" *S. cernua* (as illustrated in Figure 17a) are indicated. Positions of the plots within the grid squares is based on relative expression of the characters plotted and additional characters. Numbers are diploid chromosome numbers.
KEY

lip

△ dilated, membranaceous
△ dilated, fleshy
○ ovate, membranaceous
● ovate, fleshy
| signifies yellowish coloration

roots

↗ tuberous, descending
→ tuberous, horizontal
← slender, horizontal

leaves

↑ long-petiolate, fugaceous
↓ long-petiolate, persistent
↓ short-petiolate, persistent

Prairie Complex

Northeast Complex

S. magnicamporum (30)
(60) ○ (60) △
(60) △
(60) △ (45)

S. ochroleuca (30)
(45) (60) △
(ca.60) (61) ○
S. cernua (60)
FIGURE 13: Distribution of polyploids exhibiting two prairie complex morphologies. Compare these maps with the distribution of *S. magnicamporum* (Figure 10).

a: Tuberous roots (defined as thickness in excess of 4 mm.), based on herbarium specimens and field observations. Root tuberosity is general in the western portion of the region, but roots are too infrequently collected to provide a one-to-one correlation with the distribution map for *S. cernua* (Figure 11).

b: Peloria (lip an essentially unmodified third petal).
FIGURE 14: Distribution of combinations of three characters in *S. magnicamporum* and *S. cernua* in the western Great Lakes region based on specimens at ILL, ILLS, MIL, and collections made by the author. Specimens are plotted as leafy (black) or leafless (white). Lip characters are ranked on arbitrary scales of 1 to 5 (shape: ovate-oblong without basal dilation = 1, with an orbicular dilated base = 5; & texture: strongly thickened and fleshy = 1, wholly membranaceous = 5). Known chromosome numbers (2n) are plotted adjacent to the appropriate columns.

a: Scatter diagram of combinations of the two lip characters.

b: Lip character combinations in “a” expressed as a function of a hybrid index (shape X texture).

Left: The line plots two-point sliding means of the total sample.

Right: The lines plot two-point sliding means of the leafy and leafless components of sample.
FIGURE 15:
*Spiranthes odorata*

a: plant, X 0.4; *Sheviak 814*, Manatee Co., Florida (from photograph, *in hort.*).
b: flower, lateral view, X 3.1; *Sheviak 814*, Manatee Co., Florida (from photograph, in the field).
c: flower, lateral view, X 3.1; *Sheviak 817*, Collier Co., Florida (from photograph).
d: lip, X 3.2; *Sheviak 917*, Sarasota Co., Florida.
e: flower, front view, X 3.1; *Sheviak 817*, Collier Co., Florida (from photograph).
FIGURE 16

*Spiranthes ochroleuca*

a: plant, X 0.6; *Sheviak* 877, Sullivan Co., New Hampshire (from photograph).
b: flower, lateral view, X 2.7; *Sheviak* 915, Sagadahoc Co., Maine (from photograph).
c: flower, front view, X 2.7; *Sheviak* 915, Sagadahoc Co., Maine (from photograph).
d: lip, X 3.2; *Sheviak* 1962, Cattaraugus Co., New York.

*Spiranthes magnicamporum*

e: plant, X 0.5; *Sheviak & Sheviak* 1302, Richland Co., North Dakota (from photograph).
f: flower, lateral view, X 2.8; *Sheviak* 362b, Lake Co., Illinois (from photograph).
g: flower, front view, X 2.8; *Sheviak* 362b, Lake Co., Illinois (from photograph).
h: lip, X 3.1; *Sheviak* 362b, Lake Co., Illinois.
FIGURE 17

Spiranthes cernua

The characteristic form of moist sandy and peaty soils throughout the Northeast, the Great Lakes region, and along the Appalachians. The "sand prairie ecotype" of Sheviak (1974b). 2n=60.

a: plant, X 0.6; Sheviak s.n., Lake Co., Illinois (from photograph).
b: flower, lateral view, X 3.2; Sheviak 2169, Orleans Co., New York (from photograph).
c: flower, front view, X 3.2; Sheviak 2169, Orleans Co., New York (from photograph).
d: lip, X 4.0; Sheviak 891, Worcester Co., Massachusetts.
e: lip, X 4.0; Sheviak & Sheviak 1313, Winnebago Co., Illinois.
f: lip, X 4.0; Jones 16673, Kankakee Co., Illinois.
g: lip, X 4.0; Catling s.n., Halburton Co., Ontario.
h: lip, X 4.0; Sheviak 988/1, Erie Co., Pennsylvania.
FIGURE 18

Spiranthes cernua

Forms typical of moist roadcut banks and similar sites in New England and adjacent New York. These plants commonly occur with S. ochroleuca and more typical forms of S. cernua, and occasionally with the form illustrated in Figure 19a-d.

a-d: 2n=45.

a: plant, X 0.8; Sheviak & Sheviak 1123, Belknap Co., New Hampshire (from photograph).
b: flower, lateral view, X 3.6; Sheviak & Sheviak 1123, Belknap Co., New Hampshire (from photograph).
c: flower, front view, X 3.6; Sheviak & Sheviak 1123, Belknap Co., New Hampshire (from photograph).

e-h: 2n=60.

e: plant, X 0.8; Sheviak 875, Merrimack Co., New Hampshire (from photograph).
f: flower, lateral view, X 3.6; Sheviak & Sheviak 1036h, Sullivan Co., New Hampshire (from photograph).
g: flower, front view, X 3.6; Sheviak & Sheviak 1036h, Sullivan Co., New Hampshire (from photograph).
h: lip, X 3.6; Sheviak & Sheviak 1036h, Sullivan Co., New Hampshire (from photograph).

i-l: 2n=61.

i: inflorescence, X 0.8; Sheviak & Sheviak 1036b, Sullivan Co., New Hampshire (from photograph).

j: flower, lateral view, X 3.6; Sheviak & Sheviak 1036b, Sullivan Co., New Hampshire (from photograph).
k: flower, front view, X 3.6; Sheviak & Sheviak 1036b, Sullivan Co., New Hampshire (from photograph).
l: lip, X 3.6; Sheviak & Sheviak 1036b, Sullivan Co., New Hampshire.
FIGURE 19

*Spiranthes cernua*

a-d: A form common in dry to moist sand, especially in excavated sites, in New England and New York. Perhaps var. *major* Eaton. 2n=ca. 60.

a: plant, X 0.8; *Sheviak & Sheviak 1043c*, Windham Co., Vermont (from photograph).

b: flower, lateral view, X 2.4; *Sheviak 884*, Middlesex Co., Massachusetts (from photograph).

c: flower, front view, X 2.4; *Sheviak 884*, Middlesex Co., Massachusetts (from photograph).

d: lip, X 3.6; *Sheviak 1654c*, Hamilton Co., New York.

e-j: Variation common in the western Great Lakes region. 2n=60.

e: inflorescence, X 0.7; *Sheviak 398*, Lake Co., Illinois (from photograph).

f: flower, lateral view, X 2.2; *Sheviak 398*, Lake Co., Illinois (from photograph).

g: flower, front view, X 2.2; *Sheviak 398*, Lake Co., Illinois (from photograph).

h: lip, X 3.9; *Sheviak 182*, Cook Co., Illinois.

i: lip, X 3.9; *Sheviak 402*, Lake Co., Illinois.

j: lip, X 3.9; *Sheviak 179*, Lake Co., Illinois.
FIGURE 20

*Spiranthes cernua*

a-d: The "low prairie race" of Sheviak (1973, 1974b); a plant of low, calcareous, black-soil prairies in Illinois, Wisconsin, and Iowa. 2n=45.

a: plant, X 0.8; Sheviak et al. 1314, Dekalb Co., Illinois (from photograph).
b: flower, lateral view, X 2.7; Sheviak et al. 1314, Dekalb Co., Illinois (from photograph).
c: flower, front view, X 2.7; Sheviak et al. 1314, Dekalb Co., Illinois (from photograph).
d: lip, X 3.6; Sheviak 698, Kankakee Co., Illinois.

e-h: The "old field ecotype" of Sheviak (1974b); a plant of acidic old fields and woodland openings in the lower Midwest and South. 2n=60.

e: plant, X 0.7; Sheviak 706, Pope Co., Illinois (from photograph).
f: flower, front view, X 3.6; Sheviak 706, Pope Co., Illinois (from photograph).
g: flower, lateral view, X 3.6; Sheviak 706, Pope Co., Illinois (from photograph).
h: lip, X 3.6; Sheviak et al. 985, Champaign Co., Illinois.
FIGURE 21

*Spiranthes cernua*

Typical forms of the southern prairies complex. $2n=60$.

a: plant, X 0.5; *Sheviak et al. 981/2*, Bond Co., Illinois (from photograph).
b: flower, lateral view, X 2.4; *Sheviak et al. 981/2*, Bond Co., Illinois (from photograph).
c: flower, front view, X 2.4; *Sheviak et al. 981/2*, Bond Co., Illinois (from photograph).
d: lip, X 3.6; *Sheviak et al. 981/2*, Bond Co., Illinois.
e: plant, X 0.5; *Sheviak et al. 981a*, Bond Co., Illinois (from photograph).
f: flower, front view, X 2.4; *Sheviak et al. 981a*, Bond Co., Illinois (from photograph).
g: flower, lateral view, X 2.4; *Sheviak et al. 981a*, Bond Co., Illinois (from photograph).
h: lip, X 3.6; *Sheviak et al. 981a*, Bond Co., Illinois.
FIGURE 22

*Spiranthes cernua*

Typical forms of the southern prairies complex.

a-d: 2n=60.

a: plant, X 0.5; *Sheviak & Sheviak 976f*, Bourbon Co., Kansas (from photograph).
b-c: flowers, lateral view, X 2.4; *Sheviak & Sheviak 976f*, Bourbon Co., Kansas (from photograph).
d: lip, X 3.6; *Sheviak et al. 981c*, Bond Co., Illinois.

e-g: Cleistapogamous form. 2n=62.

e: plant, X 0.5; *Sheviak 1015*, Bond Co., Illinois (from photograph).
f: flower, lateral view, X 2.4; *Sheviak 1015*, Bond Co., Illinois (from photograph).
g: lip, X 3.6; *Sheviak 1016*, Bond Co., Illinois.

h: Cleistapogamous form from sand prairies in the western Great Lakes region. Base of plant, X 0.5. Otherwise as in e-g; *Sheviak & Niemann 900a*, Kankakee Co., Illinois.
FIGURE 23

*Spiranthes cernua*

A peloric form which is an important member of the southern prairies complex in eastern Kansas and adjacent areas. \(2n=\text{ca. } 60\).

a: plant, X 0.6; Sheviak & Niemann 947, Waubansee Co., Kansas (from photograph).
b: flower, lateral view, X 2.4; Sheviak & Niemann 947, Waubansee Co., Kansas (from photograph).
c: flower, front view, X 2.4; Sheviak & Niemann 947, Waubansee Co., Kansas (from photograph).
d: lip, X 3.6; Magrath 4913, Washington Co., Kansas.