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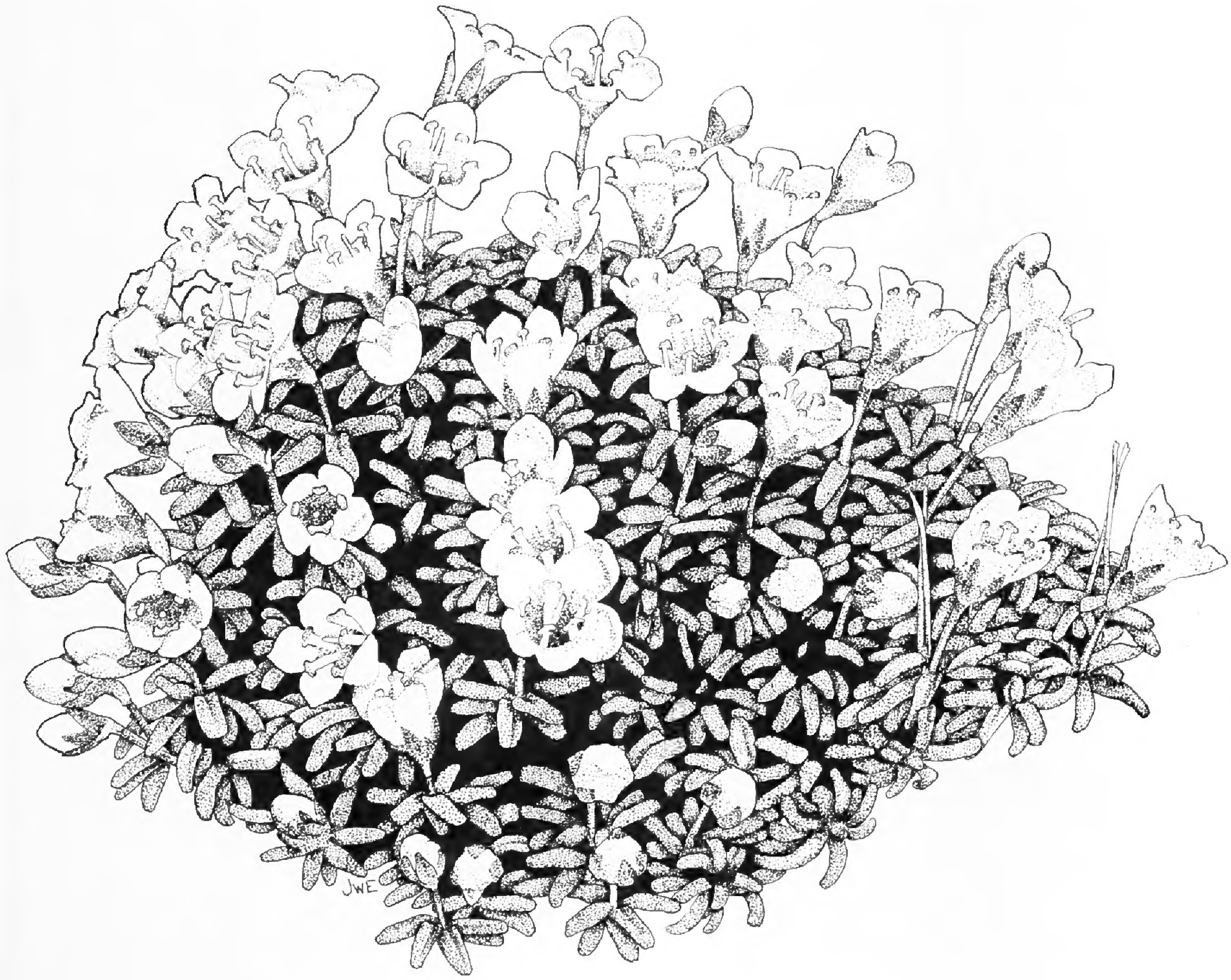

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Diapensia lapponica L. ssp. *lapponica*. Found on the higher mountains of northern New England, this Arctic circumpolar early-blooming tussock plant is a rare disjunct to New England. Original artwork by Josephine Ewing.

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REPRODUCTIVE LIMITATIONS OF A LOCALLY RARE *ASCLEPIAS*

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AND ROBERT E. ENGEL

ABSTRACT

Reproduction in populations of *Asclepias quadrifolia* and *A. syriaca* was examined at a western Vermont study site. While both field and forest populations of *A. syriaca* appeared to be heavily pollinated by *Apis* spp. and *Strymon* spp., observed pollinia insertion rates for the locally rare *A. quadrifolia* were among the lowest reported for the genus. Pollen and resource availability together are shown to closely account for the observed fruit production of <.007 fruits per *A. quadrifolia* flower. Comparisons of data for *A. quadrifolia* in Missouri, where the species is common, suggest that reproductive limitations may be an important factor contributing to the scarcity of *A. quadrifolia* in Vermont.

Key Words: reproductive limitations, *Asclepias,* rarity, biogeography, Vermont

INTRODUCTION

Biological rarity in plants has proven to be a highly subjective matter difficult to quantify and define (Drury, 1974, 1980; Harper, 1981; Krukeberg and Rabinowitz, 1985; Rabinowitz et al., 1986). Nevertheless, in recent times scientific interest in rarity has increased, perhaps partly because of the human-caused loss of biological diversity currently occurring on earth (Wilson, 1989). While globally rare species often are too endangered for rigorous scientific study, organisms which are locally rare provide an ethically more acceptable opportunity to investigate biological aspects of rarity.

One approach to understanding any form of rarity is to examine

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the process of reproduction and attempt to identify limiting factors. Reproductive comparisons of sympatric rare and common congeners may be a useful technique for gaining insight into the causes and consequences of biological rarity and commonness (Fiedler, 1987; Ornduff, 1989). Comparing data obtained at a location where a species is rare, with data where the species is common, may further enhance our understanding of rarity and the factors which limit reproduction (Ward, 1981).

Although reproductive ecology of *Asclepias* has been relatively well studied (reviewed by Shannon and Wyatt, 1986), there still is no consensus as to the relative importance of factors that determine levels of fruit initiation and maturation. *Asclepias syriaca* L. and *A. quadrifolia* Jacq. (Asclepiadaceae) are sympatric in the understory of a deciduous forest in western Vermont. While *A. syriaca* is commonly found in fields, roadsides, and newly created forest openings throughout North America, *A. quadrifolia* is the only *Asclepias* studied that grows in low-light forest understories throughout its range (Chaplin and Walker, 1982).

Only two studies of *Asclepias quadrifolia* have been published (Chaplin and Walker, 1982; Pleasants and Chaplin, 1983); both took place in Missouri, where this species is fairly common. Chaplin and Walker (1982) found for several populations of *A. quadrifolia* in Missouri that stem height was significantly correlated with total plant, root, and aboveground energy content (determined by bomb calorimetry). They also found that flower and fruit production in this species appeared to be limited by available energy reserves; plants under the threshold of 33–34 cm stem height (32–33 kilo joules total energy) are apparently unable to mature a seed pod successfully, likely due to the relatively high energetic cost (10.40 kj/pod).

The present study examines reproduction in *Asclepias quadrifolia* in Vermont, where this species approaches the northeastern edge of its range and is classified by the Vermont Nongame and Natural Heritage Program as "uncommon in the state" (Thompson, 1990). Energetic constraints and levels of pollination are assessed for their roles in limiting reproduction at the Vermont study site. In an effort to better understand why this species is locally rare, data from the Vermont populations of *A. quadrifolia* are also compared with data from sympatric populations of *A. syriaca* and Missouri populations of *A. quadrifolia* obtained from the two studies cited above.

MATERIALS AND METHODS

Species and Study Site

Asclepias is a widespread genus with 108 species and 9 subgenera distributed over three geographic regions: temperate to tropical North America, subtropical South America, and southern and eastern Africa (Woodson, 1954). *Asclepias syriaca* is a robust species often considered a "troublesome weed" in North America; underground rhizomes may form large clones of up to several thousand stems (Gleason, 1952). In contrast, *A. quadrifolia* is one of the smallest milkweeds (Woodson, 1954; Chaplin and Walker, 1982) and is incapable of asexual reproduction, with most plants producing a single stem from the rootcrown each spring (Chaplin and Walker, 1982; Cabin, pers. obs.). This species is typically found in low-light forest understories throughout the Appalachian and Ozark Mountains (Chaplin and Walker, 1982).

In the summer of 1989, two plots of *Asclepias quadrifolia* and two populations of *A. syriaca* were studied. All plants are located within the Vermont Nature Conservancy's 110 ha Shaw Mountain Preserve, located near the southern tip of Lake Champlain, in the town of Benson, Rutland County, Vermont. The mountain consists of a limestone uplift which rises over 150 m from the surrounding land and hosts a variety of plants considered rare in Vermont (Vermont Nongame and Natural Heritage Database, 1990). On Shaw Mountain, *A. quadrifolia* is found primarily in grassy meadows in mature, mixed deciduous forests. At this site, *A. quadrifolia's* whitish to pinkish flowers are borne on no more than two umbels per stem, with most umbels containing 5–15 flowers. The majority of flowering stems on Shaw Mountain bloomed from about mid-June to the end of that month. As most *A. syriaca* stems in the study area did not bloom until early July, there was little overlap in the flowering phenology of these two *Asclepias* species. Individual stems of *A. syriaca* produced an average of four umbels, with each umbel containing about 40 flowers.

Asclepias quadrifolia

Two plots of *Asclepias quadrifolia* were established in the study area. The first plot was chosen to represent a typical stand of the species as it occurs on Shaw Mt. (scattered individuals growing at $\cong .2$ stems/m^2). The plot measured 14 × 37 m and is dominated by scattered mid-size trees including *Acer saccharum* Marsh., *Carya ovata* (Mill.) K. Koch, *Pinus strobus* L., *Quercus alba* L. and *Ostrya virginiana* (Mill.) K. Koch, and contains low grasses and sedges in the understory. The second plot is about .5 km SE of the first and was chosen because it contained the highest density of flowering *A. quadrifolia* observed on Shaw Mountain ($\cong 4$ stems/m^2); aside from this distinction the two plots were otherwise similar in habitat characteristics. In both plots the number of leaves per stem and height (ground to most distal leaf node) were measured for all *A. quadrifolia* stems. Each flowering stem was labeled and the number of umbels, flowers per umbel, and number of fruits was recorded at regular intervals. Due to the rarity of *A. quadrifolia* in Vermont, direct measurements of plant energy were not performed. Instead, plant energy was estimated using Chaplin and Walker's (1982) equation for converting stem height (in cm) to total plant energy (in kj) as follows: $\log_{10}$ total plant energy content = 0.014 (stem height) + 1.050 ($r = .75$, $P < .001$).

Asclepias syriaca

Two populations of *Asclepias syriaca* were studied on Shaw Mt. The first is located in an abandoned field about .5 km E from the first plot of *A. quadrifolia*; the second lies within the forest about 1 km S from the old field and is located in a substantial light gap created by recent logging. For the old field population, 20 flowering stems were randomly selected, labeled, and regularly monitored for fruit production; flowers from both populations were also examined for pollination levels (see below).

Pollination

In *Asclepias* flowers, pollen grains are enclosed in paired, waxy structures called pollinia; each pollinium generally contains enough pollen to fertilize an entire fruit (Bookman, 1984; Morse, 1985). Pairs of pollinia from adjacent anther-sacs of separate stamens are connected by translator arms to a common clip, the corpusculum. The entire structure of pollinia, translator arms, and corpusculum is called a pollinarium (plural pollinaria); each indi-

Table 1. Comparisons of flowering and nonflowering *Asclepias quadrifolia* stems on Shaw Mountain in Vermont with flowering ones in Missouri. Data for Missouri obtained from Chaplin and Walker (1982) and Pleasants and Chaplin (1983). Numbers are means ± 1 SE.

	Shaw Mt., VT		Columbia, MO
	Flowering ($n = 65$)	Nonflowering ($n = 118$)	Flowering
Stem Height (cm)**	30.5 ± 0.7	20.6 ± 0.6	≈40
# Leaves per Stem*	7.3 ± 0.2	6.1 ± 0.1	≈12
Energy per Stem (kj)	30.0[a]	21.8[a]	≈40.7
# Flowers per Stem	8.9 ± 0.8		29.6
# Umbels per Stem	1.2 ± 0.1		≈2

[a] Energy per stem calculated using Chaplin and Walker's (1982) equation for converting stem height (in cm) to kj (see text).

* $P < 0.01$, ** $P < 0.001$ (Vermont flowers only).

vidual flower contains two ovaries and five pairs of pollinia which straddle the five stigmatic chambers.

The pollinaria of *Asclepias* facilitate accurate quantification of both male (pollinium removal) and female (pollinium insertion) reproductive functions. To estimate pollinial movement on Shaw Mountain, flower samples of both milkweed species were collected throughout the flowering period and examined under a dissecting microscope for pollinaria removals and pollinia insertions. Flowers of *A. quadrifolia* were obtained at 2-day intervals from randomly selected plants occurring in the general vicinity of the two established plots. In addition, some sampling of the flowers within plot 2 was conducted to determine whether this unusually dense stand was differentially attracting pollinators. Flower samples of *A. syriaca* were collected from randomly-selected individuals in the old field population at 2-day intervals; flowers from the forest population were collected only once.

RESULTS

Data from the two *Asclepias quadrifolia* plots on Shaw Mountain (combined in Table 1) show that flowering stems were significantly taller and produced more leaves than nonflowering stems ($P < .001$ and $.01$, respectively). Compared to data reported by Chaplin and Walker (1982) in Missouri, the flowering stems ob-

Table 2. Comparative pollination of *Asclepias quadrifolia* in Vermont and Missouri with *A. syriaca* in Vermont. The pollinaria removal and insertion data for Missouri are taken from Pleasants and Chaplin (1983). Numbers are means ± 1 SE.

	A. syriaca flowers (Shaw Mt.)		*A. quadrifolia* flowers	
	Field ($n = 155$)	Forest ($n = 40$)	Shaw Mt., VT ($n = 234$)	Columbia, MO ($n = 27$)
Pollinaria Removed (per flower)	2.48 ± 0.21	2.08	0.64 ± 0.11	2.23 ± 0.18
Pollinia Inserted (per flower)	0.81 ± 0.15	0.82	0.02 ± 0.01	1.28 ± 0.18
Insertions/Removals (%)	32.7%	39.4%	3.8%	57.4%

served on Shaw Mountain were smaller in size and produced a much more modest floral display.

Table 2 compares pollination levels between populations of *Asclepias quadrifolia* and *A. syriaca* on Shaw Mountain with Pleasants and Chaplin's (1983) populations of *A. quadrifolia* in Missouri. Despite the differences in density, the insertion and removal rates of the two plots of *A. quadrifolia* on Shaw Mountain were not significantly different and thus are combined in Table 2. The observed insertion rate per *A. quadrifolia* flower on Shaw Mountain (.02) is among the lowest reported for the genus. In addition, the number of observed pollinia insertions for this species is less than 4% of the observed pollinaria removals, while in Missouri this same percentage exceeds 55%. These results suggest that *A. quadrifolia* flowers studied on Shaw Mountain are pollinated with much lower frequency and efficiency (i.e., more pollen is wasted by vectors removing but not inserting pollinia) than in the Missouri populations. Despite repeated observations, potential pollinators for *A. quadrifolia* were never observed. In contrast, both field and forest populations of *A. syriaca* were often covered with insect visitors, most frequently *Apis* spp. and *Strymon* spp.

Fruit initiation and maturation comparisons between *Asclepias quadrifolia* and *A. syriaca* on Shaw Mountain show that fruit production was much greater in *A. syriaca,* even when the comparison is made on a per flower basis (Table 3). While *A. syriaca* showed considerable fruit abortion on Shaw Mountain (> 65%

Table 3. Comparisons of fruit set between flowering stems of *Asclepias* species on Shaw Mountain, Vermont, shown with ± 1 SE. There are no significant differences between the two plots of *A. quadrifolia.*

	A. quadrifolia		*A. syriaca*
	Plot 1 (*n* = 28)	Plot 2 (*n* = 37)	Field only (*n* = 20)
Total Fruit Initiated	5	2	132
Mean Fruit Initiated (per stem)	0.179 ± 0.116	0.054 ± 0.038	6.6 ± 5.540
Mean Fruit Initiated (per flower)	0.009 ± 0.006	0.006 ± 0.005	0.05 ± 0.006
Total Fruit Matured (as of Aug. 12)	4	2	46
Mean Fruit Matured (per stem)	0.143 ± 0.112	0.054 ± 0.038	2.3 ± 0.250
Mean Fruit Matured (per flower)	0.007 ± 0.005	0.006 ± 0.005	0.023 ± 0.004

as of Aug. 12), only one initiated *A. quadrifolia* fruit in the two plots failed to mature, and this failure was due to herbivory rather than abortion.

In contrast, Chaplin and Walker (1982) reported that 80–90% of the initiated *Asclepias quadrifolia* pods in their Missouri populations were lost within 3 weeks of the end of flowering, nearly all due to fruit abortion. Nevertheless, 50% of their pod-producing plants not damaged by herbivores successfully matured at least 1 pod (Pleasants and Chaplin, 1983).

Despite the size and, presumably, energy differences between *Asclepias quadrifolia* from Missouri and Vermont, all the pod-producing stems on Shaw Mountain are above the height and energy thresholds found in Missouri. By assuming that each pollinium inserted into a flower on a stem taller than 33 cm (i.e., a stem with sufficient energy to mature a pod) resulted in the initiation of 1 fruit, actual fruit production in the two *A. quadrifolia* plots on Shaw Mountain can be predicted with remarkable accuracy (Table 4). The two plots on Shaw Mountain contained a combined 183 stems, of which 65 produced at least one flower. Of these 65 stems, 22 were at or above the minimum size of 33–34 cm stem height apparently needed for pod maturation. Multiplying these 22 plants by their own mean number of flowers per

Table 4. Comparisons of actual fruit set with predicted fruit set of *Asclepias quadrifolia*. Predictions calculated by assuming that each pollinium inserted into the stigmatic chamber of a flower on a mature plant (i.e., a plant with sufficient stored energy to mature a seed pod; see text) resulted in the initiation of one fruit.

	A. quadrifolia in Vermont		
	Plot 1	Plot 2	Total
Flowering Stems	28	37	65
No. stems > 33 cm	8	14	22
Mean no. Flowers (per stem)	13.88	10.79	11.9
Mean no. Insertions (per flower)	0.03	0.02	0.024
Predicted Fruit (insertions × no. flowers × no. stems)	3.33	2.56	6.29
Actual Fruit (as of Aug. 12)	4	2	6

stem (11.9) times the mean insertion rate per flower (.024) (the average of plot 2 and random flower samples), equals a total of 6.29 insertions for these 22 stems; the actual number of total fruits as of August 12 was six.

DISCUSSION

The results of this study suggest that both energetic constraints and low rate of pollination limited reproductive output in *Asclepias quadrifolia* on Shaw Mountain in 1989. Of the plants studied, only about 10% were apparently large enough to mature pods; low pollinia insertion rates appeared to further restrict fecundity. The observation that pollination levels were not significantly different for the most dense stand of *A. quadrifolia* found at Shaw Mountain suggest that the pollinators of this species may not be responsive to local floral density.

Their larger size and increased levels of pollination apparently enabled sympatric *Asclepias syriaca* stems to initiate many more fruits per flower than *A. quadrifolia*. Even though about two-thirds of the initiated *A. syriaca* pods failed to mature, primarily as a result of fruit abortion, pod maturation per *A. syriaca* flower still was an order of magnitude greater than that observed for *A. quadrifolia*. If asclepiads are capable of selective fruit abortion (Bookman, 1984), it is conceivable that the low fruit initiation and apparent lack of fruit abortion observed for *A. quadrifolia* in this study may result in seeds of lower quality than those matured by nearby *A. syriaca* stems or by *A. quadrifolia* in Missouri, where fruit abortion rates can reach 80–90% (Chaplin and Walker, 1982). Whether there is any general pattern of seed quality and pollination intensity gradually decreasing as populations of *A. quadrifolia* and/or other species approach the edges of their geographical distributions was not investigated.

Suitable habitat patches of open, sparse forest understories may further limit the distribution and abundance of *Asclepias quadrifolia* on Shaw Mountain and perhaps in northern New England as well. At other sites in Vermont known to have harbored populations of *A. quadrifolia,* one of us (R.C.) found that recent forest succession often invaded large sections of what had been grassy, clear patches where *A. quadrifolia* once grew. In many areas of Vermont it thus appears likely that forest succession may eliminate suitable habitat for this species before a given *A. quadrifolia* seed can germinate and store enough energy to flower and set seed (if and when the flower is pollinated). Future studies are needed to clarify what creates and maintains these types of habitats, and why this particular habitat is more common in the southern Appalachian and Ozark Mountains. Additional work on Shaw Mountain and other sites in Vermont could also help determine if the low levels of pollination and pod production for *A. quadrifolia* found in this study accurately reflect larger spatial and temporal patterns for this species in northern New England.

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MORPHOLOGICAL DIFFERENTIATION IN *PHACELIA DUBIA* AND *P. MACULATA*

FOSTER LEVY[1]

ABSTRACT

In a common garden experiment, three morphological characters, corolla lobe length, corolla lobe width, and degree of leaf dissection, reliably distinguished the three varieties of *Phacelia dubia* as well as the closely related *P. maculata.* The taxonomic merit of *P. dubia* var. *interior* was confirmed by this analysis, but prior reports that this taxon is dwarfed in habit were not verified. Significant intra-varietal variation among populations occurred in *P. dubia* var. *georgiana* and *P. maculata,* two taxa endemic to granite outcrops in the southeastern United States. The occurrence of *P. dubia* in South Carolina was documented, but the varietal identity of these populations remains unclear; these plants probably represent an incipient variety.

Key Words: *Phacelia,* endemics, granite outcrops, common garden experiment, southeastern U.S.

INTRODUCTION

Much of our knowledge of phylogenetic relationships and differences among species is based on morphological systematics. However, in most instances, the genetic basis of morphological differences and hence the degree of genetic differentiation among taxa is unknown. The first step in an analysis of genetic differences is to determine which characters vary in response to environmental factors and which have a genetic basis. In this study, I use common garden experiments (Clausen et al., 1948) to address problems of varietal delineation and character differentiation among varieties within *Phacelia dubia* (L.) Trel. and within a closely related species, *P. maculata* Wood. Because three of the four recognized taxa in the study are narrow endemics, these results are also used to evaluate the hypothesis that narrowly-endemic plants are characterized by a lack of genetically based morphological variation.

In *Phacelia dubia,* the necessity of comparing plants grown in a common environment became evident as a result of a combination of field observations and preliminary growth experiments.

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In the field, both *P. dubia* and *P. maculata* can vary from small (< 10 cm), single-stemmed individuals with small leaves and few flowers to forms possessing highly branched stems, each terminating in long inflorescences. These drastically different phenotypes were observed in different years at similar locations within populations. Furthermore, plants grown in the greenhouse were much more robust than plants from natural populations. These observations suggested that morphology was subject to a high degree of phenotypic plasticity. As a consequence, in this group comparisons based upon field collections and herbarium specimens may not accurately reflect patterns of genetic divergence.

PHACELIA DUBIA

Recognized varieties

Phacelia dubia (L.) Trel., a winter annual that is a member of the subgenus *Cosmanthus,* occurs throughout the southeastern United States (Constance, 1949). Three varieties within *P. dubia* have been described. *Phacelia dubia* var. *dubia* (herein referred to as var. *dubia*) is found in alluvial or rocky woods and roadbanks from Pennsylvania into North Carolina. McVaugh (1943) described *Phacelia dubia* var. *georgiana* McVaugh (herein referred to as var. *georgiana*), endemic to granite outcrops in Georgia and Alabama, solely on the basis of increased leaf dissection relative to var. *dubia.* Murdy (1966) later showed that a combination of calyx length and sepal hair length could also distinguish these taxa.

The status of both var. *dubia* and var. *georgiana* has been accepted but a long-standing controversy surrounds the third variety, *Phacelia dubia* var. *interior* Fern. (herein referred to as var. *interior*). Fernald (1944) proposed var. *interior* on the basis of ovate rather than narrow sepals, shallowly lobed leaves, and small stature. Although Fernald (1944) referred to plants with these characteristics from a locality in Alleghany County, Virginia, var. *interior* is now regarded as endemic to cedar glades in the Nashville Basin of Tennessee (Baskin and Baskin, 1986, 1988, 1989). Constance (1949) included Fernald's var. *interior* in var. *dubia,* stating that similar dwarfed plants occur throughout the range of var. *dubia.* Murdy (1966), who also noted the dwarfed habit of plants from central Tennessee, stated that these plants possess larger corolla lobes than var. *dubia,* but no measurements were given. Putman (M.A. thesis, Emory University, Atlanta, GA, 1967) did provide data showing that the corolla lobes of var. *interior* were larger than those of var. *dubia.* However, the confusion over the status of var. *interior* has continued: for example Baskin and Baskin (1971, 1973, 1978) referred to plants from central Tennessee as var. *dubia,* but later they accepted var. *interior* (Baskin and Baskin, 1988, 1989). The need for clarification of the status of var. *interior* is especially important in light of the current emphasis on the conservation of genetic resources in rare and endemic species, since the variety is entirely restricted to cedar glades in central Tennessee.

The primary goal of this study was to identify characters that reliably distinguish the three recognized varieties of *Phacelia dubia.* These data test the validity of prior taxonomic determinations and test the hypothesis that narrow endemics lack significant genetic variability. Toward this goal two primary tasks were undertaken: 1) to determine the status of var. *interior* by testing whether the dwarfed habit is environmentally induced or genetically based and whether additional morphological differentiation separates this taxon from other varieties, and 2) to determine if floral characters, in addition to leaf dissection, separate var. *georgiana* from other varieties. These data provide baseline estimates of the range and bounds of variation in character expression within and between varieties to be used to test hypotheses concerning hybrids. The morphological characteristics of *P. maculata* and two newly proposed putative varieties were also analyzed to determine their similarity to varieties within *P. dubia*

Putative varieties

The distribution and varietal identity of *Phacelia dubia* in South Carolina, between the documented ranges of var. *dubia* and var. *georgiana,* is unclear. In his map of the distribution of *P. dubia* var. *dubia,* Murdy (1966) largely followed Constance (1949) in omitting var. *dubia* from South Carolina except for one site near the North Carolina border. Murdy (1968) later showed var. *dubia* extending into the southern piedmont of South Carolina. Coffey (M.A. thesis, U.S.C., Columbia, SC, 1964) did not include *P. dubia* in her species list of granite outcrops throughout the piedmont of South Carolina. Both McVaugh (1943) and Murdy (1966) stated that var. *georgiana* is absent from South Carolina and is restricted to Georgia and Alabama. However, *P. dubia* is not absent from South Carolina. With the aid of information from J. Allison, several populations of *P. dubia* were located in the northern and central piedmont of South Carolina. Although all populations were found on granite outcrops, the typical habitat of var. *georgiana,* the plants did not have the characteristic appearance of that variety. These populations, because of their location to the north of var. *georgiana* and south of var. *dubia* may be, a) of recent hybrid origin, b) part of a var. *dubia*–var. *georgiana* cline, or c) varietally distinct. Plants from this previously neglected region, herein referred to as the putative variety *P. dubia* var. "imitator" (herein referred to as "imitator"), were included in this study to distinguish between these hypotheses.

In the course of collecting plants from populations within the range of var. *dubia,* two large populations were visited in southwestern Virginia, the plants of which were restricted to a narrow zone of gravel-covered cinders on railroad embankments. In both these populations, herein referred to as a putative variety, *P. dubia* var. "railroad" (= "railroad"), male sterile individuals were frequently encountered. Male sterile plants were not noted in any other population visited. When crossed with plants of nearby var. *dubia* populations, plants from these two variant populations were partially reproductively isolated from var. *dubia* by a nuclear-cytoplasmic barrier (Levy, unpub. data). Because of the unusual habitat of these populations, somewhat reminiscent of the var. *georgiana* habitat, and the partial reproductive barrier, these plants were included in the present study to determine whether morphological divergence has accompanied reproductive and ecological divergence.

PHACELIA MACULATA

Phacelia maculata is also an endemic of southeastern granite outcrops (Murdy, 1966). A shared chromosome number of $n = 5$, unique to *P. dubia* and *P. maculata* and the lowest number in the genus, in addition to shared derived morphological characters (Constance, 1949) provides evidence that these are sister taxa. *Phacelia maculata* can readily be separated by the presence of paired corolla lobe spots, the absence of capitate glands on leaves and stems, and unbranched rather than basally branched stems

(Constance, 1949; Murdy, 1966). The two species are completely reproductively isolated (Gillett, 1964; Murdy, 1966) and the specific status of both is not questioned. Plants from two populations of *P. maculata* were sampled to determine whether characters useful in delineating varieties within *P. dubia* could provide evidence of the relationship of *P. maculata* to the varieties of *P. dubia* and to test whether there is variation among populations within *P. maculata.* Both Constance (1949) and Murdy (1966) have stated that *P. maculata* is a morphologically uniform taxon throughout its range; this observation suggests it is a genetically homogeneous taxon.

METHODS

Experimental design

Seeds were collected from the field in the spring of 1986, stored at room temperature to permit after-ripening (Baskin and Baskin, 1971), and in December 1986, germinated in petri dishes on moist filter paper at 15–18°C. Upon emergence of the cotyledons, seedlings were transplanted into a gravel-sand-vermiculite potting mixture and placed in a random arrangement in the greenhouse. Plants were watered once daily and supplemented weekly with an application of fertilizer. Floral measurements on each plant were taken at the time of peak flowering, approximately 10 weeks after transplanting.

The characters analyzed were:

1. Leaflet pairs—the number of pairs of leaflets proximal to the terminal leaflet, counted on the fifth leaf of the basal rosette.
2. Corolla lobe length (mm)—measured from the corolla lobe apex to base.
3. Corolla lobe width (mm)—measured at the widest point on the corolla lobe.
4. Filament length (mm)—measured from the base of the filament to the insertion of the anther.
5. Style length (mm)—measured from the tip of the ovary to the apex of the stigma.

Emphasis was placed on floral characters in this and later experiments because of their possible correlation with reproductive barriers. Measurements of the four floral characters were taken on ten plants from each of the 14 populations listed in Table 1. These characters were measured with a ruler under a dissecting microscope. On a subset of three populations, preliminary work had shown little intra-plant variation in floral characters. Similar results were obtained in hybridization experiments, consequently, one measurement per plant was taken. The number of pairs of leaflets was counted on 37–70 seedlings per population (mean = 47 per population).

Statistical analysis

The balanced design for each of the floral characters was analyzed with the ANOVA procedure of SAS (SAS Institute, 1982). The character of leaflet pairs was analyzed by the GLM procedure. In each analysis, only the eight populations of the three recognized varieties were included to facilitate separation of these varieties. A subsequent analysis, based upon patterns of variation uncovered in this test, would determine whether the putative varieties differed from the recognized varieties. In all analyses, the significance of a varietal main effect was tested using type III mean squares; the varietal mean square was tested against the nested effect, the mean square of populations within varieties. If the varietal effect was significant, an LSD test of population means was executed (SAS Institute, 1982).

Applying the data obtained in the previous analysis of recognized varieties, a series of Hotelling T^2 tests was performed to test whether populations of the putative varieties could have been sampled from one or more of the recognized varieties (Morrison, 1976). Unlike a discriminant analysis in which a test sample is always assigned to one of the previously classified entities, the Hotelling T^2 calculates the multivariate probability that an unknown sample could have been drawn from one, several, or none of the known entities. In this case, it provides a test of the affinities or uniqueness of putative varieties.

The Hotelling T^2 statistic was calculated for each population of the two putative varieties and for *Phacelia maculata* with respect to each of the three recognized varieties. The difference in character means between the test population and that of a particular variety forms a vector. This vector pre- and post-multiplies the pooled character covariance matrix to arrive at a T^2 value. The resultant T^2 value can then be used to generate an F-statistic

Table 1. Populations of *Phacelia* sampled for morphological analysis.

Taxon	Population	Habitat	Location
Phacelia dubia var. *dubia*	d-1	alluvial forest	High Rock, NC
	d-2	upland forest	Claytor Lake, VA
	d-3	shale barren	Bath Co., VA
P. dubia var. *georgiana*	g-1	granite outcrop	Appling, GA
	g-2	granite outcrop	Kiokee Creek, GA
	g-3	granite outcrop	Echol's Mill, GA
P. dubia var. *interior*	i-1	cedar glade	Cedars-of-Lebanon St. Pk., TN
	i-2	cedar glade	Davidson Co., TN
P. dubia var. "imitator"	p-1	granite outcrop	York Co., SC
	p-2	granite outcrop	Kershaw Co., SC
P. dubia var. "railroad"	r-1	railroad embankment	Radford, VA
	r-2	railroad embankment	Bertin, VA
Phacelia maculata	m-1	granite outcrop	Kershaw Co., SC
	m-2	granite outcrop	McCormick Co., SC

Table 2. Analysis of variance comparisons of the three taxonomically recognized varieties of *Phacelia dubia* for each of five morphological characters.

Character	Source	df	F	*P*
Leaflet pairs	among recognized varieties	2,5	54.20	<0.0001
	populations within varieties	5,400	2.64	0.023
Corolla lobe length	among recognized varieties	2,5	8.77	0.023
	populations within varieties	5,72	4.50	0.0001
Corolla lobe width	among recognized varieties	2,5	33.59	0.0001
	populations within varieties	5,72	4.00	0.003
Filament length	among recognized varieties	2,5	1.37	0.336
	populations within varieties	5,72	5.59	<0.0001
Style length	among recognized varieties	2,5	2.49	0.178
	populations within varieties	5,72	2.64	0.030

with an associated probability value; this is the probability that the population or variety of unknown identity could be a member of the variety with which it is being compared. Morphological differences among populations of *Layia* were analyzed in a similar fashion by Gottlieb et al. (1985).

Four characters were included in the Hotelling T^2 analysis: corolla lobe length, corolla lobe width, and leaflet pairs were

Table 3. Population means ($\bar{x}$) in mm, and standard deviations (SD) of characters measured in the common garden experiment. LSD tests on population means (for recognized varieties only) were performed on characters exhibiting significant varietal variation. Means followed by the same letter were not significantly different from each other.

		Recognized Varieties				
		interior		*dubia*		
Character	Population:	i-1	i-2	d-1	d-2	d-3
Leaflet pairs	$\bar{x}$	0.67^a	0.76^a	1.04^b	1.27^b	1.35^b
	SD	0.71	0.69	0.53	0.43	0.48
Corolla lobe length	$\bar{x}$	6.15^a	6.34^a	5.57^b	4.84^c	5.65^b
	SD	0.60	0.48	0.36	0.39	0.57
Corolla lobe width	$\bar{x}$	4.79^a	5.09^a	3.86^b	3.90^b	4.42^c
	SD	0.40	0.26	0.25	0.54	0.41
Filament length	$\bar{x}$	4.44	5.16	4.28	4.08	4.89
	SD	0.48	0.68	0.46	0.44	0.36
Style length	$\bar{x}$	4.95	5.34	4.91	4.29	4.79
	SD	0.59	0.57	0.35	0.50	0.44

included because each exhibited significant varietal variation in the univariate analysis. Filament length was included because it added significantly to the maximum F value of Roy's Greatest Root test (Morrison, 1976), which indicates that in combination with the other three characters, filament length provided additional varietal resolution.

RESULTS

For all five characters there was significant variation among populations within varieties (Table 2). A significant varietal component of variation was noted in only two of the four floral characters, corolla lobe length and corolla lobe width, as well as in the number of leaflet pairs per leaf. LSD comparisons among means revealed complete varietal separation in two characters, corolla lobe width and leaflet pairs (Table 3). Corolla lobe length was capable of distinguishing var. *interior* from var. *dubia* and var. *georgiana* but the latter two could not be resolved by this character.

The Hotelling T^2 test showed that neither of the putative varieties were morphologically unique, at least based upon the characters chosen for analysis; each population of these varieties could be unambiguously assigned to one of the recognized varieties

Table 3. Continued.

Recognized Varieties			Putative Varieties					
georgiana			"railroad"		"imitator"		*P. maculata*	
g-1	g-2	g-3	r-1	r-2	p-1	p-2	m-1	m-2
1.86^{c}	2.00^{c}	2.05^{c}	1.26	1.36	1.11	1.89	1.60	2.88
0.62	0.56	0.44	0.50	0.47	0.50	0.57	0.50	0.58
5.28^{bc}	5.04^{c}	5.08^{c}	5.71	5.86	5.98	5.38	6.70	6.16
0.29	0.40	0.42	0.46	0.55	0.67	0.43	0.48	0.48
3.35^{d}	3.25^{d}	3.19^{d}	4.47	4.57	3.88	3.89	5.38	5.74
0.34	0.24	0.30	0.31	0.34	0.44	0.51	0.26	0.38
4.09	4.37	4.31	4.43	4.78	4.54	4.38	5.32	5.36
0.17	0.57	0.55	0.35	0.51	0.58	0.42	0.47	0.53
4.66	4.82	4.74	5.00	5.41	4.79	4.71	5.38	5.30
0.47	0.57	0.28	0.49	1.16	0.76	0.54	0.34	0.65

Table 4. F-statistics associated with the Hotelling T^2 values testing for the varietal affinities of *Phacelia maculata* and putative varieties within *P. dubia* against each of the recognized varieties within *P. dubia*. The Hotelling T^2 value in each case is ten times the F value and is therefore omitted. Degrees of freedom = 2,4; probabilities associated with F values are, * = 0.05, ** = 0.01, *** = 0.005.

Test Taxon and Population	Recognized Variety		
	dubia	*interior*	*georgiana*
"railroad" r-1	2.18	8.78*	26.32***
"railroad" r-2	1.08	9.98*	23.49**
"imitator" p-1	1.37	13.36*	19.24**
"imitator" p-2	16.37*	40.82***	2.35
P. maculata	27.40***	47.41***	15.34*

(Table 4). Both "railroad" populations were inseparable from var. *dubia,* but they differed significantly from var. *interior* and var. *georgiana.* Neither of the two populations of "imitator" was unique, but each was assigned to a different recognized variety; "imitator" (p-1) and (p-2) were classified as var. *dubia* and var. *georgiana* respectively. The uniqueness of *Phacelia maculata* was confirmed by the Hotelling T^2 test; *P. maculata* was significantly different from each of the varieties within *P. dubia.*

DISCUSSION

Validity of the recognized varieties

Evidence for the taxonomic validity of all three varieties was provided by genetically based differentiation in vegetative (leaf dissection) and reproductive (corolla lobe length, corolla lobe width) characters. Supplementing McVaugh's original reliance upon leaf dissection, var. *georgiana* was shown to differ from the other two varieties in corolla lobe width and to differ from var. *interior,* but not var. *dubia,* in corolla lobe length (Table 3). The common garden experiment has conclusively demonstrated that var. *interior* can be distinguished by the same characters separating var. *dubia* and var. *georgiana.* Although it is true that in the field var. *interior* plants are often dwarfed (as is often the case with var. *georgiana* plants), cultivation in the greenhouse showed this was a phenotypic response to the cedar glade environment rather than a genetically fixed varietal characteristic. Vegetatively, var. *interior* plants were as tall and luxuriant as plants from the other varieties. Morphologically, var. *interior* possessed a large corolla whose corolla lobes were longer and wider than either of the other varieties. Vegetatively, var. *interior* was distinguished by having the least dissected leaves in the complex. The morphological distinctiveness of var. *interior*, combined with its restriction to a unique habitat and a distribution allopatric to the other varieties, should dispel any doubts about the validity of this taxon (Baskin and Baskin, 1986, 1988, 1989; Constance, 1949; Fernald, 1944; Murdy, 1966; Putman, M.A. thesis, Emory University, Atlanta, GA, 1967).

Putative varieties: hybrids or incipient varieties?

The hypothesis that the morphology of "railroad" populations fell within the limits of variation in var. *dubia* was not rejected (Hotelling T^2 analysis, Table 4). Despite the occurrence of these populations in an unusual habitat and the presence of a partial reproductive barrier when crossed with var. *dubia* (Levy, unpub. data), there was no evidence of morphological divergence within this putative variety.

Neither of the two populations of "imitator" was morphologically unique, but each was indistinguishable from a different recognized variety; the more northerly located p-1 was similar to var. *dubia* while p-2, located in the central piedmont of South Carolina, was like var. *georgiana* in morphology (Table 4). Although morphologically and ecologically similar to either var. *dubia* or var. *georgiana*, "imitator" is characterized by an allopatric distribution and a unique reproductive specificity, that is, inter-varietal hybrids exhibit partial sterility (Levy, unpub. data).

Given the lack of morphological intermediacy, the hypothesis that "imitator" is the midpoint in a var. *dubia*–var. *georgiana* cline can only be supported if, (*i*) the cline proceeds step-like, that is, the transition from one morphological state to the other occurs abruptly rather than continuously (Endler, 1977), and (*ii*) the cline encompasses differences in reproductive compatibility. The clinal hypothesis cannot be rejected but an additional possibility for the identity of "imitator" remains; it may represent a derivative of var. *dubia* or var. *georgiana* within which reproductive, but not morphological, divergence has occurred. Because the three taxonomically recognized varieties are all allopatric, partially reproductively isolated from each other, and morphologically unique, the lack of distinguishing morphological characters would render it inappropriate to afford the putative variety "imitator" equivalent taxonomic rank. Rather, it should be regarded as an incipient variety, which after sufficient time may attain a level of genetic differentiation characteristic of formally recognized varieties in this complex.

Relationships of *Phacelia maculata*

The combination of large corolla lobes, long filaments, and highly dissected leaves found in *Phacelia maculata* was unlike that of any form of *P. dubia* (Table 4). The Hotelling T^2 analysis has shown that *P. maculata* can be separated from *P. dubia* on the basis of the same characters that distinguish varieties within *P. dubia* but from these analyses it is not possible to determine which variety of *P. dubia* is most closely related to *P. maculata.* Furthermore, the variation among just two populations within *P. maculata* showed that this taxon is not, as had previously been suggested (Constance, 1949; Murdy, 1966), morphologically uniform throughout its range. Retention of morphological differences in a common garden demonstrated the presence of genetic variability within this geographically and ecologically restricted endemic.

Because of significant morphological differentiation, allopatric ranges, and partial reproductive isolation, one could reasonably argue that var. *interior* and var. *georgiana* be elevated to species. However, current taxonomic nomenclature in the subgenus *Cosmanthus* accurately reflects genetic relationships: species are characterized by morphological differentiation (Constance, 1949) and complete inter-sterility (Gillett, 1964); varieties of *Phacelia dubia* are morphologically differentiated but only partially reproductively isolated from each other (Levy, unpub. data); putative varieties are partially reproductively isolated but lack morphological differentiation from the recognized varieties.

Genetic variation in endemics

Recent conservation efforts to preserve the gene pools of rare and endemic species highlight the need for analyses of genetically based morphological variation. Ideas on the nature of genetic variation in narrow endemics have historically embraced the hypothesis correlating geographic and ecologic restriction with a lack of genetic variation (Stebbins, 1942; Drury, 1974). Within *Phacelia dubia,* significant variation among populations for each of the five morphological characters demonstrated the presence of intra-varietal genetic variation in excess of variation among varieties. Significant morphological variation was found in two (var. *georgiana* and *P. maculata*) of the three endemics analyzed. In a review of species inhabiting rock outcrop communities, Baskin and Baskin (1988) cited references to several endemics in each of which significant morphological variation was also found. They concluded that a high light requirement, rather than a lack of genetic variation, was the primary factor restricting the endemics to rock outcrops. The recognition of both morphological and allozymic variation in several rare species led Stebbins (1980) to abandon his original hypothesis of genetic depletion in endemics in favor of a more synthetic viewpoint which included ecological factors.

Ecological divergence and morphological change

It is a straightforward task to determine whether a correlation exists between habitat and morphology. However, because of the frequent correlation of these two forms of divergence, it is impossible to infer causation. Two alternative hypotheses can be posited to account for the occurrence of similar morphological characters in different habitats: first, more than one genetic pathway can lead to adaptation to a particular habitat, but in both a similar morphology is selected for; or second, morphological differentiation may occur without regard to the habitat factors (for example, it may arise as a result of random genetic drift).

In *Phacelia dubia,* the recognized varieties occupy very different habitats, and although each has unique morphological characteristics, the two forms of divergence are confounded. In var. *georgiana,* a highly dissected leaf and short narrow corolla lobes were correlated with the granite outcrop habitat. *A. priori,* one may be tempted to assume these morphological characteristics had been selected for during invasion of the outcrop habitat. But two independent sources of information (characters in "imitator" (p-1) and in "railroad") demonstrated that successful colonization of habitats similar to those occupied by var. *georgiana* can occur without the characteristic morphology of var. *georgiana.* The granite outcrops of South Carolina are obviously unlike the rocky and alluvial woods which var. *dubia* inhabits but it is on these outcrops that "imitator" exhibits a var. *dubia*-like morphology. In terms of observable features such as aspect, size, species composition, plant cover, and soil accumulation, the South Carolina outcrops resemble those occupied by var. *georgiana* in Georgia. However, the possibility that subtle differences between these regions has resulted in selection for different morphological characteristics cannot be ruled out. Reciprocal transplant experiments may clarify this problem, but at present, it appears that both morphological forms can and have colonized the outcrop habitat.

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THE OCCURRENCE OF *ACICARPHA TRIBULOIDES* (CALYCERACEAE) IN EASTERN NORTH AMERICA

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ABSTRACT

Acicarpha tribuloides Juss. (Calyceraceae) has a natural distribution in southern Brazil, Uruguay, Paraguay, and northeastern-central Argentina. This species has also been collected in the United States, and Small (1933) reported it as being naturalized in northern Florida. Recent herbarium studies reveal that *Acicarpha tribuloides* occurred as a ballast plant in Pennsylvania, New Jersey, Alabama and Florida. Small's account was based on two specimens collected by Curtiss in 1885; no specimens of *Acicarpha tribuloides* collected after 1888 are known. *Acicarpha tribuloides* appears to be a well adapted weed in South America based on its abundance, multiple adaptations for dispersal, and on its ability to invade disturbed habitats and cultivated fields. This species may have failed to become naturalized in the United States due to: (1) climatic and edaphic barriers; (2) inability to compete with native and naturalized species; (3) low reproductive capacity.

Key Words: *Acicarpha tribuloides,* ballast plants, Calyceraceae, distribution, United States

INTRODUCTION

Acicarpha tribuloides Juss. (Figure 1) is one of five species of the South American genus *Acicarpha,* and occurs in Southern Brazil, Uruguay, Paraguay, Bolivia, Peru, and northeastern-central Argentina (Figure 2). The epithet "tribuloides" no doubt refers to the five persistent, spine-like calyx lobes protruding from the center of each achene, much in the same fashion as the genus *Tribulus* (Zygophyllaceae). Both *Acicarpha* and *Tribulus* exhibit fruits which in shape resemble a Roman tribulus (a device once used to impede calvary).

The first known specimens of *Acicarpha tribuloides* from the United States were collected sometime between 1867 and 1876 (Burk, 1877; Table 1). Additional specimens from the Eastern United States were collected between 1885 and 1888. Small (1933) reported the species from northern Florida, and Shetler and Skog (1978) listed *A. tribuloides* as an introduced annual. These reports provided a stimulus to investigate the distributional history and current status of *Acicarpha tribuloides* in the United States.

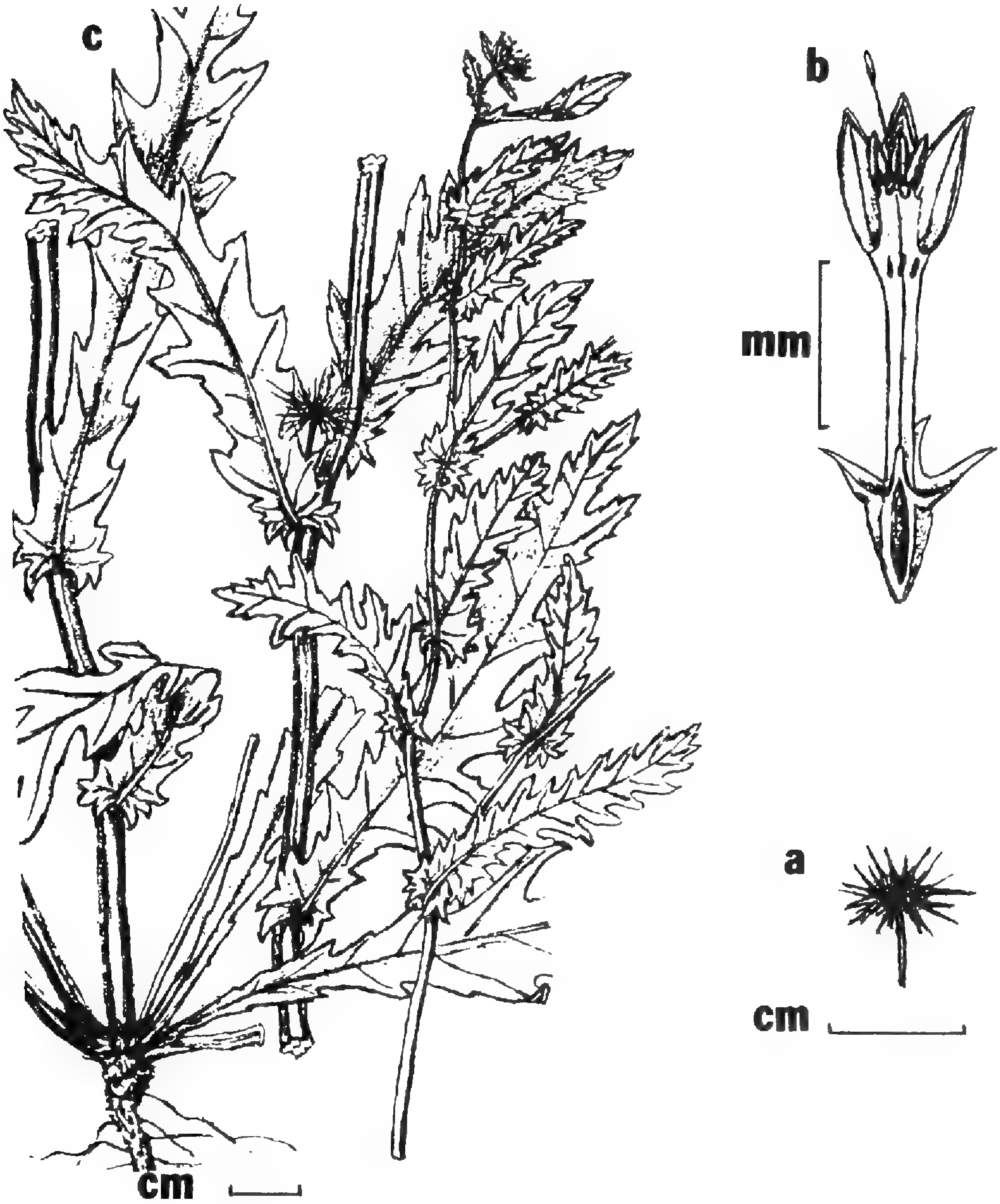

Figure 1. *Acicarpha tribuloides* Juss. **a**, capitulum; **b**, flower; **c**, habit. From Miers (1860: Plate 51).

NATURAL HABITAT AND MEANS OF DISPERSAL

Cabrera and Zardini (1978) noted that *Acicarpha tribuloides* commonly inhabits grasslands of deltas, river banks, and sandy ravines, and is an invader of cultivated fields. Flowers are borne in capitula (0.3–0.8 cm in diameter) attached to slight peduncles. At maturity, the calyx lobes of the peripheral achenes (central flowers are female-sterile) persist, and are adnate to the achene.

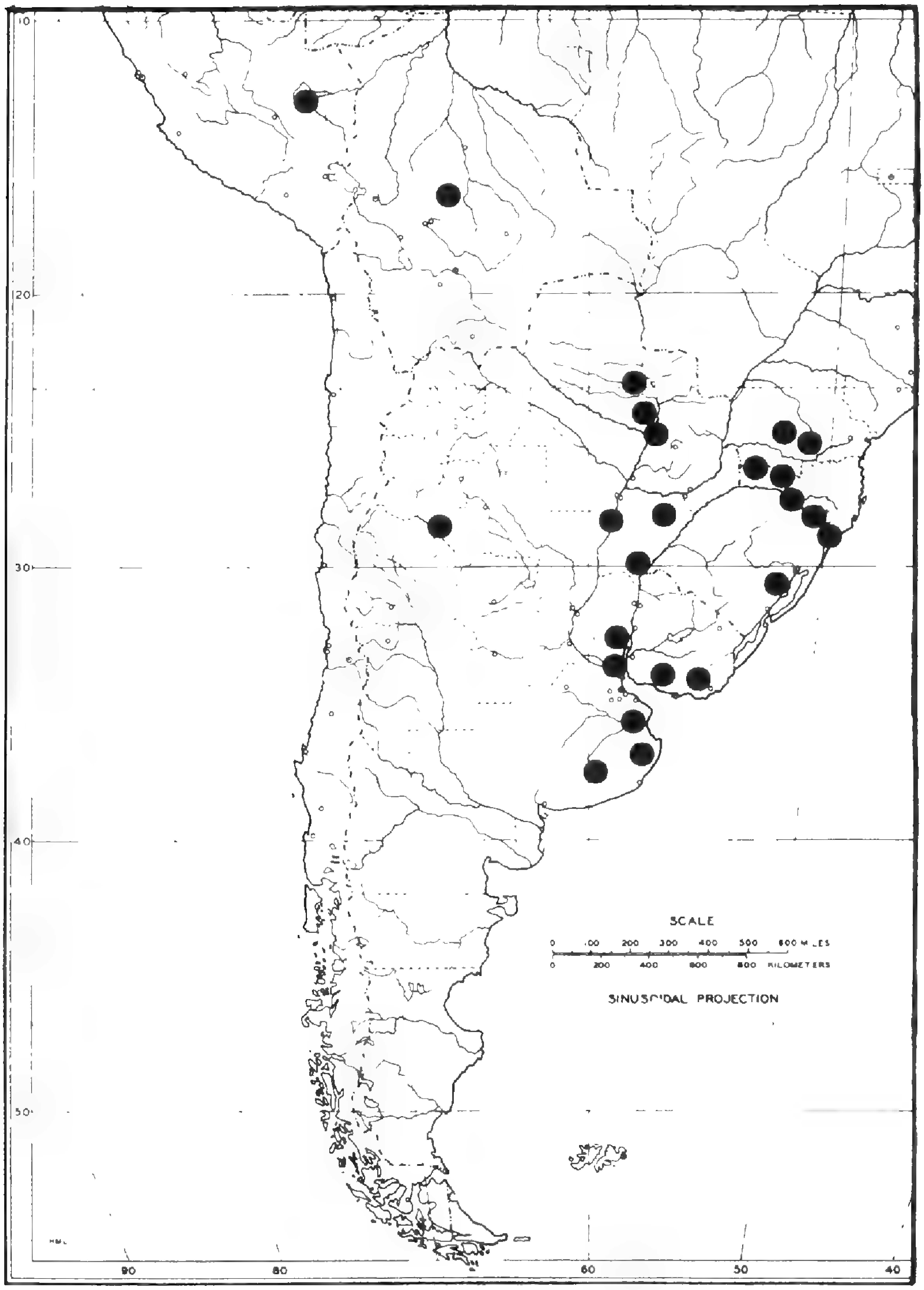

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Figure 2. Map showing the natural distribution of *Acicarpha tribuloides* Juss. in southern South America.

Table 1. Collections of *Acicarpha tribuloides* Juss. from the eastern United States.

Collection Site	Collector*	Number of Specimens	Year	Location of Voucher Specimens
Philadelphia, PA	Burk	3	1867–75	F (310981, 319640), GH
Camden, NJ	Parker	1	1887	NY
North Carolina	McCarthy	2	1888	US (42101, 53061)
South Carolina	McCarthy	1	1888	GH
Walton County, FL	Curtiss	1	1885	GH
Pensacola, FL	Curtiss	1	1885	GH
Mobile, AL	Mohr	1	1888	US (53144)

* No collection numbers are recorded for these voucher specimens.

The achenes and receptacle fuse together and form an ovate, rigid, spiny, disseminule that detaches from the spindly peduncle (Figure 1).

Ridley (1930) hypothesized that plants with adherent calyces are almost certainly dispersed by wandering mammals. The ripened capitula of *Acicarpha tribuloides* may break off and become attached to a passing animal. Since the species is common along river banks, the spiny capitula may be transported by animals using these sites as watering places. Disseminules may also be wind-blown. Annual herbs inhabiting deserts, steppes, or praires often are dispersed when their inflorescenses become detached and are blown across open areas (Ridley, 1930). Morphologically, the detached capitula of *Acicarpha* could easily be tumbled across a sandy deltaic plain or river bank by wind.

Many specimens of *Acicarpha tribuloides* examined have been collected from river banks or ravines. In all likelihood, capitula are transported downstream and deposited on sandy river banks and bars. Species of *Acicarpha* appear to be well adapted weeds in South America based on their abundance, multiple adaptations for dispersal, and their ability to invade disturbed habitats and cultivated fields.

SITES OF INTRODUCTION IN THE UNITED STATES

The earliest known occurrence of *Acicarpha tribuloides* in the United States is near the Philadelphia area in 1867 (Table 1).

Burk collected plants from a ballast dump at Kaighn's Point which he identified as *Calycera balsamatifolia* (Burk, 1877). Careful examination of Burk's collections reveals that all three specimens are *A. tribuloides.*

Two specimens of *Acicarpha tribuloides* collected in the late 1880's from ballast sites in Camden, New Jersey, and Mobile, Alabama serve as evidence of later introductions of the species. Other specimens from North Carolina (1888) and Walton County, Florida (1885), lack label information regarding the specific locality (Figure 3).

MEANS OF INTRODUCTION

Ridley (1930) described six ways plants can be introduced: (1) as impurities with cereals, vegetables, and bird seeds; (2) as attachments to fleeces and hides of domesticated animals; (3) in animal fodder; (4) in packing materials; (5) as escapes from cultivation; and (6) in ships' ballast and exported soil. During the late 1880's ballast disposal was a common means by which alien plants were introduced. Ships usually took sand and gravel from a near-shore area at the beginning of a voyage, and discharged it at the port of destination. This practice continued until the early 20th century when water became the material used to weight ships. Burk (1877) noted that "improvements" made by the Pennsylvania Railroad and the American Steamship Company increased the number of vessels entering Philadelphia to export produce and merchandise. Marshland surrounding the harbor was covered with mud and sand dredgings and ballast was constantly added. Brown (1879) watched vessels dumping ballast day and night on Gowanus Creek in New York City. Late 19th century botanists not only observed ballast dumpings, but also made careful observations of the plants growing in the sites and traced their origins.

A large portion of ballast dumped in Philadelphia was oolite or chalk, materials indigenous to the British Coast. Many plants reported from the Kaighn's Point site were native to the British Isles. Others were South American or Southern European in origin, and such plants captured the imagination of Burk "either from their rarity or the place of nativity." The circumstances possibly responsible for the introduction of *Acicarpha tribuloides* are intriguing.

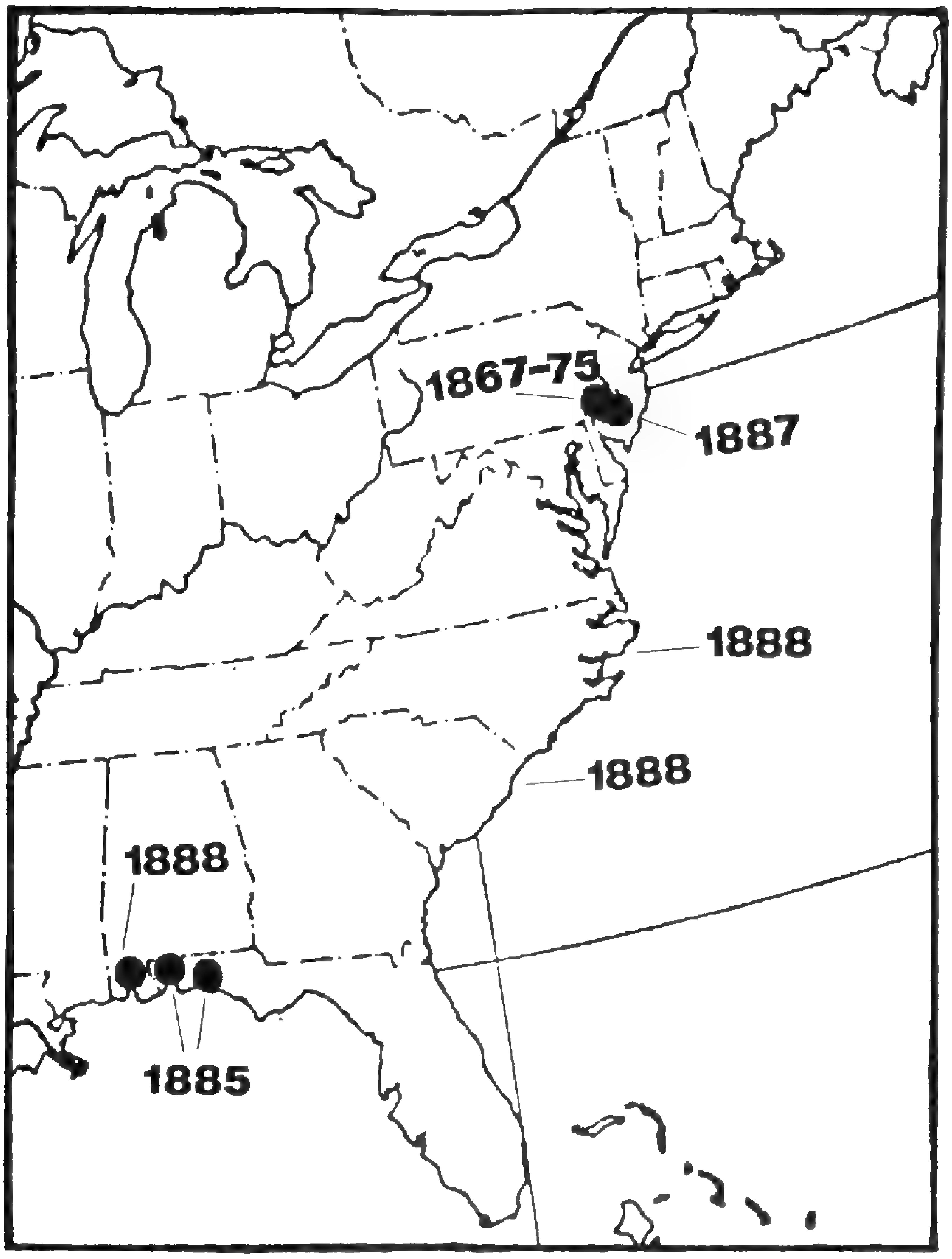

Figure 3. Sites of introduction of *Acicarpha tribuloides* Juss. in eastern North America.

On 26 December 1864 the Paraguayan dictator Francisco Salano Lopez invaded Brazil. Brazil formed a coalition with Argentina and Uruguay against Paraguay that lasted until the Brazilian lancers killed Lopez in the mid-1870's (Mooney, 1981). During the beginning of the Paraguay-Brazil conflict, the United States and the Confederacy were engaged in the Civil War. When defeat was inevitable, some Confederates formed colonization societies to promote emigration from North America. One popular choice of a new rebel homeland was Brazil, a country glamorized in books Southerners read before the war (Harter, 1985). Some colonists failed to adapt to Brazil and were returned to the United States by vessels belonging to the Brazilian Squadron. Such ships as the *Kansas, Portsmouth,* and *Quinnebaug* protected United States citizens and economic interests during the Paraguay-Brazil War (Harter, 1985). Two ships belonging to this war squadron commonly traveled in the region of South America where *Acicarpha tribuloides* occurs naturally.

The *Wasp* was a small iron-hulled sidewheel steamer that joined the Brazilian Squadron after she was repaired in Philadelphia in 1867. She cruised the Plata and Uruguay Rivers during the war and remained in Uruguay after the war transporting diplomats and " guarding American interests." A second vessel, the *Juaniata,* patrolled the coast of Brazil as far south as Buenos Aires. In 1867 this steam sloop-of-war returned to Philadelphia and docked with monitors and ironclads in the Old Navy Shipyard (Coletta and Bauer, 1985; Mooney, 1981). The fact that Burk collected *Acicarpha tribuloides* in a Philadelphia ballast dump between 1867 and 1876 suggests that the plant may have been introduced via a naval vessel.

The circumstances responsible for later introductions of *Acicarpha tribuloides* are very sketchy. One possible means of introduction may have been by ships transporting farm equipment. The Argentinian economy boomed during the 1880's as a result of wheat cultivation. Lands previously utilized as sheep and cattle range lands were allocated for wheat. A great need for quality farm equipment resulted in strong trade relationships between the United States and Argentina and an increase in shipping (Koebel, 1912; Ross and McGann, 1982; Williams, 1975).

CURRENT STATUS

No specimens of *Acicarpha tribuloides* collected after 1888 are known. Burk (1877) observed a great variety of ballast plants, most of which survived a single growing season. Futhermore, herbarium studies reveal that Small's account was based on two specimens collected by Curtiss in 1885 (Table 1). Dr. Robert Godfrey (pers. comm.) has never discovered a population of *A. tribuloides* in his 35 years of botanizing in northern Florida. It appears that this species never became naturalized in the United States.

Some taxa have become naturalized after being introduced in ships' ballast. *Apium leptophyllum* (Apiaceae), native to Florida, Texas, and South America, became naturalized in Europe, West Africa, China, Japan, Australia, New Zealand and Polynesia. *Cakile maritima* (Brassicaceae), *Glaucium leuteum* (Papaveraceae), and *Plantago coronopus* (Plantaginaceae) were probably introduced to Southern Australia in ballast (Ridley, 1930). It is surprising that *Acicarpha tribuloides* never became established in Alabama or Florida. The species appears to be an abundant weed in regions of South America that are physiographically similar to southeastern United States.

Acicarpha tribuloides probably failed to become naturalized for a number of reasons. Any plant native to South America is likely to encounter some climatic and edaphic barriers to establishment. Seedlings are especially affected by these two factors since they lack the tolerance and vigor of a mature plant (Smith, 1978). If the seedling survives it is forced to compete with native and naturalized individuals. Ross and Harper (1972) suggested that an individual's ability to capture resources is restricted by the number and proximity of neighboring plants. Even if the founder is capable of scattering seed or reproducing vegetatively, the resulting population may be small and vulnerable due to low reproductive capacity and slow population growth (Smith, 1978). A small population of *A. tribuloides* growing in a constantly disturbed ballast dump site would be an excellent candidate for eradication.

Acicarpha tribuloides, as well as other members of Calyceraceae, possess capitula. The family bears a striking morphological resemblance to Asteraceae. The aggregation of flowers into a capitulum is believed to be the result of selection acting on the flowering phase of the plant. During the fruiting phase, the capitulum is vulnerable to herbivory (Burtt, 1978). To date, the only secondary compounds known to exist in Calyceraceae are monoterpenoid cyclopentanoid lactones called iridoids (Jensen et al., 1975). Cronquist (1988) speculates that the lack of diversification in Calyceraceae is not due to floral or vegetative morphology, but to limited chemical defenses that have evolved in the family. Cronquist's theory will be tested in the future when more is known about the biology and secondary compounds in the Calyceraceae. Currently, no members of the Calyceraceae occur as weeds outside South America, even though the family includes such weedy species as *Boopis gracilis* Phil., *Boopis anthemoides* Juss., and *Acicarpha tribuloides.*

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HYDROPHILY: PHYLOGENETIC AND EVOLUTIONARY CONSIDERATIONS

C. THOMAS PHILBRICK

ABSTRACT

The two forms of abiotic pollination, hydrophily and anemophily, exhibit contrasting taxonomic, ecological and phylogenetic patterns. Anemophily is widespread among angiosperms whereas hydrophily occurs in only one dicot and seven monocot families. Ecological limitations of hydrophily likely parallel those of anemophily, yet the processes involved in the former are not well understood. Although hydrophily is in all probability polyphyletic, the phylogenetic relationships among hydrophilous groups are unresolved. Specialization in reproductive structures that accompany hydrophilous pollination makes the recognition of homology difficult, thus phylogenetic hypotheses in groups in which hydrophily occurs are tentative. Hydrophily and anemophily are both geographically widespread, yet the general trend of decreasing incidence of anemophily with decreasing latitude is lacking in the distribution of hydrophily. This contrast may be associated with markedly different geographic patterns of species richness in aquatic versus terrestrial habitats.

Key Words: hydrophily, species richness, geographic distribution, phylogeny, evolution

INTRODUCTION

Hydrophily, water-mediated cross-pollination, entails dramatic modifications of the floral systems of terrestrial angiosperms. These changes arise from adaptation to provide for the release, transport and capture of water-borne, often wet, pollen. Hydrophilous taxa are infrequent in angiosperms; only 140 of the total of ca. 225,000 angiosperms (R. Thorne, pers. comm.) are hydrophilous (.00062%). The infrequency of hydrophily has no doubt contributed to the perception that this pollination system is "unimportant" in angiosperm evolution. In fact, an understanding of hydrophily may provide a unique perspective on the evolution of angiosperm reproductive systems. Hydrophilous systems are perhaps the best examples of the evolutionary "plasticity" of the angiosperm floral biology; i.e., in hydrophily the "aerial" floral system that dominates angiosperms has been essentially abandoned. Furthermore, the restricted occurrence of hydrophily makes it possible to gain an overall understanding of its evolution, an understanding which is perhaps unattainable in virtually all other, much more widespread pollination systems.

Two general, but sometimes rather arbitrary, forms of hydrophily are recognized: 1) epihydrophily; pollination via pollen transport at the water surface (two-dimensional), and 2) hypohydrophily; pollination via pollen transport below the water surface (three-dimensional). The distinctions between the two are not always clear and both may operate in some species. For the sake of discussion, the two are combined in this paper.

In most works on pollination biology, the two forms of abiotic pollination, anemophily and hydrophily, are treated conceptually as similar systems that operate in different media. There are no doubt similarities between anemophily and hydrophily that reflect their abiotic nature. However, it is evident that the two systems reflect contrasting ecological and evolutionary patterns. Several workers (e.g., Whitehead, 1969, 1986; Regal, 1983) have addressed the evolution of anemophily, especially in an ecogeographic context, but the evolution of hydrophily has been largely neglected. In fact, it may be informative to contrast these two abiotic pollination systems with the hope of elucidating the distinctions between them and to place these differences in an evolutionary context.

Many basic questions concerning the evolution of hydrophily remain unaddressed, or even unasked. For instance, although hydrophily characterizes all marine angiosperms, it is unclear whether it was a prerequisite for, or a consequence of, the invasion of the marine environment (Philbrick, 1988). Why is hydrophily most common in monocots, and virtually absent in dicots? What might this discrepancy suggest about the evolutionary histories of the monocots versus dicots? Are monocots, or certain groups within the monocots, somehow evolutionarily "predisposed" for hydrophily?

An enhanced understanding of the evolution of hydrophily may be attainable via consideration of the relationships among hydrophilous and nonhydrophilous taxa, the ecogeographic pattern of hydrophily, and its similarities and differences relative to anemophily. The purpose of this contribution is to consider these issues. First, our current understanding of the taxonomic and phylogenetic distribution of hydrophily will be summarized. Secondly, the ecogeographic distribution of hydrophily will be considered relative to anemophily, as well as several ecological and/

Table 1. The taxonomic distribution of hydrophily. Modified from Les (1988). The genera are followed by the number of species/type of hydrophily: E, epihydrophily; H, hypohydrophily. Taxonomy of monocots follows Dahlgren and Rasmussen (1983).

Dicot:	
Nymphaeales	
Ceratophyllaceae—cosmopolitan.	
Ceratophyllum	6/H
Monocot:	
Hydrocharitales	
Hydrocharitaceae—cosmopolitan, mainly warm regions.	
Appertiella	1/E
Elodea	5/E
Enhalus	1/H
Halophila	8/H
Lagarosiphon	9/E
Nechamandra	1/E
Thalassia	2/H
Vallisneria	2/E
Zosterales	
Najadaceae—cosmopolitan.	
Najas	30–50/H
Posidoniaceae—Mediterranean, S. W. Asia, Australia.	
Posidonia	3/H
Potamogetonaceae—(re: *Ruppia*) temperate and subtropical regions.	
Ruppia	1–7/E
Zosteraceae—temperate coasts, excluding South America and S.W. Africa.	
Heterozostera	1/H
Phyllospadix	5/H
Zostera	12/H
Zannichelliaceae—cosmopolitan.	
Althenia	2/E
Lepilaena	4/E
Zannichellia	1–5/H
Cymodoceaceae—tropical and subtropical.	
Amphibolis	2/H
Cymodocea	4/H
Halodule	6/H
Syringodium	2/H
Thalassodendron	2/H

or biological factors that may influence its distribution. Through a consideration of these two general topics I seek to focus attention on some of the important issues that remain to be adequately addressed regarding the evolution of hydrophily.

TAXONOMIC AND PHYLOGENETIC CONSIDERATIONS

The difference in taxonomic distribution of hydrophily in dicots versus monocots is striking. The Ceratophyllaceae is the single dicot family for which hydrophily has been documented. Although the Callitrichaceae is often cited as containing hydrophilous species, the available evidence suggests otherwise (Philbrick and Anderson, unpubl. data). In contrast, hydrophily is considerably more widespread in monocots, where it occurs in seven families (Table 1) and ca. 134 species (.0026% of monocots). If we consider the extent of hydrophily among aquatic angiosperms as a group, 1.5% of dicots, and ca. 28% of monocots are hydrophilous (Philbrick, 1990).

It has long been recognized that hydrophily has evolved several times. Yet, the taxonomic versus phylogenetic relationships are unclear; it is not evident how often it has evolved. In some instances, the taxonomic distribution of hydrophily, versus various manifestations of autogamy that have been misinterpreted as hydrophily, is still being clarified (cf. Philbrick, 1984, 1988). In addition, our understanding of the relationships among groups where hydrophily occurs is still tentative.

Hydrophily is likely monophyletic in dicots; it occurs only in the Ceratophyllaceae. Its phylogenetic history among monocots is much more complex. The seven monocot families in which hydrophily occurs are in two orders: Hydrocharitales and Zosterales (Table 1). There has been much speculation concerning relationships among the families in these orders, yet study is plagued by the extreme modification of floral structure that masks homology. A recent cladistic analysis by Dahlgren and Rasmussen (1983) provided perhaps the best phylogenetic hypothesis of relationships among the families in these orders (Figure 1).

If we use the traditional idea that hydrophily arises from an aerial-flowered most recent ancestor, then the Dahlgren and Rasmussen phylogeny (Figure 1) suggested that hydrophily has evolved a minimum of four times in monocots: once in the Hydrocharitaceae (D), and at least three times in the Zosterales clade (A, B, C). If we include the possibility of reversals from hydrophily to aerial pollination systems, several additional scenarios are possible. For instance, hydrophily may be synapomorphic at E in Figure 1, with a subsequent reversal to aerial pollination in *Potamogeton* (Potamogetonaceae) (Figure 1f). This latter "reversal-

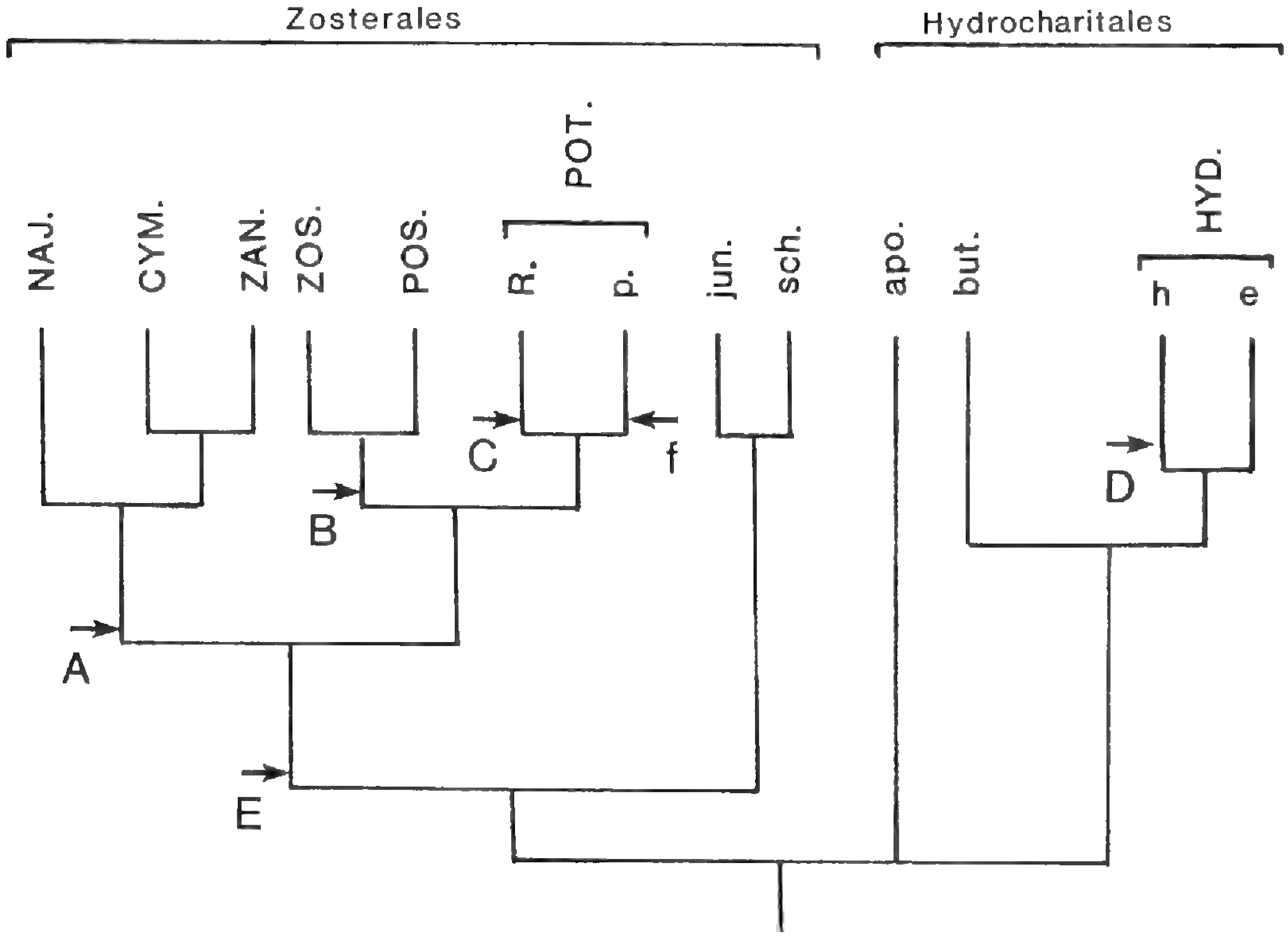

Figure 1. A cladogram modified from Dahlgren and Rasmussen (1983). The synapomorphies that support each node are not included but are listed in Dahlgren and Rasmussen's Figure 10, p. 359. Families in which hydrophily occurs are in upper case letters; those in which aerial pollination occurs are in lower case letters. The arbitrary division of the Hydrocharitaceae into hydrophilous (h) and entomophilous (e) taxa is mine. Upper case letters adjacent to arrows designate where hydrophily may have arisen; lower case letters adjacent to arrows designate reversals from hydrophily to aerial pollination systems. NAJ., Najadaceae; CYM., Cymodoceaceae; ZAN., Zanichelliaceae; ZOS., Zosteraceae; POS., Posidoniaceae; R., *Ruppia*; p., *Potamogeton*; jun., Juncaginaceae; sch., Scheuchzeriaceae; apo., Aponogetonaceae; but., Butomaceae; HYD., Hydrocharitaceae; POT, Potamogetonaceae.

scenario" requires one less step than does the former. However, the reversal-scenario requires the evolution of aerial pollination from a hydrophilous precursor, which is contrary to the traditional belief that aerial pollination systems are primitive. Yet, in principle there is no reason to refrain from reversing this polarity. Could aerial floral systems in some groups be derived from hydrophilous ones? At the species level there is no *a priori* reason why an aerial floral system cannot be derived from a hydrophilous precursor. In fact, it may be heuristic to consider just such alternatives, with the hope of gaining a new perspective on the problem. It is noteworthy that the resolution that involves the fewest

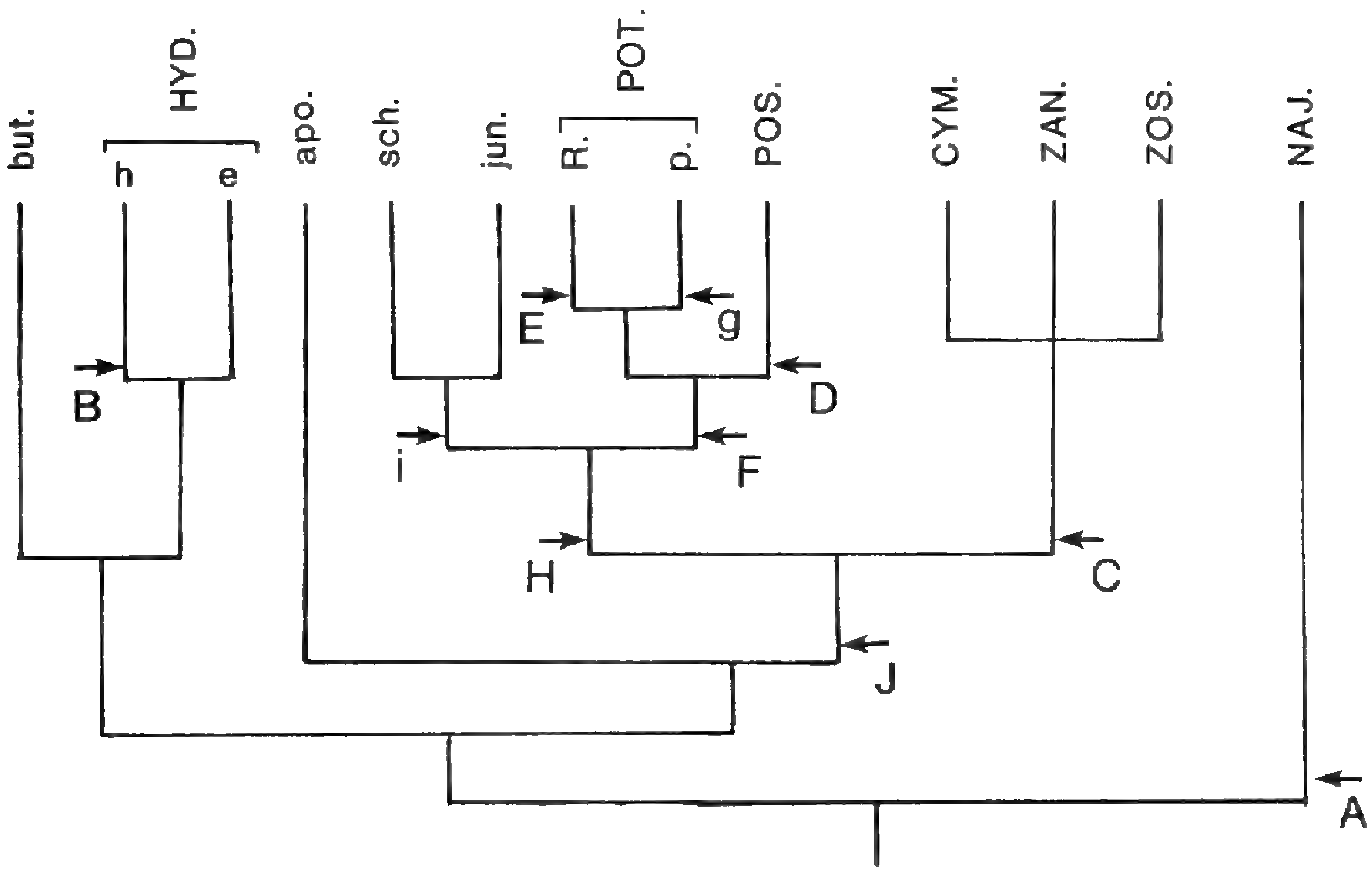

Figure 2. An intuitive phylogeny of Robert Thorne (pers. comm., 1990) illustrating the proposed relationships between the same families shown in Figure 1. Families in which hydrophily occurs are in upper case letters, those in which hydrophily does not occur are in lower case letters. For the sake of illustration the Hydrocharitaceae are arbitrarily divided into taxa that exhibit hydrophily (h) and those that are entomophilous (e). Upper case letters adjacent to arrows indicate where hydrophily may have originated; lower case letters represent reversals from hydrophily to aerial pollination systems. apo., Aponogetonaceae; sch., Scheuchzeriaceae; jun., Juncaginaceae; POT., Potamogetonaceae; R., *Ruppia*; p., *Potamogeton*; POS., Posidoniaceae; CYM., Cymodoceaceae; ZAN., Zanichelliaceae; ZOS., Zosteraceae; NAJ., Najadaceae; HYD., Hydrocharitaceae; but, Butomaceae.

steps (the reversal-scenario) includes a single reversal from hydrophily to aerial pollination.

It may be useful here to compare the cladogram from Dahlgren and Rasmussen with another phylogenetic pattern that has been proposed for the Zosterales. Figure 2 is the intuitive phylogenetic tree of Robert Thorne (pers. comm.). Several features of the Thorne phylogenetic tree contrast with that of Dahlgren and Rasmussen, e.g., Thorne's placement of the Najadaceae relative to the Zosteraceae. Using the same reasoning as above, the Thorne phylogenetic tree suggests that hydrophily has evolved at least five times in monocots (Figures 2A, B, C, D, E). If reversals to aerial pollination systems are included, the most parsimonious resolution would still require five steps. For instance, if hydrophily arose at A and B, to account for its occurrence in the Najadaceae and Hydrocharitaceae, respectively, and at J, a minimum of two reversals (g, i) would be necessary. Thus, the Dahlgren and Rasmussen topology (Figure 1) provides a more parsimonious (fewer steps) resolution of the distribution of hydrophily than does the phylogenetic tree of Thorne (Figure 2).

The complexity of interpretation of floral structure throughout the Zosterales has been an obstacle in establishing confidence in phylogenetic hypotheses for this order (Dahlgren and Clifford, 1982; Dahlgren and Rasmussen, 1983; Posluszny and Tomlinson, 1977; Tomlinson, 1982). This difficulty has been attributed to modification of reproductive structures that accompany the evolution of hydrophily. However, the presence of non-hydrophilous taxa in this order also leads to phylogenetic puzzles. Taxa such as *Lilaea* and *Triglochin* (Juncaginaceae) and *Scheuchzeria* (Scheuchzeriaceae) display floral features that are difficult to assess as homologous with those in other monocot groups (Tomlinson, 1982). Thus, it appears that there are factors other than hydrophily itself that make interpretation of phylogenetic relationship difficult in the Zosterales. A reassessment of some of the basic ideas we have concerning floral system evolution, such as the evolutionary polarity of aerial versus hydrophilous pollination, may provide a new perspective.

It is important to note that neither the Dahlgren and Rasmussen (Figure 1) nor Thorne (Figure 2) phylogenies provide resolution for relationships among taxa in the Hydrocharitaceae (nor are they meant to). Yet, this family deserves special consideration here, given its diversity of pollination types. The Hydrocharitaceae is the only family in which entomophily, epihydrophily and hypohydrophily all occur (cf. Cook, 1982). Unfortunately, little phylogenetic work has been carried out in the Hydrocharitaceae (C. D. K. Cook, pers. comm.) and it is unclear whether hydrophily is mono- or polyphyletic in the family. Kaul (1968, 1970) included a diagram of floral evolution derived from his studies of floral and inflorescence anatomy. He showed that modifications of floral and inflorescence structures that accommodate hydrophily may have occurred via several developmental pathways. This evidence suggests that hydrophily is polyphyletic within the family. A phylogenetic framework against which to assess the evolution of pollination types would allow us to address whether one form of hydrophily has led to another (e.g., epihydrophily to hypohydrophily) or whether they have arisen independently.

TAXONOMIC, GEOGRAPHIC, LIMNOLOGICAL AND BIOLOGICAL CONSIDERATIONS

Anemophily versus hydrophily: taxonomic distribution

The differences in taxonomic distribution of anemophily and hydrophily are striking. Anemophily is taxonomically widespread and occurs in virtually every major angiosperm group. Anemophilous groups are often species-rich; for instance, *Quercus* (Fagaceae) encompasses ca. 600 species, *Salix* (Salicaceae) ca. 400 species, and *Poa* (Poaceae) ca. 500 species. In addition, the Poaceae, a largely anemophilous family, has perhaps 6000 species. Thus, it is reasonable to say that speciation in these groups does not seem to have been hindered by an anemophilous pollination system.

Hydrophily, in contrast, is restricted to eight angiosperm families (Table 1). Groups that include hydrophily are generally species-poor (Les, 1988); in fact, *Najas* with its ca. 50 species is the most species-rich hydrophilous genus. The next largest hydrophilous genus is *Zostera* which has only 12 species. The remaining genera contain 10 or fewer species. Whether it is hydrophily itself or the associated attributes of life in the aquatic milieu which limit speciation is an issue which has been addressed to some degree by Les (1988), although it remains largely unresolved.

Geographic considerations

Although there are relatively few hydrophilous species, hydrophily itself is as geographically widespread as anemophily, yet the two abiotic pollination types show different geographic patterns. Anemophily increases in incidence with increasing latitude and/or altitude (Whitehead, 1969; Regal, 1983; Berry and Calvo, 1989). Anemophily is the primary mode of pollination across large geographic areas, e.g., northern boreal forests and grasslands. However, anemophily is relatively uncommon in tropical regions. In contrast, hydrophilous species seem to be equally common in temperate and tropical regions, but make up a small component of the flora throughout. All eight families in which hydrophily occurs are geographically widespread, and five of the eight families exhibit broad geographic ranges across temperate and many tropical regions (Table 1).

The broad distribution of hydrophily is illustrated by the num-

Table 2. Summary of the total number of species (A-C) and genera(D) that occur per 10 degrees of latitude. The taxa in each latitudinal increment are not necessarily mutually exclusive. A. The number of species of *Najas* in Central and North America (modified from Haynes, 1979). B. The number of species of *Najas* in the Neotropics (modified from Lowden, 1986). C. The number of species of *Najas* in Malaysia (modified from de Wilde, 1972). D. The number of genera of seagrasses worldwide (modified from den Hartog, 1970).

Degrees Latitude	*Najas*			Seagrasses
	A	B	C	D
70				
	—	—	—	2
60				
	2	—	—	2
50				
	5	—	—	4
40				
	7	4	—	6
30				
	5	4	—	8
20				
	5	5	4	8
10 N				
	—	5	3	8
0				
	—	5	7	8
10 S				
	—	3	—	8
20				
	—	4	—	11
30				
	—	2	—	8
40				
	—	—	—	2
50				

ber of representative taxa that occur in temperate and tropical latitudes. For instance, Haynes (1979) and Lowden (1986) provided distribution data for species of *Najas* throughout Central and North America, and the Neotropics, respectively. The numbers of species of *Najas* per 10 degrees of latitude (Tables 2A, B) shows a relative overall geographic uniformity. The similar incidence of najad species in tropical and temperate regions contrasts markedly with what one would predict if the distribution of anemophily were used as a model: increasing incidence with increasing latitude. The distribution of *Najas* in Malaysia (de Wilde, 1972) also illustrates the extent of this genus in tropical regions (Table 2C). The temperate-tropical distribution of hydrophily is further illustrated by the worldwide distribution of the genera of sea-grasses (Table 2D). In fact, the number of genera per 10 degrees of latitude is somewhat higher in tropical than temperate regions.

The nature of the comparisons that are being attempted here lead to several questions. For instance, is this a meaningful comparison given the vastly different sample sizes? That is, there are only 140 species of hydrophilous angiosperms, compared with the thousands of anemophilous taxa from which to assess distribution patterns. No doubt our perception of the distribution of hydrophily is colored by the distribution of relatively few species. However, this problem is inherent in the nature of the pattern being discussed, that is, comparing a ubiquitous to a rare pollination system. Secondly, although anemophily is infrequent in tropical regions relative to biotic pollination, how many tropical taxa are in fact anemophilous? Could it be that on a taxon-by-taxon basis anemophily is as frequent, or more frequent, in tropical regions as hydrophily? Although, this frequency comparison may or may not be true, the significance of the comparison being made lies in the incidence of the pollination system throughout broad geographic areas, not in its proportion relative to other pollination systems within a particular flora.

Limnological factors

Our understanding of hydrophily might benefit from a discussion of the factors that limit its distribution, an approach taken regarding anemophily (Whitehead, 1969; Regal, 1983; Daubenmire, 1972). The ecogeographic distribution of hydrophily is no doubt a result of a complex array of interactions of limnological and biological factors. Although we run the risk of over-simplification, it may be useful nonetheless to attempt to construct generalized patterns.

Aquatic habitats are considered fairly uniform regardless of latitude (Arber, 1920; Sculthorpe, 1967; den Hartog, 1970; Tiffney, 1981; Les, 1988). Although differences in water chemistry, growth season duration and temperature do affect aquatic plant communities, the aquatic habitat seems to be more uniform than terrestrial habitats, in part due to the thermal properties of water.

Environmental cues that initiate flowering in hydrophilous species may be insensitive to latitudinal change. The seagrasses (Cymodoceaceae, Hydrocharitaceae [*Enhalus, Thalassia*], Posidoniaceae, Zosteraceae) provide a good example, where tidal cycles have been implicated in stimulation of flowering (cf. Pettitt, 1984). Although the amplitude of the tidal cycle varies with latitude, the cycle itself is ubiquitous. Similar ubiquitous cues may also be instrumental in the flowering of freshwater hydrophilous taxa. However, pollination systems in freshwater hydrophilous species are little studied. Therefore, possible environmental cues that would indicate the most appropriate environmental conditions for pollen release, transport, and capture have yet to be elucidated.

Nothing is known about the patterns of pollen flow (e.g., effective "pollen shadow," dispersal distance, etc.) relative to population structure, in hydrophilous species (cf. Les, 1988). The biotic and abiotic limits to pollen flow have not been identified. Nonetheless, some general assumptions are not unreasonable. An important component of the physical boundaries of aquatic habitats (the margins of the body of water) are insensitive to geography. That is, the physical boundaries to water-mediated pollen flow within a body of water will be the same regardless of latitude. This fact would certainly serve to "standardize" a major factor that limits pollen flow. Furthermore, the overall limnological processes that would influence pollen dispersal in water bodies of similar size would likely be the same in temperate and tropical regions. For instance, the yet poorly understood diurnal turnover of the water column in the littoral zone may provide a predictable vector for pollen flow within a population.

Biological factors

An important difference between aerial and underwater floral systems is the spectrum of potential pollen vectors: both biotic and abiotic (wind) vectors are available to aerial floral systems. In contrast, the aquatic medium itself is the only vector available to submerged flowers. Although a specialized fauna is well developed in aquatic plant communities, there is no evidence to suggest that biotically mediated pollination occurs in submerged flowering species. Thus, in underwater aquatic habitats, unlike in aerial systems, an increasing spectrum of biotic pollination vectors with decreasing latitude would have little bearing on the incidence of hydrophily. Some forms of epihydrophily (e.g., in *Elodea, Nechamandra, Vallisneria,* Hydrocharitaceae) offer a different set of evolutionary riddles than does hypohydrophily. Many aspects of epihydrophilous pollination are essentially aerial in nature. Why epihydrophily is the method of pollen dispersal in some taxa of Hydrocharitaceae and anemophily or biotic pollination is not, is an intriguing yet unaddressed issue.

A consideration of species diversity in terrestrial versus aquatic habitats is also revealing. It is generally agreed that species diversity is highest in the tropics and decreases with increasing latitude (e.g., Pianka, 1966 and references therein). For the angiosperms, this trend is based principally on terrestrial taxa. Although aquatic habitats in general display lower species diversity than their terrestrial counterparts, it is as yet unclear how aquatic plant communities vary latitudinally. A preliminary comparison of temperate and tropical aquatic habitats reveals that the species diversity of aquatic angiosperms in temperate regions is generally uniform with that found in the tropics (G. E. Crow, unpubl. data). Thus, the inverse relationship between species diversity and distance between individuals within a population, which serves to limit the effectiveness of anemophily (Daubenmire, 1972), is less a factor in aquatic communities. Cook (1988) reported that the incidence of anemophily in both temperate and tropical aquatic angiosperms was similar (ca. 33%). This observation too may suggest that species diversity in aquatic communities is similarly low in tropical and temperate regions.

But, how does this low diversity relate to abiotic pollination? Daubenmire (1972) proposed that the distance between individuals of a species restricts the effectiveness of anemophily; that is, the greater the distance the less effective is the pollination system. Furthermore, an inverse relationship exists between species diversity and distance between conspecifics. Thus, the high species diversity in tropical latitudes is strongly associated with the low incidence of anemophily in tropical regions. It is reasonable to assume that hydrophily is much like anemophily in that the distance between conspecifics is critical for effective pollination. Therefore, it is reasonable to predict that at a particular interplant distance, the effectiveness of hydrophily will also break down. Thus, the generally uniform distribution of hydrophilous species in temperate and tropical regions may reflect the relative uniform species diversity in aquatic habitats throughout both regions as well.

Assessment of the relative importance of seed set in the propagation of hydrophilous species is complicated by the high incidence of clonal growth. Les (1988) has discussed the apparent lack of genetic variability in many hydrophilous taxa and has suggested that in some groups sexual reproduction may be "essentially a relictual condition of uncertain consequence to their present reproductive biology." The rather sporadic episodes of flowering in some taxa supports this notion. However, when flowering does occur in these species, seed are produced. Thus the sexual apparatus, both structurally and functionally, is maintained.

Najas and *Zannichellia* are exceptional hydrophilous genera in being annual, and perhaps by necessity, exhibiting abundant seed production (Les, 1988). Both genera have as broad a geographic distribution as any of the clonal hydrophilous taxa (e.g., *Ceratophyllum*). The high seed set throughout the ranges of these genera provides strong evidence that hydrophily can also function throughout. Thus, sexual as well as clonal growth may both be important factors that provide for such broad geographic ranges of hydrophilous taxa. Perhaps the high incidence of clonal growth in aquatic taxa would also promote low conspecific distances within aquatic communities.

CONCLUSIONS

Hydrophily and anemophily present contrasting phylogenetic, biological and ecogeographic patterns. The broad systematic distribution of anemophily indicates a polyphyletic phylogenetic history. However, phylogenetic relationships among aquatic monocots are largely unresolved, and thus whether hydrophily is ancestral or derived in each group is unclear. If in each group hydrophily is derived, it may well have evolved as many as five times in monocots. Yet, if hydrophily is primitive in certain groups, relative to aerial (e.g., anemophilous) pollination systems, we will have to reassess the traditional perception of pollination system evolution. It is equally unclear whether hydrophily has evolved once or numerous times in the Hydrocharitaceae, a family that exhibits a remarkable range of pollination systems.

Because hydrophily and anemophily are both abiotic systems, many of the overall factors that limit their effectiveness are likely to be similar. However, different geographic patterns of species diversity between terrestrial and aquatic habitats may play a role in the contrasting geographic distributions of the two abiotic pollination systems.

Many of the mechanisms of water-mediated pollination are being reevaluated and ecological perspectives are becoming refined (e.g., Cox, 1988). However, a reliable phylogenetic base upon which to anchor our understanding of the ecological diversity is yet lacking. Because the ability to assess homology between hydrophilous and non-hydrophilous groups is clouded by the degree of specialization and reduction in hydrophilous flowers, it is desirable to construct phylogenetic hypotheses via data sets that are divorced from the reproductive structures themselves; e.g., the use of molecular based data sets in hydrophilous groups is certainly an exciting prospect.

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THE IDENTITY OF *CAREX ALBOLUTESCENS*, *C. FESTUCACEA*, AND *C. LONGII* (CYPERACEAE)

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ABSTRACT

Carex albolutescens and *C. longii* (section *Ovales*) are considered conspecific by some authors. A survey of herbarium material revealed that they are morphologically distinct and simply represent a misapplication of species names. On the other hand, *C. albolutescens* is easily confused with a third species, *C. festucacea*. Diagnostic characters useful in identifying these three species are reviewed and new ones suggested. A species key and descriptions are provided.

Key Words: *Carex albolutescens, C. festucacea, C. longii,* section *Ovales,* Cyperaceae, North America

INTRODUCTION

Species of *Carex* L. from section *Ovales* (Kunth) Christ deserve a reputation for difficulty in their identification. Typically, a successful understanding of the species requires close attention to mature perigynia to perceive subtle differences in shape, color, and texture. Confusion over this sedge group in the nineteenth century was so great that one exasperated botanist, in trying to apply a taxonomy formulated by S. T. Olney, scrawled across an herbarium sheet "since Olney has manipulated them, it's not for ordinary mortal to name them."

Mackenzie's (1931) monograph of North American *Carex* culminated a long series of papers by himself, Bailey, Fernald, and others dealing with the taxonomy and nomenclature of section *Ovales*. His treatment brought order to the group and has been largely incorporated in eastern North American regional floras. However, at least one species in Mackenzie's monograph remained improperly typified. Upon reexamination of the type for *C. straminea* Willdenow *ex* Schkuhr, Svenson (1938) discovered that the name *C. straminea* should be applied to *C. richii* (Fernald) Mackenzie. This change, in turn, required the name *C. albolutescens* Schweinitz be revived for the taxon treated as *C. straminea* by Mackenzie.

Since Svenson's correction of nomenclature, regional floras have contained conflicting classifications of *Carex albolutescens* and *C. longii* Mackenzie. Several floras, notably those of Gleason (1952), Radford et al. (1964), and Seymour (1969), reduced *C.*

longii to synonymy with *C. albolutescens.* On the other hand, floras by Fernald (1950) and Voss (1972) maintained that two distinct species may be recognized. The present study was initially undertaken to clarify the taxonomy of *C. longii.* While reviewing herbarium material from the southeastern United States, the heart of the geographical range of *C. albolutescens,* it became apparent that part of the disagreement stems from confusion between *C. albolutescens* and a third taxon, *C. festucacea* Schkuhr *ex* Willdenow. As a result, true *C. longii* is recorded as *C. albolutescens* while true *C. albolutescens* is cataloged with *C. festucacea.* This paper reviews the diagnostic characters used currently in regional manuals, seeks additional characters of diagnostic value, and reviews the nomenclature of each of these species.

MATERIALS AND METHODS

This study was based on over 700 specimens of *Carex* from the following herbaria: BH, CU, GA, GH, IND, MICH, MO, NCU, NY, PAC, PH, SIU, TENN, and VPI. A sample of ninety-seven specimens was scored for 7 qualitative and 34 quantitative characters. The characters studied included but were not limited to those used by recent authors. Eight characters were derived from freehand, midculm cross-sections. Characters of perigynia, achenes, and pistillate scales were measured at 30 × magnification. The base of the perigynium beak was estimated as the point at which margin curvature deflects towards the beak tip. All references to the width and shape of perigynium include the thin, winged margin. After rejecting four quantitative characters on the basis of likely genetic redundancy, principal components analysis (PCA) was applied to 30 quantitative characters (Table 1) using NTSYS-PC (Rohlf, 1987). The F-statistic of ANOVA also aided in discerning which quantitative characters are of greatest value in delimiting morphological boundaries. Holotypes of *Carex albolutescens* and *C. longii* were examined to verify use of these names. Since the type of *C. festucacea* is apparently lost (A. A. Reznicek, pers. comm.), Schkuhr's (1801) illustration of his holotype was consulted to determine the application of the name.

RESULTS AND DISCUSSION

Section *Ovales* is the largest North American section in the genus *Carex.* Species in this group have gynaecandrous spikes,

Table 1. List of characters subjected to principal components analysis.

1. Mature culm height
2. Longest leaf sheath length/culm height
3. Length of ventral hyaline band
4. Culm diameter
5. Culm wall thickness
6. Number of culm lacunae
7. Number of culm vascular bundles
8. Radial thickness of largest culm fiber bundle
9. Tangential thickness of largest culm fiber bundle
10. Anticlinal length of culm epidermal cell
11. Periclinal length of culm epidermal cell
12. Inflorescence length
13. Number of spikes
14. Length of female portion of lateral spike
15. Length of male portion of lateral spike
16. Width of lateral spike
17. Length of perigynium body
18. Width of perigynium
19. Perigynium length from widest point
20. Beak length
21. Midbeak width
22. Length of serrulate margin/length of perigynium
23. Length of dorsal beak suture
24. Length of ventral beak suture
25. Number of dorsal perigynial nerves
26. Number of ventral perigynial nerves
27. Achene length/width
28. Achene width
29. Achene length from widest point
30. Style: amplitude of lateral sinuosity

wing-margined perigynia and hollow culms. Mackenzie (1931) placed *C. albolutescens* and *C. longii* in subsection *Alatae* within *Ovales* because they both have obovate perigynium bodies and strong ventral nerves on the leaf sheaths. Members of *Alatae* also tend to have relatively slender achenes. Subsection *Alatae* seems to be a natural grouping in North America which includes *C. alata, C. cumulata,* and *C. silicea. Carex festucacea* is classified in subsection *Festucaceae,* characterized by perigynia widest near or below the middle. Other members of this subsection include *C. molesta, C. normalis,* and *C. tenera. Carex festucacea,* according to Mackenzie, may be further distinguished by its combination of suborbicular perigynium bodies, long beaks, and moniliform inflorescences. *Carex albolutescens* and *C. longii,* on the other hand, are recognized by Mackenzie on the basis of the color and density of inflorescence, shape of perigynium beak, apex of pistillate scales, and thickness of culm.

Typification

The holotype for *Carex albolutescens,* deposited at PH, is a collection by Rev. Schweinitz labeled as "Nobis junior lagopod" from Salem [North Carolina] and Bethlehem [Pennsylvania]. The type locality cannot be determined more precisely since both Moravian towns were undoubtedly visited by Schweinitz and both are within the known range of this species. Although collected at the immature fruiting stage, *C. albolutescens* may be characterized as a slender plant which clearly has obovate perigynia with narrow beaks, acute-tipped pistillate scales, and short inflorescences. The holotype for *C. longii,* also on deposit at PH, is a collection by B. Long from Cape May County, New Jersey on 24 July 1907. In contrast to *C. albolutescens, C. longii* displays broad beaked obovate perigynia and obtuse pistillate scales. In addition, spikes of this specimen are congested with appressed-ascending perigynium beaks rather than spreading beaks. Achenes are oblong, less than 1 mm wide, and bear straight styles. Schkuhr's illustration of the holotype for *C. festucacea* depicts a plant with some anthesis of male flowers. Schkuhr's plant had perigynia with narrow beaks and very acute-tipped pistillate scales, much like *C. albolutescens.* On the other hand, at least three characters associated with *C. festucacea* are clearly depicted: oval shape of the perigynium body; long tapered bases of lateral spikes; and a long inflorescence. Also, Schkuhr illustrated the achene as somewhat ovoid with a straight style. Unfortunately, he only provided a dorsal view of the perigynium, so that the nervation of the ventral face is in doubt. Nonetheless, the illustration clearly represents *C. festucacea* as interpreted here, and serves to fix the application of the name.

General Character Analysis

Both quantitative and qualitative characters distinguish these three taxa at the species level. Vegetative as well as reproductive characters may be of value in species recognition; clearly, however, mature reproductive characters are of most use.

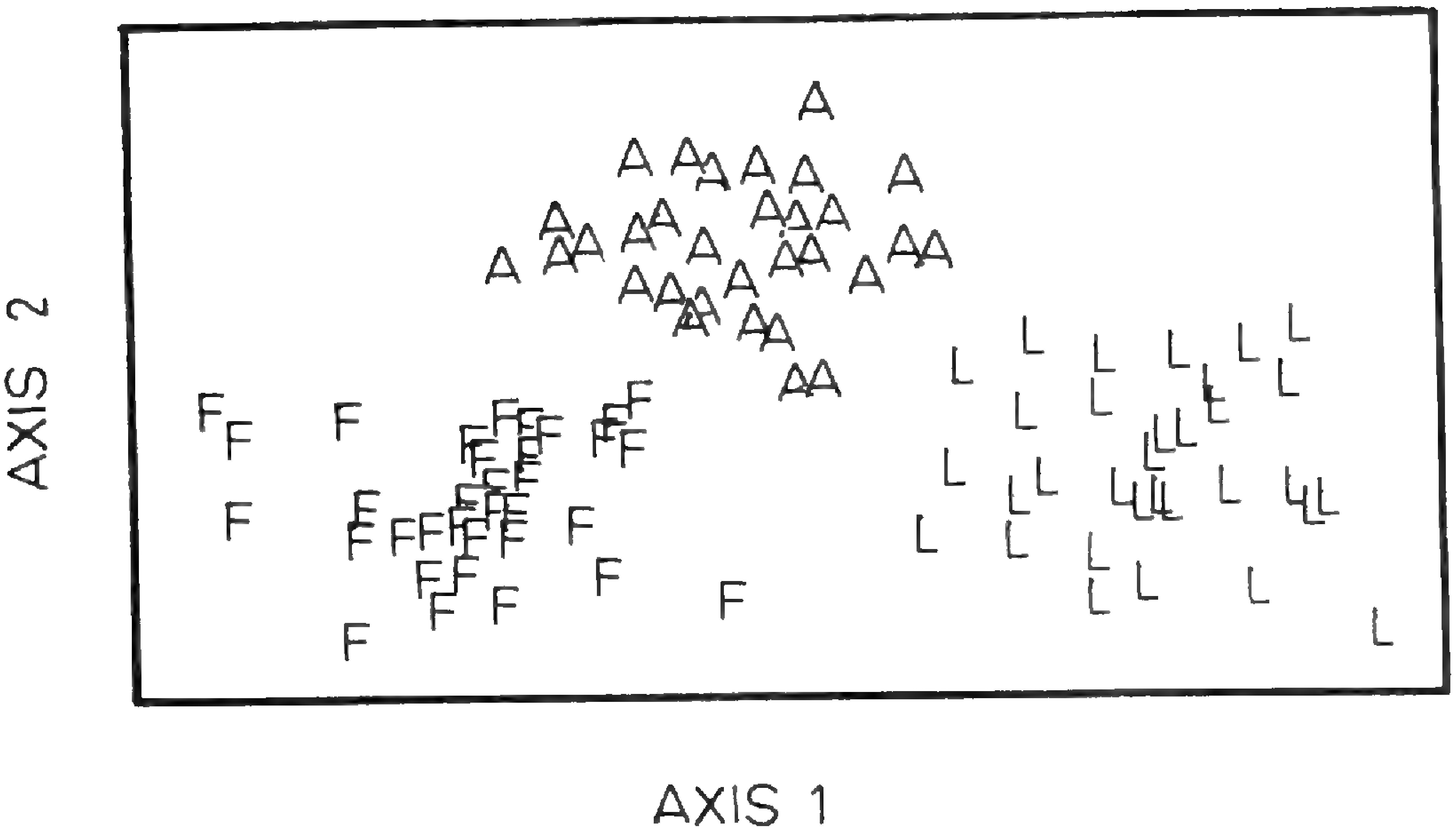


Figure 1. Ordination of *Carex albolutescens* (A), *C. festucacea* (F), and *C. longii* (L) along principal components axes 1 and 2. Axis 1 accounts for 20% of the total variation, while axis 2 accounts for 11%.

Principal components analysis of 30 quantitative characters shows three clusters of points which correspond to the three species typified above (Figure 1). The first component, accounting for 20% of the total variation, clearly separates *Carex festucacea* from *C. longii* and, to large degree, *C. albolutescens* from *C. longii.* There is overlap of *C. albolutescens* and *C. festucacea* in the first component. The second component, with a few exceptions, separates *C. albolutescens* from *C. festucacea* and *C. longii.* The second component explains 11% of the total variation in the data. An additional 8% of total variation is contained within the third principal component. However, this vector displays no separation into species groupings. The characters which show the greatest weighting in the first principal component (Table 2) include perigynium length from base to widest point, midbeak width, length of perigynium body, length of male portion of spikes, and achene length/width ratio. The greatest weightings in the second principal component include amount of style sinuosity and features of culm anatomy. These anatomical features include radial and tangential thickness of culm fiber bundles as well as anticlinal and periclinal length of epidermal cells adjacent to fiber bundles.

Of the 30 quantitative characters analyzed, 17 yielded F-ratios greater than 10 when subjected to ANOVA (Table 2). Among the highest F-ratios was 137.7 for midbeak width, demonstrating that

Table 2. Mean, interquartile range, eigenvalue and F-ratio for 17 quantitative characters distinguishing *C. albolutescens* (A), *C. festucacea* (F), and *C. longii* (L). Eigenvalues from axis two are marked **; all others are from axis one. F-ratios are significant at a level of less than 0.001.

Character		Mean	Interquartile Range	Eigen-value	F-Ratio
Leaf sheath length vs. mature culm height ratio	A	0.36	0.29–0.39	0.44	10.6
	F	0.30	0.23–0.37		
	L	0.40	0.34–0.46		
Culm epidermal cell length (anticlinal) (μm)	A	4.7 μm	3.3–5.6	−0.52 **	47.5
	F	5.4	4.4–5.6		
	L	7.5	6.7–8.9		
Culm epidermal cell length (periclinal) (μm)	A	9.0 μm	7.8–10.0	−0.65 **	25.1
	F	10.5	8.9–11.1		
	L	12.2	11.1–13.3		
Radial thickness of largest culm fiber bundle (μm)	A	40.2 μm	34.4–45.6	−0.71 **	17.4
	F	55.9	50.0–61.3		
	L	54.2	42.5–64.4		
Tangential thickness of largest culm fiber bundle (μm)	A	86.6 μm	75.0–97.5	-0.61 **	12.3
	F	112.5	100.0–125.0		
	L	97.9	79.4–113.8		
Inflorescence length (mm)	A	29.6 mm	25.1–33.9	−0.49	19.3
	F	39.6	32.0–47.5		
	L	29.7	26.3–34.6		
Number of spikes per inflorescence	A	4.7	4.0–5.5	−0.41 **	10.2
	F	5.7	5.0–6.0		
	L	5.7	5.0–6.1		
Spike length: male portion (mm)	A	3.4 mm	2.5–3.9	−0.70	39.3
	F	4.4	3.0–6.1		
	L	1.6	1.0–2.0		
Spike length: female portion (mm)	A	6.2 mm	5.8–6.9	0.51	19.8
	F	6.2	5.9–7.0		
	L	7.8	7.2–8.6		
Perigynium body length (mm)	A	2.2 mm	2.1–2.4	0.70	30.5
	F	2.1	1.9–2.2		
	L	2.6	2.3–2.8		
Perigynium width (mm)	A	2.1 mm	1.9–2.3	0.47	15.7
	F	1.9	1.7–2.0		
	L	2.2	2.0–2.3		
Perigynium length from base to widest point (mm)	A	1.5 mm	1.3–1.6	0.84	85.2
	F	1.1	1.0–1.2		
	L	1.7	1.6–1.9		

Table 2. Continued.

Character		Mean	Interquartile Range	Eigen-value	F-Ratio
Midbeak width (mm)	A	0.31 mm	0.25–0.35	0.77	137.7
	F	0.32	0.30–0.35		
	L	0.56	0.50–0.60		
Number of ventral nerves	A	4.7	4.0–5.0	0.52	24.9
	F	2.9	2.0–4.0		
	L	4.9	4.0–6.0		
Achene length/width ratio [length excludes style base]	A	1.67	1.59–1.76	0.62	35.3
	F	1.40	1.28–1.50		
	L	1.71	1.55–1.87		
Achene width (mm)	A	0.90 mm	0.85–0.95	−0.53	40.1
	F	1.03	1.00–1.10		
	L	0.90	0.85–0.96		
Style: amplitude of lateral sinuosity (mm)	A	0.23 mm	0.17–0.25	0.80	201.5
	F	0.03	0.00–0.05	**	
	L	0.02	0.00–0.05		

beaks of *Carex longii* are wide ($\bar{x}$ = .56 mm) compared to those of *C. albolutescens* and *C. festucacea* ($\bar{x}$ = .31 and .32). A second character with a high F-ratio of 85.2 was perigynium length from base to widest point. *Carex festucacea,* with its oval rather than obovate body, had the smallest length ($\bar{x}$ = 1.1 mm). Other vegetative and inflorescence characters with significant F-ratios are detailed below.

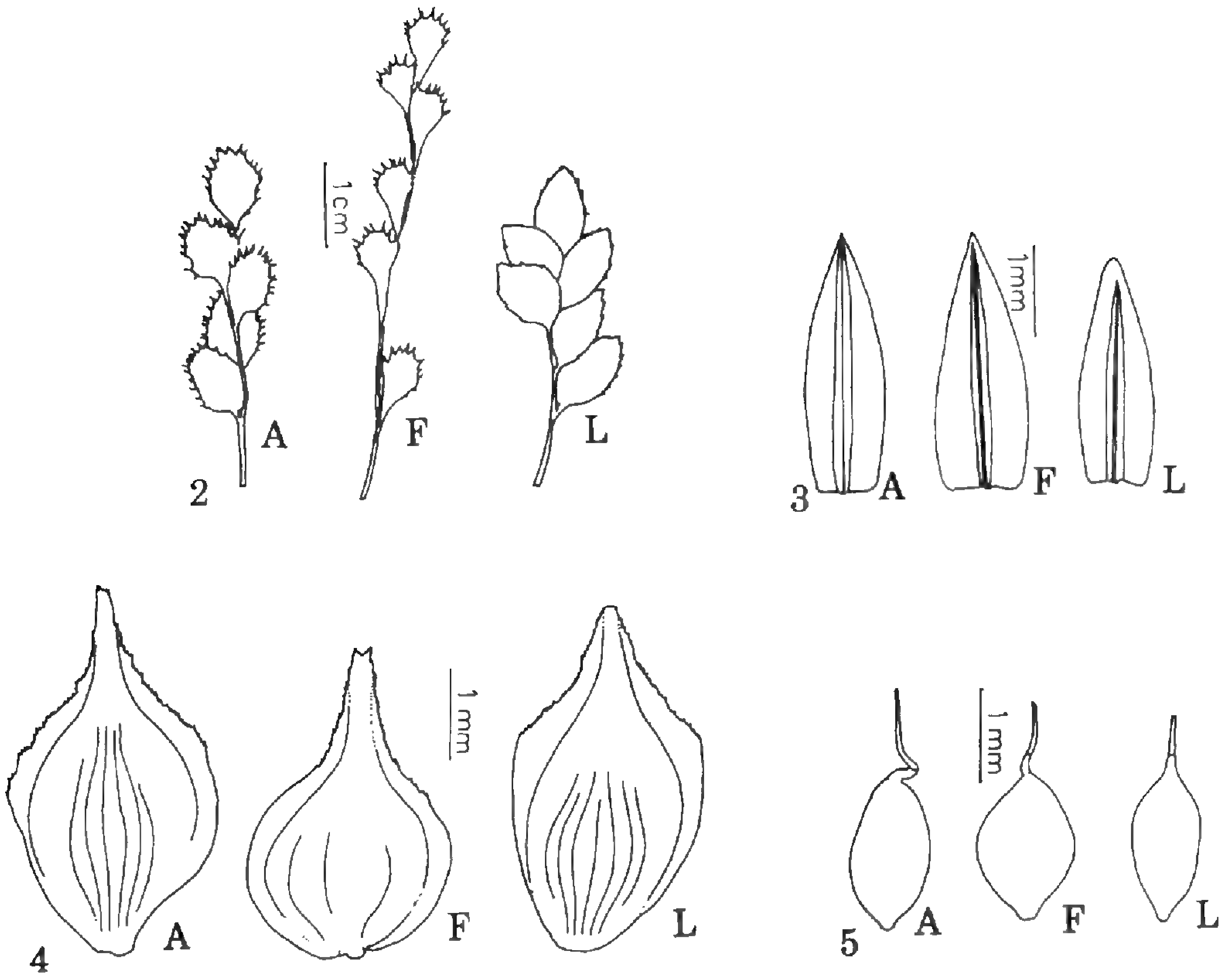
LEAVES AND CULMS. All three species have a similar caespitose habit and similar range of leaf widths. *Carex festucacea* has the shortest leaf sheath relative to the length of mature culms (Table 2); *C. festucacea* has a mean ratio of only .30, compared to .36 for *C. albolutescens* and .40 for *C. longii.* In evaluating this character, only fully mature culms can be used since culms continue to increase in length during fruit ripening.

Mackenzie (1931) maintained that the ventral hyaline band of the leaf sheath of *Carex festucacea* can be a useful diagnostic character. If indeed this character is diagnostic, it is difficult to interpret. In most specimens of *C. festucacea,* a thin hyaline area with fine veins occurs ventrally near the mouth of the sheath and usually becomes indistinct several mm below that region. Some leaf sheaths of *C. albolutescens* and *C. longii* may have identical hyaline areas, while other leaf sheaths of these species maintain strong venation to near the mouth of the sheath and have a distinct boundary between hyaline and non-hyaline areas.

Both Mackenzie (1931) and Fernald (1950) described some difference in culm stiffness. In attempting to quantify this difference, midculm diameter, wall thickness, and the cross sectional thickness of fiber bundles were assessed. Midculm thickness and thickness of the wall had only slight if any statistical difference in the three species. The radial thickness of fiber bundles did vary strongly between taxa (F = 17.4, Table 2). *Carex albolutescens* had the least fiber development with a mean of 40.2 μm as compared with means of greater than 54 μm for both *C. longii* and *C. festucacea.* In addition to the differing degrees of fiber development, culm cross-sections revealed a size differential in epidermal cells lying adjacent to fiber bundles; of the three species, *C. longii* had the largest cells with an average anticlinal length of 7.5 μm and periclinal length of 12.2 μm. *Carex albolutescens* had much smaller epidermal cell lacunae ($\bar{x}$ = 4.7 × 9.0 μm), while *C. festucacea* was intermediate ($\bar{x}$ = 5.4 × 10.5 μm).

INFLORESCENCE AND SPIKE. As shown in Table 2, inflorescence length differs significantly among the three species (F = 19.3); inflorescences of *Carex festucacea* are longest, typically greater than 3.0 cm. In addition to this greater inflorescence length, spikes of this species frequently have long tapered bases bearing numerous male flowers and rounded apices formed by spreading perigynium beaks (Table 3, Figure 2). In contrast, inflorescences of *C. albolutescens* seldom reach more than 3.0 cm in length. Their spikes have acute to sometimes long tapering bases and are rounded apically. For this reason they may be easily confused with those of *C. festucacea.* The inflorescences of *C. longii* occasionally reach the length of 3.5 cm or more, within the range of variation present in *C. festucacea.* The congestion and shape of spikes of *C. longii* are singular. *Carex longii* spikes exhibit rounded bases and, most importantly, seldom have spreading perigynium beaks. As a result of the ascending, appressed beaks, the spikes frequently have an acute to obtuse apex (Figure 2).

Pistillate scale apices of *Carex longii* (Figure 4) are bluntish in contrast to the sharply acute apices of *C. albolutescens* (Voss, 1972). A survey of a large number of specimens showed this observation to be constant. Its application may at times be limited



Figures 2–5. **2.** Inflorescences, **3.** Perigynia, **4.** Pistillate scales, and **5.** Achenes of *C. albolutescens* (A), *C. festucacea* (F), and *C. longii* (L).

by having frayed or curled scales or by failure to recognize that scales near the spike apex tend to be more acute. The pistillate scales of *C. albolutescens* and *C. festucacea* are similar in size, shape, and apex. Their acute tips are flat, rather than convex as in *C. longii,* with the midrib usually reaching to the very tip of the scale.

PERIGYNIA. Perigynia possess a number of traits of diagnostic value. The perigynium body length of *Carex festucacea* perigynia tends to be the shortest of the three species, typically 1.9–2.2 mm (Table 2). The body length in *C. albolutescens* and *C. longii* is seldom below 2.1 mm. In addition to size differences, *C. festucacea* perigynia have more oval to orbicular bodies (Figure 3). The widest point is ca. 1.1 mm from the base in contrast to 1.5 mm for *C. albolutescens* and 1.7 mm for *C. longii.*

Fernald (1950) described the beak of *Carex longii* as broad, triangular and gradually tapering into the body (Figure 3). Beaks of *C. albolutescens* and *C. festucacea* tend to be narrower (mean midbeak width ca. .3 mm) and arise more abruptly from the body.

Table 3. Qualitative characters distinguishing *C. albolutescens* (A), *C. festucacea* (F), and *C. longii* (L).

Character		Description
Spike arrangement	A	approximate, not congested
	F	separated
	L	frequently congested
Lateral spike base	A	acute or tapered; sometimes rounded
	F	acute to long tapered
	L	rounded; sometimes acute
Spike apex	A	rounded, beaks spreading
	F	rounded, beaks spreading
	L	obtuse to acute, beaks appressed-ascending
Pistillate scale	A	flat, apex acute, midrib to tip
	F	flat, apex acute, midrib usually to tip
	L	usually convex with flat margins, apex obtuse, midrib ending short of tip
Perigynial body [includes winged margin]	A	obovate
	F	orbicular to oval
	L	obovate
Mature perigynium color	A	straw colored
	F	straw colored
	L	brown
Perigynial beak	A	narrow, wing ending 0.2–0.4 mm below apex
	F	narrow, wing ending 0.2–0.4 mm below apex
	L	broad, ± winged to apex
Style	A	strongly sinuous laterally
	F	straight or bent dorsiventrally
	L	straight

The wing margins of these beaks end approximately .2 mm short of the beak apex. Quantification of these characters confirmed that they are highly significant statistically (Table 2). Although differences in beak shape hold throughout the range of these species, a noteworthy geographical variation occurs in inland populations of *C. longii,* which frequently have smaller perigynia and correspondingly narrower beaks.

Other perigynium characters are also helpful in species distinction. In *Carex longii,* the perigynia can take on a dull brown color as they mature, while those of the other two species mature into a bronze-tinged straw color. Finally, the perigynia of *C. festucacea* seem to have a textural difference in that they tend to be more coriaceous and on average have 3 or fewer strong ventral

Figure 6. Distribution of *C. albolutescens* (A), *C. festucacea* (F), and *C. longii* (L) in eastern United States and Canada.

nerves. *Carex albolutescens* and *C. longii* generally have 4 to 7 distinctly raised ventral nerves.

ACHENE AND STYLE. Morphology of the achene and style has apparently not been previously studied in these three species. Achenes of *C. festucacea* are significantly wider (F = 40.1, Table 2), with an interquartile range of 1.00–1.10 mm. Achenes of *C. albolutescens* and *C. longii* seldom reach more than .95 mm in width and exhibit an oblong shape compared to more ovoid achenes of *C. festucacea* (Table 2).

Variation in style form is even more striking. Styles observed in *Carex albolutescens* show a strong lateral deflection or sinuosity of ca. .2 mm (Table 2, Figure 5) rather than the straight form in *C. longii*. *Carex festucacea* styles vary from straight to dorsiventrally bent at the base. None have the degree of sinuosity typical of *C. albolutescens* as evidenced by the high F-ratio of 201.5 for this character (Table 2).

DISTRIBUTION AND HABITAT. According to herbarium records, all three *Carex* species broadly overlap in their ranges and habitat requirements. *Carex albolutescens* has its greatest frequency in moist, acidic woodland soils of the Piedmont, especially in the Carolinas (Figure 6). It also occurs sporadically inland as far west as Lake Michigan and into parts of the Mississippi Valley. *Carex longii* (Figure 6) is the most common and widespread of these species, thriving in seasonally wet, sandy soils of the Coastal Plain from Texas north to Massachusetts and southern Nova Scotia. Sporadic inland stations are known as far west as Illinois and Arkansas. It also is reported from mountainous areas of Mexico, Central America, and western South America as well as from

Bermuda and Haiti. Recently it has been introduced into Hawaii. In North America, *C. longii* seems to favor less shaded habitats than either *C. albolutescens* or *C. festucacea. Carex festucacea* (Figure 6) is most frequently found from eastern Pennsylvania to western Missouri, with its range extending into southern Ontario and as far south as the Gulf states. It prefers moist, open woods or brush and soils with less sand content than typical for *C. albolutescens* and *C. longii.*

KEY TO THE SPECIES

1. Perigynium bodies oval or orbicular, often with 3 or fewer nerves ventrally; mature achenes 1.0 mm or more wide and styles straight or bent dorsiventrally; inflorescences usually greater than 3.0 cm long, spikes separated and long tapered at base . . . . *C. festucacea*
1. Perigynium bodies obovate, typically with 4 to 7 ventral nerves; mature achenes less than .95 mm wide and styles straight or with strong lateral sinuosity; inflorescences usually less than 3.0 cm long, spikes of longer inflorescences congested and rounded at base 2
    2. Beaks of perigynia broad (midbeak width ca. .5 mm), appressed-ascending, winged margins extending to apex of beak; pistillate scales with obtuse apex, convex, midrib ending short of tip; styles straight . . . . *C. longii*
    2. Beaks of perigynia slender (midbeak width usually < .35 mm), spreading, winged margins ending ca. .2 mm below apex of beak; pistillate scales with acute apex, flat, midrib reaching to tip; styles laterally sinuous . . . . *C. albolutescens*

SPECIES DESCRIPTIONS

1. **Carex albolutescens** Schweinitz, Ann. Lyceum Nat. Hist. N.Y. 1:66. 1824. TYPE: Salem and Bethl. [N.C. and Pa.]. "Nobis junior lagopod." Ex herbarium Schweinitz (HOLOTYPE: PH!).

Culms caespitose. Fertile culms 2.5–12 dm tall; culm bases pale to brownish-black, 1.0–2.5 mm thick; aphyllopodic. Longest leaf sheaths ¼ to about ½ as long as mature culms. Ligules prolonged, often somewhat loose. Leaves 3–5 to a fertile culm; broadest leaves 2–3.5 mm wide; upper blades 5–25 cm long. Inflorescences

1.5–4.0 cm (rarely longer) and composed of 2–8, usually approximate, gynaecandrous spikes with spreading beaks. Lowest bracts scale-like to setaceous. Spikes 5–13 × 4–6.5 mm, rounded at apex, acute to tapered at base. Pistillate scales shorter and narrower than perigynia, flat with acute apex. Perigynia papery, green to straw colored at maturity, 2.6–4.5 × 1.5–2.7 mm, the body obovate with 4–7 raised nerves on ventral face and many nerves on dorsal face. Perigynium beaks ⅓ to ¾ as long as body, abruptly tapered from body, narrow with wing ending below apex. Body of achenes 1.3–1.7 mm long and .75–1 mm wide, oblong. Styles strongly bent or sinuous laterally.

As demonstrated by Svenson (1938), the name *Carex straminea* was erroneously applied to this species by Mackenzie (1922, 1931). Gleason (1952) and Radford et al. (1964) treated this taxon as conspecific with *C. festucacea.*

2. **Carex festucacea** Schkuhr *ex* Willdenow, Sp. Pl. 4: 242. 1805. TYPE: Habitat in America boreali.

Culms caespitose. Fertile culms 4.5–10 dm tall; culm bases brownish-black, 1.5–2.5 mm thick, aphyllopodic. Longest leaf sheaths ⅙ to ⅖ as long as mature culm. Ligules prolonged and generally tight. Leaves 3–5 to a fertile culm; broadest leaves 1–5 mm wide; upper blades 5–30 cm long. Inflorescences 2.5–6 cm long and composed of 3–10 usually separated, gynaecandrous spikes with spreading beaks. Lowest bracts scale-like to setaceous. Spikes 6–16 × 5–6.5 mm, rounded at apex, acute to long tapered at base. Pistillate scales shorter and narrower than perigynia, flat with acute to acuminate apex. Perigynia subcoriaceous, green to straw colored at maturity, 2.5–3.5 × 1.5–2.2 mm, the body orbicular to oval with 2–4 usually short and inconspicuous nerves on the ventral face and many nerves on dorsal face. Perigynium beaks ⅓ to ¾ as long as body, abruptly tapered from body, narrow with wing ending below apex. Body of achenes 1–1.6 mm long and .95–1.25 mm wide, ovoid. Styles straight or somewhat bent dorsiventrally.

3. **Carex longii** Mackenzie, Bull. Torrey Bot. Club 49: 372–373. 1923. TYPE: Cold Spring, Cape May County, New Jersey, 24 July 1907. B. Long *s.n.* (HOLOTYPE: PH!).

Culms caespitose. Fertile culms (2) 3–12 dm tall; culm bases pale to brownish-black, 1.2–3.0 mm thick, aphyllopodic. Longest leaf sheaths ⅓ to ½ as long as mature culms. Ligules prolonged, often somewhat loose. Leaves 2–4 to a fertile culm; broadest leaves 2–4 mm wide; upper blades 5–25 cm long. Inflorescences 1–4.5 cm long and composed of 3–10 usually aggregated, gynaecandrous spikes with appressed-ascending beaks. Lowest bracts scale-like to setaceous. Spikes 6–13 × 3.8–7 mm, obtuse to broadly acute at apex, rounded at base. Pistillate scales shorter and narrower than perigynia, often convex, obtuse or occasionally acute at apex with midrib ending below apex. Perigynia papery, green to drab brown at maturity, 3–4.5 × 1.6–2.6 mm, the body obovate with 4–7 raised nerves on ventral face and many nerves on dorsal face. Perigynium beaks ⅓ to ½ as long as body, gradually tapered from body, the wing reaching to apex. Body of achenes 1.3–1.7 mm long and .75–1 mm wide, oblong. Styles straight.

This species is referred to as *Carex albolutescens* by Gleason (1952), Radford et al. (1964), and Seymour (1969).

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My thanks are given to herbarium curators for loan and use of collections under their care. Special gratitude is extended to C. S. Keener and A. A. Reznicek for their help and encouragement. Partial support for this work was received from the Taylor University Fund for Faculty Scholarship.

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APPENDIX

Representative specimens

Carex albolutescens

Alabama: Hale Co., Payne Lake Rec. Area, 30 April 1987, *Bryson 5579* (MICH). **Arkansas**: Hot Springs Co., Magnet Cove, 2 May 1937, *Demaree 14811* (MO). **Georgia**: Murray Co., floodplain of Conasauga River, 9 May 1969, *Bowers & Morton 43525* (NY, TENN). **Indiana**: Jackson Co., 5 mi. W of Freetown, 5 June 1940, *Deam 59606* (CU, IND). **Kentucky**: Bath Co., Olympian Springs, 9 June 1938, *Wharton 2524* (GH, MICH). **Louisiana**: East Baton Rouge Parish, Comite River, 22 April 1928, *Brown 1922* (MICH). **Maryland**: Prince Georges Co., Beltsville, 13 June 1943, *Hermann 10859* (NY). **Massachusetts**: Bristol Co., Dighton, 29 June 1961, *Seymour 19292* (MO). **Mississippi**: Itawamba Co., .8 mi. NE of Kirkville, 27 May 1986, *Bryson 4404* (MICH). **North Carolina**: Granville Co., 1.4 mi. E of Creedmoor, 16 June 1961, *Radford 43925* (NCU); Hertford Co., NE of Como, 30 May 1958, *Ahles & Duke 41661* (NCU, GA). **New Jersey**: Camden Co., Pensauken, 15 June 1918, *Long 19103* (GH). **New York**: Suffolk Co., Greenport, Long Island, 20 June 1916, *Chase 7389* (CU). **Ohio**: Columbiana Co., Tritton Marsh, Center Twp., 12 July 1989, *Bissell et al. 1989:197* (MICH). **Pennsylvania**: Chester Co., S of Nottingham, 22 June 1912, *Pennell 3752* (PAC). **South Carolina**: Clarendon Co., 2½ mi. SSW of Summerton, 20 April 1957, *Radford 21233* (NCU). **Tennessee**: Coffee Co., Tullahoma, 2 June 1938, *Svenson 8720* (BH, TENN); Franklin Co., Huntland, 29 May 1954, *Svenson 13090* (GH, TENN). **Texas**: Wood Co., E of Quitman, 12 May 1989, *S. & G. Jones & Powell 2778* (MICH). **Virginia**: Stafford Co., 3½ mi. E of Falmouth, 8 June 1940, *Hermann 10558* (CU, NY). **West Virginia**: Greenbrier Co., SW of Crawley, 12 July 1983, *Brant 291* (SIU, VPI).

Carex festucacea

Ontario: Essex Co., 7 km WSW of Kingsville, 19 June 1983, *Reznicek et al. 7171* (MICH). **Connecticut**: Fairfield Co., Norwalk, 19 June & 1 July 1941, *Eames 12066* (BH, IND, NCU). **Georgia**: Ben Hill Co., 16.3 mi. ENE of Fitzgerald, 27 April 1968, *Faircloth 5098* (GA, NCU). **Illinois**: Jackson Co., 2 mi. N of DeSoto, 20 May 1960, *Mohlenbrock & Dillard s.n.* (SIU); Randolph Co., Rock Castle Creek, 26 May 1970, *Evans 1057* (SIU); St. Clair Co., wet places, 31 May 1893, *Eggert s.n.* (BH, MO). **Indiana**: Knox Co., 2¾ mi. N of Bicknell, 7 June 1912, *Deam 10060* (IND); Laporte Co., 2 mi. S of South Wanatah, 29 May 1927, *Deam 44352* (IND). **Kansas**: Cowley Co., 7 mi. W of Winfield, 11 August 1966, *Koch 1837* (NCU).

Massachusetts: Hampshire Co., Hadley, 12 June 1980, *Ahles 87995c* (BH). **Mississippi**: Clay Co., 10 mi. SE of West Point, 16 May 1982, *Bryson 3292* (VPI). **Missouri**: Lincoln Co., T49N R2E S½ sec. 2, 1 June 1985, *Brant et al. 598* (MO). **New York**: Tompkins Co., Cayuga Heights, 9 June 1918, *Wiegand 9438* (MO). **North Carolina**: Orange Co., vic. of Chapel Hill, *Ashe s.n.* (CU, NCU). **Pennsylvania**: Berks Co., 1⅔ mi. E of Bernville, 24 May 1959, *Berkheimer 19125* (VPI); Centre Co., Ingleby, 30 May 1938, *Wahl 82* (NCU, PAC). **Tennessee**: Montgomery Co., 5 mi. SW of Clarksville, 7 May 1950, *Brown & Clebsch s.n.* (NCU). **Texas**: Franklin Co., .3 mi. S on Hwy. 115 from its jcn. w/ FM 3122, 12 May 1989, *S. & G. Jones & Powell 2800* (MICH). **Virginia**: Lunenberg Co., 12 mi. SE of Lunenburg, 3 June 1986, *Wieboldt 5992* (VPI); Sussex Co., 4½ mi. N of Sussex, 4 June 1986, *Wieboldt 6024* (VPI).

Carex longii

Arkansas: Saline Co., Benton, 16 May 1942, *Demaree 22969* (MO, NY). **Delaware**: Sussex Co., Rehoboth, 19 June 1926, *True 73* (GA). **Florida**: Lake Co., vic. of Eustis, 1–15 June 1894, *Nash s.n.* (CU, GH, MICH); Leon Co., betw. Tallahassee & Lake Bradford, 31 May 1955, *Godfrey 53340* (NY, NCU). **Georgia**: Chatham Co., SW of Savannah, 31 March 1929, *Miller & Maguire 271* (BH); Dougherty Co., 4 mi. S of Albany, 28 June 1947, *Thorne 4999* (CU, GH, GA); Glynn Co., S end of Jekyll Island, 3 September 1948, *Thorne & Muenscher 8873* (CU, GA). **Indiana**: Jasper Co., 2½ mi. SE of Tefft, 5 July 1937, *Deam 57961* (IND, MICH). **Louisiana**: Washington Parish, Sheridan, 13 May 1972, *Rogers 8045* (NCU). **Massachusetts**: Barnstable Co., Harwich, 20 July 1918, *Fernald s.n.* (CU, GH, IND, MICH, NCU, GA, TENN). **Michigan**: Kalamazoo Co., 2 mi. NW of Vicksburg, 9 July 1937, *Hermann 9007* (CU, MICH, NY). **Mississippi**: Harrison Co., Biloxi, 28 April 1898, *Tracy s.n.* (MICH, MO, NY); Lamar Co., Purvis, 17 May 1972, *Rogers 8106* (NCU, TENN). **New Jersey**: Middlesex Co., South Amboy, 8 July 1906, *Mackenzie 2171* (IND). **New York**: Nassau Co., NE of Hempstead, 23 June 1908, *Harper s.n.* (GH, NY). **North Carolina**: Pamlico Co., Janeiro, 5 July 1958, *Radford 36003* (NCU); Washington Co., 3 mi. E of Hoke, 15 June 1958, *Radford 35068* (GH). **Pennsylvania**: Lackawanna Co., E of Old Forge, 28 June 1946, *Glowenke 6906* (PAC). **Rhode Island**: Bristol Co., Bristol, 11 August 1961, *Seymour 19459* (MO); Washington Co., Westerly, 11 July 1913, *Woodward s.n.* (GH, PAC). **South Carolina**: Colleton Co., 8 mi. SE of Walterboro, 18 July 1927, *Wiegand & Manning 409* (CU, GH). **Texas**: Houston Co., 5 mi. W of Crockett, 26 May 1959, *Correll et al. 22366* (NY). **Virginia**: City of Virginia Beach, Sandbridge, 22 June 1971, *Uttal 8146* (VPI); Lancaster Co., 3 mi. W of Westland, 9 June 1940, *Hermann 10579* (CU, NY).

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TAXONOMY OF *PRIMULA* SECTS. *ALEURITIA* AND *ARMERINA* IN NORTH AMERICA

SYLVIA KELSO

ABSTRACT

In North America the genus *Primula* has several representatives in section *Aleuritia* Duby and section *Armerina* Lindley. These sections were originally treated as related subsections in the large section *Farinosae* Pax. Their members have been the subject of much misinterpretation, particularly in arctic and boreal North America where few collections and no modern systematic treatment existed. North American members of these two sections are reviewed here with particular attention to the arctic and boreal taxa. Section *Aleuritia* ($x = 9$) is represented by 4 diploid species: *P. alcalina, P. anvilensis, P. mistassinica,* and *P. specuicola,* and 4 polyploid species: *P. borealis* ($4x$), *P. incana* ($6x$), *P. laurentiana* ($8x$), and *P. stricta* ($14x$). Section *Armerina* ($x = 11$) is represented by a diploid species, *P. nutans* (formerly *P. sibirica*), and a tetraploid species, *P. egaliksensis.*

Key Words: Primulaceae, *Primula* sect. *Aleuritia, Primula* sect. *Armerina, Primula* sect. *Farinosae,* taxonomy, phytogeography, Arctic, North America

INTRODUCTION

The large genus *Primula* L. (Primulaceae) is widely distributed throughout the northern latitudes of Eurasia and North America. Of ca. 500 species now recognized, the majority are found in the mountains of Asia. In North America, there are approximately twenty-five species representing five sections of the genus. Of these, members of sect. *Armerina* Lindley and sect. *Aleuritia* Duby have been especially subject to taxonomic confusion due to their morphological and ecological similarity, and to their distribution in remote northern areas where field studies have been limited or nonexistent.

This paper provides a comprehensive taxonomic treatment of sections *Aleuritia* and *Armerina* in North America with special attention given to poorly understood arctic and boreal taxa. It is appropriate to discuss these sections together for several reasons. They were initially treated (Bruun, 1932; Smith and Fletcher, 1943) as closely related subsections in a section then called *Farinosae* Pax. Many of the taxa superficially resemble one another and some grow sympatrically. Analyses by Wendelbo (1961) and Schwarz (1968) have showed some fundamental differences between these sections in Eurasia, but until now the North American taxa have not been examined. This study supports recognition of two distinct sections on the basis of cytology, anatomy, and morphology. There are eight members of section *Aleuritia* in North America (*Primula alcalina* Cholewa & Henderson, *P. anvilensis* Kelso, *P. borealis* Duby, *P. incana* M. E. Jones, *P. laurentiana* Fernald, *P. mistassinica* Michaux, *P. specuicola* Fernald, and *P. stricta* Hornemann) and two members of section *Armerina* (*P. egaliksensis* Wormskjold and *P. nutans* Georgi, formerly *P. sibirica* Jacq.).

TAXONOMIC HISTORY

Monographic treatments of *Primula* were done by Lehmann (1817), Duby (1844), Pax (1889, 1890), Pax and Knuth (1905), and Smith and Fletcher (1943). Although the work of Smith and Fletcher was based on morphological interpretations of taxa and limited material of some species, it stands as the most comprehensive taxonomic treatment of the genus to date.

Infrageneric arrangement of *Primula* by Duby (1844) was based on gross morphology without regard to the more phylogenetically relevant characters in cytology, anatomy, or chemistry seen as essential in contemporary systematics. This arrangement was revised by Balfour (1913), Bruun (1932), Smith and Forrest (1928), and Wendelbo (1961), with additional modification by Schwarz (1968).

No comprehensive examination of the North American primulas has been carried out to date. Fernald (1928) revised section *Farinosae* and Williams (1936) provided a brief overview of the genus in western North America. Since these papers were published, several new taxa have been described, the descriptions of others have been modified, and considerably more has been learned about the ecology and biogeography of the genus in North America.

MATERIALS AND METHODS

Field studies were carried out in Alaska at numerous locations from the Seward Peninsula, the Alaska Range around Denali National Park, along the Tanana River in Fairbanks, the Delta River near Donnelly Creek, and the Northway region along the upper Tanana River. In the Yukon, populations were studied along the Donjek River, the confluence of the White and Koidern Rivers, and from Kluane Lake. In addition, live material from various arctic regions was cultivated in gardens in Fairbanks.

Morphological characteristics of approximately 1300 herbarium specimens from ALA, ALTA, BM, BRY, CAN, CAS, COLO, DAO, E, GH, ID, ISC, K, NDG, NY, PH, RS, S, T, UBC, UPS, US, UTC, and WTU were examined. These specimens represented *Primula* taxa over their entire range.

Chromosome numbers reported here are original counts or are referenced as literature reports. Methodology for the cytological and anatomical analysis and complete lists of specimens examined are given in Kelso (Ph.D. dissertation, Univ. of Alaska, Fairbanks, 1987).

TAXONOMIC CHARACTERS IN *PRIMULA*

Although large and geographically widespread, *Primula* is not a morphologically diverse genus. Species of *Primula,* and likewise genera in the Primulaceae, are often distinguished by a combination of characters rather than by a single attribute. These diagnostic attributes can change with ontogeny. For example, height of the scape can increase six-fold during blooming, farina that is dense on young leaves almost disappears on individuals in fruit, arching pedicels at anthesis stiffen and become erect as capsules ripen. Furthermore, individuals are often phenotypically plastic in their vegetative and reproductive responses to environmental conditions. However, while it is necessary in northern species of *Primula* to allow for generous morphological amplitude according to the effects of phenology and environment, all taxa discussed here show a coherent and identifiable phenotype.

It is critical to recognize the importance of reproductive biology in the taxonomy, ecology, and evolution of *Primula.* While *Primula* has long been known for its high incidence of distyly (Darwin, 1889), and a considerable amount is known about the genetic basis for this complex reproductive, morphological, and biochemical system (see, among others, Ganders, 1979; Charlesworth and Charlesworth, 1979; Richards, 1986), little attention has been paid to distyly and homostyly as taxonomic characters or to their evolutionary significance in related species. Due to the strong intramorph incompatibility reaction, distylous individuals are virtually obligate outcrossers, while homostylous individuals are self-fertile and probably highly autogamous due to the proximity of the reproductive organs.

In the two sections treated here, there are both distylous and homostylous taxa. Distyly and homostyly are reliable taxonomic markers: in several thousand individuals examined during this study, taxa were either completely distylous or completely homostylous. Contrary to the misconception that arctic plants must have facultative selfing capacity to cope with a short growing season, several arctic species of *Primula* are distylous with concomitant obligate outcrossing. Other arctic primulas, often widespread polyploids, are homostylous and self-fertile.

To some extent, homostyly and polyploidy are linked in *Primula*. Diploid species tend to be distylous, tetraploids can be distylous or homostylous, and higher polyploids are all homostylous. *Primula* section *Aleuritia,* with a base number of $x = 9$, contains taxa ranging from $2x$ to $14x$. Although chromosome reports in the literature suggest that some species have several chromosome races, almost all cases can be shown to be the result of faulty determination of the taxa examined. Section *Armerina* ($x = 11$) contains a distylous diploid species and a homostylous tetraploid one. Chromosome number is thus a very strong taxonomic character in at least these two sections of *Primula,* both on an intersectional and an interspecific basis.

The chemical nature of the powdery exudate known as "farina" that is common in some species of *Primula* has been of interest to a number of authors (Blasdale, 1945, 1947; Harborne, 1968; Wollenweber, 1974; Sellmair et al., 1977). While all species appear to have at least a few relictually farinipotent glands, glandular development is most pronounced on species with abundant farina. The farina is composed primarily of flavones of varying chemical composition (Harborne, 1971), but it is not clear that the chemical composition has systematic significance or whether farina composition remains constant throughout a species, throughout a population, or throughout a growing season. The common occurrence of efarinose individuals or populations in normally farinose species, and the dramatic drop in farina production on farinose individuals toward the end of the growing season indicates that it is unwise to rely heavily on this character.

At the anatomical level, sections and sometimes species, can be distinguished by the glands and pollen grains. All species of *Primula* have either articulated hairs or glands on at least some of their vegetative parts. Members of section *Aleuritia,* where farina is common, have glands with a large apical cell and one to three smaller basal cells, while members of section *Armerina,* all of which are efarinose, have articulated hairs. *Primula egaliksensis,* although efarinose, also contains a few glands similar to those in section *Aleuritia.* While pollen grains have been used as taxonomic and phylogenetic markers at the generic level in the Primulaceae (Wendelbo, 1961; Nowicke and Skvarla, 1977), until now little attention has been given to a comparative study of pollen morphology at the subgeneric level, or to the effects of polyploidy on that morphology.

Exine ornamentation can be diagnostic at the sectional level for North American primulas. The number of colpi per pollen grain correlates with polyploidy and can thus be a useful character at the species level. Members of section *Aleuritia,* for example, have microreticulate exine, with diploids and tetraploids having tricolpate grains. Both the hexaploid *Primula incana* and the octoploid *P. laurentiana* have 4-colpate grains, and the decatetraploid *P. stricta* has 5-colpate grains. In section *Armerina, P. nutans* shows the broadly reticulate exine and 6-stephanocolpate pollen that is typical of Eurasiatic members (Nasir, 1987).

The most useful characters for identifying species in sections *Armerina* and *Aleuritia* are certain aspects of floral and vegetative morphology. The following features are important:

1. LEAF SHAPE. Members of section *Armerina* are strongly petiolate, with a thin, efarinose, oval or elliptical blade with entire margins. Members of section *Aleuritia* have spathulate leaves that are often farinose and denticulate on the upper margins. Because most primulas bloom early, their leaves are not fully expanded at anthesis. Enlargement occurs over the growing season, and by the time capsules are ripe, leaves may be up to four times their size at early anthesis. In addition, vegetative growth in *Primula* is responsive to nutrient availability, and luxuriant forms can be seen in protected or nutrient-rich areas such as in sites with resident bird populations. These forms are particularly dramatic in normally dwarf tundra species, and led to some of the early taxonomic confusion when authors described taxa based on few specimens and no field experience.

2. Bracts. All species of *Primula* have several involucral bracts subtending the umbel. The shape at the tip (involute or flat), the shape at the base (flat or saccate), and the presence or absence of auricles of these bracts can be useful at both the sectional and the specific level.

3. Height. Scape height is most reliable as a taxonomic marker when measured at full (when most of the flowers in the umbel are in bloom) or late anthesis. Several arctic species begin blooming early when plants are virtually ascapose. Elongation of the scape continues throughout anthesis until the capsules are ripe, and the fruiting plant can be several times as tall as the plant in first bloom. The increase is most noticeable in the taller species like *P. incana* or *P. laurentiana* which are frequently misidentified as their shorter relatives *P. stricta* and *P. mistassinica,* respectively.

4. Pedicels. As capsules ripen and elongation of the scape slows and eventually ceases, elongation and stiffening of the pedicels occurs. At anthesis, the length and posture of pedicels are both strong taxonomic markers at the species level. In fruit, however, the shape of the umbel is very different, and neither length nor posture of the pedicels is a reliable character for distinguishing between species.

5. Flower Number. The number of flowers per umbel of any individual plant is to a certain extent species specific, but it can also be influenced by length of the growing season. Individuals with multi-flowered umbels bloom asynchronously, and those plants that emerge early from snow cover have a longer season in which to develop flowers than those blooming later.

6. Calyx. Significant differences in the shape and degree to which the calyx is divided are diagnostic at the sectional level. In both sections examined here, the calyx bears lanceolate teeth. In sect. *Armerina,* it is cylindrical, ribless, and divided less than one quarter of its length. In comparison, members of section *Aleuritia* have a campanulate obscurely ribbed calyx that is divided one third to one half its length. Calyx size in *Primula* is generally

correlated with overall size of the individual plant and is not a useful character.

7. COROLLA. The length of the corolla tube relative to the calyx can be diagnostic at the species level. This is consistent during the period of anthesis; however, in all taxa the tube elongates rapidly between the bud stage and time of flower opening. Relative sizes can be measured accurately only when flowers are in full bloom.

Corolla size, as measured by width across the limb, can also be a useful character at the species level. To a certain extent, flower size is correlated with the breeding system: pollinator-dependent distylous species tend to have larger flowers than self-fertile homostyles.

Two species in section *Aleuritia* (*Primula alcalina* and *P. anvilensis*) have consistently white flowers. Other species in both sections *Aleuritia* and *Armerina* have lavender flowers, although *P. egaliksensis* has equally abundant white and lavender forms, and *P. mistassinica* has a white form common in Newfoundland. Flower color is deepest in young flowers, and gradually fades with maturity. Herbarium specimens can be deceptive since drying causes many lavender flowers to fade and appear white.

8. CAPSULES. Capsule shape follows sectional lines. Members of section *Aleuritia* have elliptical to broadly cylindrical capsules, while members of section *Armerina* have narrowly cylindrical capsules. With the exception of *Primula stricta* which has characteristic short capsules, it is difficult to distinguish the capsules of related species. Fruiting specimens of *Primula* are the most difficult to identify on the basis of morphology alone, and for these individuals, anatomical and/or ecological features may be helpful.

9. ECOLOGY. All North American species of *Primula* show a preference for cool, moist, open habitats disturbed by frost action, flooding, or downslope movement. Members of section *Aleuritia* show a strong affinity for alkaline soils. Among these, *P. borealis* is confined to salt marshes, *P. incana* to inland clay soils, and *P. specuicola* to canyon walls. Other members, particularly the widespread *P. mistassinica,* have less specific habitat requirements, and can be found on lake shores, along stream beds or roadsides,

or around hot springs. In section *Armerina, P. nutans* on the west coast of Alaska is restricted to salt marshes, but in the interior of the state and in the Yukon it is found in freshwater marshes.

EVOLUTIONARY HISTORY

SECT. *Aleuritia.* The polyploid complex in sect. *Aleuritia* can be explained by the secondary contact model described by Stebbins (1950, 1985). In this model, an initially widespread taxon is fragmented into disjunct populations by a catastrophic event such as climate change, but these gene pools do not differentiate enough for complete reproductive isolation. If the ecological or geological barriers are removed, taxa can come into secondary contact forming a complex pattern of allopolyploid hybrids. The success of these polyploids is promoted by the availability of new open habitats. I suggest this model may be applicable for sect. *Aleuritia* as follows:

Prior to the late Quaternary glaciation, a diploid similar to *Primula mistassinica* was widespread across North America in the boreal regions. At this time Alaska was isolated by the confluence of the Cordilleran and Laurentide ice, and a remnant of this diploid remained there in the Bering Strait region as *P. anvilensis* of today. South of the ice sheets, there was further fragmentation of the ancestral diploid. Vogelmann (Ph.D. dissertation, Univ. of Michigan, 1956) has suggested that *P. mistassinica* survived Pleistocene glaciation in separate refugia, including Newfoundland, the Appalachians, and the Midwest. It seems likely that the narrow endemics *P. alcalina* in Idaho and *P. specuicola* in the Southwest were completely isolated and adapted *in situ* to the local conditions as the climate became warmer and drier in postglacial times. In contrast, the eastern populations of *P. mistassinica* rejoined as they migrated north following glacial retreat, and now show only infraspecific variation as local races.

The concatenation of eastern populations provided the basis for a polyploid complex. The hexaploid *Primula incana* and the octoploid *P. laurentiana* can be seen as the result of hybridization between the partially differentiated diploid populations. As self-fertile homostyles, these polyploids were able to become established and spread rapidly into the deglaciated regions where they are found today.

In Europe there is a parallel situation with the diploid species *Primula farinosa* L., the hexaploid *P. scotica* Hook. and the octoploid *P. scandinavica* Bruun. Like *P. mistassinica, P. farinosa* probably survived glaciation in several refugia and these populations rejoined to form allopolyploids. The amphi-Atlantic species *P. stricta,* a 14-ploid, may be a hybrid between *P. scotica* and *P. scandinavica* as suggested by Knaben (1982), but the North American *P. incana* and *P. laurentiana* are equally probable progenitors. The contemporary distribution of *P. stricta* is not convincing evidence for postglacial migration in either direction. Its range is larger in North America than in Europe, but this may only be due to more suitable habitat in the Canadian Arctic Archipelago. The heritage of *P. stricta* remains an open question until further genetic evidence can be obtained.

The origin of the tetraploid *Primula borealis* of the Bering Sea coast is somewhat problematic as well. It has a close morphological affinity with the Japanese species *P. modesta* Bisset & Moore *s. lat.*, and on biogeographic grounds it is reasonable to suggest that *P. borealis* is a recent tetraploid derivative of the Asian *P. farinosa–P. modesta* complex rather than of the North American *P. mistassinica* line.

SECT. *Armerina.* On the basis of morphology, anatomy, and cytology, members of this primarily Asiatic section are distinguishable from those belonging to sect. *Aleuritia,* and recognition of these as phylogenetically separate is clearly justified. The wide distribution of *Primula nutans* across Eurasia suggests that it is an old taxon. Mäkinen and Mäkinen (1964) have described how Pleistocene isolation may have resulted in the Fennoscandian subspecies *finnmarchia,* which differs only in a short corolla tube. The scattered populations of *P. nutans* found in North America are probably Pleistocene survivors that persisted in unglaciated Alaska and the Yukon. If *P. nutans* once extended further east, it must have been extirpated there by the late glacial ice sheets.

Primula egaliksensis is a homostylous tetraploid with such a strong resemblance to *P. nutans* that Fernald (1928) and Smith and Fletcher (1943) assumed it was a derivative of that species without knowing the cytological status of the two. As for the polyploids in sect. *Aleuritia,* a change in the breeding system from distyly to homostyly brought self-fertility and the potential for colonizing recently deglaciated habitats. Today *P. egaliksensis* is widespread across North America from Alaska to Newfoundland in areas that were covered by ice until the late Pleistocene.

TAXONOMIC TREATMENT

KEY TO THE SECTIONS OF *PRIMULA* IN NORTH AMERICA

1. Leaves broadly dentate at the apex, capsules globose, seeds with flanged edges . . . . sect. *Cuneifolia*
1. Plants not as above 2
    2. Corolla lobes entire . . . . sect. *Crystallophlomis*
    2. Corolla lobes cleft or notched 3
        3. Flowers magenta pink, often glandular at base of corolla tube, leaves lanceolate to broadly spathulate, capsules broadly cylindrical, rarely ovate . . . . . . sect. *Parryi*
        3. Flowers lavender pink or white, eglandular, leaves spathulate to ovate, capsules elliptical or narrowly cylindrical 4
            4. Leaves distinctly petiolate, blades ovate or elliptical, plants efarinose, capsules narrowly cylindrical . . . . sect. *Armerina*
            4. Leaves indistinctly petiolate to spathulate, plants usually farinose, rarely efarinose, capsules elliptical to ovate . . . . sect. *Aleuritia*

Primula sect. **Aleuritia**

Primula sect. **Aleuritia** Duby, in DeCandolle, Prodromus 8: 41. 1844.—*pro parte.* Emend. Wendelbo, Aarbok Univ. Bergen, Mat.-Naturvitensk. Ser. 1961: 37. 1961. TYPE: *P. farinosa* L.

Section *Farinosae* Pax, Bot. Jahrb. Syst. 10: 194. 1889.—*pro parte.*

Plants usually farinose or with farinipotent glands, lacking rhizomes. Leaves with revolute vernation, blades decurrent, lanceolate to spathulate, glabrous. Inflorescence a simple umbel subtended by involucral bracts usually saccate or gibbous at base, rarely plane; pedicels usually erect, sometimes flexuous. Corolla lilac, pink, or white; lobes notched or cleft. Capsules elliptical to broadly ovate. Chromosome base number: $x = 9$.

KEY TO SECTION *ALEURITIA*

1. Flowers distylous 2
  2. Involucral bracts saccate or gibbous at base; plants of coastal salt marshes .... *P. borealis*
  2. Involucral bracts plane at base; plants not of coastal salt marshes 3
    3. Corolla limb always white 4
      4. Plants farinose; pedicels erect at anthesis, shorter than bracts .... *P. alcalina*
      4. Plants efarinose; pedicels arching at anthesis, longer than bracts .... *P. anvilensis*
    3. Corolla limb lavender, rarely white 5
      5. Leaves heavily white farinose .... *P. specuicola*
      5. Leaves yellow farinose or efarinose .... *P. mistassinica*
1. Plants homostylous 6
  6. Corolla limb 8–16 mm in diameter, leaf margins distinctly crenate .... *P. laurentiana*
  6. Corolla limb 4–8 mm in diameter, leaf margins entire to denticulate at apex only 7
    7. Leaves and calyces slightly farinose; capsules ovate, only slightly longer than the calyx .... *P. stricta*
    7. Leaves and calyces heavily farinose; capsules elliptical and strongly exserted from the calyx .... *P. incana*

Primula alcalina A. Cholewa & D. Henderson, Brittonia 36: 59–62. 1984. Figure 1A. TYPE: U.S.A. IDAHO. Lemhi Co., 10 mi. north of Blue Dome along Birch Creek, *Henderson and Cates 1372* (HOLOTYPE: ID; ISOTYPE: NY!).

Plants farinose only when young, efarinose in age. Scape 6.5–24 cm high. Leaves elliptic-oblanceolate, blade narrowing gradually onto winged petiole, 1–4 cm long, margins crenulate or denticulate, sometimes entire. Involucral bracts plane at base, .4–.7 cm long, lanceolate, apex obtuse or acute. Umbel 3–10 flowered, pedicels erect, to .5 cm long. Flowers distylous. Calyx campanulate, somewhat farinose, obscurely ribbed, .4–.6 cm long, green or with purple striations, lobed about one third its length, teeth with capitate glands. Corolla white, throat yellow; tube .4–.7 cm long; limb .6–1 cm wide, lobes deeply cordate. Stamens ca. 1.5 mm long, anthers located toward the middle of the corolla tube.

Pollen 3-syncolpate. Stigma capitate, in pin plants located in upper third of corolla tube, positions reciprocal in thrum plants. Capsules not seen.

CHROMOSOME NUMBER. $n = 9$ (Idaho: Cholewa and Henderson, 1984).

HABITAT. Wet alkaline meadows.

DISTRIBUTION. Endemic to Idaho west of the Lemhi Range.

Primula anvilensis S. Kelso, Sys. Bot. 12: 9–13. 1987. Figure 1B.
P. parvifolia sensu Fernald (non Duby), Rhodora 30: 93. 1928; Hultén, Fl. Alaska and Yukon, Acta Univ. Lund 4: 1273. 1948. TYPE: U.S.A. ALASKA. Nome area: Anvil Mt., *Kelso 83-136* (HOLOTYPE: ALA!; ISOTYPES: CAN!, COLO!, NY!).

Plants slender, efarinose. Scape 2–10 (12.5) cm tall. Leaves bright green, cuneate or spathulate, including the petioles .5–1 (2) cm long, margins strongly denticulate near the apex; the blade .2–.4 cm wide, gradually narrowing onto a winged petiole .2–.4 cm long. Involucral bracts lanceolate, .2–.5 cm long, plane at the base. Umbel 1–5 (7) flowered; pedicels filiform, .5–1 cm long. Flowers distylous. Calyx efarinose, campanulate, obscurely ribbed, .2–.4 cm long, green or with purple striations, divided to one third its length, teeth lanceolate with capitate glands. Corolla white with a yellow throat; limb .5–.8 cm wide, emarginate; tube equal to the calyx or only slightly longer. Stamens .5–.75 mm long, anthers located in the lower third of the corolla tube in pin plants. Pollen 3-syncolpate. Stigma capitate, located in the upper third of the corolla tube in pin plants, positions reciprocal in thrum plants. Capsule cylindrical, .3–.5 cm long, .2–.3 cm in diam., strongly exserted from the calyx; seeds brown, strongly reticulate, .3 mm long.

CHROMOSOME NUMBER. $2n = 18$ (Nome: *Kelso 83-136,* at ALA).

HABITAT. Frost boils, late snowbeds, creek banks and gravel bars with calcareous substrates.

DISTRIBUTION. Endemic to and common on the Seward Peninsula, northwestern Alaska.

The species we now know as *Primula anvilensis* was first described by Fernald (1928), using the incorrect name *P. parvifolia.* The latter epithet came from a brief diagnosis of Duby, based on material collected by Langsdorff in 1805 from the southern Bering

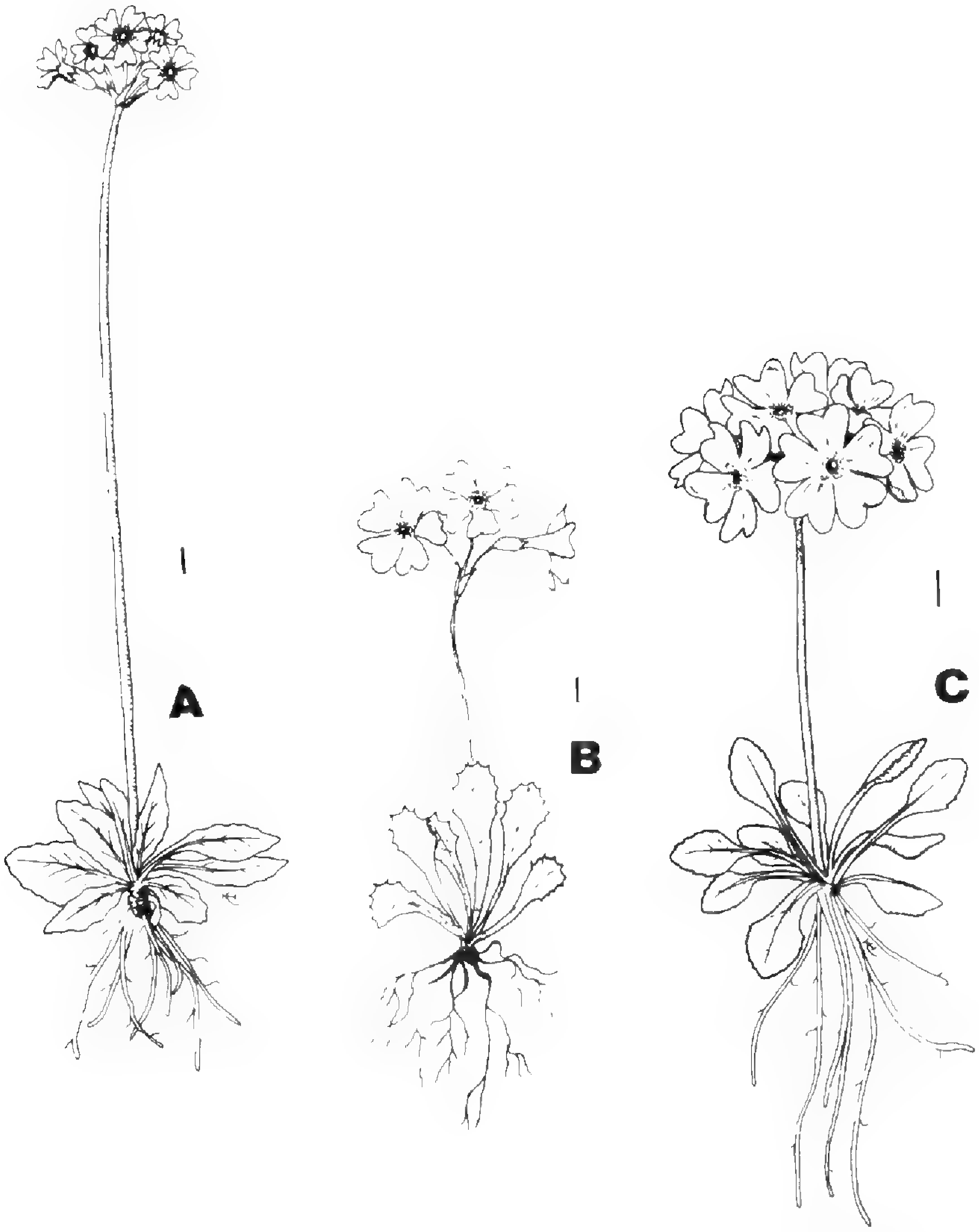

Figure 1. A. *Primula alcalina*, B. *P. anvilensis*, C. *P. borealis*. Bar equals 1 cm.

Sea region. These plants were given to Fischer at Leningrad, with duplicates sent to Kew and Edinburgh under the name *P. araboides* from herb. Fischer (Smith and Fletcher, 1943). When the name *P. parvifolia* was shown by Smith and Fletcher (1943) to be a synonym of *P. borealis*, the distinctive nature of the Seward Peninsula material was obscured in spite of Fernald's detailed description. It was not until recently that the Seward Peninsula material was separated from *P. borealis* by Kelso (1987) and given the name *P. anvilensis*.

Primula anvilensis is endemic to the Seward Peninsula of northwestern Alaska. While there are a number of plant taxa restricted to the Bering Strait region, *P. anvilensis* is unusual in having a wholly North American distribution.

Primula borealis Duby, Mem. Soc. Phys. d'Hist. Nat. Génève 10: 31. 1843; in DeCandolle, Prodromus 8: 43. 1844. Figure 1C. TYPE: U.S.A. ALASKA. Shishmaref, *Chamisso & Eschscholtz in 1816* (LECTOTYPE here designated: LE, photograph E!).

Primula mistassinica sensu Chamisso & Schlechtendal (*non* Michaux), Linnaea 1: 213–215. 1826.

Primula parvifolia Duby, in DeCandolle, Prodromus 8: 42. 1844. *Primula borealis* var. *parvifolia* (Duby) Pax, in Engler, Pflanzenreich, Primulaceae, 81. 1905. TYPE: "*Ad fretum Beering*" as *P. araboides, nomen nudum,* in herb. Fischer (HOLOTYPE: LE?; ISOTYPES: E!, K!, NY!).

Primula tenuis Small, Bull. Torr. Bot. Club 25: 320. 1898. TYPE: U.S.A. ALASKA. Pastolic, 25 Jun 1871, *Dall s.n.* (HOLOTYPE: NY!, photograph E!).

Primula chamissonis Busch, Fl. Sib. & Orient. Extrem. 4: 28. 1926. TYPE: U.S.A. ALASKA. Kotzebue, 1816–17, *Chamisso s.n.* (HOLOTYPE: LE, Photo GH!).

Plants growing in dense clusters or single, farinose in youth, becoming more or less efarinose in age. Scape (1) 2–10 cm tall. Leaves including petiole 1–2 (3.5) cm long, .1–.7 cm wide, spathulate, elliptical, or rhombic, margins crenate to remotely denticulate. Involucral bracts gibbous or saccate at base, involute above, .2–.5 cm long. Umbel (1) 3–8 (12) flowered. Pedicels .2–.8 cm long, erect or spreading but not capillary. Flowers distylous. Calyx campanulate, green or with purple striations, ca. .3 cm long, obscurely ribbed, divided up to ½ its length with lanceolate teeth covered with capitate glands. Corolla lavender, rarely white, throat yellow; tube .6–.8 cm long, at anthesis 1.5 times length of the calyx; limb (.8) 1–1.5 cm wide, lobes slightly or deeply emarginate. Stamens ca. 1 mm long, anthers located near middle of the corolla tube in pin plants. Pollen 3-syncolpate. Stigma capitate, in pin plants located at or just above the annulus. Positions reciprocal in thrum plants. Capsule cylindrical, .3–.6 cm long, .2–.3 cm in diam., strongly exserted from the calyx. Seeds strongly reticulate, ca. .3 mm long.

CHROMOSOME NUMBER. $2n = 36$ (Alaska: *Kelso 84-115, 83-292,* at ALA; Johnson and Packer, 1968; Northeast Siberia: Zhukova, 1965, 1966, 1982; Zhukova and Tikhonova, 1971; Zhukova et al., 1973). $2n = 18$ (Alaska: Thomas, 1951; Siberia: Zhukova, 1980; Zhukova and Petrovsky, 1980, q.v. *P. mistassinica*).

HABITAT. Coastal estuarine marshes.

DISTRIBUTION. In North America from the Bering Sea coast to Cape Bathurst in the Northwest Territories. Total range in Asia uncertain, but clearly present along the coast from the Chukotsk Peninsula to the Kolyma River.

In 1816–17, Chamisso and Eschscholtz travelled through the Bering Strait with the Kotzebue expedition, collecting at Unalaska, St. Lawrence Bay (Chukotka), St. Lawrence Island, and Shishmaref (then spelled Schischmareff). In a later enumeration of the plants from this expedition, Chamisso misidentified several specimens as *Primula mistassinica.* The formal description of *P. borealis* was not made by Duby until several decades later, based on the collections of Chamisso ("*in Americae occidentali-borealis sinubus schischmareff et Sancti Laurentii*"). Although Bunge is also listed as a collector of type material, this cannot be correct since he never visited the area. Duby was possibly referring to specimens from herb. Bunge, collected by Chamisso and Eschscholtz. It is appropriate, therefore, to designate the Chamisso material as the lectotype of *P. borealis.*

Primula borealis is variable in height, leaf morphology, and amount of farina, all of which are influenced by ecological and phenological factors. Dune populations contain individuals less than 2 cm in height, whereas individuals growing in more stable, nutrient-rich sites can attain over 10 cm. Leaf length increases over a growing season, and the amount of farina present appears to be related to phenology. Young leaves are heavily farinose, but later in the summer only a few traces of farina may remain.

Floral morphology is consistent in *Primula borealis.* The wide corolla limb, full symmetrical umbel, and short pedicels on top of a short scape make the plants appear top-heavy at anthesis. Individuals growing in environmentally stressed areas, however, often have depauperate umbels. The specimens described by Small as *P. tenuis* are typically of this growth form. In live material, the involucral bracts are consistently saccate or gibbous but this character may be difficult to detect in some herbarium material.

Primula borealis is always found in saline habitats. It can be sympatric with *P. nutans,* and herbarium sheets frequently contain both species. *Primula nutans* is easily distinguished from *P. borealis* by its ovate petiolate leaves and auriculate bracts.

The collection from the interior of the Yukon reported in Porsild (1966) and Porsild and Cody (1980) as *Primula borealis* was based on a misidentification of *P. mistassinica.* Because of insufficient specimens available for inspection, the range of *P. bo-*

realis in Siberia beyond the coast of Chukotka is unclear. Soviet literature (Yurtsev et al., 1979; Tolmatchev and Yurtsev, 1980; Kozhevnikov, 1981) reports the species as far west as the Lena River. However, the chromosome number attributed to *P. borealis* there (Zhukova and Petrovsky, 1980) is diploid rather than the tetraploid given in numerous other reports. The Eurasiatic taxon *P. farinosa* L. is a diploid and is found throughout northern Siberia, including the Lena River basin. It can resemble *P. borealis* and it is likely that there has been some confusion between the two species. Consequently, I hesitate to accept the conclusion of Smith and Fletcher (1943) that the Siberian *P. stricta* var. *jacutensis* Busch is entirely synonymous with *P. borealis.* They are certainly correct that it is not a form of *P. stricta.* However, I suspect that the specimens cited by Busch from the mountainous region along the Lena River, and the specimens identified as *P. borealis* with the diploid chromosome number reported by Zhukova and Petrovsky (1980) from the Anyui Mountains, should be allied with *P. farinosa* rather than with *P. borealis.*

South of the Chukotsk Peninsula, it is difficult to separate the range of the North Pacific species *Primula modesta s. lat.* from that of *P. borealis.* No recent systematic work has been done on the Asiatic members of sect. *Aleuritia,* but there is clear affinity between *P. borealis* and *P. modesta* in their large flowers, symmetrical umbels, and rhomboid leaves. *Primula modesta* is known to be diploid (Shimizu, 1982) and the other diploid chromosome counts reported for *P. borealis* in Siberia are from the mountains along the Sea of Ochotsk (Yurtsev et al., 1979), near the range of *P. modesta.* I suspect that the lower chromosome numbers attributed to *P. borealis* in this region are applicable instead to one of the varieties of *P. modesta.*

Primula incana M. E. Jones, Proc. Cal. Acad. Sci. 5: 706. 1895. Figure 2A. *P. farinosa* var. *incana* (M. E. Jones) Fernald, Rhodora 9: 16. 1907. *P. farinosa* subsp. *incana* (M. E. Jones) Smith and Forrest, Notes Roy. Bot. Garden Edinburgh 16: 24. 1928. TYPE: U.S.A. UTAH. Tropic, *Jones 5312* (HOLOTYPE: RSA!).

Primula americana Rydberg, Bull. Torrey Bot. Club 28: 500. 1901. TYPE: U.S.A. MONTANA. Deer Lodge, *Rydberg 2746* (HOLOTYPE: NY!).

Plants slender and heavily farinose, occasionally efarinose. Scape

Figure 2. A. *Primula incana,* B. *P. laurentiana,* C. *P. mistassinica.* Bar equals 1 cm.

to 46 cm tall. Leaves elliptic or oblanceolate, including the petioles to 6 cm long, blade .3–1.6 cm wide, margins denticulate, blade gradually narrowing onto a broadly winged petiole. Involucral bracts oblong, densely covered with white farina, flat above, saccate or gibbous at the base, .5–1 cm long. Umbels capitate, (4) 7–19 flowered, pedicels .3–.9 cm long. Flowers homostylous. Calyx green, heavily farinose, cylindrical, obscurely ribbed, .4–.7 (1) cm long, divided up to one third its length by lanceolate teeth covered with capitate glands. Corolla lavender with yellow throat; limb .4–.8 cm wide, tube equal to or slightly longer than calyx, limb emarginate. Stamens ca. 1 mm long, located in upper portion of corolla tube. Pollen 4-syncolpate. Stigma capitate, located adjacent to anthers. Capsule cylindrical to slightly elliptical, .8–1.8 cm long, .2–.3 cm in diam. Seeds brown, reticulate, ca. .2 mm long.

CHROMOSOME NUMBER. $2n = 54$ (Alaska: *Kelso 83-350, 84-53, 84-91*; Yukon: *Kelso and Holmes 84-37,* all at ALA). $2n =$ ca. 50 (Colorado: *Wittmann and Wittmann 2542,* at ALA). $2n = 72$ (Colorado: Vogelmann, 1960).

HABITAT. Alkaline clay soil in river flood plains and open meadows.

DISTRIBUTION. Utah and Colorado north to Alaska.

Primula incana is a generally well-marked species with heavily farinose leaves, tall scape, and flat-tipped bracts subtending tight umbels of small homostylous flowers. Many northern collections have been misidentified as the smaller *P. stricta* because flowering begins when the scape is relatively short. Elongation of the scape continues throughout anthesis and pedicels lengthen as seeds ripen. Thus, the characteristic tight umbels do not persist beyond anthesis, and individuals in fruiting stage may be many times taller than those in early flowering stage. While most plants are heavily farinose, some individuals in otherwise farinose populations may be efarinose. *Primula incana* is most similar to *P. laurentiana.* The latter is distinguished by larger flowers, longer pedicels, broader, more denticulate leaves and involute rather than flat bracts.

A single octoploid count for *Primula incana* has been reported (Vogelmann, 1960) from a population in South Park, Colorado, but I have obtained a hexaploid count from the same locale. The consistency of chromosome number at the species level in sect. *Aleuritia,* the number of hexaploid counts for this species, and the complete lack of morphological or anatomical differences between northern specimens and the southern populations are evidence that the octoploid count may be in error and the species is consistently hexaploid.

Primula laurentiana Fernald, Rhodora 30: 68–72. 1928. Figure 2B. *P. farinosa* L. var. *macropoda* Fernald, Rhodora 9: 16. 1907. *P. mistassinica* Michx. var. *macropoda* (Fernald) Boivin, Nat. Can. 93: 644. 1966. TYPE: CANADA. QUEBEC. Le Bic, *Fernald and Collins 243* (HOLOTYPE: GH; ISOTYPE: MN!).

Primula laurentiana f. *chlorophylla* Fernald, Rhodora 30: 72. 1928. TYPE: CANADA. NEWFOUNDLAND. Dog Peninsula, St. Margaret Bay, *Fernald et al. 28913* (HOLOTYPE: GH!).

Plants usually heavily farinose, glabrous. Scape 10–30 (48) cm tall. Leaves including petiole 3–10 cm long, oblanceolate to spathulate, rounded or acute at the apex with crenate margins, blade .4–1.3 cm wide, gradually narrowing into winged petioles, densely farinose below with white or cream-colored farina. Involucral bracts saccate at base, involute above, .6–.8 cm long. Umbel 3–12 flowered; pedicels up to 1 cm long, elongating greatly in fruit. Flowers homostylous. Calyx campanulate to tubular, green, obscurely ribbed, .5–.8 cm long, divided up to ⅓ its length by lanceolate teeth, densely covered with capitate glands. Corolla lavender with a yellow throat, tube .6–.9 cm long, 1.5–2 times the length of the calyx at anthesis; limb to 1.6 cm wide, lobes to 0.7 cm wide, emarginate. Stamens ca. 1 mm long, anthers located adjacent to the stigma in the upper ⅓ of the corolla tube. Pollen 4-syncolpate. Capsule elliptical, up to 1.4 cm long, .3–.5 cm in diam., exserted from the calyx. Seeds brown, ca. .3 mm long, reticulate.

CHROMOSOME NUMBER. $2n = 72$ (unknown location: Bruun, 1938; Labrador and Quebec: Vogelmann, 1960; Quebec: Gervais and Cayouette, 1985). $2n = 54$ (Labrador: Vogelmann, 1960).

HABITAT. Open areas on limestone, along riverbanks.

DISTRIBUTION. Common on the Gaspé Peninsula of Quebec and in limestone regions of western Newfoundland, infrequent west to Hudson Bay and south to northeastern Maine.

Primula laurentiana is most similar to *P. incana* M. E. Jones. The latter species is also usually tall and heavily farinose, but has smaller flowers, flat bracts, a more western distribution, and is a hexaploid. While a single hexaploid count has been published for *P. laurentiana,* the number of other octoploid counts suggests that this may be erroneous, although further cytological investigations in Newfoundland would be helpful.

The efarinose form of *P. laurentiana* described by Fernald as f. *chlorophylla* is a common variant occurring throughout the range. Because efarinose individuals can be found in virtually all farinose populations, I do not believe they deserve taxonomic recognition.

Primula mistassinica Michaux, Fl. Bor.-Amer. 1: 124. 1803. Figure 2C. *P. farinosa* var. *mistassinica* (Michaux) Pax, Bot. Jahrb. Syst. 10: 200. 1889. *P. farinosa* subsp. *mistassinica* (Michaux) Pax and Knuth, Das Pflanzenreich 4(237): 85. 1905. *P. sibirica* var. *mistassinica* (Michaux) Kurtz, Bot. Jahrb. Syst. 19: 394. 1894.—*pro parte.* TYPE: CANADA. QUEBEC. Rivière des Goelands, Lake Mistassini. "*Ad locus mistassins Canadam inter et fretum Hudsonis,*" 1792, *Michaux s.n.* (HOLOTYPE: P).

Primula intercedens Fernald, Rhodora 30: 86–87. 1900. *P. mistassinica* var. *intercedens* (Fernald) Boivin, Nat. Canad. 93: 644. 1966. *P. mistassinica* f. *intercedens* (Fernald) J. Cayouette, Nat. Canad. 111: 443–445. 1984. TYPE: *P. farinosa sensu* Nuttall, Gen. 1: 119. 1818, "calcareous gravel shores of the islands of Lake Huron around Michilimakinak, Bois Blanc, and St. Helena in the outlet of Lake Michigan," and *P. farinosa* var. *americana* Torrey, Fl. North. & Midl. U.S. 1: 213. 1824, "shores of Lake Huron, Lake Michigan, etc. *Douglass* and *Nuttall*" (LECTOTYPE here designated: PH!, *Douglass s.n.*, Lake Huron, ex herb. Schweinitz).

Primula mistassinica var. *noveboracensis* Fernald, Rhodora 30: 19. 1928. TYPE: U.S.A. NEW YORK. Triphammer Falls, Fall Creek, Ithaca, *Eames 4804* (HOLOTYPE: GH!).

P. maccalliana Wiegand, Bull. Torr. Bot. Club 27: 389. 1900. TYPE: CANADA. ALBERTA. Banff. *Maccalla 2433* (HOLOTYPE: CU; ISOTYPE: K!).

Plants usually efarinose, glabrous, sometimes with traces of farina on vegetative parts. Scape 5–15 cm tall. Leaves including the petiole .5–7 cm long, spathulate or elliptical, margins widely denticulate to almost entire; blade .2–1.6 cm wide, gradually narrowing to winged petiole. Involucral bracts lanceolate, plane at base, .3–.5 cm long, involute above, acute or somewhat obtuse at the tip. Umbel 1–5 (10) flowered. Pedicels .5–2.0 cm long, capillary. Flowers distylous. Calyx green or with purple striations, campanulate, obscurely ribbed, .3–.5 cm long, divided up to ½ by lanceolate teeth sparsely covered with capitate glands. Corolla lavender, sometimes white; throat usually yellow, rarely lavender; tube .5–.8 cm long, at anthesis 1.5–2 times the length of the calyx; limb .8–1.4 cm wide, lobes emarginate. Stamens ca. 1 mm long, anthers located in pin plants in bottom third of corolla tube. Pollen 3-syncolpate. Stigmas capitate, located in pin plants in upper third of corolla tube, positions reciprocal in thrum plants. Capsule cylindrical to elliptical, .3–.6 cm long, .2–.3 cm in diam., seeds ca. .3 mm long, reticulate.

CHROMOSOME NUMBER. $2n = 18$ (Yukon: *Kelso and Holmes 84-15,* at ALA; Michigan, New York, Nova Scotia, Quebec: Vogelmann, Ph.D. dissertation, Univ. of Michigan, 1956, 1960).

HABITAT. Open meadows and riverbanks, lakeshores, and around hot springs, in the southern portion of the range on cool, wet, north-facing slopes and cliff faces; calcareous substrates.

DISTRIBUTION. Across boreal America from Alaska to Newfoundland, south to northern Vermont, New York, Illinois, Michigan, and Minnesota.

Primula mistassinica is one of the most polymorphic North American species in sect. *Aleuritia.* Previous authors (cf. Fernald, 1907, 1928; Vogelmann, *loc. cit.*) have recognized several infraspecific taxa. While *P. mistassinica* varies in size, leaf morphology, and the amount of farina, it is consistent in habit, chromosome number, and floral morphology. The infraspecific taxa lack clear geographic coherence, intermediate forms are abundant, and it is often difficult to assign material to varietal level. Among the taxa recognized by previous authors, individuals belonging to var. *intercedens* (distinguished by the presence of yellow farina) are particularly abundant around the Great Lakes. However, individuals with variable amounts of farina can be found throughout the range of *P. mistassinica.* Similarly, individuals belonging to var. *noveboracensis* (distinguished by smaller flowers and lack of a yellow eye) are abundant in Newfoundland and in the Northwest, but can also be found throughout the range. For these reasons, I believe *P. mistassinica* is best treated as a single polymorphic species without infraspecific designations.

The range of *Primula mistassinica* is generally sympatric with the boreal forest of North America. In the northwestern portion of the range, *P. mistassinica* becomes increasingly rare and is recognized as threatened or endangered in several Canadian provinces. In northwestern Canada and Alaska it is better documented by herbarium specimens than previously believed, although it should still be considered rare. Many of the specimens from the continental Northwest Territories and Yukon initially identified as the homostylous *P. stricta* are actually the distylous *P. mistassinica.* Two populations from the interior Yukon (*Spetzman 311, 312,* DAO!) identified by Porsild (1966) as *P. borealis* are also *P. mistassinica. Primula mistassinica* differs from *P. borealis* in its more slender habit, plane involucral bracts, and fewer-flowered

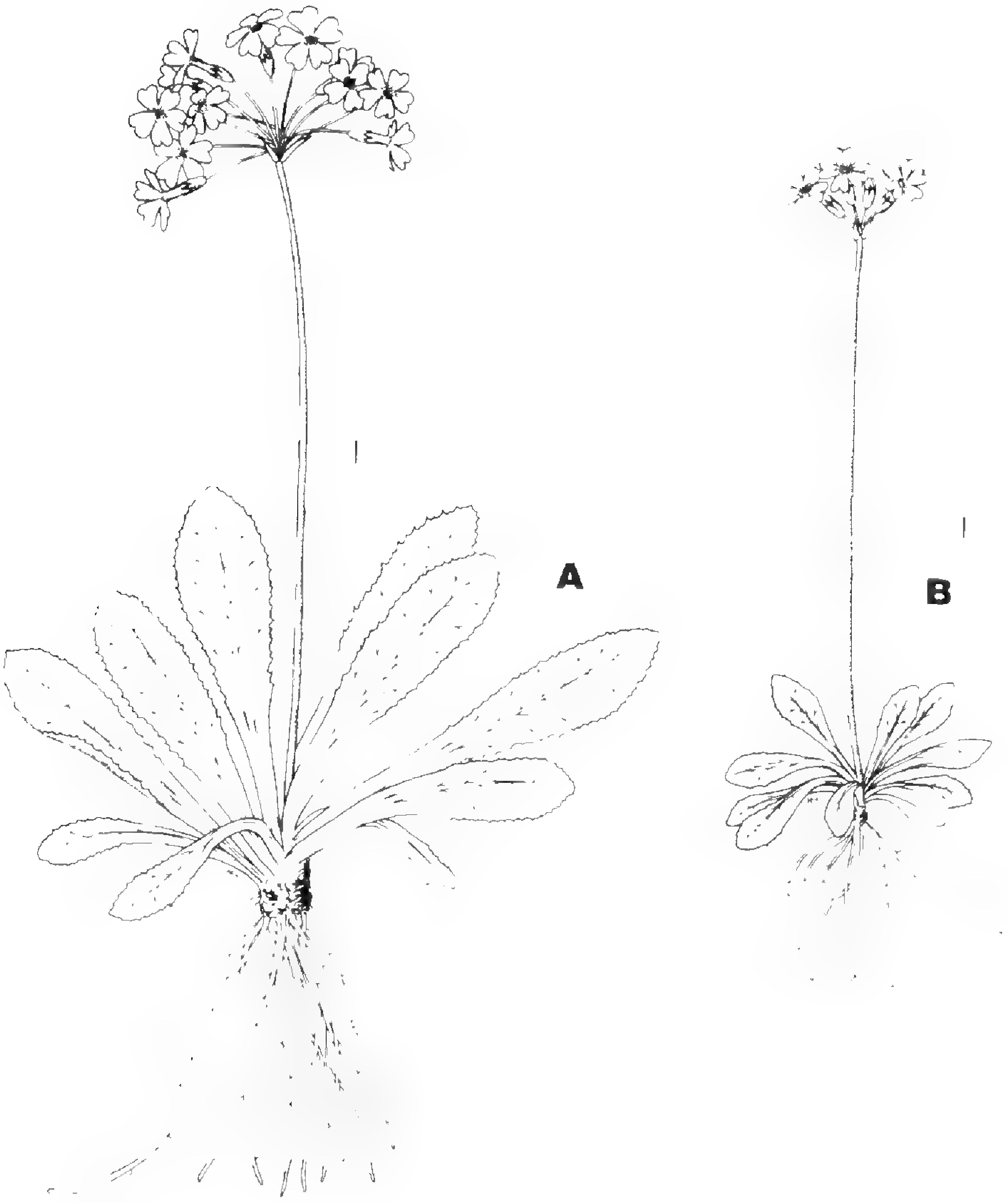

Figure 3. A. *Primula specuicola*, B. *P. stricta*. Bar equals 1 cm.

umbel on longer pedicels, as well as by the lower chromosome number.

Primula specuicola Rydberg, Bull. Torrey Bot. Club 40: 461–462. 1913. Figure 3A. TYPE: U.S.A. UTAH. San Juan River, near Bluff (HOLOTYPE: *Rydberg 9882*, NY!).

Primula hunnewellii Fernald, Rhodora 36: 117. 1934. TYPE: U.S.A. ARIZONA. Coconino County, north rim of the Grand Canyon (HOLOTYPE: *Hunnewell 10883* in Hunnewell Herbarium; ISOTYPE: GH!).

Plants heavily farinose. Scape to 25 cm tall. Leaves spathulate, including petioles to 13 cm long, blade to 2 cm wide, margins strongly sinuate-dentate, blade gradually narrowing to a broadly winged petiole. Involucral bracts lanceolate, plane at base and involute above, a broadly winged petiole. Involucral bracts lanceolate, plane at base and involute above, .5–1 cm long. Umbels loose, (6) 10–25 flowered, pedicels ascending, 1–3 cm long. Flowers distylous. Calyx green, campanulate, obscurely ribbed, .3–.5 cm long, divided to ⅓ its length by lanceolate teeth covered with capitate glands. Corolla violet, with a yellow throat; limb 1–1.6 cm broad, tube .8–1 cm long, twice the length of the calyx. Anthers ca. 1.5 mm long, stamens located in the middle of the corolla tube in pin plants. Pollen 3-syncolpate. Stigma capitate, located in upper ⅓ of corolla tube in pin plants, positions of anthers and stigma reciprocal in thrum plants. Capsule elliptical, .3–.5 cm long, ca. .3 cm in diam. Seeds ca. .5 mm long, reticulate.

CHROMOSOME NUMBER. $2n = 18$ (Vogelmann, 1960).

HABITAT. Moist seepage areas on carbonate canyon walls along the Colorado River and its tributaries.

DISTRIBUTION. Southern Utah and northern Arizona.

Primula specuicola is a distinctive species with large corollas, long pedicels, and long, sharply dentate, farinose leaves. A few specimens with short pedicels superficially resemble *P. incana* but the latter is distinguished by its smaller, homostylous flowers and longer capsules as well as its higher chromosome number.

A specimen from the Grand Canyon with a more exserted capsule than in the type material from Utah was given the name *Primula hunnewellii* by Fernald (1934). The Arizona plant resembles the type of *P. specuicola* in all other aspects of morphology, cytology, and ecology, and I believe that *P. hunnewellii* is merely a local variant of *P. specuicola.*

Primula stricta Hornemann, in Oeder, Flora Danicae 8(24): t. 1385. 1810. Figure 3B. *P. hornemanniana* Lehm. Monogr. Gen. Prim. 55. 1817—*pro parte.* TYPE: NORWAY. Tolgen and Roraas, *Hornemann s.n.* (HOLOTYPE: C, microfiche ALA!). *P. farinosa* var. *groenlandica* Pax in Engler, Pflanzenr. Primulaceae 84. 1905.—*pro parte.*

Plants efarinose or sparingly farinose. Scape 8–15 (18.5) cm tall. Leaves including petiole 1–6 cm long, oblanceolate to spathulate, margins slightly denticulate to almost entire, blade .3–1.1 cm broad, gradually narrowing onto winged petioles. Involucral bracts lanceolate, acute at the tip, saccate at base, involute above,

.6–1.0 cm long. Umbel 2–9 flowered, pedicels .1–.8 cm long, elongating slightly in fruit. Flowers homostylous. Calyx green or with purple striations, campanulate, obscurely ribbed, .4–.6 cm long, divided up to ⅓ by lanceolate teeth, with capitate glands on the margins, somewhat white farinose on the inner surface. Corolla tube .4–.7 cm long, slightly exserted from calyx at anthesis, limb .5–.8 cm wide, lobes slightly emarginate. Stigmas capitate, located just below the annulus. Stamens ca. .75 mm long, anthers adjacent to stigma. Pollen 5-syncolpate. Capsules ovoid-elliptical, .5–.7 cm long, .3–.4 cm in diam. Seeds strongly reticulate, ca. .3 mm long.

CHROMOSOME NUMBER. $2n = 126$ (unknown location: Bruun, 1930; Iceland: Löve and Löve, 1956; Manitoba: Löve and Ritchie, 1966). $2n > 90$ (Norway: Laane, 1967).

HABITAT. Coastal regions including marshes, stable dunes and beach ridges, more rare inland along rivers.

DISTRIBUTION. In North America throughout the southern islands of the Canadian Arctic Archipelago and Hudson Bay region, east through Greenland and Scandinavia to Novaya Zemlya.

The arctic species *Primula stricta* was originally described and illustrated by Hornemann from specimens collected in Norway. Its nature was confused, however, by Lehmann's use of the name *P. hornemanniana* for the same material, coupled with his description of the taxon based on what he erroneously thought was additional material from the Tyrol. This material was probably *P. farinosa* L., and thus the description and illustration in Lehmann's monograph refer to a chimera of *P. stricta* and *P. farinosa. Primula stricta* is not found in the Alps, and Hornemann's original name and description are correct for the species as we now understand it.

In its most typical form, *Primula stricta* is a short plant with capitate umbels, small emarginate corolla lobes, and broadly elliptical capsules barely longer than the calyx. Although height and number of flowers can vary, the morphology of the species remains generally consistent across the range in the Canadian and European Arctic. This consistency in *P. stricta,* however, has been obscured in North America by confusion with *P. incana.*

While some of the smaller forms of *Primula incana* resemble *P. stricta,* the typical forms are easy to distinguish. *Primula stricta* is less than one third the height of *P. incana,* lacks the dense farina of the latter except on the inner surface of the calyx, and has involute rather than flat-tipped involucral bracts. *Primula stricta* also has broader and shorter capsules than *P. incana,* and there are cytological differences between the two species: *P. stricta* is 14-ploid ($2n = 126$) and *P. incana* is a hexaploid ($2n = 54$).

In western North America, *Primula stricta* has been erroneously reported in the Yukon Territory and Alaska (Hultén, 1968; Porsild, 1966; Scoggan, 1979). Most of the records west of the Mackenzie Basin are based on misidentified specimens of *P. incana.* The confusion of the two taxa here is understandable, since in the interior of the Yukon, particularly in the saline clay pans around Kluane Lake, *P. incana* has a small efarinose form with depauperate umbels very similar to *P. stricta.* When transplanted to gardens in Fairbanks, these plants regained the tall farinose appearance typical of *P. incana.* Chromosome counts confirm that the Yukon populations are *P. incana* and not *P. stricta.*

In Alaska, Hultén (1948, 1968) reported *Primula stricta* in the interior, on the Seward Peninsula and on the arctic seacoast. These records are also based on misidentifications. The Seward Peninsula specimens are *P. anvilensis* (e.g., *Hutchinson 313-318, 313-331,* E!, K!), on the arctic coast they are *P. borealis* (e.g., *Johansen 265,* CAN!), and in the interior of Alaska they are *P. incana* (Copper Center: *Heideman 46,* US!). The specimens of *P. stricta* cited from the Yukon by Hultén (Five Finger Rapids: *Tarleton 78*; Lewes River: *Gorman 1052,* both at US!) are also *P. incana.*

Primula sect. **Armerina**

Primula sect. **Armerina** Lindley, Edward's Bot. Reg. 32: t. 31. 1846. TYPE: *P. involucrata* Wallich.

Section *Farinosae* subsection *sibirica* Bruun, Symb. Bot. Upsal. 1: 67. 1932. TYPE: *P. sibirica* Jacquin.

Plants efarinose but with jointed hairs, sometimes rhizomatous. Leaves with revolute vernation, distinctly petiolate on slender, elongate petioles; blades entire or slightly undulate, glabrous. Inflorescence a simple umbel subtended by involucral bracts that are saccate and usually conspicuously auriculate at base; pedicels flexuous. Corolla lilac, pink, or white, lobes notched or cleft. Capsules narrowly cylindrical. Chromosome base number $x = 11$.

Schwarz (1968) divided section *Armerina* into two subsections: *Armerina* (including *Primula nutans*) and *Chamaecome* (including *P. egaliksensis*). He distinguished the latter section by its persistent rhizomes, in contrast to subsection *Armerina* with rhizomes lasting only a single growing season. At best this distinction seems weak, and at least in Alaska, completely false. Consequently, I do not follow the divisions of Schwarz, and treat all the species related to *P. nutans* as members of a single section.

KEY TO SECTION *ARMERINA* IN NORTH AMERICA

Involucral bracts distinctly auriculate at the base; flowers 8 mm or more in diameter .... *P. nutans*

Involucral bracts saccate at base but not auriculate; flowers less than 8 mm in diameter .... *P. egaliksensis*

Primula egaliksensis Wormskjold *ex* Hornem., Fl. Danicae 9: 2, t. 1511. 1816. Figure 4B. TYPE: GREENLAND. Igaliko, 1813, *Wormskjold s.n.* (HOLOTYPE: C; ISOTYPE: E!).

P. stricta var. *groenlandica* Warming, Kongl. Svenska Vetenskapsakad. Handl. 12: 21. 1887. *P. farinosa* var. *groenlandica* (Warming) Pax, in Engler, Das Pflanzenreich, Primulaceae 84. 1905.—*pro parte*. *P. groenlandica* (Warming) Balfour, J. Royal Hort. Society 34: 182. 1913. *P. egaliksensis* f. *violacea* Fernald, Rhodora 30: 98. 1928. TYPE: GREENLAND. Itivnek, Holsteinborg District, 13 Jul 1884, *Warming & Holm s.n.* (HOLOTYPE: C; ISOTYPES: GH!, K!).

P. sibirica Hooker, Fl. Bor. Am. 2: 121. 1838.—*pro parte*. *P. sibirica* var. *minor* Duby, in DeCandolle, Prodromus 8: 43. 1844.

Plants slender, completely efarinose. Scape 4–12.5 cm tall. Leaves distinctly pedicellate, including the petiole 1.5–5.5 cm long, blade elliptical, to .9 cm wide, .7–2.5 cm long, margins entire, obscurely undulate or slightly denticulate in age. Involucral bracts lanceolate, to .6 cm long, distinctly saccate but not auriculate at the base, somewhat involute above. Umbel 1–3 (6) flowered, pedicels pendant, .2–.9 cm long. Flowers homostylous. Calyx cylindrical, obscurely ribbed, .4–.6 cm long, green or with purple stripes, divided to ⅓ by teeth with glandular cilia on the margins. Corolla white or lavender, throat yellow; limb .6–.8 cm wide, slightly emarginate, tube .6–.8 cm long, equal to or slightly exserted from the calyx. Stamens ca. .75 mm long, anthers located adjacent to stigmas in upper one third of corolla tube. Pollen

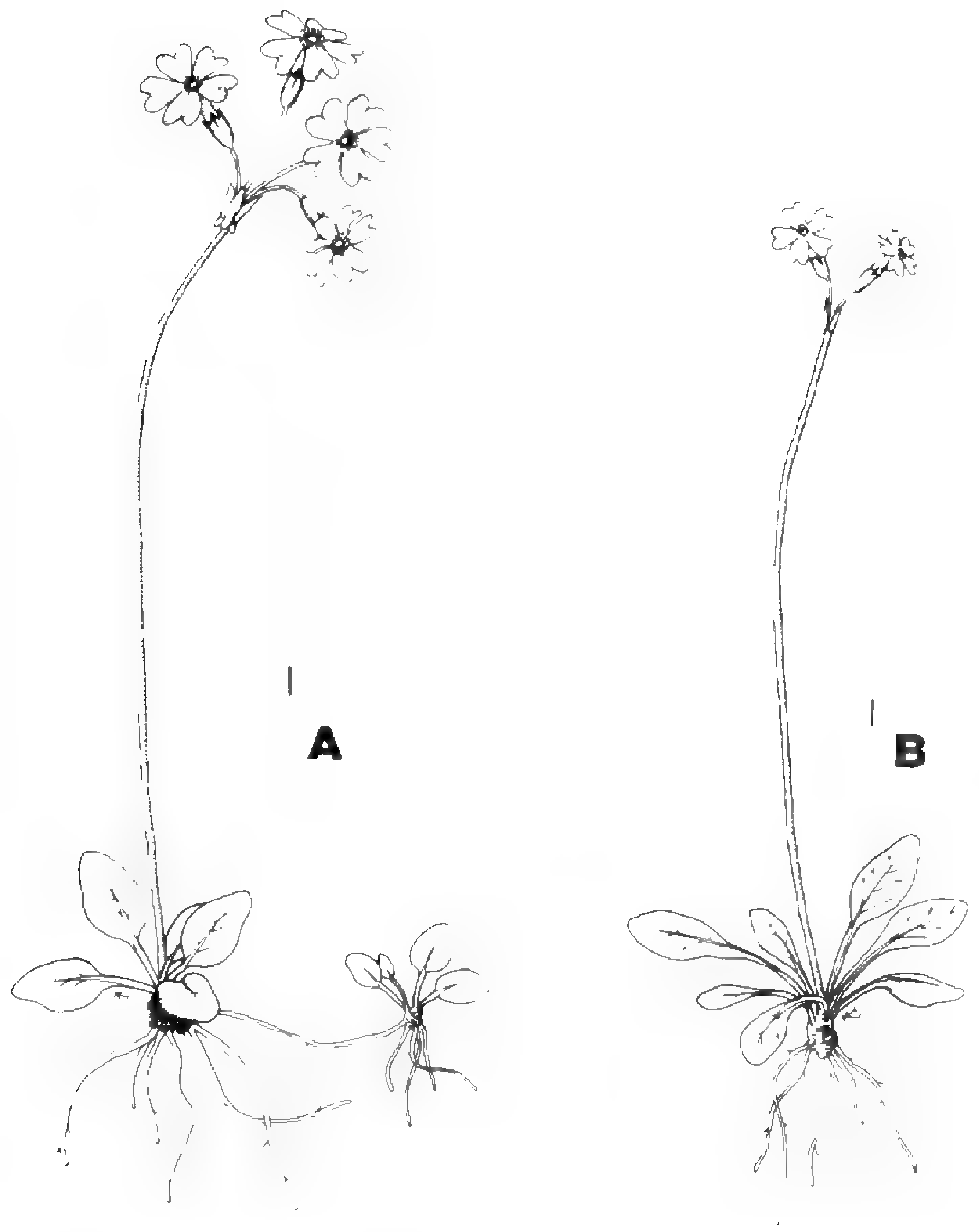

Figure 4. A. *Primula nutans*, B. *P. egaliksensis*. Bar equals 1 cm.

5-syncolpate. Stigma cylindrical. Capsule narrowly cylindrical, up to 1.2 cm long, ca. .1 cm in diam. Seeds green to light brown, obscurely reticulate, to .3 mm long.

CHROMOSOME NUMBER. $2n$ = 36 (Alaska: *Kelso 85-10, Parker 2007,* both at ALA; Colorado: Löve et al., 1971; Greenland: Jørgenson et al., 1958). $2n$ = ca. 36 (Alaska: Johnson and Packer, 1968). $2n$ = 40 (Northeast Siberia: Zhukova et al., 1973; Zhukova, 1982). $2n$ = ca. 40 (Labrador: Hedburg, 1967).

HABITAT. Damp silt along streambanks.

DISTRIBUTION. Across North America from Alaska to Greenland, known in the south from disjunct locations in Colorado and northwestern Wyoming; in Asia, known from the Chukotsk Peninsula.

Primula egaliksensis is easily distinguished by its inflorescence of 1 or 2 small homostylous flowers and its elliptical efarinose leaves. Both white and violet flowers are equally common and adjacent populations can occur. This dimorphism confused

Warming who allied the lilac form in Greenland to *P. stricta* rather than to the white-flowered taxon described by Wormskjold. This error was corrected by Fernald who examined Warming's material, removed it from *P. stricta,* and renamed it as a color variant of *P. egaliksensis.*

Primula egaliksensis has a wide geographic range but it is not locally abundant. Because of the small flowers and generally short stature, individual plants are inconspicuous even during the brief flowering period.

Primula nutans Georgi, Bemerk. Russ. Reich 1: 200. 1775. Figure 4A. TYPE: *J. G. Gmelin,* Fl. Sib. 4: t. 46. 1769. "*Ab Ob fluvio ad transbaicalensis usque ad regiones*" (HOLOTYPE: LE?).

P. sibirica Jacquin, Misc. Austr. 1: 161. 1778. Based on the same type as *P. nutans.*

Plants slender, efarinose, sometimes rhizomatous. Scape 5–20 cm tall. Leaves distinctly pedicellate, including petioles to 3 cm long; blade ovate to slightly elliptical, to 2 cm wide, 1–2 cm long, margins entire. Involucral bracts .4–.6 cm long, oblong, obtuse at the tip, saccate and prominently auriculate at the base. Umbel 2–4 flowered; pedicels nodding, 3 times the length of the bracts. Flowers distylous. Calyx cylindrical, .4–.7 cm long, distinctly ribbed, divided to ¼ its length by obtuse to somewhat acute teeth, with prominent ciliolate glands on the margins. Corolla violet with a yellow throat, tube .7–1 cm long, strongly exserted from the calyx in North American specimens; limb .9–2 cm wide, lobes cordate. Stamens 1.5–2 mm long, located in middle of corolla tube in pin plants and near top of corolla tube in thrum plants. Pollen 6-stephanocolpate. Stigma cylindrical, located in pin plants slightly above the annulus of corolla tube, and in thrum plants near middle of tube. Capsules narrowly cylindrical, to 1.4 cm long, .2–.4 cm in diam. Seeds light brown, ca. .4 mm long, rounded, reticulate.

CHROMOSOME NUMBER. $2n = 22$ (Alaska: *Kelso 84-05,* at ALA; Yukon: *Kelso and Holmes 84-21,* at ALA; Kamchatka: Sokolovskaya, 1968; Northeast Siberia: Zhukova et al., 1973; Norway: Engelskon, 1979; Borgen and Elven, 1983). $2n = 20$ (Mongolia: Hanelt, 1973; Lake Baikal, Siberia: Belaeva and Siplivinsky, 1975).

HABITAT. Salt marshes and estuaries along the coast, inland in sloughs and river flood plains.

DISTRIBUTION. Fennoscandia across northern and central Asia, coastal Alaska, rare in the interior of Alaska and the Yukon.

Until recently, *Primula nutans* has been known as *P. sibirica* Jacq. By the rules of the International Code of Botanical Nomenclature, the name *P. nutans* must be used because it antedates Jacquin's name by three years. Both Georgi and Jacquin used an unnamed Siberian primula (Gmelin, 1769) as the basis for their species. Jacquin apparently was not aware of Georgi's treatment when he named it *P. sibirica. Primula sibirica* was used by Duby (1844) in his monograph of the genus as the name *P. nutans* slipped into obscurity. Smith and Fletcher (1943) were aware of Georgi's treatment and listed *P. nutans* as a synonym of *P. sibirica,* but gave a later and erroneous date of publication (1797). Since the true date of publication of the name *P. nutans* is 1775, it takes precedence over *P. sibirica,* published in 1778. *Primula nutans* Georgi predates *P. nutans* Delavey, from China (section *Soldanelloides* Pax) which now becomes *P. flaccida* Balakr.

Although *Primula nutans* is geographically widespread, it is morphologically consistent. The only significant variation is in the relative lengths of calyx and corolla tube. Specimens from Fennoscandia have a corolla tube only slightly longer than the calyx; in Asiatic and North American specimens the corolla tube is twice the length of the calyx. The Scandinavian taxon is now treated as *P. nutans* subsp. *finnmarchia* (Jacquin) A. Löve & D. Löve (Löve and Löve, 1961; Mäkinen and Mäkinen, 1964).

In western Alaska *Primula nutans* is commonly found in estuarine marshes. It can be sympatric with *P. borealis* and the two species are often found mixed on herbarium sheets. *P. nutans* is easily distinguished from *P. borealis* by its ovate pedicellate leaves and auriculate bracts. It blooms approximately two weeks later than *P. borealis,* and unlike the latter, tolerates continually saturated soil.

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BOOK REVIEW

Peter Goldblatt and Dale E. Johnson, Eds. 1990. *Index to Plant Chromosome Numbers 1986–1987.* Pp. vi + 243. Monographs in Systematic Botany from the Missouri Botanical Garden 30. Missouri Botanical Garden, St. Louis, MO ($15.00)

The *Index to Plant Chromosome Numbers 1986–1987* is the most recent installment of a series invaluable to systematists, plant breeders, horticulturalists and other botanists as a guide to chromosome numbers of taxa at any level, or simply as an index to current research on a taxon. The number of periodicals reviewed (approximately 250) ensures that few chromosome counts have been missed, although the many counts reported in *Systematic Botany Monographs* are not cited.

The current volume covers the Fungi, Algae, Bryophytes, Pteridophytes, and Spermatophytes. Within each of the major taxa, families are in alphabetical order, with genera and species following in alphabetical order. Some users may find this treatment of all spermatophytes as a single taxon to be inconvenient—the *Pinaceae,* for example, falls between the *Phytolaccaceae* and the *Piperaceae.* Chromosome numbers provided for more than 10,000 taxa are either gametic or sporophytic numbers as cited in the original publication, and indicate pairing relationships (numbers of univalent, bivalents, etc.) where the original author(s) described these.

As with previous volumes in this series, the format is clear and information is easy to retrieve. The editors have included the ISSN and OCLC numbers of the periodicals reviewed to facilitate inter-library loan requests for articles cited. The editors also indicate that chromosome number citations from the years 1982–1987 will soon be available on-line, making the citations more easily accessible.

A striking, and somewhat distressing observation derived from scanning the pages of the *Index* is that few chromosome counts were reported from North American species, or by North American systematists. The omission of *Systematic Botany Monographs* may be a reason for this apparent under-representation, but this raises the concern that few systematists are using chromosome numbers in their work. In addition to the value of chromosome data in assessing systematic relationships, isoenzyme, or even nuclear DNA studies, cannot be done reliably without a knowledge of the chromosome numbers, pairing relationships, or ploidy levels of the organism as the basis for analysis.

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MEETING ANNOUNCEMENT
NEW ENGLAND BOTANY GRADUATE STUDENTS

The sixth annual New England Botany Graduate Student Meeting will be held at the University of Connecticut, Storrs, on Saturday, April 6, 1991. Graduate students from all New England states are invited to give short presentations on completed research or work in progress in all areas of botany. All interested persons are encouraged to attend. For more information, registration and abstract forms, please contact:

Jeanette Whitton (203) 486-4053 or -3937
or Thomas Mione (203) 486-1890

Department of Ecology and Evolutionary Biology
The University of Connecticut
Storrs, CT 06269-3042

NEBC AWARD
FOR THE SUPPORT OF BOTANICAL RESEARCH

The 1990 New England Botanical Club Award was given to Alison C. Dibble from the University of Maine for her project entitled, "Status of *Amelanchier nantucketensis,* Nantucket shadbush (Rosaceae: Maloideae), a narrow endemic of coastal Massachusetts."

The New England Botanical Club will again offer an award of $1000 in support of botanical research to be conducted in relation to the New England flora during 1991. This award is made to stimulate and encourage botanical research on the New England flora, and to make possible visits to the New England region by those who would not otherwise be able to do so. The award will be given to the graduate student submitting the best research proposal dealing with field studies in systematic botany, biosystematics, plant ecology, and plant conservation biology, but proposals for research in other areas of botany will also be considered. This award is not limited to graduate students at New England institutions, nor to members of the New England Botanical Club. Papers based on this research must acknowledge the NEBC's support, and it is encouraged that they be submitted to *Rhodora,* the Club's journal, for possible publication—subject to standard review processes.

Applicants should submit a proposal of no more than three double-spaced pages, a budget (the budget will not affect the amount of the award), and a curriculum vitae. Two letters, one from the student's major professor, in support of the proposed research are also required. Proposals and supporting letters should be sent before 28 February 1991 to:

Awards Committee
The New England Botanical Club
22 Divinity Avenue
Cambridge, MA 02138

The recipient of the award will be notified by 30 April 1991.

THE NEW ENGLAND BOTANICAL CLUB

22 Divinity Avenue
Cambridge, MA 02138

The New England Botanical Club is a non-profit organization that promotes the study of plants of North America, especially the flora of New England and adjacent areas. The Club holds regular meetings, has a large herbarium of New England plants, and a library. It publishes a quarterly journal, RHODORA, which is now in its 93rd year and contains about 400 pages a volume.

Membership is open to all persons interested in systematics and field botany. Annual dues are $30.00, including a subscription to RHODORA. Members living within about 200 miles of Boston receive notices of the Club meetings.

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Vol. 92, No. 872, including pages 213–314, was issued October 19, 1990

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Submission of a manuscript implies it is not being considered for publication simultaneously elsewhere, either in whole or in part.

Manuscripts should be submitted in **triplicate** (an original and two xerographic copies) and *must be double-spaced* (at least 3/8") **throughout** including tables, figure legends, and literature citations. The list of legends for figures and maps should be provided on a separate page. Footnotes should be used sparingly. Do not indicate the style of type through the use of capitals or underscoring, particularly in the citation of specimens. Names of genera and species may be underlined to indicate italics in discussions. Specimen citations should be selected critically, especially for common species of broad distribution. Systematic revisions and similar papers should be prepared in the format of "A Monograph of the Genus *Malvastrum,*" S. R. Hill, Rhodora 84:1–83, 159–264, 317–409, 1982, particularly with reference to indentation of keys and synonyms. Designation of a new taxon should carry a **Latin diagnosis** (rather than a full Latin description), which sets forth succinctly just how the new taxon is distinguished from its congeners. Papers of a floristic nature should follow, as far as possible, the format of "Annotated List of the Ferns and Fern Allies of Arkansas," W. Carl Taylor and Delzie Demaree, Rhodora 81: 503–548, 1979. For bibliographic citations, refer to the Botanico-Periodicum-Huntianum (B-P-H, 1968) which provides standardized abbreviations for journals originating before 1966. All abbreviations in the text should be followed by a period, except those for standard units of measure and direction (compass points). For standard abbreviations and for guidance in other matters of biological writing style, consult the *CBE Style Manual,* 5th ed. (original title: *Style Manual for Biological Journals*). In preparing figures (maps, charts, drawings, photos, etc.) please remember that the printed plate will be 4 × 6 inches; be sure that illustrations are proportioned to reduce correctly, and indicate by blue pencil the intended limits of the figures. (Some "turn-page" figures with brief legends will be 3½ × 6 in.) Magnification/reduction values given in text or figure legends should be calculated to reflect the actual printed size. An Abstract and a list of Key Words should be supplied at the beginning of each paper submitted, except for a very short article or note. All pages should be numbered in the upper right-hand corner. Brevity is urged for all submissions.

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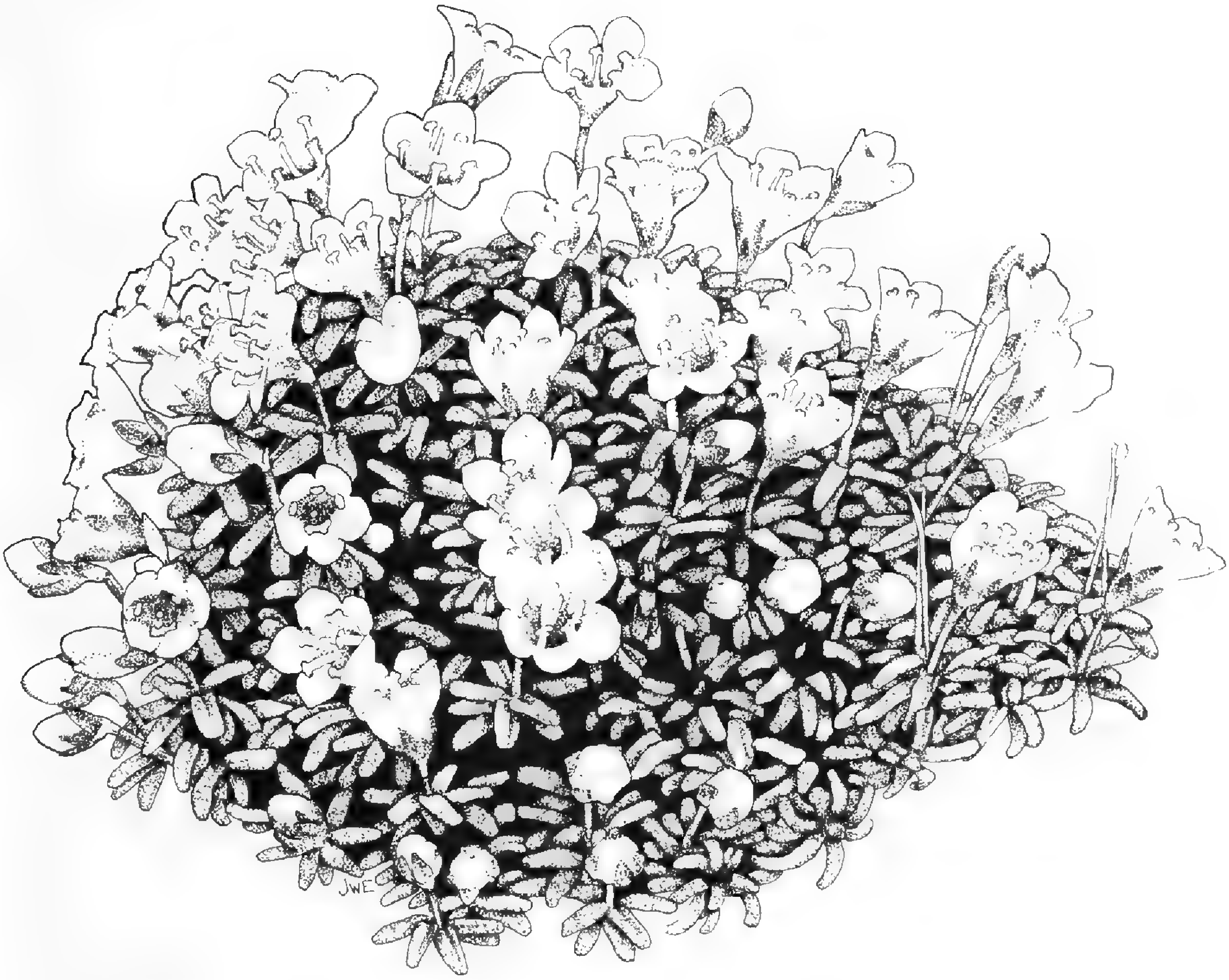

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Cover Illustration

Diapensia lapponica L. ssp. *lapponica*. Found on the higher mountains of northern New England, this Arctic circumpolar early-blooming tussock plant is a rare disjunct to New England. Original artwork by Josephine Ewing.

Rhodora

JOURNAL OF THE

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RHODORA, Vol. 93, No. 874, pp. 105–122, 1991

ADIANTUM VIRIDIMONTANUM, A NEW MAIDENHAIR FERN IN EASTERN NORTH AMERICA

Cathy A. Paris

ABSTRACT

Recent systematic work on the *Adiantum pedatum* L. complex has demonstrated that the serpentine maidenhair fern in eastern North America, to which the name *A. pedatum* L. var. *aleuticum* Rupr. has traditionally been applied, is a disjunct member of the western North American lineage, a lineage divergent at the species level from the typical maidenhairs of the eastern woodlands. Also present in eastern North America is a previously unrecognized tetraploid species, the allopolyploid derivative of a sterile hybrid between the serpentine and the typical maidenhair ferns. Here a description of the new species is provided and a new combination is proposed for the western North American maidenhairs, including the disjunct serpentine populations in eastern North America. Although phenotypic plasticity, the existence of the previously unrecognized allotetraploid, and the presence of backcross hybrids have obscured species boundaries, the three species in North America are morphologically distinct and can be reliably separated using non-technical characters.

Key Words: *Adiantum*, maidenhair ferns, serpentine vegetation, Vermont

The *Adiantum pedatum* complex, the northernmost element of a genus widespread in the Old and New World tropics, is widely distributed in temperate regions of North America, eastern Asia, and the Himalayas. In eastern North America, two taxa have traditionally been recognized, *A. pedatum* L. *sensu stricto* and a smaller maidenhair of serpentine substrates, first reported by Fernald from the Shickshock Mountains of Québec (Fernald, 1905). Fernald referred this new maidenhair to *A. pedatum* L. var. *aleuticum* Rupr., the common maidenhair of wet rocks and ravines from California and Idaho north to Alaska. The occurrence of *A. pedatum* var. *aleuticum* and other western cordilleran species on the Gaspé Peninsula later figured in Fernald's argument that large areas of the Gulf of St. Lawrence region remained unglaciated during the Pleistocene (Fernald, 1925; Paris, 1989). *Adiantum pedatum* var. *aleuticum* was subsequently located on numerous serpentine outcrops throughout southeastern Canada and New England (Jolley, 1922; Rugg, 1922; Mousley, 1923; Gawler, 1983; Zika and Dann, 1985).

Cody (1983) re-evaluated the relationship of the eastern serpentine maidenhair to those of the western mountains and concluded that Fernald was mistaken. After having examined more than 400 sheets of *Adiantum pedatum* from various habitats on both sides of the continent, Cody concluded that non-serpentine populations in western North America were even more distinct from the serpentine maidenhair than they were from the typical variety. He thus removed the serpentine maidenhair from *A. pedatum* var. *aleuticum* and described a new taxon, *A. pedatum* L. ssp. *calderi* Cody, comprising the maidenhairs on serpentine and sometimes dolomitic substrates in northeastern North America, Washington, and California. A chromosome count of $n = 29$ was provided for the new taxon, the same as for ssp. *pedatum* and ssp. *aleuticum* (Cody, 1983).

The relationship of the serpentine and the typical maidenhairs was recently clarified in a systematic study of the *Adiantum pedatum* complex in eastern North America (Paris and Windham, 1988). Results of an electrophoretic survey of two serpentine and six woodland (i.e., typical) populations showed that the two taxa are well differentiated genetically: the mean genetic identity value of .49 obtained for between-taxon population comparisons is typical in the ferns of congeneric species, not subspecies or varieties (Haufler, 1987). The low genetic identity of the two maidenhairs indicated that they are probably not related as progenitor and derivative. On the basis of preliminary isozyme evidence, Paris and Windham (1988) proposed that the eastern serpentine maidenhair was most closely allied to those of the western mountains, the relationship originally suggested by Fernald. Another important result of the study was the detection of a third species in eastern North America, an allotetraploid derived from a sterile hybrid between the serpentine and typical maidenhairs. The new species is so far known only from a few serpentine outcrops in north-central Vermont. Evidence for the allopolyploid origin of the new species has been presented elsewhere (Paris and Windham, 1988).

Ongoing isozyme and chloroplast DNA studies of the *Adiantum pedatum* complex worldwide indicate that maidenhairs in North

America represent two discrete lineages: *A. pedatum sensu stricto,* the typical maidenhair of eastern woodlands; and a western lineage, to which Ruprecht (1845) gave the name var. *aleuticum.* Results of these molecular studies confirm that the maidenhair on serpentine in eastern North America is a disjunct member of the western lineage (Paris and Stein, 1989; Paris, unpubl. data).

The new information on evolutionary relationships within the *Adiantum pedatum* complex demonstrates that taxonomic revision of the group is in order. The purpose of the present contribution is to provide a description of the new tetraploid species, to make a new combination at the species level for the western North American lineage in the *A. pedatum* complex, and to supply a key to the three species in North America.

LEAF ARCHITECTURE IN *ADIANTUM PEDATUM* S.L.

Fundamental to an accurate and comprehensible description of taxa in the *Adiantum pedatum* complex is a correct understanding of leaf architecture in the group. The *A. pedatum* leaf has traditionally been misinterpreted as pedately divided, with arching pinnae borne on the upper side of a dichotomizing rachis. This description is unlikely, however, in that dichotomizing axes are otherwise unknown in the Polypodiaceae *sensu lato.* Apparently the developmental program in this group of ferns is dedicated to the production of a pinnate leaf. Although Slosson (1906) provided a largely accurate explanation of *A. pedatum* leaf architecture, and Wagner (1952, 1956) subsequently improved upon it, these works have not yet influenced the way maidenhair leaves are described in the literature. The observations of Slosson and Wagner are summarized here as a basis for an accurate description of the maidenhair leaf in this and subsequent contributions.

Adiantum pedatum shows a heteroblastic series from simply pinnate leaves to leaves with the basal pinnae progressively elaborated. Leaf complexity is increased in successively older plants by increasing enlargement and dissection of the basal basiscopic segments of the first and second basal pinnae, a pattern that is reiterated in higher order divisions of the basal pinnae (Slosson, 1906, *see* p. 42, plate 3, figs. 9 & 10). Because it is always the basal basiscopic segment that is elaborated, without proliferation of the corresponding acroscopic segment, each order of dissection features paired segments with the basal acroscopic member simple and the basal basiscopic member compound. This pattern produces a leaf in which isolated simple segments (the acroscopic members of segment pairs) alternate with pinnate axes along what appears to be the acroscopic side of an arching dichotomous rachis (Figure 1). Spatial constraints on the pattern of reiterated basal basiscopic development produce the familiar fan-shaped leaf blade. The major fork in the blade axis is produced by the departure of the much enlarged first basal pinna from the rachis, and so does not represent a true dichotomy (Wagner, 1952). The second basal pinna, though similarly enlarged, does not form a conspicuous fork.

Leaf architecture in *Adiantum pedatum* follows from a simple modification of the standard pattern of leaf development in the higher ferns; thus it is both appropriate and advisable to use standard terminology (Tryon, 1960) to describe the maidenhair leaf. The rachis of the maidenhair leaf is a continuation of the petiole axis, as it is in most ferns, but it has been displaced laterally by the greatly enlarged first basal pinna (Figure 1). Located to the other side of the rachis is the main axis of the second basal pinna. The next "branches" outward from these two are the proliferated basal basiscopic segments of the basal pinnae, and so forth. The term *pseudopedate* is suggested for the modified-pinnate type of leaf architecture found in *A. pedatum* and a few of its congeners (e.g., *A. aleuticum, A. hispidulum, A. oatesii, A. patens*), in preference to *pedate,* which describes a palmate leaf design.

NEW SPECIES

Adiantum viridimontanum Paris *sp. nov.* (Figure 2)

Ab *Adianto pedato* L. et *A. aleutico* (Rupr.) Paris indusio falso longiore saepe plus quam 3.5 mm, sporis grandioribus circa 51.3 μm in diametro differt; illo segmentis ultimis triangularibus acutis, chartaceis, marginibus basiscopicis obliquis; hoc petiolulis longioribus.

Medium-sized terrestrial fern. Rhizomes slender, 2.0–3.5 mm diam., short-creeping, branching occasionally; rhizome scales concolorous bronzy-fulvous, lustrous, lanceolate, attenuate, with an ephemeral, filiform, ± tortuous apex, entire, conform, loosely appressed. Leaves deciduous, 30–75 (–90) cm long, arching to stiffly erect, often densely clustered, anadromous (in some leaves, the higher order divisions catadromous); petioles castaneous to

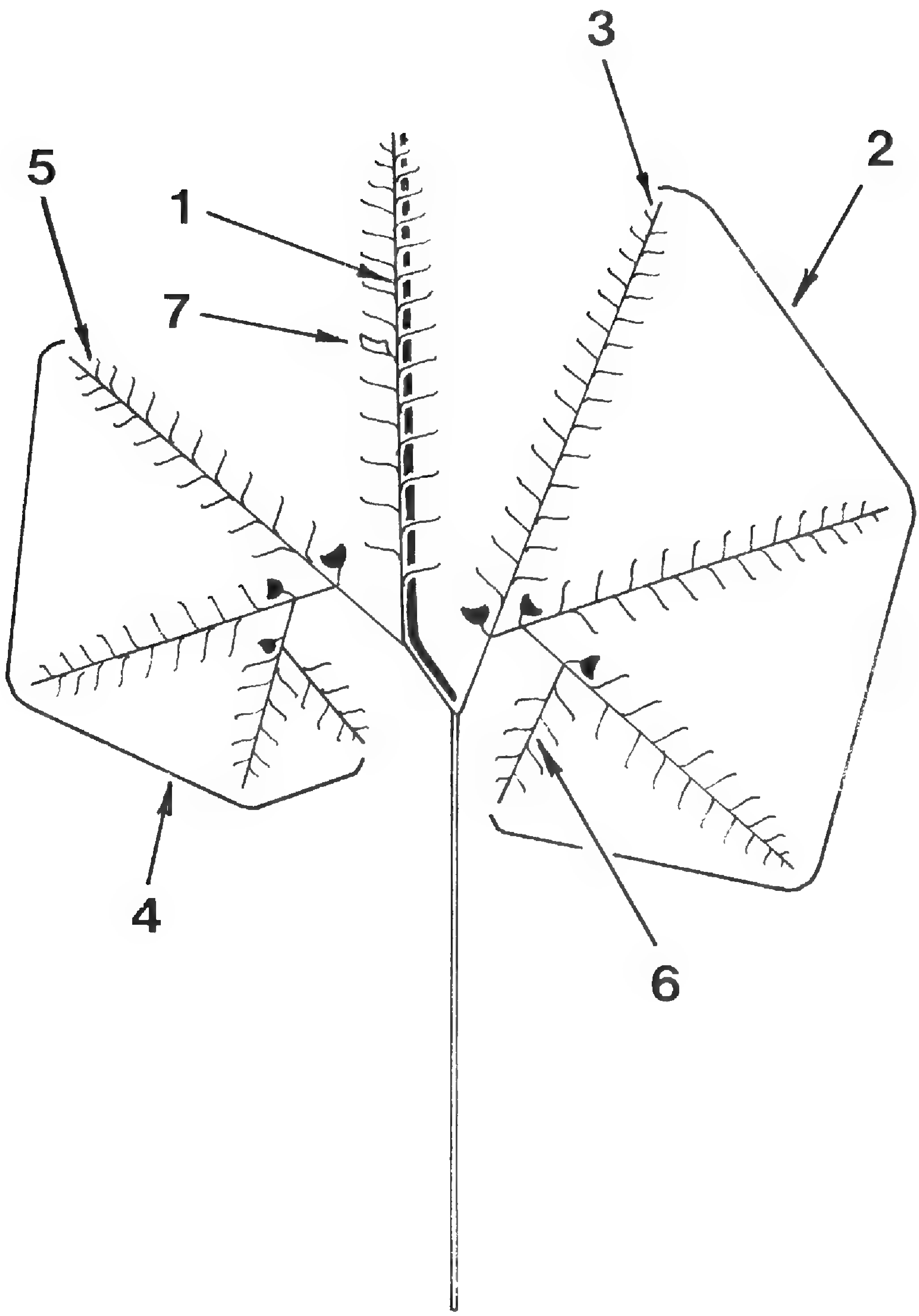

Figure 1. Schematic representation of the pseudopedate leaf of *Adiantum pedatum* and several of its congeners, including *A. aleuticum* and *A. viridimontanum*. **1** = rachis (shaded); **2** = first basal pinna; **3** = axis of first basal pinna; **4** = second basal pinna; **5** = axis of second basal pinna; **6** = highest-order axis; 7 = medial ultimate segment. Shaded segments are the simple acroscopic members of segment pairs, which alternate with pinnate axes along what appears to be the acroscopic side of an arching dichotomous rachis.

Figure 2. Holotype of *Adiantum viridimontanum* (Belvidere Mountain, Eden, Vermont, 28 August, 1985, *Paris 856* (VT)).

atropurpureous, lustrous, 2.0–3.0 mm diam., with a single, gutter-shaped vascular bundle, petiole scales similar to the rhizome scales but more or less spreading, tortuous, fugacious except at petiole base; blades flabellate in shade to funnel-shaped in full sun (flattened in pressed specimens), pseudopedate, 10–35 × 10–

35 (–45) cm, basal pinnae (2–) 3–7-pinnate and much enlarged basiscopically, blade 1-pinnate above, the apical part of the blade narrowly oblong to lanceolate, scarcely exceeding the basal pinnae; rachis castaneous to atropurpureous, lustrous, straight, displaced somewhat by the first basal pinna, 1–2 mm diam., glabrous. Ultimate segments long-triangular, 9.5–22.5 × (3.8–) 4.2–7.5 mm, ca. 2.5 times as long as broad; borne in the plane of the blade in shade, often twisted out of the plane of the blade in full sun; the acroscopic margin lobed, the lobes separated by narrow (usually less than 1.0 mm) incisions; the basiscopic margin oblique; the apex acute, usually entire; firm-herbaceous to chartaceous; glabrous; stalks short, (0.4–) 0.6–1.5 (–1.9) mm, the dark color commonly passing into the segment base; fertile segments with marginal lobes recurved to form conspicuous false indusia, these transversely oblong, mostly 2–5 (–10) × 0.6–1.4 mm, dark brown at maturity, with scarious margins. Sori more or less round, subterminal on veins that end in the false indusium, borne on the abaxial surface of the false indusium. Spores tetrahedral-globose, yellow, mostly 45–58 μm diam. (mean = 51.4 μm diam.), perispore smooth. Gametophytes superficial, cordate, glabrous. n = 58 (Paris and Windham, 1988).

Sporulating summer-fall. Restricted to serpentine sites, where it occurs in rock clefts, on talus slopes, and in well-developed serpentine soils. 245–800 m. North-central Vermont.

TYPE: U.S.A. Vermont. Lamoille Co., Eden: Belvidere Mountain, exposed SE-facing talus slope at the pit of the old asbestos mine, 800 m, 28 August, 1985, *Paris 856* (HOLOTYPE: VT; ISOTYPES: GH, US).

ADDITIONAL SPECIMENS EXAMINED: U.S.A. Vermont: Lamoille Co.: **Eden**: Belvidere Mountain, exposed SE-facing talus slope at the old asbestos mine, 800 m, *Paris 341* (NY); dry embankment, road to the old asbestos mine, in rocky but well-developed soil, 770 m, *Paris 337* (VT); road to the old asbestos mine, in well-developed soil, in shade, 750 m, *Paris 208* (VT); *Mrs. Jolley, s.n.* in July 1922 (GH); Orleans Co.: **Lowell**: dunite roadcut, N & S sides of Vt. Rte. 58, ca. 0.5 mi. W of Vt. Rte. 100, 275 m, *Dann & Zika 6156* (VT); dunite roadcut, E side of Vt. Rte. 100, at the Lowell town line, 260 m, *Paris 888 & 889* (VT); E- and W-facing dunite outcrops, Brown's Ledges, 450 m, *Dann & Zika 6168 & 6169* (VT); **Westfield**: dunite knob near Mineral Springs Brook, 245 m, *Dann 8323* (VT); Franklin Co.: **Montgomery**: *Mrs. Jolley s.n.* in 1924 (GH).

Adiantum viridimontanum, the Green Mountain maidenhair fern, is the allotetraploid derivative of a hybrid between *A. pe-*

datum sensu stricto and *A. aleuticum* (Paris and Windham, 1988). The species reproduces sexually and 64 normal spores are formed at meiosis. Presumed to be of recent origin, it is at present known from only five locations, all on serpentine, in north-central Vermont. Mrs. F. L. Jolley first located the plant (identified as *A. pedatum* var. *aleuticum*) in 1922, at the asbestos mine on Belvidere Mountain. The other four stations were found by Vermont botanists Peter Zika and Kevin Dann (Zika and Dann, 1985). Mrs. Jolley's 1924 Montgomery station has not been relocated. Additional populations of the species may eventually be discovered elsewhere in Vermont and southern Québec, particularly in the vicinity of the asbestos mines in the Black Lake area of Megantic Co.

NEW COMBINATION

Adiantum aleuticum (Ruprecht) Paris, *stat. et comb. nov.*

Adiantum pedatum L. var. *aleuticum* Ruprecht, Distr. crypt. vasc. Ross. 3: 49. 1845. Lectotype (here chosen): Unalaschka, *Chamisso* (fragment ex LE, NY!). The remaining syntype is: Kadiak, Langsdorf. *A. pedatum* L. ssp. *aleuticum* (Ruprecht) Calder & Taylor, Canad. J. Bot. 42: 1388. 1965.

A. pedatum L. var. *subpumilum* Wagner in Wagner & Boydston, Canad. J. Bot. 56: 1727. 1978. Type: British Columbia: Brooks Peninsula, NW Vancouver Island, 27 June, 1977. *J. Pojar & F. Boas 770191* (Holotype: MICH; isotypes: V, UBC!). *A. pedatum* L. subsp. *subpumilum* (Wagner *in* Wagner & Boydston) Lellinger, Amer. Fern J. 74: 62. 1984.

A. pedatum L. ssp. *calderi* Cody, Rhodora 85: 93. 1983. Type: Québec, Gaspé County, cold, sheltered ravines, Mt. Albert, 14 August, 1905. *J. F. Collins & M. L. Fernald s.n.* (Holotype: DAO; isotype: GH!)

Adiantum boreale K. Presl, Tent. Pterid. 158. 1836, *nom. nud.* Collection cited: Unalaschka, *Chamisso.*

Adiantum aleuticum is the common maidenhair of the Sierra Nevadas, the Cascades, and the Coast Range, from central California north to Glacier Bay, Alaska, and west through the Aleutian Islands. Disjunct populations occur in the northern Rocky Mountains of Idaho, where it is part of the Cascadian floristic element there (Alverson, 1989), and on serpentine in southeastern Canada and northeastern U.S.A. Collections have also been reported from dolomites in Newfoundland (cited in Cody, 1983); these reports may be in error, as the taxon does not occur on dolomites elsewhere in northeastern North America.

Adiantum aleuticum occurs in a variety of habitats throughout its range. In western North America, it is most common in humid, wooded ravines and on creek banks, but it is also found on sunny talus slopes, serpentine barrens, wet rock fissures, and coastal headlands. In eastern North America it is limited to serpentine. Although there are morphological differences among populations in these diverse habitats, the differences are not consistent or predictable. More significantly, genetic divergence among populations in these various habitats is limited, as shown by the results of chloroplast DNA and isozyme studies of the group (Paris and Stein, 1989). In consequence, infraspecific taxa are not here recognized within *A. aleuticum.*

KEY TO THE *ADIANTUM PEDATUM* COMPLEX IN NORTH AMERICA

The following key is written to work equally well with living or preserved materials; characters not observable in most herbarium specimens are therefore excluded. Problematic individuals may be backcross or diploid hybrids and should be examined for abortive spores.

1. Medial ultimate segments ± oblong; blade lax-arching, flabellate; plants generally growing in shade . . . . 2.
    2. Medial ultimate segments usually less than 3.2 times as long as broad, the apices with rounded, crenulate or crenato-denticulate lobes, these separated by shallow sinuses 0.1–2.0 (–3.7) mm deep, incisions in acroscopic margin narrow, generally less than 1.0 mm broad, borne on stalks ca. 0.6–0.9 mm; eastern North America . . . . *A. pedatum*
    2. Medial ultimate segments usually more than 3.2 times as long as broad, the apices with angular, sharply denticulate lobes, these separated by deeper sinuses 0.6–4.0 mm, incisions in acroscopic margin broader, mostly greater than 1.0 mm broad, borne on stalks up to 0.6 mm long; western North America . . . . *A. aleuticum*
1. Medial ultimate segments ± long-triangular; blade arching to stiffly erect, flabellate to funnel-shaped; plants generally growing in exposed situations . . . . 3.
    3. Medial ultimate segments borne on stalks shorter than 0.9 mm; false indusia mostly less than 3.5 mm long; spores mostly less than 47 μm diam.; western North America, disjunct on serpentine in eastern North America . . . . *A. aleuticum*

3. Medial ultimate segments borne on stalks generally longer than 0.9 mm; false indusia longer, the longest frequently exceeding 3.5 mm; spores mostly greater than 47 μm diam.; serpentine outcrops in north-central Vermont . . . . *A. viridimontanum*

PATTERNS OF VARIATION AND TAXONOMIC CHARACTERS

Although *Adiantum pedatum* and its allies occur in a region whose flora is among the best known in the world, a satisfactory taxonomic treatment of the group has so far eluded botanists despite several worthy efforts in that direction. Disagreement has occurred because patterns of variation within the *A. pedatum* group are complex, and there is a general incongruence of the genetic and phenetic units within it, especially in *A. aleuticum.* Nevertheless, the species are distinct and can be reliably separated using standard morphological characters (Table 1).

Intraspecific Variation in *Adiantum aleuticum*

A particular challenge to the maidenhair-fern taxonomist has been presented by *Adiantum aleuticum,* a species in which phenotypic plasticity is superimposed on abundant genetic variation. Based on field observations (my own and others', e.g., Fernald, 1905; Alverson, pers. comm.), degree of exposure, particularly to light, is the key environmental variable to which morphology is responding in that species. In full sun, *A. aleuticum* has stiffly erect, funnel-shaped leaf blades and small ultimate segments twisted on their stalks; in the shade it bears a greater resemblance to *A. pedatum,* with lax-arching leaf blades and larger ultimate segments borne in the plane of the blade. Morphological variation in *A. aleuticum* presents itself as an array of forms that grade insensibly into one another according to degree of insolation; there are no gaps delimiting subspecies. Nevertheless, several subspecific taxa have been recognized and so deserve comment.

The serpentine maidenhair fern, referred by Fernald (1905) to *Adiantum pedatum* var. *aleuticum,* was recognized by Cody (1983) as a distinct taxon, *A. pedatum* subsp. *calderi.* Considering the evidence, I concur with Fernald, though I recognize *aleuticum* as specifically distinct from *pedatum,* as stated previously. To fairly evaluate the status of the serpentine maidenhair fern, it must be considered in the context of the species as a whole. In eastern North America, the serpentine and the non-serpentine maidenhair ferns represent different species. The former, part of *A. aleuticum,* is almost always stiffly erect, whereas the latter, *A. pedatum,* is lax–arching. Thus the two are seldom confused, although species boundaries have been blurred to some extent by hybridization and allopolyploidy. In western North America, however, maidenhairs are all part of the ecologically diverse and morphologically variable *A. aleuticum*; in the west, plants on serpentine are dubiously distinct from those in exposed but non-serpentine localities. Compare, for instance, a serpentine collection (e.g., *Paris 268,* [VT], Scheele Mine, Twin Sisters Mountain, Washington) with one from an exposed non-serpentine site (e.g., *Van Dyke 67,* [GH], Unalaska, Alaska—the type locality for subsp. *aleuticum*). Both collections have leaf blades equivalently small and stiffly erect, with ultimate segments twisted on their stalks. By contrast, plants growing in shaded microsites on serpentine barrens (e.g., *Paris XX.C,* [VT], Horse Mountain, Trinity Mountains, California) have lax leaves similar to plants in wooded non-serpentine sites (e.g., *Paris 274,* [VT], Perry Creek Trail, Mt. Baker–Snoqualmie National Forest, Washington). Although variation in characters such as stature and leaf attitude is obviously related to habitat in *A. aleuticum,* such variation is not entirely the result of phenotypic plasticity. Results of common garden trials show that the distinctive characters of plants from serpentine areas and other exposed sites persist to some extent in common culture, indicating that the character state differences have a genetic basis. Thus it appears that ecotypic differentiation is occurring under different light regimes in *A. aleuticum*; the maidenhairs of serpentine soils and other open, sunny sites on lithosolic substrates might best be considered a set of ecotypes. Recognition of the serpentine maidenhair as a distinct subspecies, however, is untenable.

Another taxon that has been recognized in the lineage now designated *Adiantum aleuticum* is *A. pedatum* subsp. *subpumilum* (Wagner *in* Wagner and Boydston) Lellinger, a dwarf maidenhair of coastal cliffs in the Pacific Northwest. This taxon, well known to horticulturalists, was only recently (in 1977) located in nature; currently three stations are known. Plants referred to subsp. *subpumilum* are diminutive in stature and have imbricate ultimate segments with excavate basiscopic margins, characters for which

Table 1. Comparison of *Adiantum pedatum*, *A. aleuticum*, and *A. viridimontanum*. The eastern serpentine maidenhair (part of *A. aleuticum*) is also shown separately (ES). Asterisks mark the characters that best discriminate species. Nu-

	Species	
Character	*A. pedatum*	*A. aleuticum*
PLANT HEIGHT	40–75 cm	15–110 cm
RHIZOME		
*Internode length	2.0–10.0 mm	1.0–5.0 mm
*Branching	occasionally to frequently (rhizome not congested)	occasionally to frequently (rhizome congested or not)
LEAF		
Attitude	lax-arching	lax-arching to stiffly erect
BLADE		
Shape	flabellate	flabellate to funnel-shaped
Recurvature, highest order axes of basal pinnae	recurved toward petiole	recurved to spreading or ascending
Dissection, basal pinnae	3–9-pinnate	(1–) 2–7-pinnate
Rachis, length relative to axis of first basal pinna	0–30 mm	0–54 mm
Apex	obtuse to acute	acute to occasionally obtuse
MEDIAL ULTIMATE SEGMENTS		
Shape	oblong	oblong, long-triangular, or occasionally reniform
Length	14–26 (–28) mm	6–34 mm
Width	5–9 mm	4–9 mm
L/W ratio	2.2–3.7 (–4.0)	1.4–4.4 (–4.8)
Attitude	in plane of blade	in plane of blade in shade, twisted out of plane in full sun
Breadth of incisions, acroscopic margin	0.0–0.9 (–1.1) mm	0.2–3.0 mm
Basiscopic margin	straight	straight, oblique, or occasionally excavate
Apex	obtuse, with rounded, crenulate, or crenato-denticulate lobes, these separated by shallow sinuses	obtuse, with angular, sharply denticulate lobes, these separated by deeper sinuses; or acute, entire

merals in the righthand column indicate treatments in which a given character was used in keys or diagnoses. 1 = Ruprecht, 1845; 2 = Fernald, 1950; 3 = Calder and Taylor, 1968; 4 = Cody, 1983; 5 = Lellinger, 1985.

Species		
A. aleuticum (ES)	*A. viridimontanum*	Treatments
15–59 (–64) cm	30–75 (–90) cm	1, 4
1.0–2.0 mm	4.0–7.5 mm	2, 3, 4
frequently (rhizome congested)	occasionally (rhizome seldom congested)	2
mostly stiffly erect	arching to stiffly erect	2, 3, 4, 5
mostly funnel-shaped	flabellate to funnel-shaped	2
mostly ascending	usually spreading to ascending	2, 3, 4, 5
1–6 (–7)-pinnate	(2–) 3–7-pinnate	1, 3
0–30 mm	3–45 mm	
acute to occasionally obtuse	acute	5
long-triangular	long-triangular	
6–18 (–21) mm	9–23 mm	2, 3, 4, 5
3–7 (–8) mm	4–8 mm	
1.4–3.0 (–3.5)	(1.4–) 1.7–3.5	
in plane of blade in shade, twisted out of plane in full sun	in plane of blade in shade, twisted out of plane in full sun	2
0.0–0.9 (–1.1) mm	0.0–1.0 (–1.2) mm	3, 4
oblique	oblique	
acute, entire	acute, usually entire	3, 5

Table 1. Continued.

Character	Species *A. pedatum*	 *A. aleuticum*
Color	bright green	bright to bluish-green, occasionally glaucous
Texture	weakly herbaceous to herbaceous	herbaceous to chartaceous
*Stalk length	0.5–1.5 (–1.7) mm ($\bar{x}$ = 0.9 mm)	0.2–0.9 (–1.3) mm ($\bar{x}$ = 0.6 mm)
FALSE INDUSIUM		
Length	1.0–3.0 mm	0.2–3.5 (–6.0) mm
Width	0.3–1.0 mm	0.2–1.3 mm
*SPORE SIZE (diameter)	32–42 (–46) μm ($\bar{x}$ = 37.0 μm)	(31–) 34–53 μm ($\bar{x}$ = 43.6 μm)
CHROMOSOME NUMBER	$n = 29$	$n = 29$
HABITAT	deciduous woodlands, often on humus-covered talus	moist, wooded ravines, serpentine areas, coastal cliffs, etc.

the plants breed true (Wagner and Boydston, 1978). Although the dwarf maidenhairs differ from other members of the species in several noteworthy characteristics, observations of the plants in nature call their subspecific status into question. At the one station I have visited, typical "subpumilum-type" plants occur on cliff faces exposed to the sea, but away from the cliffs and back up the canyons, plants look more like normal *A. aleuticum.* Between the two extreme forms, a range of intermediates exists. This pattern of variation along an environmental gradient suggests that the dwarf plants of the cliff faces represent an ecotype, not a subspecies. In consequence, subsp. *subpumilum,* like subsp. *calderi,* is not maintained in the present treatment.

Interspecific Comparisons

In eastern North America, *Adiantum pedatum sensu stricto* and *A. aleuticum* are most reliably distinguished using attributes of the ultimate segments, though they also differ in size, rhizome habit, leaf attitude, texture, color, dissection, mean spore size, and habitat preference (Table 1). More problematic is distinguishing

Table 1. Continued.

Species		
A. aleuticum (ES)	*A. viridimontanum*	Treatments
usually bluish-green, glaucous	bright to bluish-green	2, 3, 4, 5
mostly chartaceous	firm-herbaceous to chartaceous	2
0.3–1.3 mm ($\bar{x}$ = 0.7 mm)	(0.4–) 0.6–1.5 (–1.9) mm ($\bar{x}$ = 1.1 mm)	
0.8–2.9 (–3.4) mm	2.0–5.0 (–10.0) mm	2, 3, 4, 5
0.5–1.3 mm	0.6–1.4 mm	
(31–) 34–52 (–53) μm ($\bar{x}$ = 43.0 μm)	(35–) 41–62 (–69) μm ($\bar{x}$ = 51.4 μm)	
n = 29	n = 58	
serpentine	serpentine	

A. pedatum from *A. aleuticum* as it appears in moist, wooded ravines, its most common habitat in the American West. Although the western maidenhair fern (as *A. pedatum* ssp. *aleuticum*) has been described as having "branches (of the fronds) usually strongly ascending" (Calder and Taylor, 1968; Cody, 1983), that character is by no means diagnostic: in the shade, *A. aleuticum* has a lax–arching leaf blade much like that of *A. pedatum*. The species can be distinguished, however, using characters of the medial ultimate segments. Medial ultimate segments of *A. aleuticum* are relatively long and narrow, with broad incisions in the acroscopic margin that give them a "saw-toothed" appearance. Segment apices have angular lobes with sharply denticulate margins. Medial ultimate segments of *A. pedatum*, by contrast, are broader relative to their length, have narrower, less prominent incisions, and their apices are round–lobed with crenulate or crenato-denticulate margins. The two species also differ in several attributes of the leaf blade: in *A. aleuticum*, the leaf is less dissected (i.e., has fewer "branches"), the rachis tends to be conspicuously longer than the axes adjacent to it, and the segments on each axis taper to an acute apex. These characteristics, taken together, suggest a human hand. For this reason, *A. aleuticum* is sometimes called the "five-finger fern," a name never applied to *A. pedatum,* which has a decidedly more fan-shaped leaf blade. The two species also differ in rhizome habit and in spore size (Table 1).

Structural variation in response to light level, common in *Adiantum aleuticum,* also occurs in the tetraploid *A. viridimontanum.* Intermediate (*sensu* Barrington, 1986) between its progenitor diploids in most structural characters, the tetraploid bears a generally greater resemblance to *A. aleuticum* as it appears on serpentine and other exposed sites, having stiffly erect, funnel-shaped leaf blades and small ultimate segments twisted on their stalks (e.g., *Paris 856,* VT, GH, US). In the shade, however, it bears a greater resemblance to *A. pedatum,* with lax–arching, fan-shaped leaf blades and larger ultimate segments borne in the plane of the blade (e.g., *Paris 208,* VT). *Adiantum viridimontanum* is best separated from both *A. pedatum* and *A. aleuticum* by its longer false indusia, which often exceed 3.5 mm, by the longer stalks of the ultimate segments, and by its larger spores (mean diameter = 51.3 μm).

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OCCURRENCE OF AN ANTHOCYANIN-LACKING FORM OF ELEPHANT'S-HEAD LOUSEWORT, *PEDICULARIS GROENLANDICA* (SCROPHULARIACEAE)

R. J. STANIFORTH, P. F. MAYCOCK, AND J. SVOBODA

ABSTRACT

A new, pale form of *Pedicularis groenlandica* Retz. (elephant's-head lousewort) from Churchill, Manitoba is described as forma *chlorina* Staniforth, Maycock & Svoboda. Individuals of this form lack the normal reddish anthocyanin pigment found throughout foliage, stems and flowers of the type variety. Six mature plants possessed old infructescences that predated their discovery by three years. These structures, together with the observation of numerous seedlings and presence of developing seeds in capsules, suggested that the colony is well established. Information regarding a new far-northern record of the white flowered form (f. *alba* Cody) of *P. lanata* Cham. & Sch. is provided.

Key Words: *Pedicularis groenlandica,* forma *chlorina,* Manitoba

INTRODUCTION

The herbaceous genus *Pedicularis* (louseworts), family Scrophulariaceae, is represented in Canada by twenty-two species (Scoggan, 1978), many of which have brightly colored flowers, strong fragrances, and intricate flower forms. In many species, local populations have been described which differ from the type species with respect to flower color, corolla shape and degree of pubescence (*see* Scoggan, 1978). In July 1985, the authors discovered a population of pale green, white-flowered individuals of the normally purple-red *P. groenlandica* Retz. (elephant's-head lousewort) near Churchill, Manitoba. This form has not been previously described.

DESCRIPTION OF FORMA *CHLORINA*

The purplish anthocyanin pigments in the leaves, stems, sepals and petals of normal plants were absent in this form, so that the plants appeared greenish-yellow and the flowers white. A diagnosis of this new form follows:

Pedicularis groenlandica Retz. f. **chlorina** *forma nova*

A typo differt corollis albis non pupureis, et caulibus foliisque chlorinis non purpureis.

Ramets of forma *chlorina* were collected and preserved as the form holotype in the herbarium of Erindale College, University of Toronto (TRTE). Lepage (1951) described two new forms of *Pedicularis groenlandica* from Fort George in northern Quebec: forma *pallida* and forma *gracilis.* The former has white flowers (drying to yellowish) with purplish bases, and the latter was a slender plant with normal, colored flowers and vegetative parts. Abrams (1951) lists subspecies *surrecta* (Benth.) Piper which has pale flowers and long beaks on the galeas and capsules. None of these forms is the same as that described here.

Pedicularis groenlandica forma *chlorina* was identical to the pigmented plants, apart from coloration and vigor (Figure 1). The population of forma *chlorina* was at the same stage of maturity; i.e., flowering was three-fourths completed by July 29, 1985. Plant height (mean 30.4 cm), numbers of reproductive spikes per plant (mean 3.2), numbers of blossoms and/or capsules per spike (mean 30.0) as measured for forma *chlorina* appeared comparable to that of the normal form, for which data are unfortunately not available. An opened capsule contained numerous white, ripening seeds, which appeared to be as well-developed as those from adjacent, normally-pigmented plants. They were obviously viable since there was a dense carpet of seedlings under the plants. The stems of the green plants appeared more robust, as if the energy required to produce the red pigment was shunted into some other function.

SITE AND HABITAT DESCRIPTION

A total of six reproductively mature plants of forma *chlorina* was found amongst 32 normally-pigmented plants along a 15 m section of a drainage ditch. Plants of *Pedicularis groenlandica* have clustered stems from stout caudices (Hultén, 1968); the absence of creeping rhizomes indicates that clumps and seedlings are distinct individuals and not merely asexually produced sprouts.

→

Figure 1. **A.** Drainage ditch near Churchill, northern Manitoba, the site of *Pedicularis groenlandica* f. *chlorina.* Plants of this form are located to the right of the ranging pole. Spikes of the normal, purplish plants are found throughout the ditch. **B.** Purplish pigmented (normal) plants of *P. groenlandica* growing near Churchill, Manitoba. **C.** Flowering spikes of plants of f. *chlorina.*


A
C

Normally-pigmented plants were abundant over the remaining 0.75 km of the ditch but no additional individuals of forma *chlorina* were found. The ditch was located 0.6 km south of Akudlik and 5.0 km southeast of Churchill, Manitoba, running westward from Goose Creek Road to the Canadian National Railway line. The six plants were located within 60 cm of a small stream in the center of the ditch. Vascular plant cover was approximately 70%, and exposed substrate surfaces were covered by algal and bryophyte mats. Species in proximity to individuals of forma *chlorina* were: *Carex aquatilis* Wahl., *C. capillaris* L., *Triglochin maritimum* L., *T. palustre* L., *Juncus arcticus* Willd., *J. balticus* Willd., *J. triglumis* L., *Salix brachycarpa* Nutt., *S. calcicola* Fern. & Wieg., *Betula glandulosa* Michx., *Pinguicula vulgaris* L., *Pedicularis flammea* L., and *Aster borealis* (T. & G.) Provancher. Vegetation surrounding the ditch was subarctic forest dominated by *Picea glauca* (Moench) Voss, *Larix laricina* (Du Roi) Koch, *Salix* spp., *Vaccinium uliginosum* L., *Empetrum nigrum* L., and *Carex* spp.

ECOLOGY

Plants of this new form are striking for their combination of elaborate flower design, pale green foliage and brilliant white flowers. Albinism in corolla color is not infrequent in plants and is usually attributed to the mutation of a single gene, which results in the lack of pigment production (Strickberger, 1985). The ability of white mutants of brightly colored, entomophilous species (like *P. groenlandica*) to attract pollinators effectively is of interest because it would determine pollination success, seed production and consequently, survival of the mutant. The authors assume that pollination was successful in forma *chlorina* because its capsules contained almost ripe seeds, and because of the abundance of nearby seedlings. Normally, the flowers would be pollinated by worker bumble-bees (*Bombus* spp.) which cause resonance in the blossoms by means of peculiar wing beats (Faegri and van der Pijl, 1971). Pollen is then released onto the bee. Unfortunately, we observed no bumble-bees or any other insects visiting flowers of either form during our studies. Selfing would seem improbable because the stamens and stigmas are physically separated by the corolla tube ("elephant's trunk"). However, a large ratio in favor of seedlings of forma *chlorina* suggested that selfing may have been more frequent than originally thought. Selfing would result

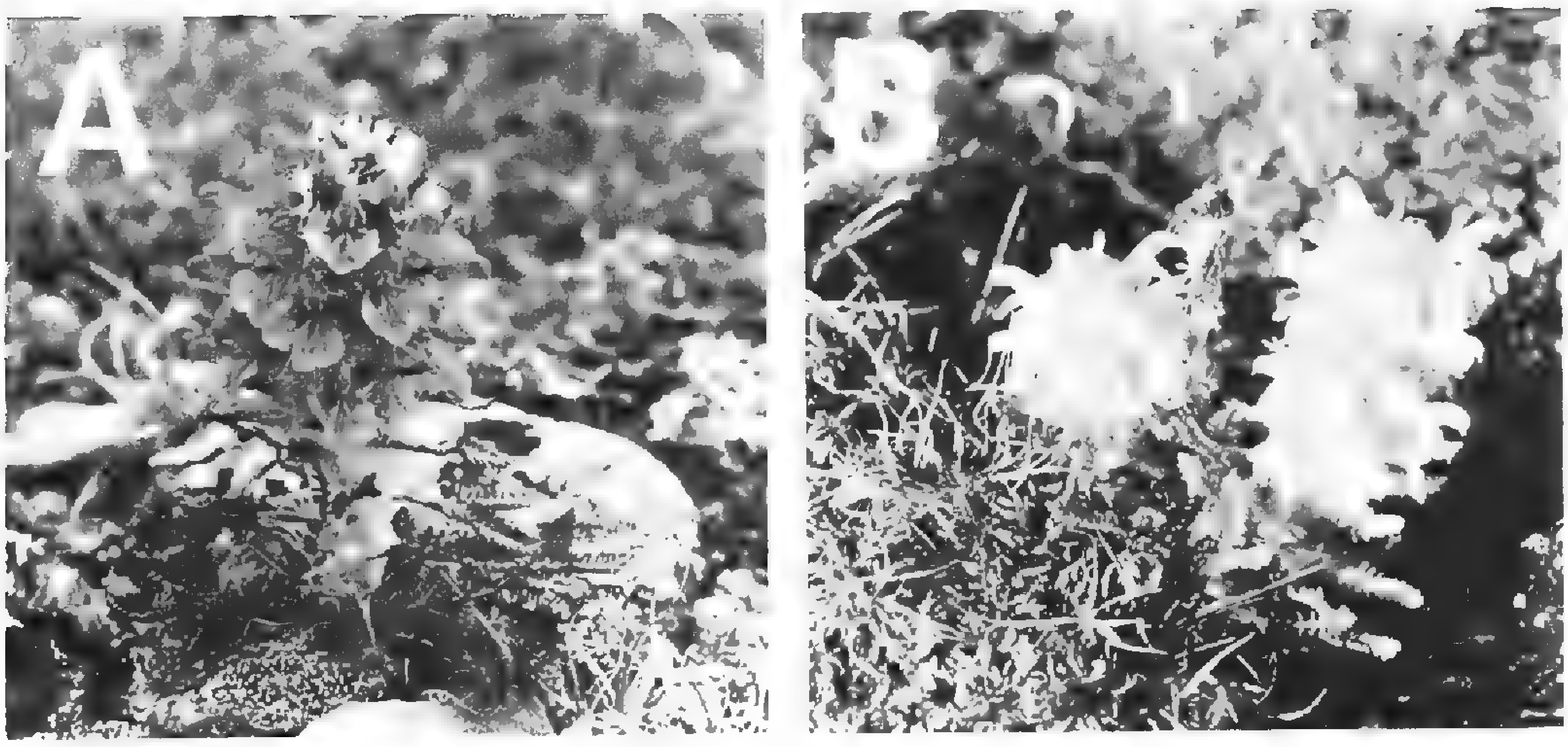

Figure 2. **A.** Purple-flowered (normal) plant of *Pedicularis lanata,* growing in the Truelove Lowlands, Devon Island, N.W.T. **B.** White-flowered f. *alba* found growing near the plant shown in 2A.

in an increase in homozygosity of recessive alleles (such as albinism), and this fact would account for the large number of seedlings of forma *chlorina* in the vicinity of their parent plants. The scarcity of normal-colored seedlings in proximity to many mature normal plants would support this contention.

The question arises as to whether the plants of forma *chlorina* are genetically normal plants reacting to a toxin (perhaps herbicides from the railway line). Such a toxin might block or induce the breakdown of anthocyanin. However, observations of intermixing by normal and pale plants, and that the plants of forma *chlorina* were found well away from sources of disturbance, do not support the suggestion that a toxin could be the causal factor. Growing seeds in the greenhouse and noting the color of the seedlings likely would be difficult due to probable hemi-parasitism in this species.

Three large plants possessed old flowering spikes from 1983 and 1984, hence the colony dates to at least 1982. The number of seedlings of forma *chlorina* outnumbered those of the pigmented form by 10:1, even though reproductively mature plants were less frequent (1.0:6.5). The reversal in ratios for mature plants may indicate that forma *chlorina* will become abundant relative to the typical form in future years, unless seedling mortality in this form is very high, due to other unfavorable factors. The visibility of this interesting population will make it a suitable subject for studies on population size and dispersal ecology.

A further observation on relationships of albino forms and dispersal ecology in this genus should be included. In July 1985, J.S. found an albino form of *Pedicularis lanata* Cham. & Sch. (woolly lousewort) in the Truelove Lowland, Devon Island, North West Territories, Canada. The single individual was a twin-stemmed plant, growing in a high arctic tundra community. Both stems were flowering but the season was too early for observations to be made on seed viability. The plant was not collected due to its rarity. The white coloration of the petals and pale green leaves and stems contrasted strongly with those of the common, purple-colored form. No pale-colored seedlings were observed around the plant (Figure 2). The specimen appears to fit the description of forma *alba* Cody, described from Southampton Island, N.W.T., Canada (65°N), by Cody (1951). The specimen observed on Devon Island (75°N) represents a site approximately 800 km north of the previous records.

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STUDIES ON THE *STELLARIA LONGIPES* COMPLEX (CARYOPHYLLACEAE)–TAXONOMY

C. C. CHINNAPPA AND J. K. MORTON

ABSTRACT

Based on previously published biosystematic data, we conclude that variation in the *Stellaria longipes* group is due to a complex interaction of phenotypic plasticity and genetic variability. Only a single species (*S. longipes*) is recognized, with two intraspecific taxa, *Stellaria longipes* subsp. *longipes* and *S. longipes* subsp. *arenicola, comb. nov.*

Key Words: *Stellaria longipes*, taxonomy, Caryophyllaceae, Canada, northern hemisphere

Stellaria longipes was described by Goldie in 1822 from material which he had collected three years earlier "in the woods near Lake Ontario" (Goldie, 1822), probably along the shores of the Bay of Quinte. In Goldie's diary (Goldie, 1967) for 14 June 1819, when he travelled from Kingston as far as the Bay of Quinte, he noted that "Today I have met with a number of interesting plants, some of which are new to me . . ." No specimen of *Stellaria longipes* collected by Goldie has been located either by ourselves or by previous workers. There can be no doubt, however, as to the plant referred to by Goldie, for it still grows in the area through which Goldie travelled and no other component of the *Stellaria longipes* complex occurs in that part of North America. Material from the type locality and elsewhere was used in our experimental studies of this complex (Chinnappa, 1985a, 1985b; Chinnappa and Morton, 1974, 1976, 1984; Cai and Chinnappa, 1989a, 1989b; Gifford and Chinnappa, 1986; Macdonald and Chinnappa, 1988, 1989; Macdonald et al., 1984, 1986, 1987, 1988). Since Goldie described this species in 1822, many new names have been created for components of the complex in other parts of its broad range of distribution.

The taxonomic problems of the group were recognized at an early stage by Hooker (1829–1834) who, in discussing some of the taxa, commented, "I scarcely know whether they should constitute species or rather be described as varieties." The same problem has confronted subsequent writers of regional floras, who have chosen either to combine all or most of the entities within

Stellaria longipes, or to recognize several species. The first attempt at a world-wide revision of the complex was that of Hultén (1943), who recognized six species: *S. longipes, S. ciliatosepala* Trautv., *S. laxmanni* Fischer *ex* Ser., *S. crassipes* Hultén, *S. laeta* Richardson and *S. monantha* Hultén. Hultén's work was based on a study of herbarium material and distribution, together with field observations. In a revision of his views, Hultén (1968) used the name *S. edwardsii* R. Br. for *S. ciliatosepala* and considered *S. laxmanni* to be a similar plant "of obscure status." *Stellaria stricta* Richardson, previously treated as a synonym of *S. ciliatosepala,* was included in *S. longipes.* Porsild (1963) in a similar revision (but with much more material at his disposal) recognized nine species in this complex: *S. longipes, S. crassipes, S. arenicola* Raup, *S. stricta, S. subvestita* E. Greene, *S. monantha, S. laeta, S. edwardsii* and an unnamed species "*S. laxmanni, sensu* Hultén." At the other extreme Polunin (1940, 1959) recognized only a single species, *S. longipes,* throughout the arctic range of this complex, commenting that "it grows in a wide variety of situations . . . being among the most familiar and ubiquitous of arctic inhabitants."

The first attempt at a biosystematic approach to the problems of variation in this complex was that of Böcher (1951), who worked primarily with material from Greenland and Scandinavia and recognized the six species of Hultén (1943). From a consideration of ecology, geographical distribution, and the limited cytological data available, Böcher tentatively concluded that, ". . . the species of the *longipes* group are not sharply separated but the variation is not continuous either. The species perhaps represent particularly well-balanced gene complexes with a specific ecology." More recently Philipp (1972), working with Böcher on material from northwestern Greenland, concluded that there is no correlation between chromosome number and morphology (or taxonomy) and that in certain instances the plants do not fit into the six species recognized by Böcher and Hultén. Porsild (1963) concluded from his taxonomic study of this complex that it was necessary to ". . . leave the final decision to the future when the taxonomy and genetics . . . have been studied more fully and, preferably, on material grown under controlled conditions of light and temperature." The present study developed from discussions with Dr. Porsild by one of us (JKM) in 1968. His intimate knowledge of this complex, both in the field and the herbarium, and his insight into the problems that it presents were invaluable to us during our work on the complex.

TAXONOMIC IMPLICATIONS

Though the *Stellaria longipes* complex is exceptionally variable, this variation cannot be satisfactorily treated by orthodox taxonomic methods. Those characters that are under genic control are scattered more or less at random throughout the range of distribution of the species (Chinnappa and Morton, 1976) and there is little or no correlation between them, with polyploidy (Chinnappa and Morton, 1974), or with the environment. All populations investigated are interfertile, and most show a high degree of phenotypic plasticity, being also affected by environmental conditions (Chinnappa and Morton, 1984). Accordingly, we are of the opinion that no useful purpose is served by giving taxonomic recognition to this variation. We believe that *S. longipes* should be treated as a single polymorphic species without infraspecific taxa. The only exception to this conclusion, which we recognize, is the morphologically and biologically distinct series of populations on the Lake Athabasca sand dunes on the borders of Saskatchewan and Alberta (Macdonald et al., 1987). These populations appear to have evolved *in situ* into distinctive genotypes, adapted to the specialized environmental conditions provided by the extensive series of dunes occurring on the south side of Lake Athabasca. These genotypes were named *Stellaria arenicola* by Raup (1936). Their evolution has been accompanied and facilitated by a possible shift in the breeding system in favor of self pollination. This entity is interfertile with other populations of *S. longipes* and intergrades with them in its natural habitat; hence, we consider that it does not justify recognition at a level above that of subspecies. Accordingly, we propose the following taxonomy and synonymy for the *Stellaria longipes* complex.

Stellaria longipes Goldie subsp. **longipes** Edinburgh Philos. J. 6: 327. 1822. TYPE: none designated and none known to exist; type locality "in woods near Lake Ontario"—in the Bay of Quinte area. NEOTYPE here designated *Morton* NA5101 (E—duplicates in CAN, K, UAC, WAT and JKM) from near Odessa, Kingston, Ontario, Canada; on natural prairie on limestone. 13 June 1972. Material from this same collection, which was grown in cultivation at Waterloo, is also lodged in E, K, UAC and JKM.

Alsine strictiflora Rydb., Bull. Torrey Bot. Club 39: 315. 1912.
Stellaria arctica Schischkin, Fl. U.S.S.R. 6: 418, 881. 1936.
S. ciliatosepala Trautv. *in* Middend. Reise Sibir. 2: 52, Tab. 8, Fig. 1. 1856.
S. crassipes Hultén, Bot. Not. 1943: 261, Fig. 1h–n and map (Fig. 3).
S. edwardsii R. Br. *in* Franklin Narr. journey Polar Sea, App. VII: 738. 1823.
S. laeta Richardson *in* Franklin, *l.c.* 1823.
S. laxmanni Fischer *ex* Ser. *in* DC. Prodr. 1: 397. 1824.
S. longipes var. *altocaulis* (Hultén) C. Hitchc., Vasc. Pl. Pacific Northwest 2: 307. 1964.
S. monantha Hultén, Bot. Not. 1943: 265 Fig. 7a–f and map (Fig. 9). inc. var. *altocaulis* Hultén and subsp. *atlantica* Hultén.
S. nitida Hook. *in* Scoresby Journal of a voyage to the Northern Whale-fishery. Edinburgh Philos. J. VIII: 411. 1823.
S. palustris Richardson *in* Franklin *l.c.* 1823.
S. peduncularis Bunge *in* Ledeb. Fl. Altaic. 2: 157. 1830.
S. stricta Richardson *in* Hook. Fl. bor.-amer. 1: 96. 1830.
S. subvestita E. Greene, Ottawa Naturalist, 15: 42. 1901.

Stellaria longipes Goldie subsp. **arenicola** (Raup) Chinnappa & J.K. Morton *comb. nov.* TYPE: Saskatchewan: on sand dunes south of William Pt., south shore of Lake Athabasca, August 16, 1935, *Raup 6882* (HOLOTYPE: GH-!; ISOTYPE: CAN-!).

S. arenicola Raup, J. Arnold Arbor. 17: 248, pl. 196. 1936.
S. longipes var. *arenicola* (Raup) B. Boivin, Naturaliste Canad. 93: 646. 1966.

(Note: Herbarium acronyms are as given in Holmgren et al., 1981, save that JKM represents the research herbarium of one of the authors.)

Goldie's type collection of *Stellaria longipes* is missing. He donated his specimens to the herbarium of the University of Glasgow which was subsequently transferred to that of the Royal Botanical Gardens, Edinburgh, where many of Goldie's collections are to be found. However, his collection of *S. longipes* has been sought by many workers including Porsild, Hultén and one of the present authors (JKM), but without success. Accordingly we hereby designate a neotype for *S. longipes* subsp. *longipes.* The collection that we have chosen is a recent one made by ourselves a few miles from the locality where Goldie is believed to have collected in 1819. It has been chosen because we are satisfied that it belongs to the same genotype as the original collection, and because we used this material in our experimental work on this species complex. Also we have adequate duplicate material for distribution to other herbaria.

For typification of the many synonyms of *Stellaria longipes* subsp. *longipes,* the reader is referred to Hultén (1943) and Porsild (1963).

Despite the major lumping of taxa that we have proposed, *Stellaria longipes* is, on occasions, difficult to distinguish from certain members of the genus because of the great range of variation that it displays. The main difficulties arise in separating *S. longifolia* ($2n = 26$) and *S. longipes* ($2n = 52$ to 104). The following characters have, however, been found to provide reliable separation. In *S. longifolia* the leaves are always very narrow and are broadest above the middle; their margins and the stems are minutely tuberculate-scabrous. In *S. longipes* the leaves can be narrowly to broadly lanceolate-triangular but are always broadest at the base, and their margins and the stem are not scabrous (though they may be ciliate).

We have not had the opportunity to study material of *Stellaria alaskana* Hultén, *S. ruscifolia* Pallas *ex* Schlange, *S. florida* Fischer, or *S. fischeriana* DC.; hence we have excluded them from the above taxonomy and synomymy. The first two species appear to us to be distinct but related to *S. longipes,* while the last two appear to be part of the *S. longipes* species complex.

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CYMOPHYLLUS FRASERIANUS (KER-GAWLER) KARTESZ & GANDHI (CYPERACEAE), THE CORRECT NAME FOR FRASER'S SEDGE

JOHN T. KARTESZ AND KANCHEEPURAM N. GANDHI

ABSTRACT

The authorship of *Cymophyllus* and *Cymophyllus fraseri* is corrected to Mackenzie *ex* Britt. *Cymophyllus fraseri,* hitherto referring to Fraser's sedge, is considered to be a taxonomic synonym of the following new combination: *Cymophyllus fraserianus* (Ker-Gawler) Kartesz & Gandhi.

Key Words: Fraser's sedge, *Carex fraseri, Carex fraseriana, Cymophyllus fraseri, Cymophyllus fraserianus,* southeastern United States

INTRODUCTION

Fraser's sedge, known hitherto either as *Carex fraseri* Andrews (Strausbaugh and Core, 1970) or more commonly as *Cymophyllus fraseri* (Andrews) Mackenzie (Britton and Brown, 1913; Small, 1933; Fernald, 1950; Clarkson, 1961; Massey, 1961; Gleason, 1963; Radford et al., 1968; Wofford, 1978, 1989; Rayner, 1979; Wiegman, 1979; Kartesz and Kartesz, 1980; Massey et al., 1983; Brown and Brown, 1984; Harvill et al., 1986; Jones and Coile, 1988; Branson et al., unpubl. ms., Endangered, threatened, and rare plants of KY) ranges from northeastern GA and adjacent SC, western NC, eastern TN, southwestern VA, through WV and extends northward to MD and southern PA (Kartesz, unpubl. ms., Distributional atlas for the North American flora). The names *Cymophyllus* (a monotypic genus) and *Cymophyllus fraseri* were originally proposed in Britton and Brown (1913). For *Cymophyllus fraseri,* the basionym (*Carex fraseri* Andrews) and the synonym (*Carex fraseriana* Ker-Gawler) were cited.

Britton and Brown's (1913) work included contributions from several authors, e.g., Gramineae by G. V. Nash (footnote, p. 107), *Carex* by K. K. Mackenzie (footnote, p. 352), etc. The text, excluding the contributions, was written by Britton (cf. title page). Hence, unless otherwise shown, all new names must be attributed to Britton. Although the names *Cymophyllus* and *Cymophyllus fraseri* were attributed to Mackenzie, there was no indication given that the *Cymophyllus* text was published for Mackenzie by Britton and Brown. Hence, the correct authorship for the genus name should be: Mackenzie *ex* Britt. Farr et al. (1979) cited the authorship as: Mackenzie *ex* Britton & Brown. As indicated above, the authorship of the name *Cymophyllus* should be credited to Britton alone, not to Britton and Brown.

As to the correct name for Fraser's sedge, both names, *Carex fraseri* Andrews and *Carex fraseriana* Ker-Gawler were published in 1811. Mackenzie (1931, p. 8) cited June 1811 as the date of Andrews' publication (Bot. Repos. 10(132): *t.* 639) and July 1811 for Ker-Gawler's publication (Bot. Mag. 34: *t.* 1391). We concur with Mackenzie regarding Ker-Gawler's date of publication, which, as reflected by the engraver's date, was found at the bottom of the plate. Stafleu and Cowan (1976, p. 578) stated that the engraver's date was generally accepted as the date of the publication of new taxa in Curtis' Botanical Magazine.

With reference to the date of Andrews' publication, no engraver's date was given on the plate 639; however, Britten (1916) and Stafleu and Cowan (1976) differed with Mackenzie's information. Stafleu and Cowan mentioned that the Botanist's Repository vol. 10(132), *t.* 639 was issued in November 1811. Britten provided additional information on Andrews' plates, stating that he ascertained Andrews' dates from the "Monthly Botanical Reports" in the Monthly Magazine for 1807–1813. According to Britten, the records showed that the Monthly Magazine reported vol. 10, parts 128–131 (plates 618–636) in June 1811 and reported vol. 10, part 132 (plates 637–640) in November 1811. Britten remarked that the date of the Magazine (November 1811, in this case) was at least one month later than the appearance of the plate in Botanist's Repository. (Furthermore, we noticed that in the specimen collection data for *t.* 638, Andrews mentioned that he received information from J. Milne in April 1811.) It is most likely that Botanist's Repository, vol. 10(132), *t.* 639 was issued in September-October 1811, and we consider Mackenzie's as well as Stafleu and Cowan's bibliographical information on the date of Andrews' publication to be an error.

Ker-Gawler (1811) gave a description of *Carex fraseriana* along with a reference to *Carex fraseri,* and mentioned the plate no. as 638, not 639. In his discussion, Ker-Gawler stated that the species was named for Mr. Fraser, who collected the species from North Carolina and introduced it into England. The preceding information is almost identical with that provided by Andrews. It is possible that Ker-Gawler had access to Andrews' manuscript and copied the data from Andrew's specimen. It is further possible that either Ker-Gawler assumed the plate number to be 638 or Andrews altered the plate number after Ker-Gawler studied it. In any event, we consider Ker-Gawler's reference to Andrews' *t.* 638 as a bibliographical error for *t.* 639 (Greuter, 1988; ICBN, Art. 33.2). The *t.* 638 refers to an Australian legume, *Daviesia latifolia* R. Br. *ex* Ait. The reason for Ker-Gawler altering the specific epithet from the original "*fraseri*" (a noun with genitive ending) to "*fraseriana*" (an adjectival form) is uncertain. Dr. A. A. Reznicek (MICH; pers. comm.) remarked that the epithet "*fraseriana*" agrees in gender with the feminine gender of the genus *Carex.*

Although both epithets, *fraseri* ("of Fraser" or "Fraser's") and *fraseriana* ("the Fraserian" or "for Fraser"), denote essentially the same thing, the former epithet must not be considered to be an orthographic variant of the latter. We consider these two epithets to be different, and since the names *Carex fraseri* and *Carex fraseriana* were based on two separate types, we believe that the name *Carex fraseri* must be treated as a taxonomic synonym of *Carex fraseriana.* The binomial *Carex fraseriana* is the earliest applicable name and accordingly we propose the following new combination.

TAXONOMY

Cymophyllus fraserianus (Ker-Gawler) Kartesz & Gandhi, *comb. nov. Carex fraseriana* Ker-Gawler, Bot. Mag. 34: *t.* 1391. Jul. 1811. HOLOTYPE: Bot. Mag. 34: *t.* 1391. Jul. 1811.

Carex fraseri Andrews, Bot. Rep. 10(132): *t.* 639. Sep.–Oct. 1811. *Cymophyllus fraseri* (Andrews) Mackenzie *ex* Britt. *in* Britton & Brown, Ill. Fl. N. U.S., ed. 2. 1: 441. 1913. HOLOTYPE: Bot. Rep. 10(132): *t.* 639. Sept.–Oct. 1811.

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FLOWERING SEQUENCE OF THE ORCHID GENUS *GOODYERA* IN THUNDER BAY DISTRICT, ONTARIO

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ABSTRACT

A two-year field study (1987 and 1989) of mixed populations of *Goodyera repens*, *G. tesselata*, and *G. oblongifolia* and a study of relevant herbarium material showed that the flowering sequence of these three species is different in Thunder Bay District, Ontario, from what has been reported for several areas in somewhat more southern regions. The sequence in more southern regions is *G. tesselata* to *G. repens* to *G. oblongifolia*. The sequence in this northern area is *G. repens* to *G. tesselata* to *G. oblongifolia*. As *G. tesselata* arose through hybridization of the other two species, this latter sequence could have important consequences for the reproductive biology of the group.

Key Words: *Goodyera*, phenology, hybridism, northwestern Ontario, Canada

INTRODUCTION

In 1986, funds made available from a bequest by Dr. Gaëtan Harvais allowed a study of the orchid genus *Goodyera* to begin. There are three species present in the Thunder Bay area: *G. repens* var. *ophioides* ($2n = 30$), *G. tesselata* ($2n = 60$) and *G. oblongifolia* ($2n = 30$). The first two species are quite common, but *G. oblongifolia* is rare and is known only from a few local populations. It has been established first by Fernald (1899) and later in detail by Kallunki (1976, 1981) that *G. tesselata* is a tetraploid (rarely a triploid) derived through hybridization between the other two species. However, some backcrossing does still occur. Kallunki (1976, 1981) has shown that in most respects *G. tesselata* is both intermediate and more variable than either of the parent species. Theoretically then, *G. tesselata* should be intermediate in its phenology, especially in flowering period, to the parent species. Kallunki (1976) did not find this assumption to be true for northern Michigan populations, but showed that *G. tesselata* flowers earlier than *G. repens* and much earlier than *G. oblongifolia*. Therefore, the order of flowering she reported was *G. tesselata*, *G. repens* and finally *G. oblongifolia*. Kallunki (1981) considered that this order of flowering is important in preventing backcrossing in mixed *Goodyera* populations, thereby leading to genetic stability in *G. tesselata*. Brown (1985), in a twenty-year study, showed the same order of flowering occurring in Ontario's Bruce Peninsula, and Whiting and Catling (1986) in *Orchids of Ontario* stated that *G. tesselata* is ". . . the earliest blooming of our rattlesnake-plantains." Our studies in the more northerly Thunder Bay area of northwestern Ontario show a different situation occurring here; this paper describes some aspects of the phenology of the three *Goodyera* species in this area.

METHODS

Study Area

The Thunder Bay District is in northwestern Ontario north of western Lake Superior. It is an area of cold winters and cool to warm summers. Precipitation is moderate with about one-third falling as snow. The whole area is underlain by rocks of the Canadian Pre-Cambrian Shield and is moderately rolling. There are areas of rock outcrops but there are also deposits of glacial drift, clay, silt, sand, and gravel. The soils are mainly brunisols and organic soils, but podzols and luvisols are also common.

Two sites were used in this study: 1. Hawkeye Lake is inland and 30 km northwest of Thunder Bay city; 2. Ravine Lake, Sibley Peninsula, is 30 km east of Thunder Bay city across part of Lake Superior.

The Hawkeye Lake biogeochemical study area is a monitored headwater catchment basin (48°40′N, 89°29′W). It is in the Port Arthur Hills at an elevation of 460 m, considerably higher than Lake Superior (183 m). There are rock outcrops, but most of the catchment is covered by morainic material with brunisols being the most common soil type. Hawkeye is in the Superior section of the Boreal Forest Region (Rowe, 1972) and is dominated by balsam fir (*Abies balsamea* (L.) Mill.), trembling aspen (*Populus tremuloides* Michx.), and white birch (*Betula papyrifera* Marsh.). The phenology study area is about 20 × 30 m on a slightly west-facing slope under a canopy of balsam fir and black spruce (*Picea mariana* (Mill.) BSP). The understory vegetation is sparse and is locally dominated by *Goodyera repens* (L.) R.Br. and *G. tesselata* Lodd. There is no *G. oblongifolia* Raf. at Hawkeye Lake.

Ravine Lake, the second study area, is at the southern end of the Sibley Peninsula (48°21′N, 88°51′W). It is one km from Lake Superior at an elevation of 260 m. The area climate is modified by Lake Superior and tends to be cooler and damper than inland areas (Wilson, 1970, Master's thesis, Lakehead University, Thunder Bay, Ontario). There is a mixed population of *Goodyera repens, G. tesselata,* and *G. oblongifolia* present on this site. There are sedimentary rocks in this area and the vegetation is dominated by balsam fir, eastern white cedar (*Thuja occidentalis* L.) and white spruce (*Picea glauca* (Moench) Voss).

Field Methods

The methods used in the two study areas had some differences. Hawkeye Lake studies were carried out in 1987 and in 1989 during the months of June to September. Fifty plants with developing scapes were marked for both *Goodyera repens* and *G. tesselata.* Initially the species were identified by leaf colour and reticulation, and after flowering began were confirmed by floral morphology. The plants were checked usually once a week until the midpoint of anthesis could be determined for each plant.

As there was high mortality due to herbivory or a pathogen in 1989, an additional 10 plants of *Goodyera repens* and 3 of *G. tesselata* were marked after the study began. If more than half of the total number of buds of a plant failed prior to anthesis, then the plant was excluded from calculations.

The Ravine Lake site is less accessible than Hawkeye Lake; weekly observations were carried out only in 1989 and did not begin until 7 August 1989. Although there are good populations of all three species of *Goodyera* at Ravine Lake, relatively few could be found with developing scapes. Plants were marked in three small areas. There were 16 *G. repens*, (all past midpoint of anthesis) 9 *G. tesselata* and 14 *G. oblongifolia.*

The midpoint of anthesis for both study areas was determined using the method of Kallunki (1981):

$$\text{Midpoint} = t0 + \frac{(t1 - t0)(0.5 \times Y+ - Y0)}{(Y1 - Y0)}$$

where

$t0$ is the observation date before the midpoint of anthesis
$t1$ is the observation date after the midpoint of anthesis
$Y+$ is the total number of buds in the inflorescence
$Y0$ is the number of flowers at $t0$
$Y1$ is the number of flowers at $t1$

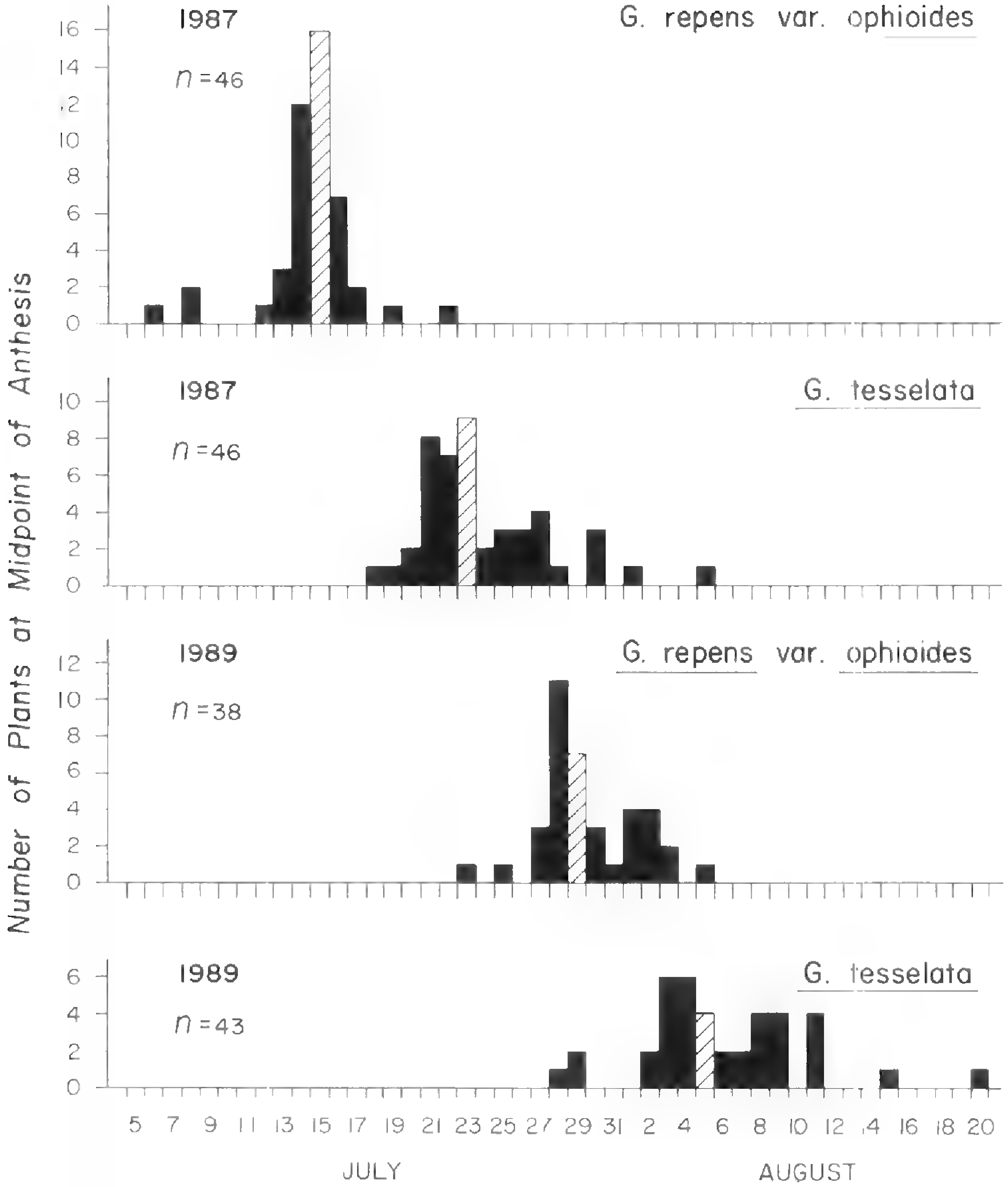

Figure 1. Flowering period at Hawkeye Lake in 1987 and 1989, based on the number of plants at midpoint of anthesis, for *Goodyera repens* var. *ophioides* and *G. tesselata.* The cross-hatched bar is the midbloom date.

Note: the "midbloom" date (Figure 1) is the arithmetic middle date of the flowering period.

Herbarium Methods

All collections of the three *Goodyera* sp. present in the Lakehead University Herbarium and collected from Thunder Bay District were checked for dates and flowering status. Variation may exist between parts of Thunder Bay District; however, comparisons were made for the district as a whole.

RESULTS

The results of the phenological study are presented in three parts in the same order as listed in the methods.

Hawkeye Lake

Figure 1 shows a 13–14 day difference in midbloom flowering dates when 1987 data are compared to 1989 data for both *Goodyera repens* and *G. tesselata.* Also, there is a significant 7–8 day difference ($P \leq .005$) between the two species in midbloom flowering dates in both study years, with *G. repens* being earlier than *G. tesselata* in both cases. When *G. repens* and *G. tesselata* are further compared there is considerable overlap in midpoint of anthesis flowering periods for these two species in both years.

Ravine Lake

At this site all 16 of the *Goodyera repens* were past the midpoint of anthesis prior to 7 August, 1989, all 9 *G. tesselata* flowered and 12 of the 14 *G. oblongifolia* flowered. The midpoint of anthesis flowering period is the same for both *G. tesselata* and *G. oblongifolia* and in 1989 was 8 August to 20 August. The midbloom date for *G. tesselata* was 11 August and for *G. oblongifolia* was 10 August. There is no significant difference between the two species in midbloom dates. The midbloom date for *G. tesselata* is six days later at Ravine Lake than at inland Hawkeye Lake.

Herbarium Study

The material in the Lakehead University Herbarium has 36 sheets of *Goodyera repens* var. *ophiodes* in flower. Dates of the collections cover the years 1936 to 1982. The flowering period for these years is shown to be 13 July to 6 September with the midbloom date being 9–10 August.

There are 23 flowering collections of *Goodyera tesselata* for the years 1951 to 1981. The flowering period begins 27 July and ends 13 September with 11–12 August as the midbloom date.

There are only four sheets of *Goodyera oblongifolia* in flower. They cover the years 1960–1982. The flowering period is 17 August to 6 September. The midbloom date appears to be the first week in September.

The midbloom dates for *Goodyera repens* and *G. tesselata* are therefore very close together. There is large overlap in flowering periods for these two species (and also with *G. oblongifolia*) but the flowering period for *G. tesselata* is later than for *G. repens.*

These data also show that the 1987 flowering period for Hawkeye Lake for both *Goodyera repens* and *G. tesselata* is one of the earliest on record for Thunder Bay District.

DISCUSSION

The most significant result of this study of flowering periods of the three *Goodyera* species is that there is a different sequence in northwestern Ontario from that of Michigan and the more southerly areas of Ontario. In Thunder Bay District the sequence is *G. repens* to *G. tesselata* to *G. oblongifolia.* This order is supported by the Hawkeye Lake data, the Ravine Lake data, and by the data from the herbarium study.

It is also clear that in Thunder Bay District there is great annual variability in time of flowering for at least *Goodyera repens* and *G. tesselata.* This variability is shown not only by the herbarium study but also by the 1987 and 1989 data from Hawkeye Lake. Flowering was two weeks later in 1989 than it was in 1987.

Temperature records for 1987 show all the months April to August had above-average temperatures, with April and June having the highest means ever recorded. In contrast, the same months in 1989 were close to the mean. It would seem logical that the warmer temperatures of more southern areas could be a cause of the differing sequences. However, in the above normal temperatures in Thunder Bay District of 1987, *Goodyera repens* was even earlier in its midbloom date than was *G. tesselata.*

All the northwestern Ontario studies show there is considerable overlap of flowering between the three species. Both *Goodyera repens* and *G. oblongifolia* overlap into the flowering period of the intermediate hybrid *G. tesselata,* and *G. repens* may even overlap into the flowering period of *G. oblongifolia.* The studies also show that as predicted by Kallunki (1976), *G. tesselata* is more variable than *G. repens* and has a longer flowering period.

What important consequences this difference in flowering sequence and the accompanying overlap in flowering periods has on the reproductive biology of mixed populations of *Goodyera* is not yet known. It is possible to state, however, that the northwestern Ontario flowering sequence of these *Goodyera* species is different from that of the areas to the south.

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VASCULAR PLANT TYPE SPECIMENS IN THE WILLARD SHERMAN TURRELL HERBARIUM (MU), MIAMI UNIVERSITY, OXFORD, OHIO

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ABSTRACT

The vascular plant type collection in MU consists of 439 sheets of mainly North American specimens representing 419 taxa. Many of the sheets are from the non-Ohio holdings of Oberlin College (OC). A brief history of the MU collection and a complete listing of the specimens are given, with annotations correcting mistakes in protologues or monographic accounts involving a few of the specimens.

Key Words: Type specimens, vascular plants, herbarium, Miami University, Oberlin College, Ohio

The herbarium at Miami University (MU) was founded about 1906, during the tenure of Dr. Bruce Fink, first chairman of the Department of Botany. After Fink's death in 1927, the curatorship was held by a succession of faculty: Arthur T. Evans (1927–29), Ethel C. Belk (1929–56), Harvey A. Miller (1956–67), Will H. Blackwell (1968–78, 1983–86, 1988–89), Wayne J. Elisens (1982–83), R. James Hickey (1987–88) and W. Hardy Eshbaugh (1967–68, 1978–82, 1989–present). The herbarium remained small and relatively inactive from its inception until 1957, when H. A. Miller initiated numerous exchanges with domestic and foreign herbaria. By 1967, the collection had grown to about 75,000 specimens. In that year, Miami University purchased the non-Ohio holdings of Oberlin College, some 140,000 specimens, which immediately made the herbarium the largest in the state (Miller, 1968). Since that time, the collection has grown rapidly through gifts and purchases. Important collections, in addition to those listed below from OC, include the following, which are listed by collector and approximate number: R. N. P. Goodall (1000, plants of Tierra del Fuego), R. D. A. Bayliss (1020, plants of South Africa), and G. Hatschbach (6000, plants of Brazil). Geographical distribution of the material in the collection is as follows: North America (except Ohio), 60%; Ohio, 13%; Latin America, 8%; Europe, 15%; Asia, 2%; Pacifica, 1%; Africa, 1%.

The herbarium at Oberlin College (OC) was a very important collection, having been built up over a period of nearly 135 years, and having been studied by many experts in different groups, including E. B. Copeland, A. S. Hitchcock, P. A. Rydberg, and T. G. Yunker. Over 30,000 sheets were sent out by Frederick O. Grover for study by experts during the period 1933 to 1958. Curators of OC included James Dascombe (1834–78), Albert A. Wright (1878–91), Worallo Whitney (1891–93), Francis D. Kelsey (1893–97), Herbert L. Jones (1897–98), F. O. Grover (1898–28), Isabel S. Smith (1928–34), F. O. Grover (1934–58) and George T. Jones (1958–present). As was stated by Miller (1968), several hundred types were contained in the OC collection, and make up the bulk of the type collection now at MU. Among important vascular plant collections from OC which are now in MU are the following, listed by collector and number of specimens: F. E. Leonard (5000), F. D. Kelsey (5800), H. L. Jones (2650), F. O. Grover (4500), M. M. Metcalfe (1300), M. F. Spencer (20550; *see* Grover, 1941), M. E. Day (1860), E. S. Steele (1650), H. C. Beardslee, Sr. (4100), H. C. Beardslee, Jr. (4760), C. A. Kofoid (4000), H. C. Cowles (1850), A. E. Ricksecker (2100), M. E. Jones (1300), C. G. Pringle (2950), and E. Wilkinson (15,000). A manuscript containing a more detailed history of OC is on file in the MU archives.

Since 1985, an active search has been conducted to find the type specimens at MU and, to date, 439 sheets representing 419 vascular plant taxa have been confirmed as holo- (3 sheets), iso- (376 sheets), syn- (47 sheets), neo- (1 sheet) or lectotypes (6 sheets), with 6 sheets of photographs of type specimens from other herbaria. Paratypes, while numerous, are not listed here, nor have they been separated out and placed in the type collection; however, cards listing paratypes in MU are maintained in the type specimen card-file. It is expected that many more types will be discovered in the future. Cryptogamic types, which are very numerous, will be discussed in separate publications.

Sources of the type specimens in MU, most of which are from OC, are as follows: I. W. Clokey, O. Degener, W. H. Eshbaugh, G. Hatschbach, R. J. Hickey, M. E. Jones, D. D. Keck, F. E. Leonard, C. G. Pringle (*ex* herbs. F. E. Leonard, C. A. Kofoid, F. D. Kelsey and E. Wilkinson), herb. Mary Fisk Spencer, E. S. Steele, herb. E. Wilkinson, and exchanges. No attempt has been made, in the listing of specimens, to indicate the source of each sheet, which can be determined in most cases from the sheet itself.

All herbarium acronyms mentioned are from Holmgren et al. (1981). Authority and publication citations follow TL-2 (Stafleu and Cowan, 1976–88), and journal citations follow, where possible, B-P-H (Lawrence et al., 1968).

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Astragalus hemigyrus Clokey, Madroño 6: 220 (1942). NEVADA: Clark Co.; 18 Apr. 1939, *I. W. & C. B. Clokey 8409.* ISOTYPE (MU43125).

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Crataegus exclusa Sarg., Rhodora 5: 108 (1903). VERMONT: Clarendon; 24 May, 5 Aug. & Oct. 1901, *W. W. Eggleston 1789.* SYNTYPES (2: MU40884, MU155483).

Crataegus jesupi Sarg., Rhodora 5: 61 (1903). VERMONT: West Rutland; 26 May, 6 Aug. & 9 Oct. 1901, *W. W. Eggleston 2227.* SYNTYPES (2: MU40818, MU155482).

Crataegus membranacea Sarg., Rhodora 5: 186 (1903). VERMONT: Middlebury; 21 Sep. 1900 & 26 May 1901, *E. Brainerd s.n.* ISOTYPE (MU18834).

Crataegus oakesiana Eggleston, Torreya 7: 35 (1907). VERMONT:

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Cryptantha abramsii I. M. Johnst., Contr. Gray Herb. 68: 52 (1923). CALIFORNIA: Los Angeles Co.; 14 Mar. 1903, *L. Abrams 3139.* ISOTYPE (MU125411).

Cryptantha polycarpa Greene, Pittonia 1: 114 (1887). CALIFORNIA: Nevada Co.; 4 Aug. 1887, *C. F. Sonne 445.* ISOSYNTYPE (MU65964).

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Arts 29: 383 (1894). Mexico: Jalisco; 6 Oct. 1893, *C. G. Pringle 4585.* Isosyntype (mu43804).

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Desmodium subspicatum S. Wats., Proc. Amer. Acad. Arts 26: 135 (1891). Mexico: San Luis Potosi; 16 Jul. 1890, *C. G. Pringle 3211.* Isotype (mu44193).

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Dioscorea hirsuticaulis B. L. Robinson, Proc. Amer. Acad. Arts 29: 324 (1894). Mexico: Jalisco; 14 Oct. 1893, *C. G. Pringle 4572.* Isotype (mu80999).

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Dioscorea pringlei B. L. Robinson, Proc. Amer. Acad. Arts 29: 323 (1894). Mexico: Jalisco; 7 Sep. 1893, *C. G. Pringle 4526.* Isotype (mu81003).

Dioscorea pusilla B. L. Robinson & Seat., Bot. Jahrb. Syst. 22:

426 (1896). MEXICO: Michoacan; 28 Jul. 1892, *C. G. Pringle 4157*. ISOTYPE (MU81005).

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Dodecatheon clevelandii subsp. *insularis* H. J. Thompson, Contr. Dudley Herb. 4: 134 (1953). CALIFORNIA: Santa Barbara Co.; 23 Mar. 1950, *H. J. Thompson 1079*. ISOTYPE (MU110450).

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Ehretia cordifolia B. L. Robinson, Proc. Amer. Acad. Arts 29: 319 (1894). MEXICO: Jalisco; 19 May 1893, *C. G. Pringle 4382*. ISOTYPE (MU66059).

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Elatine williamsii Rydb., Mem. New York Bot. Gard. 1: 260 (1900). MONTANA: Sand Coulee; 25 Aug. 1891, *R. S. Williams 855*. ISOSYNTYPE (MU53423).

Encelia adenophora Greenm., Proc. Amer. Acad. Arts 39: 109 (1903). MEXICO: Jalisco; Sep.–Oct. 1893, *C. G. Pringle 4602*. ISOTYPE (MU103530).

Encelia frutescens f. *ovata* Hall, Univ. Calif. Publ. Bot. 3: 135

(1907). ARIZONA: near Tucson; 8 May 1884, *C. G. Pringle s.n.* ISOSYNTYPE (MU103518).

Eragrostis pringlei Mattei & Tropae, Contrib. Biol. Veget. Palermo 4: 241 (1909). ISOTYPE. (See *E. pusillus.*)

Eragrostis pusillus Lams.-Scribn. *ex* Beal, Grasses of North America 2: 481 (1896). MEXICO: Jalisco; 28 Oct. 1889, *C. G. Pringle 2327.* ISOTYPE (MU90454). *non* Hack. 1896.

Eragrostis scribneriana Hitchc., Contr. U.S. Natl. Herb. 17: 361 (1913). ISOTYPE. (See *E. pusillus.*)

Ericameria martirensis Wiggins, Contr. Dudley Herb. 1: 177 (1933). MEXICO: Baja California; 18 Sep. 1930, *I. L. Wiggins & D. Demaree 4893.* ISOTYPE (MU103559).

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Erigeron heteromorphus B. L. Robinson, Proc. Amer. Acad. Arts 27: 173 (1892). MEXICO: San Luis Potosi; 9 Dec. 1891, *C. G. Pringle 3963.* ISOTYPE (MU104138).

Erigeron tardus Lunell, Amer. Midl. Naturalist 3: 344 (1914). NORTH DAKOTA: Leeds; 26 Jul. 1913, *J. Lunell s.n.* ISOTYPE (MU15729).

Eriocaulon bilobatum Morong, Bull. Torrey Bot. Club 19: 226 (1892). MEXICO: Jalisco; 7 Oct. 1891, *C. G. Pringle 3855.* ISOTYPE (MU81776).

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Eriogonum jonesii S. Wats., Proc. Amer. Acad. Arts 21: 454 (1886). ARIZONA: Cosnino; 11 Aug. 1884, *M. E. Jones 4050.* ISOTYPE (MU21901).

Eriogynia uniflora S. Wats., Bot. Gaz. (Crawfordsville) 15: 242 (1890). MONTANA: Gate of the Mountains; 4 Jul. 1888, *F. D. Kelsey s.n.* ISOTYPE (MU39037) & photograph of LE ISOTYPE (MU134986).

Eriosema multiflorum B. L. Robinson, Proc. Amer. Acad. Arts 29: 316 (1894). MEXICO: Jalisco; 7 Oct. 1893, *C. G. Pringle 4548.* ISOTYPE (MU44341).

Eryngium mexicanum S. Wats., Proc. Amer. Acad. Arts 26: 136 (1891). MEXICO: Mexico; 30 Aug. 1890, *C. G. Pringle 3229.* ISOTYPE (MU57415).

Eryngium pringlei Hemsley & J. Rose, Contr. U.S. Natl. Herb.

8: 333 (1905). MEXICO: San Luis Potosi; 10 Jul. 1891, *C. G. Pringle 3759.* ISOTYPES (2: MU57421, MU57423).

Eryngium wolffii Mathias, Ann. Missouri Bot. Gard. 16: 395 (1929). MEXICO: Mexico; 1 Aug. 1890, *C. G. Pringle 3180.* ISOTYPE (MU57481).

Erythronium helenae Applegate, Contr. Dudley Herb. 1: 188 (1933). CALIFORNIA: Napa Co.; 4 Apr. 1932, *E. I. Applegate 7037.* ISOTYPE (MU20423).

Eupatorium amblyolepis B. L. Robinson, Proc. Amer. Acad. Arts 35: 330 (1900). MEXICO: Morelos; 7 Feb. 1899, *C. G. Pringle 8034.* ISOTYPE (MU104599).

Eupatorium espinosarum var. *doratophyllum* B. L. Robinson, Contr. Gray Herb. 75: 6 (1925). MEXICO: Jalisco; 18 Nov. 1892, *C. G. Pringle 4353.* ISOTYPE (MU104898).

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Eupatorium oresbium B. L. Robinson, Proc. Amer. Acad. Arts 35: 337 (1900). MEXICO: Morelos; 15 Feb. 1899, *C. G. Pringle 8030.* ISOTYPE (MU104907).

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Euphorbia jonesii Millsp., Pittonia 2: 89 (1890). ARIZONA: Bowie; 17 Sep. 1884, *M. E. Jones 4247.* ISOTYPE (MU50104).

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Euphorbia misella S. Wats., Proc. Amer. Acad. Arts 26: 146 (1891). MEXICO: Mexico; 18 Oct. 1890, *C. G. Pringle 3305.* ISOTYPE (MU50097).

Euphorbia subpeltata S. Wats., Proc. Amer. Acad. Arts 26: 146 (1891). MEXICO: San Luis Potosi; Aug./Sep. 1890, *C. G. Pringle 3272.* ISOTYPE (MU50270).

Evolvulus prostratus B. L. Robinson, Proc. Amer. Acad. Arts 29: 320 (1894). MEXICO: Jalisco; 26 Jul. 1893, *C. G. Pringle 4445.* ISOSYNTYPE (MU64044).

Foresteria racemosa S. Wats., Proc. Amer. Acad. Arts 25: 158

(1890). Mexico: Nuevo Leon; 29 Aug. 1889, *C. G. Pringle 2394.* Isotype (mu62176).

Fragaria bracteata Heller, Bull. Torrey Bot. Club 25: 194 (1898). New Mexico: east of Santa Fe; 29 May 1897, *A. A. Heller 3615.* Isotype (mu38835).

Fuchsia pringlei B. L. Robinson & Seat., Proc. Amer. Acad. Arts 28: 106 (1893). Mexico: Michoacan; Jul. 1892, *C. G. Pringle 4140.* Isolectotype (mu56049) (per annotation of P. E. Berry, 1980).

Galactia multiflora B. L. Robinson, Proc. Amer. Acad. Arts 29: 315 (1894). Mexico: Jalisco; 1 Jul. & 24 Sep. 1893, *C. G. Pringle 4433.* Isotype (mu44374).

Garrya grisea Wiggins, Contr. Dudley Herb. 1: 172 (1933). Mexico: Baja California; 22 Sep. 1930, *I. L. Wiggins & D. Demaree 4988.* Isotype (mu59093).

Geissolepis suaedaefolia B. L. Robinson, Proc. Amer. Acad. Arts 27: 177 (1892). Mexico: San Luis Potosi; 27 Jun. 1891, *C. G. Pringle 3762.* Isotype (mu105324).

Golionema heterophylla S. Wats., Bot. Gaz. (Crawfordsville) 16: 267 (1891). Isotype. (See *Oligonema heterophylla.*)

Gomphrena pringlei Coulter & Fisher, Bot. Gaz. (Crawfordsville) 17: 349 (1892). Mexico: Mexico; 26 Aug. 1890, *C. G. Pringle 3152.* Isotype (mu24419).

Gonolobus jaliscensis B. L. Robinson & Greenm., Proc. Amer. Acad. Arts 29: 389 (1894). Mexico: Jalisco; 21 Jun. 1893, *C. G. Pringle 4402.* Isotype (mu63718).

Guardiola rotundifolia B. L. Robinson, Proc. Amer. Acad. Arts 29: 317 (1894). Mexico: Jalisco; 15 Oct. 1893, *C. G. Pringle 4571.* Isotype (mu105640).

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Gymnolomia canescens B. L. Robinson, Proc. Amer. Acad. Arts 27: 174 (1892). Mexico: San Luis Potosi; 27 Jun. 1891, *C. G. Pringle 3763.* Isosyntype (mu105744).

Gymnolomia decumbens B. L. Robinson, Proc. Amer. Acad. Arts 26: 165 (1891). Mexico: Mexico; 3 Sep. 1890, *C. G. Pringle 3263.* Isotype (mu105745).

Gymnolomia patens var. *abbreviata* B. L. Robinson & Greenm., Proc. Amer. Acad. Arts 29: 387 (1894). Mexico: Jalisco; 21 Sep. 1893, *C. G. Pringle 4595.* Isotype (mu105752).

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Hedysarum americanum f. *albiflorum* Standley, Publ. Field Colombian Mus., Bot. Ser. 8: 15 (1930). ALASKA: Davidson Glacier; 4 Jul. 1929, *W. S. Cooper & F. E. Andrews 95*. ISOTYPE (MU44548).

Hedysarum flavescens Coulter & Fisher, Bot. Gaz. (Crawfordsville) 18: 300 (1893). MONTANA: Helena; May 1892, *F. D. Kelsey s.n.* ISOTYPE (MU44557).

Hedysarum utahense Rydb., Bull. Torrey Bot. Club 34: 424 (1907). UTAH: near Salt Lake City; 26 May 1883, *F. E. Leonard 55*. ISOTYPE (MU44552).

Helianthus laevigatus reindutus Steele, Contr. U.S. Natl. Herb. 13: 374 (1911). VIRGINIA: Bath Co.; 3 Sep. 1906, *E. S. Steele s.n.* ISOSYNTYPE (MU106205).

Heliotropium pringlei B. L. Robinson, Proc. Amer. Acad. Arts 26: 170 (1891). MEXICO: San Luis Potosi; 16 Jul. 1890, *C. G. Pringle 3207*. ISOSYNTYPE (MU66179).

Hemizonia arida Keck, Aliso 4: 109 (1958). CALIFORNIA: Kern Co.; 11 May 1935, *D. D. Keck & P. Stockwell 3279*. ISOTYPE (MU106834).

Hemizonia clementina Brandegee, Erythea 7: 70 (1899). CALIFORNIA: San Clemente Island; 25 Aug. 1894, *T. S. Brandegee s.n.* ISOTYPE (MU106835).

Hemizonia conjugens Keck, Aliso 4: 109 (1958). CALIFORNIA: San Diego Co.; 16 May 1903, *L. Abrams 3521*. ISOTYPE (MU106840).

Hemizonia halliana Keck, Madroño 3: 12 (1935). CALIFORNIA:

San Luis Obispo Co.; 4 May 1933, *D. D. Keck & W. H. Heisey 2170.* Isotype (mu106863).

Hemizonia parryi subsp. *australis* Keck, Madroño 3: 15 (1935). California: Orange Co.; 29 Sep. 1933, *D. D. Keck 2537.* Isotype (mu106972).

Heuchera duranii Bacigalupi, Contr. Dudley Herb. 1: 191 (1933). California: Mono Co.; 26 Jul. 1930, *V. Duran 2817.* Isotype (mu37171).

Heuchera rubescens var. *pachypoda* f. *ambigua* Rosendahl, Butters & Lakela, Minnesota Stud. Pl. Sci. 2: 91 (1936). California: White Mountains; 3 Jun. 1930, *V. Duran 539.* Isotype (mu37290).

Hieracium jaliscense subvar. *guadalajarense* Zahn, Pflanzenreich IV. 280, Heft 79: 1114 (1972). Mexico: Jalisco; Jul. 1893, *C. G. Pringle 4461.* Isotype (mu97629).

Hieracium tolucanum Arv.-Touv., Annuaire Conserv. Jard. Bot. Genève 1: 92 (1897). Mexico: Mexico; 17 Aug. 1892, *C. G. Pringle 4183.* Isotype (mu97687).

Hilaria cenchroides var. *ciliatus* Lams.-Scribn., Proc. Acad. Nat. Sci. Philadelphia 1891: 293 (1891). Mexico: Jalisco; 17 May 1890, *C. G. Pringle 3128.* Isotype (mu90970).

Holodiscus australis Heller, Bull. Torrey Bot. Club 25: 194 (1898). New Mexico: Santa Fe Canyon; 12 Jul. 1897, *A. A. Heller 3840.* Isotype (mu39052).

Horkelia brevibracteata Wiggins, Contr. Dudley Herb. 1: 170 (1933). Mexico: Baja California; 20 Sep. 1930, *I. L. Wiggins & D. Demaree 4931.* Isotype (mu38975).

Hymenopappus arenosus Heller, Bull. Torrey Bot. Club, 25: 200 (1898). New Mexico: Santa Fe Co.; 17 May 1897, *A. A. & E. G. Heller 3542.* Isotype (mu107271).

Hyptis digitata R. Harley, Kew Bull. 40: 632 (1985). Brazil: Coias; 28 Sep. 1975, *G. Hatschbach 37241 & R. Kummrow.* Isotype (mu154337).

Ibidium incurvum Jennings, Ann. Carnegie Mus. 3: 483 (1906). Pennsylvania: Erie Co.; 25 Aug. 1905, *O. E. Jennings 18.* Isotype (mu77845).

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Arts 29: 319 (1894). Mexico: Jalisco; 30 Aug. 1893, *C. G. Pringle 4488*. Isosyntype (mu64286).

Iresene grandis Standley, North Amer. Flora 21(2): 163 (1917). Mexico: San Luis Potosi; 5 Dec. 1891, *C. G. Pringle 3962*. Isotype (mu24433).

Isoetes montezumae D. C. Eaton, Fern Bull. 5: 25 (1897). Mexico: Mexico; 28 Aug. 1890, *C. G. Pringle 3459*. Isotype (mu112001).

Isoetes vermiculata R. J. Hickey, Ann. Missouri Bot. Gard. 76: 1160 (1989). Venezuela: Territorio Federal Amazonas; 26–27 Feb. 1985, *J. A. Steyermark & B. Holst 130758*. Isotype (mu153155).

Iva oraria Bartlett, Rhodora 8: 26 (1906). Massachusetts: Boston; 18 Sep. 1905, *H. H. Bartlett s.n.* (Plantae Exsiccatae Grayanae 293). Isotype (mu98519).

Jacobinia stellata B. L. Robinson & Greenm., Proc. Amer. Acad. Arts 29: 390 (1894). Mexico: Jalisco; 16 Oct. 1893, *C. G. Pringle 4573*. Isotype (mu73824).

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Juglans mexicana S. Wats., Proc. Amer. Acad. Arts 26: 152 (1891). Mexico: San Luis Potosi; 4 Oct. 1890, *C. G. Pringle 3322*. Isotype (mu19333).

Lagophylla dichotoma subsp. *minor* Keck, Madroño 3: 16 (1935). California: Napa Co.; 29 May 1933, *D. D. Keck 2338*. Isotype (mu107401).

Lantana glandulosissima Hayek, Repert. Spec. Nov. Regni Veg. 2: 161 (1906). Mexico: Jalisco; 2 Jul. 1893, *C. G. Pringle 4431*. Isotype (mu66933).

Lasthenia conjugens Greene, Pittonia 1: 221 (1888). California: Antioch; 17 Apr. 1887, *E. L. Greene s.n.* Isotype (mu107415).

Laurentia michoacana B. L. Robinson, Proc. Amer. Acad. Arts 26: 167 (1891). Mexico: Michoacan; 8 Nov. 1890, *C. G. Pringle 3337*. Isotype (mu76716). (*Nom. nud.*, published *pro synon.*).

Laurentia ovatifolia B. L. Robinson, Proc. Amer. Acad. Arts 26: 166 (1891). Mexico: San Luis Potosi; 8 Sep. 1890, *C. G. Pringle 3302*. Isosyntype (mu76715).

Layia chrysanthemoides subsp. *maritima* Keck & Clausen, Aliso

4: 106 (1958). CALIFORNIA: Sonoma Co.; 24 May 1935, *J. Clausen 1090.* ISOTYPE (MU107478).

Layia pentachaeta subsp. *albida* Keck, Aliso 4: 107 (1958). CALIFORNIA: San Luis Obispo Co.; 9 Apr. 1935, *D. D. Keck & J. Clausen 3106.* ISOTYPE (MU107509).

Layia septentrionalis Keck, Aliso 4: 106 (1958). CALIFORNIA: Lake Co.; 29 May 1933, *D. D. Keck 2384.* ISOTYPE (MU107538).

Lechea leggettii Britton & Hollick, Bull. Torrey Bot. Club 21: 251 (1894). NEW JERSEY: Bergen Point; 7 Oct. 1876, *W. H. Leggett 5* (or *8*?). ISOTYPE (MU53676).

Leptochloa mexicana Lams.-Scribn., Proc. Acad. Sci. Phildelphia 1891: 302 (1891). MEXICO: San Luis Potosi; 28 Sep. 1890, *C. G. Pringle 3252.* ISOTYPE (MU90862).

Leptodactylon melingii Wiggins, Contr. Dudley Herb. 1: 173 (1933). MEXICO: Baja California; 18 Sep. 1930, *I. L. Wiggins & D. Demaree 4884.* ISOTYPE (MU64646).

Lesquerella peninsularis Wiggins, Contr. Dudley Herb. 1: 166 (1933). MEXICO: Baja California; 18 Sep. 1930, *I. Wiggins & D. Demaree 4919.* ISOTYPE (MU35449).

Liabum cervinum B. L. Robinson, Proc. Amer. Acad. Arts 29: 317–318 (1894). MEXICO: Jalisco; 9 Jun. 1893, *C. G. Pringle 4398.* ISOTYPE (MU107591).

Linum australe Heller, Bull. Torrey Bot. Club 25: 627 (1898). NEW MEXICO: east of Santa Fe; 17 Jun. 1897, *A. A. & E. G. Heller 3724.* ISOTYPE (MU48388).

Lippia appendiculata B. L. Robinson & Greenm., Proc. Amer. Acad. Arts 29: 390 (1894). MEXICO: San Luis Potosi; 20 Nov. 1891, *C. G. Pringle 4625.* ISOTYPE (MU67056).

Lippia linearifolia Moldenke, Phytologia 24: 454 (1972). BRAZIL: Minas Gerais; 12 Nov. 1971, *G. Hatschbach 27812.* ISOTYPE (MU129414).

Lippia myriocephaloides Briq., Annuaire Conserv. Jard. Bot. Genève 4: 235 (1900). MEXICO: San Luis Potosi; 24 Sep. 1890, *C. G. Pringle 3277.* ISOTYPE (MU66922).

Lippia rivalis Moldenke, Phytologia 45: 37–38 (1980). BRAZIL: Bahia; 12 Mar. 1979, *G. Hatschbach 42128.* ISOTYPE (MU127621).

Lithospermum revolutum B. L. Robinson, Proc. Amer. Acad. Arts 27: 182 (1892). MEXICO: San Luis Potosi; 10 Jul. 1891, *C. G. Pringle 3802* (= *Schaffner 728*). ISOTYPE (MU66332).

Lobelia calcarea F. Wimmer, Repert. Spec. Nov. Regni Veg. 38:

83 (1935). MEXICO: San Luis Potosi; 30 Nov. 1890, *C. G. Pringle 3369.* ISOSYNTYPE (MU76722).

Lobelia novella B. L. Robinson, Proc. Amer. Acad. Arts 26: 167 (1891). MEXICO: San Luis Potosi; 1 Oct. 1890, *C. G. Pringle 3288.* ISOTYPE (MU76853).

Lobelia picta B. L. Robinson & Seat., Proc. Amer. Acad. Arts 28: 112 (1893). MEXICO: Mexico; 1 Oct. 1892, *C. G. Pringle 4305.* ISOTYPE (MU76869).

Lopezia angustifolia B. L. Robinson, Proc. Amer. Acad. Arts 27: 169 (1892). MEXICO: San Luis Potosi; 30 Oct. 1891, *C. G. Pringle 3990.* ISOTYPE (MU55991).

Lophospermum scandens Sesse & Mocino *ex* D. Don, Trans. Linn. Soc. London 15: 353 (1827). MEXICO: "Nueva España"; without date, *Sesse & Mocino s.n.* Photograph of LECTOTYPE (G) (MU133051). (See Elisens, 1985a, p. 68–71.)

Loxothysanus pedunculatus Rydb., N. Amer. Flora 34: 33 (1914). MEXICO: San Luis Potosi; 24 Jun. 1890, *C. G. Pringle 3096.* ISOTYPE (MU101362).

Lycopodium × *bartleyi* A. W. Cusick, Amer. Fern J. 77: 100 (1987). OHIO: Hocking Co.; 18 Mar. 1987, *A. W. Cusick 26204.* ISOTYPE (MU150763).

Lycopodium × *habereri* House, New York State Mus. Bull. 176: 36 (1915). NEW YORK: Oneida Co.; 24 Oct. 1907, *J. V. Haberer 3022* (labelled as "8022," but this is evidently a typographical error, since the label data agree with the protologue in all other respects). ISOTYPE (MU111561).

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Margarathnus sulphureus Fernald, Proc. Amer. Acad. Arts 35: 566 (1900). MEXICO: Federal District; 4 Oct. 1899, *C. G. Pringle 8215.* ISOSYNTYPE (MU69850).

Maurandia barclaiana Lindl., Bot. Reg. 13: t.1108 (1827). MEXICO: Hort. Barclay; 1827, *Barclay s.n.* Photograph of LECTOTYPE (CGE) (MU133050). (See Elisens, 1985a, p. 43.)

Melampodium bibracteatum S. Wats., Proc. Amer. Acad. Arts 26: 140 (1890). Mexico: Mexico; 30 Aug. 1890, *C. G. Pringle 3230*. Isotype (mu107874).

Melitella pusilla Sommier, Nuovo Giorn. Bot. Ital. 14: 496–497 (1907). Turkey: Insula Gaulos; 28 Apr. 1907, *S. Sommier s.n.* Isosyntype (mu107907).

Mentzelia perennis Wooton, Bull. Torrey Bot. Club 25: 260 (1898). New Mexico: White Mountains; 21 Jul. 1897, *E. O. Wooton 184*. Isotype (mu54947).

Mertensia leonardi Rydb., Bull. Torrey Bot. Club 36: 680 (1909). Utah: Mill Creek Canyon; 31 Jul. 1884, *F. E. Leonard s.n.* Isotype (mu66357).

Mertensia longiflora Greene, Pittonia 3: 261 (1898). Washington: Medical Lake; May 1893, *J. H. Sandberg & J. B. Leiberg s.n.* Isotype (mu66408).

Mertensia pratensis Heller, Bull. Torrey Bot. Club 26: 550 (1899). New Mexico: Santa Fe Canyon; 2 Jun. 1897, *A. A. & E. G. Heller 3641*. Isotype (mu66382).

Microstylis tenuis S. Wats., Proc. Amer. Acad. Arts 26: 152 (1891). Mexico: Mexico; 27 Jul. 1890, *C. G. Pringle 3186*. Isotype (mu78225).

Montanoa purpurascens B. L. Robinson & Greenm., Proc. Amer. Acad. Arts 34: 515 (1899). Mexico: Zacatecas; 26 Oct. 1891, *C. G. Pringle 3935*. Isosyntype (mu107956). This collection was incorrectly cited in the protologue as number 3985. (See Davis, 1936, pp. 525–526.)

Muhlenbergia biloba Hitchc., Contr. U.S. Natl. Herb. 17: 294 (1913). Mexico: Chihuahua; 7 Oct. 1886, *C. G. Pringle 819*. Isotype (mu88850).

Muhlenbergia dumosa var. *minor* Lams.-Scribn. *ex* Beal, Grasses of N. Amer. 2: 261 (1896). Mexico: Jalisco; 7 Nov. 1889, *C. G. Pringle 2355*. Isotype (mu91743).

Muhlenbergia magna Hitchc., N. Amer. Flora 17: 460 (1935). Isotype. (See *Sporobolus complanatus.*)

Muhlenbergia nebulosa Lams.-Scribn. *ex* Beal, Grasses of N. Amer. 2: 247 (1896). Mexico: Jalisco; 5 Nov. 1889, *C. G. Pringle 2366*. Isotype (mu92414).

Musenium alpinum J. M. Coulter & J. Rose, Bot. Gaz. (Crawfordsville) 20: 260 (1895). Mexico: Mexico; 2 Sep. 1892, *C. G. Pringle 4247*. Isotype (mu58084).

Myrceugenia hatschbachii Landrum, Brittonia 32: 372–373 (1980).

Brazil: Parana; 22 Oct. 1965, *G. Hatschbach 13043.* Isotype (mu128664).

Myrcia jaguariaivensis Mattos & Legrand, Loefgrenia 67: 2 (1975). Brazil: Parana; 26 Nov. 1968, *G. Hatschbach 20387.* Isotype (mu129362).

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Nemastylis flava B. L. Robinson, Proc. Amer. Acad. Arts 29: 323 (1894). Mexico: Jalisco; 23 Jun. & 21 Aug. 1893, *C. G. Pringle 4400.* Isotype (mu81095).

Nissolia confertiflora var. *laxior* B. L. Robinson, Proc. Amer. Acad. Arts 29: 315 (1894). Mexico: Jalisco; 5 Jun. 1893, *C. G. Pringle 4379.* Isotype (mu46450).

Oldenlandia pringlei B. L. Robinson, Proc. Amer. Acad. Arts 27: 169 (1892). Mexico: San Luis Potosi; 27 Jun. 1891, *C. G. Pringle 3758.* Isotype (mu75003).

Oligonema heterophylla S. Wats., Proc. Amer. Acad. Arts 26: 138 (1891). Mexico: Mexico; 30 Aug. 1890, *C. G. Pringle 3236.* Isotype (mu105595).

Onagra strigosa Rydb., Mem. New York Bot. Gard. 1: 278 (1900). Montana: Helena; 1887, *F. D. Kelsey 242 (87/270).* Isosyntype (mu56316). This specimen was cited as *Kelsey s.n.* by Elisens (1985b).

Ophiocephalus angustifolius Wiggins, Contr. Dudley Herb. 1: 176 (1933). Mexico: Baja California; 18 Sep. 1930, *I. L. Wiggins & D. Demaree 4888.* Isotype (mu71849).

Opuntia charlestonensis Clokey, Madroño 7: 71 (1943). Nevada: Clark Co.; 16 Jul. 1938, *I. W. Clokey 8029.* Isotype (mu122055).

Opuntia multigeniculata Clokey, Madroño 7: 69 (1943). Nevada: Clark Co.; 13 Jul. 1939, *I. W. Clokey 8430.* Isotypes (2: mu55021, mu122093).

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Otopappus robinsonii Klatt, Ann. K. K. Naturhist. Hofmus. 9: 362 (1894). Isotype. (See *O. alternifolius.*)

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20: 204 (1924). MEXICO: Michoacan; 25 Nov. 1891, *C. G. Pringle 3955.* ISOTYPE (MU19910).

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Walton Co.; 11 Sep. 1894, *J. K. Small s.n.* ISOTYPE (MU137687).

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Solidago sciaphila Steele, Contr. U.S. Natl. Herb. 13: 371 (1911). WISCONSIN: Sauk Co.; 26 Aug. 1909, *E. S. Steele 42.* ISOTYPE (MU109807).

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Sporobolus complanatus Lams.-Scribn. *ex* Beal, Grasses N. Amer. 2: 310 (1896). MEXICO: Jalisco; 3 Nov. 1890, *C. G. Pringle 3335.* ISOTYPE (MU90191).

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Stevia pringlei S. Wats., Proc. Amer. Acad. Arts 23: 276 (1888). MEXICO: Chihuahua; 13 Sep. 1887, *C. G. Pringle 1301.* ISOTYPE (MU4880). (This collection was incorrectly cited as *Pringle 3101* by Turner (1987). (See Davis, 1936, p. 42.))

Stevia serrata var. *ovalis* B. L. Robinson, Proc. Amer. Acad. Arts 29: 317 (1894). MEXICO: Jalisco; 28 Aug. 1893, *C. G. Pringle 4491* (= *E. Palmer 309,* according to the printed label). ISOLECTOTYPE (selected by Grashoff, per B. L. Turner) (MU5870).

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Symplocos pringlei B. L. Robinson, Proc. Amer. Acad. Arts 26: 168 (1891). MEXICO: Michoacan; 10 Nov. 1890, *C. G. Pringle 3345.* ISOTYPE (MU62125).

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Townsendia formosa Greene, Leafl. Bot. Observ. Crit. 1: 213 (1906). NEW MEXICO: Grant Co.; 30 Sep. 1904, *O. B. Metcalfe 1434.* ISOTYPE (MU101651).

Tradescantia angustifolia B. L. Robinson, Proc. Amer. Acad. Arts 27: 185 (1892). MEXICO: San Luis Potosi; 14 Aug. 1891, *C. G. Pringle 3902.* ISOTYPE (MU81914).

Tridax palmeri var. *indivisum* B. L. Robinson & Seat., Proc. Amer. Acad. Arts 28: 109 (1893). MEXICO: Jalisco; 18 Nov. 1892, *C. G. Pringle 4332.* ISOTYPE (MU2778).

Trifolium virginicum Small, Mem. Torrey Bot. Club 4: 112 (1894). WEST VIRGINIA: Greenbriar Co.; 16 May 1892, *A. Brown & J. K. Small s.n.* ISOTYPES (2: MU47619, MU47620). Note: one sheet has a printed label listing only Small as collector, while the other is hand written, and lists both names.

Tripsacum dactyloides var. *angustifolium* Lams.-Scribn. *ex* Urbina, Cat. Pl. Mex. 376 (1897). MEXICO: San Luis Potosi; 14 Aug. 1891, *C. G. Pringle 3811.* ISOTYPE (MU96061).

Trisetum deyeuxioides var. *pubescens* Lams.-Scribn. *ex* Beal, Grasses N. Amer. 2: 374 (1896). MEXICO: Michoacan; 19 Nov. 1891, *C. G. Pringle 3950.* ISOTYPE (MU96076).

Trixis longifolia var. *sericea* B. L. Robinson & Greenm., Proc. Amer. Acad. Arts 40: 9 (1904). MEXICO: Hidalgo; 29 Jan. 1899, *C. G. Pringle 8051.* ISOTYPE (MU96087).

Verbesina coahuilensis var. *viridior* B. L. Robinson & Greenm., Proc. Amer. Acad. Arts 34: 546 (1899). MEXICO: Coahuila; 12 Aug., 20 Sep. 1890, *C. G. Pringle 3268.* ISOTYPE (MU3025).

Verbesina hypomalaca var. *hypochlora* B. L. Robinson & Greenm., Proc. Amer. Acad. Arts 34: 545 (1899). MEXICO: Michoacan; 7 Aug. 1892, *C. G. Pringle 4136.* ISOLECTOTYPE (per annotation of B. L. Turner) (MU2965).

Verbesina oncophora B. L. Robinson & Seat., Proc. Amer. Acad. Arts 28: 108 (1893). MEXICO: Mexico; 21 Oct. 1892, *C. G. Pringle 4310.* ISOLECTOTYPE (per annotation of B. L. Turner) (MU15038).

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175 (1892). MEXICO: Jalisco; 12 Sep. 1891, *C. G. Pringle 3845.* ISOTYPE (MU14938).

Vernonia umbellifera Gleason, Bull. New York Bot. Gard. 4: 199 (1906). MEXICO: Jalisco; 16 Oct. 1889, *C. G. Pringle 2316.* ISOTYPE (MU15687).

Viguiera potosina S. F. Blake, Contr. Gray Herb. 54: 94 (1918). ISOSYNTYPE. See *Gymnolomia canescens.*

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NEW RECORD OF THE MANGROVE *PELLICIERA RHIZOPHORAE* (THEACEAE) ON THE CARIBBEAN COAST OF NICARAGUA

LINDA C. ROTH AND ALFREDO GRIJALVA

The recorded distribution of the neotropical mangrove *Pelliciera rhizophorae* Planchon & Triana (Theaceae) has been expanded in recent years due to new discoveries of both Tertiary pollen and living populations of the species; revised interpretations of its biogeography have been advanced with each newly reported locality. One issue concerns the Quaternary distribution of *P. rhizophorae* in the Caribbean region. The discovery of a previously unreported population of this mangrove on the Caribbean coast of Nicaragua near the northern limit of its putative modern range (Figure 1) contributes to the accumulating evidence regarding the geographic history and ecology of the species.

Early accounts of *Pelliciera rhizophorae* described its contemporary distribution as restricted to the Pacific coast of America between Costa Rica and Ecuador (Kobuski, 1951; West, 1956). Palynological studies subsequently established an expanded Tertiary range of the mangrove including widespread occurrences in the Caribbean (Wijmstra, 1968; Fuchs, 1970; Graham, 1977). These workers proposed explanations for its presumed late-Tertiary disappearance from the Caribbean in terms of restrictive site requirements and poor propagative capacity (Fuchs, 1970) or interspecific competition combined with cooling climate and fluctuating sea level (Graham, 1977). Including *P. rhizophorae* among nine mangrove species believed presently limited to the Pacific coast of America, Gentry (1982) proposed that its Caribbean populations had been eliminated when Quaternary aridity relegated these mangroves to a lone refuge of moister climate in western Colombia. When living populations of *P. rhizophorae* were found on the Caribbean coast of Colombia in 1982, human influences on the dispersal of the species, including possible passage through the Panama Canal, were offered in explanation of the supposed anomaly (Calderón-Sáenz, 1983; Winograd, 1983). Jiménez (1984) cited additional Caribbean records of *P. rhizophorae* in Panama and Nicaragua, but he noted that "significant stands" of this species occur only along the Pacific shores of the Central American isthmus and suggested that further spread on

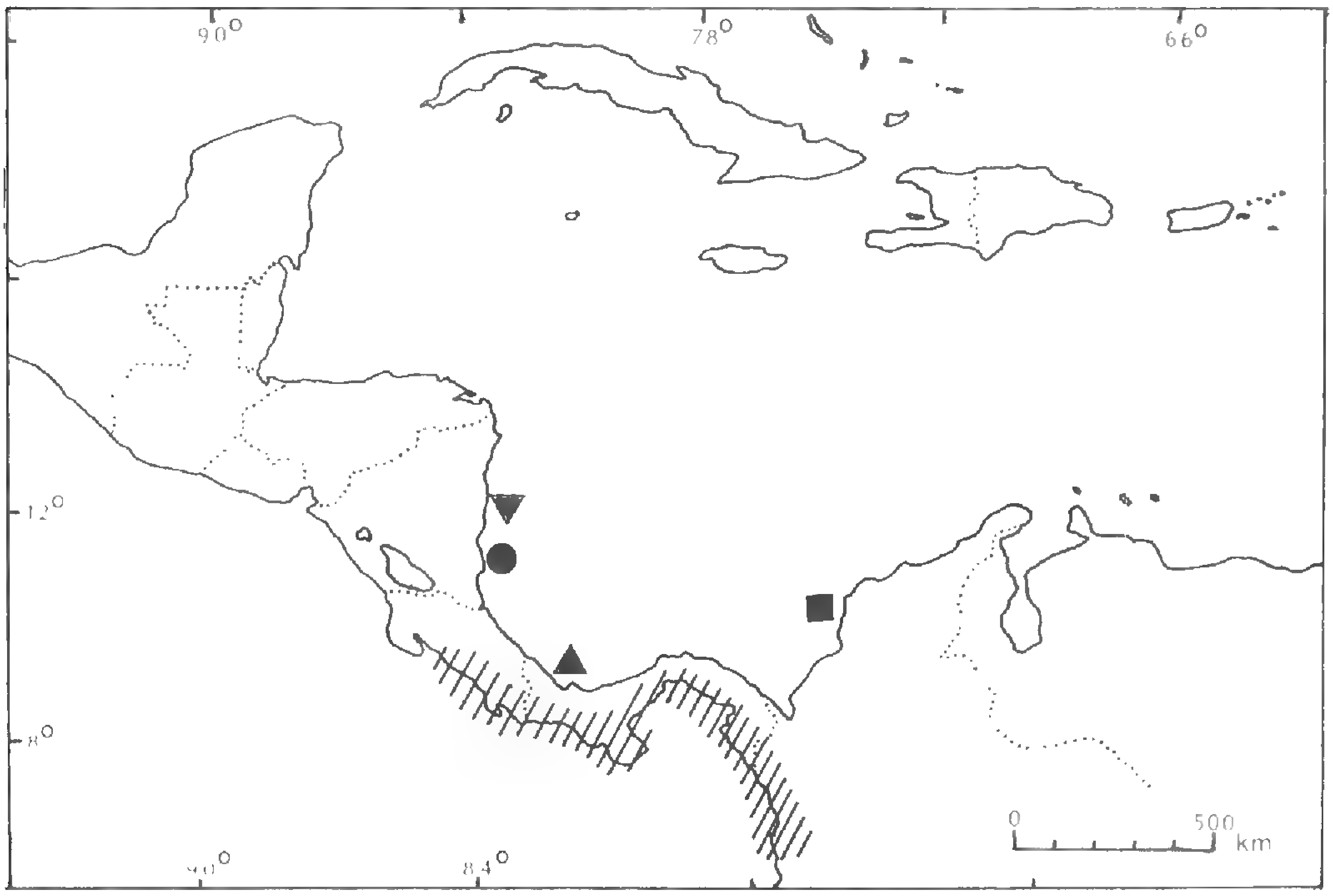

Figure 1. Map of the Central American region showing Recent distribution of *Pelliciera rhizophorae*. Shaded area indicates extent of range recognized until 1982. Subsequent findings are: (■) two small colonies reported by Calderón-Sáenz (1983); (▲) a small population reported by "Ballou and Getter, in prep." as cited in Jiménez (1984); (▼) a small population reported by "D. Neill, pers. comm." as cited in Jiménez (1984); and (●) the locality reported herein (11°55′N; 83°45′W).

the eastern side has been limited by climatic and tidal restrictions upon the extent of suitable habitat. Despite the progressively broadening recorded distribution of *P. rhizophorae* on the eastern side of the isthmus (Figure 1), these Caribbean populations are considered to be isolated relicts of a much wider Tertiary distribution (Tomlinson, 1986).

In March of 1990, vegetation sampling was conducted on Isla del Venado, a barrier island fronting the Bay of Bluefields on the east coast of Nicaragua, in order to determine the extent of mangrove regeneration after passage of hurricane Joan directly across the area in October of 1988. Although the storm had virtually destroyed the previously existing mangrove stands, the site was found amply stocked (1–2 × 10^4 ha^{-1}) with *Rhizophora mangle* L., *Avicennia germinans* (L.) L. and *Laguncularia racemosa* (L.) Gaertn. f. seedlings averaging 1.5 m in height. In addition to these more common mangrove species, 10 seedlings and one sapling of *Pelliciera rhizophorae* were found along three transects perpendicular to the water's edge, that covered a sample area of 0.15 ha. The seedlings averaged about 1 m in height. The sapling, evidently a survivor from the pre-hurricane stand, measured 4 m in height and 4 cm in trunk diameter at a height of 1.3 m. A voucher specimen has been deposited in the Nicaraguan National Herbarium in Managua. If the mean density of plants in the transects is typical of the entire stand, there could be several thousand individuals of *P. rhizophorae* on Isla del Venado; however, the small sample size precludes a reliable estimate of the population.

The fact that this locality for *Pelliciera rhizophorae* has remained unreported suggests either that the species is a recent arrival or that its presence has escaped notice. The former explanation agrees with the account of Calderón-Sáenz (1983) and Winograd (1983) and with Gentry's (1982) refuge hypothesis, although a mechanism for the recent dispersal of this mangrove into the Caribbean region remains to be demonstrated. One finding of the present study supports the second explanation. Of 11 specimens of *P. rhizophorae* encountered in the transects, 10 were found growing at distances of 25 to 57 m from the shore. The other individual was found 8 m inland from the water's edge. All of the other three mangrove species occurred throughout the length of the transects, including at points within the first few meters from shore. Several authors have remarked upon the seemingly limited microhabitat of *P. rhizophorae*, which commonly grows on slightly elevated ground inward from shore but lacking extreme salinity (Howe, 1911; Fuchs, 1970; Jiménez, 1984). A distribution pattern characterized by low densities and occurring in poorly accessible interior sections of mangrove swamps, coupled with a strong superficial resemblance of its juveniles to individuals of *R. mangle*, could explain why past collectors might have overlooked *P. rhizophorae* in parts of its range. In this case it remains to elucidate the ecological factors thus limiting this mangrove's microhabitat, population density, and perhaps size, to explain why adult trees, with their conspicuous flowers and distinctive fluted buttresses, have not been reported.

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HOLCUS MOLLIS (POACEAE) IN NEWFOUNDLAND, CANADA

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The European grass *Holcus mollis* L. (creeping fog, creeping softgrass, German velvetgrass) has been introduced in North America to many areas west of the Cascade Mountains, from California north to British Columbia (Hitchcock and Chase, 1951). In the eastern United States it is sporadically adventive at Lewis Co., NY; Camden, NJ; Delaware Co., PA (Hitchcock and Chase, 1951); Columbia, NH (Pease, 1950) and Brighton, VT (Seymour, 1985). Outside its native European distribution it has also been introduced in Chile, India, Australia and New Zealand (Häflinger and Scholz, 1981).

Previous reports for Canada (Dore, 1937; Boivin, 1967; Scoggan, 1978) are based on the 1930 collection by Herb Groh at Langley Prairie, British Columbia. A collection from Newfoundland, along the Humber Valley railway line (49°11′N, 57°20′W), is the first record of this species from eastern Canada (Green 28 VIII 1974: CAN 490598). Recent collections from Canada (at CAN and DAO) indicate that *Holcus mollis* is persisting around Langley and spreading in ruderal habitats.

In Britain, *Holcus mollis* is a common and troublesome weed growing in a wide range of moisture and soil conditions (Hubbard, 1984). Climatic parameters at Corner Brook, Newfoundland (Energy, Mines and Resources Canada, 1974) are within the range of values seen within the natural distribution in Europe. Several other species of grasses with similar native distribution in the Old World have become well established in Newfoundland (e.g., *Danthonia decumbens* (L.) DC. *in* Lam. & DC., and *Anthoxanthum odoratum* L.) suggesting that climatic conditions should not pose an obstacle to the persistence and possible spread of *H. mollis* in Newfoundland. The arrival of this grass in such a remote area probably occurred during the development and construction of the Humber Canal and Deer Lake hydroelectric project with the importation of materials in the 1920's from England by the developer Sir W. G. Armstrong, Whitworth Co. Ltd. (England).

Holcus mollis is easily distinguished from the only other member of the genus naturalized in North America, *H. lanatus* L., by the extensive creeping rhizomes (not caespitose), glabrous foliage (not villous) and a geniculate (not hooked, or curved) awn from the upper lemma.

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DODECATHEON FRENCHII (VASEY) RYDB. (PRIMULACEAE) IN ALABAMA

STEPHEN L. TIMME AND JIM LACEFIELD

ABSTRACT

Dodecatheon frenchii is reported for Alabama. Its location in the northwest portion of the state represents the most southerly distribution for the species.

Key Words: *Dodecatheon frenchii*, Hartselle sandstone, Alabama

While the senior author was conducting bryological field studies in northwest Alabama, several populations of *Dodecatheon* (Primulaceae) occurring under sandstone ledges were observed to appear somewhat different from the typical *Dodecatheon meadia* L. of limestone glades and outcrops in the area. Subsequent collections resulted in the identification of the specimens as *Dodecatheon frenchii* (Vasey) Rydb. (French's Shooting Star). As far as is known, these specimens represent first collections for Alabama.

Dodecatheon frenchii can be separated from *D. meadia* in the field by the presence of ovate leaves with blades that are abruptly narrowed to the petiole, while *D. meadia* has oblanceolate to nearly spatulate leaves with attenuate bases (Rydberg, 1932; Fassett, 1944). In addition, the filaments of *D. frenchii* are free to nearly half their length and the base of each anther is auricled. In *D. meadia,* the filaments are united nearly to the apex, and the bases of the anthers lack auricles or are only slightly auricled (Rydberg, 1932).

Dodecatheon frenchii in northwest Alabama is associated with overhangs of Hartselle sandstone, a Mississippian-aged, medium- to coarse-grained rock which forms much of the escarpment in the uplands south of the Tennessee River in Colbert County. This area is part of the physiographic province known as the "Little Mountains" section of the interior Cumberland Plateau and is highly dissected with deeply-cut ravines. The bluff tops are vegetatively characterized by *Quercus stellata* Wang. (post oak), *Q. alba* L. (white oak), *Q. falcata* Michx. (southern red oak), *Q. velutina* Lam. (black oak), *Q. prinus* L. (chestnut oak), *Carya tomentosa* (Poiret) Nutt. (mockernut hickory), *C. glabra* (Miller) Sweet (pignut hickory), and *Pinus virginiana* Miller (scrub pine). At the base of the ravines *Tsuga canadensis* (L.) Carr. (eastern hemlock), *Fagus grandiflora* Ehrhart. (beech), *Magnolia macrophylla* Michx. (umbrella tree), *Liriodendron tulipifera* L. (tulip tree), *Ilex opaca* Ait. (holly), and *Ostrya virginiana* (Miller) K. Koch. (hop hornbeam) represent the common characteristic woody plants.

Populations of *Dodecatheon frenchii* were found growing under moist, dripping sandstone overhangs. The plants were never found growing more than a few centimeters past the drip line, in regolith weathered from the overhanging rock. While some seepage of water was noted in a few places, below the overhang the soil environment is for the most part not visibly wet. The plants were not found in places where leaf litter mulched the soil extensively, but are widespread where the floor beneath the overhang was deep in the organic-poor sandy regolith. Populations were located on southern as well as northern exposures. The plants grow in homogeneous clusters, some as large as fifty square meters. Associated plants during the flowering period include *Thalictrum thalictroides* (L.) Boivin, *Plantago* sp., and *Tiarella cordifolia* L. The flowering period for *D. frenchii* in northwest Alabama is from mid-April to mid-May, with fruit maturing in June. Following seed formation, the plant dies back and becomes inconspicuous by late summer.

These northwest Alabama collections represent the most southerly distribution reported for *Dodecatheon frenchii*. Its nearest, most southern-distributed counterpart is a population located in Newton County, Arkansas. It also occurs in southern Illinois, where it was first collected, and has been reported from Pennsylvania, Minnesota, and Wisconsin (Voigt and Swayne, 1955).

Reports of *Dodecatheon frenchii* occurring under limestone overhangs north of the Tennessee River were investigated, and resulted in no populations being located. As far as is known, no populations occur outside the "Little Mountains" area of the state. The habitats of the species in this area fit well with those of collections in other states. A search for *D. frenchii* in sandstone ravines characteristic of other areas in northern Alabama may result in locating a population. These areas (Little River Canyon and Warrior River Basin), however, have been extensively studied.

Alabama: Colbert Co.: Under dripping sandstone overhangs ca. 9.6 km south of U.S. Hwy. 72 and 1.2 km north of County

Rd. #41. Cane Creek Drainage. James Lacefield Farm. Sec. 15 & 16, R12W, T5S; *Timme 9431,* with Jim Lacefield and Frank Bowers. *Timme 9734,* with Jim Lacefield.

Specimens are deposited in KSP; duplicates are available.

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SAGINA JAPONICA (SW.) OHWI (CARYOPHYLLACEAE), AN OVERLOOKED ADVENTIVE IN THE NORTHEASTERN UNITED STATES[1]

RICHARD S. MITCHELL AND GORDON C. TUCKER

In his taxonomic revision of the genus *Sagina* L., Crow (1978) cited specimens of *S. japonica* from western North America, but not the eastern United States. This introduced species is readily distinguished from our native, annual pearlwort, *S. decumbens* (Ell.) T. & G., by seed, capsule, leaf and pubescence characters (Crow, 1978, 1981). Our attention was first called to eastern North American occurrences of *S. japonica* when a specimen collected by Virginia L. Magee from the Mitchell College campus in New London, Connecticut, was sent by the junior author to Garrett Crow for identification. Subsequent study by the senior author, in conjunction with current preparation of a flora of New York State, turned up three specimens from New York and four from Massachusetts in the collections of the New York State Museum (NYS), which were not consulted by Crow during his study. Pamela Weatherbee provided a list of three additional specimens which she also had checked by Crow and by us. Arthur Cronquist also found a specimen from New York State in the herbarium of The New York Botanical Garden (NY). No additional specimens of *S. japonica* were found in the collections of the Connecticut Botanical Society (NCBS) or Yale University (YU).

Since New York and Massachusetts specimens were collected early in the 1940's, it is apparent that *Sagina japonica* has been an established introduction in the area for 50 years or more. Because of the small size of the plants and their superficial resemblance to *S. procumbens* L., our other introduced *Sagina,* they have been filed with it in herbaria. Their annual growth habit and pubescent peduncles make them readily distinguishable from that species. *Sagina japonica* has spread in the Northeast since its introduction, but it has probably been overlooked and under-collected in the disturbed, often urban, settings where it becomes established. In examining specimens from the northeastern United States, both Garrett Crow (pers. comm.) and the authors noted variability in the tuberculate condition of the seeds of *S. japonica.*

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At least one specimen (*Wilkins 14621*) has prominently and densely tubercled seeds, while the remaining specimens from our area have pebbled seed surfaces. Crow (pers. comm.) suggests that this variation may imply multiple introduction of the species into eastern North America.

For those wishing to identify *Sagina* species in New York and New England, the following diagnostic key is provided:

KEY TO *SAGINA* SPECIES IN THE NEW ENGLAND—NEW YORK AREA

1. Petals not showy, about equaling the length of sepals; flowers terminal, solitary, or a second one borne at the ultimate node; upper leaf axils not bearing succulent short-shoots . . . . (2)
    2. Perianth parts in 5's; annuals with ascending or decumbent, often capillary stems and slender taproots, not strongly tufted or spreading by offshoots . . . . (3)
        3. Seeds pale, triangular with a dorsal groove; capsules longer than broad; pedicels usually glabrous (sepals may be minutely glandular at base); leaves not succulent . . . . *S. decumbens*
        3. Seeds dark brown, plump, lacking a dorsal groove; capsules globose; pedicels glandular pubescent (at least the upper halves); leaves succulent . . . . *S. japonica*
    2. Perianth parts in 4's (rarely 5's on the same plant); matted, wiry perennials, spreading by offshoots . . . . *S. procumbens*
1. Petals showy, about twice the length of sepals; flowers often more than 2 per inflorescence; upper leaf axils bearing dense, succulent short-shoots . . . . *S. nodosa*

SPECIMENS EXAMINED: **Connecticut**: New London Co.: New London, Mitchell College Campus, dry soil by building, 7 July 1988, *Magee s.n.* (CONN, NCBS, NEBC, NHA). **Massachusetts**: Berkshire Co.: Egremont, Jug End Road, 27 June 1990, *Weatherbee 2990* (NHA); Florida, base of Torrey Mountain Road, 23 June 1990, *Weatherbee 2986* (NHA); Williamstown, driveway, 17 June 1990, *Weatherbee 2948* (NHA). Hampshire Co.: Northampton, streets, 27 June 1941, *O. L. Schreiber 234* (NYS); Amherst, "Inwood" lawn, 23 June 1950, *R.E. Torrey s.n.* (NYS); Amherst, Sunset Avenue, 18 June 1973, *H.D. Hammond 6801-b* (NYS); Hadley, North Maple Street, 3 July 1978, *H.E. Ahles 85437* (NYS). **New York**: Bronx Co.: Pelham Bay Park, Sect. 29, 14 June 1947, *H.E. Ahles 1409* (NYS); Chemung Co.: Elmira, curbings and lawns, "1945," *S.J. Smith 4797* (NYS); Kings Co.: Prospect Park, Brooklyn, N.Y. in grassy soil, 8 June 1957, *Monachino 597* (NY); Ulster Co.: Moon Hollow Rd. 2 mi. w. of W. Shokan, Town of Olive, growing in dampish soil of shaded roadside, 15 July 1987, *Karl Brooks 7074 & Paul Huth* (NYS). **Pennsylvania**: Berks Co.: lawn of Reading Museum Grounds, *Wilkens 14621* (NHA).

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THE STATUS OF *SALIX PELLITA* (SALICACEAE) IN NEW YORK STATE

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ABSTRACT

The only record of *Salix pellita* in New York is based on a single sterile herbarium specimen. Visits to the collection locality revealed that the specimen is misidentified, and the taxon remains undocumented in the state flora.

Key Words: *Salix pellita,* Bergen Swamp, New York

Salix pellita Anderss., satiny willow, is primarily an eastern Canadian species, with disjunct populations in the northeastern United States. The species is rare in Michigan (Voss, 1985) and Vermont (Thompson, 1989), but is more frequent along riparian corridors in northern New Hampshire (Pease, 1964) and in northern Maine. New York reports of *Salix pellita* (Mitchell, 1986; Clemants, 1989) are founded on a single collection made in 1944, from a sphagnum bog at Bergen Swamp, Genesee County (*White & Matthews s.n.* NYS). The collectors tentatively identified their specimen as *S. candida* Flugge forma *denudata* (Anderss.) Rouleau. In 1948 C. R. Ball annotated the sheet to *Salix pellita.*

The New York collection is sterile, presenting the standard identification difficulties in this variable genus; it is a September collection. The mature herbage is essentially glabrous, and thus closely resembles the hairless forms of three species reported in the state by Mitchell (1986): *Salix candida, S. pellita* and *S. viminalis* L. A thorough inventory of Bergen Swamp by Muenscher (1946, 1951) found 15 species of willows, including *Salix candida,* but neither *S. pellita* nor *S. viminalis.*

To relocate New York's only reported station for satiny willow, I visited Bergen Swamp in September 1989. Sphagnum-rich boggy margins were easy to locate in marly openings. Unfortunately, extensive browsing by white-tailed deer had removed most of the available willow foliage from these habitats. Typical *Salix candida* was present, but I found no *S. pellita* and no *S. viminalis.*

In early summer 1990, I revisited the resprouted willows and found typical *Salix candida* was common (*Zika 10847* NYS). Its

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glabrous form was rare (*Zika 10848, 10851* NYS). Both forms were fertile, and thus their identifications were easy to confirm. *Salix candida* forma *denudata,* with pedicels ca. 1 mm in length, was separable from *S. viminalis* which has pedicels < .5 mm long. *Salix candida* forma *denudata* had capsules with curly pubescence and was separable from *S. pellita,* which has straight hairs on the capsules. The herbage of *S. candida* forma *denudata* immediately suggested the sterile collection by White and Matthews at NYS, which was attributed to *S. pellita.*

Seymour (1982) and Voss (1985) indicated *Salix pellita* is found primarily on riverbanks and shores in the United States; my New England observations agree. Only in the Gaspé Peninsula have I seen it in the variety of other habitats noted by Scoggan (1950). Thus the New York habitat, a sphagnum bog, seems improbable for *Salix pellita* at the southern limit of its range.

The solitary sterile New York specimen called *Salix pellita* matches extant material from the collection locality shown to be *Salix candida* forma *denudata,* a superficially similar taxon. With no historical or contemporary data to the contrary, I conclude that *Salix pellita* remains undocumented from New York state.

There remains the possibility that *Salix pellita* still might be found in suitable habitats along the northern reaches of the Hudson River, or on tributaries to the St. Lawrence River in New York. If it is located there, it can safely be considered a new discovery for the state.

ACKNOWLEDGMENTS

I thank the New York Natural Heritage Program, The Nature Conservancy, and the New York Department of Environmental Conservation for supporting this field work. I am grateful to Patricia Martin and the Bergen Swamp Preservation Society for access to Bergen Swamp, and to Al Schotz for field assistance. Herbarium collections and resources at the New York State Museum (NYS) were invaluable, and I am indebted to curator and staff.

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RHODORA, Vol. 93, No. 874, pp. 198–199, 1991

NEW ENGLAND NOTE

SCIRPUS POLYPHYLLUS (CYPERACEAE) IN NEW HAMPSHIRE[1]

GORDON C. TUCKER

Scirpus polyphyllus Vahl is the only sedge of eastern North America with two-ranked leaves, a morphological feature that generally characterizes grasses rather than sedges (Tucker, 1987). Unlike *S. atrovirens* Willd. and *S. hattorianus* Makino, which are similar in having spikelets in glomerules, *S. polyphyllus* is never viviparous and it has curled bristles longer than the achenes.

During recent visits to NASC and NHA, I noted two specimens (both previously identified as "*Scirpus atrovirens* Willd.") that are in fact *Scirpus polyphyllus*, a new record for the flora of New Hampshire:

New Hampshire: Strafford Co.: Durham, Johnson Creek shore, 6 Oct. 1969, *Hellquist, Haines & Hodgdon 306* (NASC 8842); Sullivan Co.: Meriden, 1876, *Dr. N. Barrows s.n.* (NHA).

Scirpus polyphyllus, a widespread native of the eastern United States, was previously known to occur from Vermont, New York, Ohio (but not Ontario), and Illinois south to Georgia, Alabama, and Arkansas (Schuyler, 1967; Tucker, 1987). In New England it has been reported from Champlain Valley of Vermont (Zika, 1988), Massachusetts (Connecticut Valley), and Connecticut (Connecticut Valley and southwestern parts of the state) (Seymour, 1982). I have examined specimens from the herbaria listed below to confirm the range of *Scirpus polyphyllus*; in so doing, no other collections from New Hampshire were found.

On 10 September 1988, I visited Meriden, New Hampshire and spent a half-day attempting to re-locate *Scirpus polyphyllus*, assisted by J. Denison Tucker. Both *S. atrovirens* (*4166, 4168*, NYS) and *S. hattorianus* (*4169, 4180*, NYS) were plentiful along streams and in wet meadows bordering many of the town roads, but we were unable to find any *S. polyphyllus*.

---

[1] Contribution #672 from the New York State Museum and Science Service.

ACKNOWLEDGMENTS

I thank the curators of CCNL, CLEMS, CONN, DUKE, GH, KIRI, MASS, MT, MTMG, NASC, NCSC, NCU, NEBC, NHA, NYS, SMU, TRT, TRTE, VT, and YU for lending specimens or providing access to collections.

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BIOLOGICAL SURVEY
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THE STATE EDUCATION DEPARTMENT
ALBANY, NY 12230

RHODORA, Vol. 93, No. 874, pp. 200–201, 1991

BOOK REVIEW

C. B. McQueen. 1990. *Field Guide to the Peat Mosses of Boreal North America.* Pp. xiv + 138 (+ 8 pp. of colored plates). University Press of New England, 17½ Lebanon St., Hanover, NH 03755. (Price: $22.95, soft cover).

Sphagnum, commonly called "peat moss" or sometimes "bog moss," is probably the single most important moss in nature and the one of most value to humankind. More uses have been found for *Sphagnum* in everyday and commercial life than for any other moss. It is very common and widespread in the northern part of North America, especially in the boreal regions. According to the author, Cyrus McQueen, who is an authority on *Sphagnum,* the moss covers approximately 500 million acres of North America. The plants are frequently seen and collected by scientists and naturalists who want to know their identity. Therefore, one would think that there would be many manuals such as this one to help identify the approximately 60 species known for the continent, but this certainly is not the case. In fact, this is the first field guide to *Sphagnum* for North America.

The book has a short introduction describing the morphology and terminology of peat mosses as well as their life cycle. Line drawings show types of branch fascicles, capitula and branch leaf arrangements while photographs show a gametophyte with the sporophyte attached and a spore viewed under a scanning electron microscope.

An interesting section on ecology describes the habitat zonation of *Sphagnum* and how this feature can be used to help identify species. First, zonation along a wet-to-dry gradient is discussed; the author explains how certain species only occur in some parts of wetlands depending on the amount of moisture available. A second zonation, along a nutrient gradient, limits distribution of some species within a certain pH range and is closely associated with the wet-to-dry gradient; e.g., the driest habitat, hummock tops, are also the most acidic. A final zonation, based on degree of exposure (i.e., tolerance to sunlight), provides useful identification aids since some species grow only in shaded habitats while others grow only in open habitats. Different types of peatlands, especially bogs, fens and swamps, are defined and briefly discussed. The ecology section ends with a discussion on succession and the different stages in formation of a bog.

Approximately two-thirds of the book is devoted to keys, descriptions, illustrations and color photographs, all aimed at field identification of *Sphagnum*. There are three keys in the book; the only equipment necessary to identify the plants is a 10× to 20× hand lens, tweezers and metric ruler. A random access key is provided as a quick means of identifying 26 species and one variety of the most common *Sphagnum* found in boreal regions of Canada and the United States. The key employs 67 characteristics utilizing macroscopic features of stem and branch leaves, number of spreading branches per fascicle, capitulum, color, exposure, ecology and habitat. The second key, a traditional descriptive key to the same 27 Sphagna, follows with the taxa keying out to one of seven sections in the genus, the user then referring to the individual section key to identify the species. Each species has a short description of the plant's field characters, including relevant remarks on how to distinguish it from other species with which it may be confused. Line drawings of a stem leaf and sometimes a branch leaf accompany each description. Finally, the third key, which is also a traditional one and somewhat similar to the second key with its use of sections, includes the majority of taxa (46) found in northeastern North America. A glossary and short list of books about *Sphagnum* and their identification that the author recommends for further reading conclude the book.

The keys are clear and are based on easy-to-use macroscopic characters that should present few problems to the user. The color plates of 30 taxa of *Sphagnum* are an important and useful feature of this attractive book. Although the plates are small, ca. 4 × 6 cm, the photos are generally very clear and the color of the plants in most cases seems to be very close to their color in nature. The small size of the book, ca. 11 × 23 cm, makes it easy to carry which is essential for a field guide.

Amateur naturalists, students and professional biologists, especially ecologists, will find this attractive book to be of immense help in identifying the peat mosses that are so commonly seen in boreal wetlands of North America. Because the majority of the species have a circumpolar distribution, the guide should also be useful outside North America. The book is highly recommended for those learning to identify peat mosses because of the clear and simplified approach.

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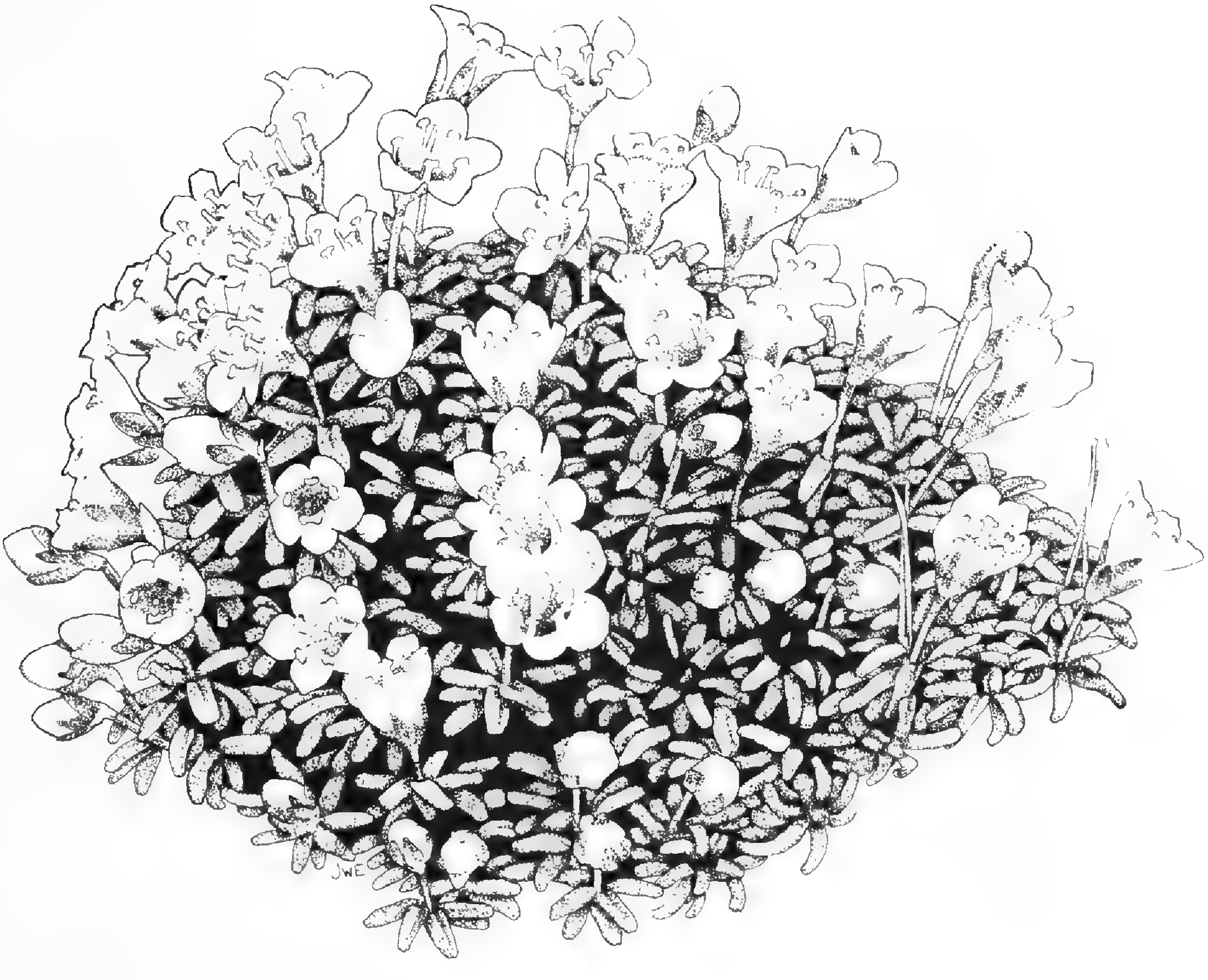

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Cover Illustration

Diapensia lapponica L. ssp. *lapponica.* Found on the higher mountains of northern New England, this Arctic circumpolar early-blooming tussock plant is a rare disjunct to New England. Original artwork by Josephine Ewing.

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RHODORA, Vol. 93, No. 875, pp. 205–225, 1991

ISOZYME EVIDENCE AND PHENETIC RELATIONSHIPS AMONG SPECIES IN *ASTER* SECTION *BIOTIA* (ASTERACEAE)

Warren F. Lamboy,[1] Daniel L. Nickrent,
and Almut G. Jones

ABSTRACT

Aster section *Biotia* is an eastern North American group of asters having a base chromosome number of $x = 9$. Phenetic analyses of isozyme gene frequency data show that the species native to the eastern deciduous forest region, *Aster divaricatus* ($2n = 18$), *A. chlorolepis* ($2n = 36$), *A. schreberi* ($2n = 54$), and *A. macrophyllus* ($2n = 72$) are very closely related and perhaps form an increasing polyploid series. Isozyme data reveal that the two species whose ranges are restricted to the Piedmont, *A. mirabilis* ($2n = 18$) and *A. jonesiae* ($2n = 54$), are very closely allied and are more distantly related to the previous group. The endemic and midwestern *A. furcatus* ($2n = 18$) is isozymically most unlike the other species in the section. Isozyme data do not rule out the possibility that the hexaploids, *A. schreberi* and *A. jonesiae,* originated by retrogressive polyploidy rather than by progressive (increasing) polyploidy. The hypothesis that *A. chlorolepis* arose from *A. divaricatus* by autopolyploidy is supported by the electrophoretic data. The relationships of the diploids to one another and the mode of origin of *A. macrophyllus* are not clarified by the isozyme analyses.

Key Words: *Aster* section *Biotia,* isozymes, electrophoresis, phenetics, eastern North America

INTRODUCTION

The North American species of *Aster* form a large, taxonomically difficult and evolutionarily complex assemblage (Allen, 1984, 1986; Dean and Chambers, 1983; Gray, 1880, 1882, 1884; Jones,

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1980a, 1980b; Semple and Brouillet, 1980a, 1980b; Shinners, 1941; Torrey and Gray, 1841). Taxonomic difficulties in the genus mostly involve species delimitations (Allen, 1984, 1986; Jones, 1980b, 1984), but even in cases where species are well defined, relationships between them are not. Hybridization and introgression (Avers, 1953; Wiegand, 1928, 1933), polyploidy (Dean and Chambers, 1983), and phenotypic plasticity (Jones, 1978a, 1978b) have been cited as the primary contributors both to blurring of species boundaries and to uncertainty about phylogenetic relationships.

From all other *Aster* groups, the eastern North American *Aster* L. section *Biotia* DC. ex Torrey and A. Gray can be distinguished by the following combination of characteristics: long-petiolate basal and lower cauline leaves with cordate-based, toothed blades; upper cauline leaves with toothed margins; mature cypselas that are fusiform with 7 or more prominent ribs; heads with the outermost phyllaries densely ciliolate and obtuse to rounded at the apex; capitulescences corymbiform; and base chromosome number $x = 9$. Judging by morphology, the most closely related groups are subgenus *Aster* subsection *Spectabiles* A. Gray and subgenus *Doellingeria* (Nees) A. Gray from eastern North America, and subgenus *Aster* section *Radulini* (Rydberg) A.G. Jones from western North America (Jones, 1980a; Jones and Young, 1983).

Aster section *Biotia* comprises three diploids: *A. divaricatus* L., *A. furcatus* Burgess in Britton and Brown, and *A. mirabilis* Torrey and A. Gray; one tetraploid: *A. chlorolepis* Burgess in Small; two hexaploids: *A. jonesiae* Lamboy and *A. schreberi* Nees; and one octoploid: *A. macrophyllus* L. Three of these species, *A. divaricatus, A. schreberi,* and *A. macrophyllus,* are common in New England (Lamboy, 1990, Ph.D. dissertation, University of Illinois, Urbana; Seymour, 1969), and *A.* ×*herveyi* A. Gray, a hybrid between *A. macrophyllus* and *A. spectabilis* Aiton, is endemic to New England and New York.

The seven members of *Aster* section *Biotia* and the one hybrid may be distinguished by means of the following taxonomic key.

KEY TO *ASTER* SECTION *BIOTIA* AND ONE SYMPATRIC HYBRID

1. Plants with stipitate-glandular hairs on the phyllaries and peduncles 2

2. Blades of lower cauline leaves broadly ovate or ovate, cordate at the base; innermost phyllaries usually less than 7 mm long, never reflexed, squarrose, or twisted at the apex; rhizomes long stoloniform; in deciduous or coniferous forest areas, eastern North America . . . . *A. macrophyllus*

2. Blades of lower cauline leaves ovate to narrowly ovate, rounded to cordate at the base; innermost phyllaries always more than 7 mm long, at least some of them reflexed, squarrose, or twisted at the apex; rhizomes caudiciform or short to long stoloniform; usually in sandy soil of coniferous forest areas, New England . . . . *A.* ×*herveyi*

1. Plants without stipitate-glandular hairs on the phyllaries and peduncles 3

3. At least some of the phyllaries squarrose 4

4. At least some of the phyllaries obovate or oblanceolate; ray florets usually 16 or more, white or lavender; disk florets 50 or more; phyllaries usually more than 50; North and South Carolina . . . . *A. mirabilis*

4. Phyllaries ovate, elliptic, or lanceolate; ray florets usually 15 or fewer, blue or violet; disk florets usually 25 or fewer; phyllaries fewer than 50; Georgia and Alabama . . . . *A. jonesiae*

3. None of the phyllaries squarrose 5

5. Leaves scabrous above, rough below; primary and secondary veins particularly prominent below; disk florets yellow at anthesis, turning greenish with age; on substrates of or derived from limestone or sandstone; Iowa, Missouri, Illinois, Wisconsin, Michigan, and Indiana . . . . *A. furcatus*

5. Leaves glabrous to scabrous above, glabrous below; primary and secondary veins not particularly prominent below; disk florets yellow at anthesis, turning magenta with age; on various substrates; United States east of the Mississippi River, southern Ontario, and southern Quebec 6

6. Blades of lower cauline leaves broadly ovate to ovate, cordate with broad sinuses at the base, usually with more than 30 teeth along each

side of the leaf; plants often forming large clonal patches of mostly sterile basal rosettes; southern Ontario, and northeastern United States, scattered localities in the Appalachian Mountains and Midwest ...... *A. schreberi*

6\. Blades of lower cauline leaves ovate, cordate at the base with sinuses lacking or very narrow, usually with fewer than 30 teeth along each side of the leaf; never forming large patches of mostly sterile basal rosettes 7

  7\. Longest peduncles usually longer than 2.0 cm; heads wider than 2.5 cm when the rays are fully extended; involucre 0.5–1.0 cm tall; high mountains in Virginia, Tennessee, North Carolina, and Georgia ... . *A. chlorolepis*

  7\. Longest peduncles usually shorter than 2.0 cm; heads narrower than 3.0 cm when the rays are fully extended; involucre 0.35–0.75 cm tall; at lower altitudes throughout eastern North America .. *A. divaricatus*

Possible interspecific relationships, which have been postulated on the basis of morphology, geography, and chromosome number (Lamboy, 1990, op. cit.), are shown in Figure 1. The only phylogenetic statement that can be made with a reasonable degree of certainty, though, is that the montane tetraploid, *Aster chlorolepis,* arose from *A. divaricatus* by autotetraploidy (Lamboy, 1991, at review). The former species is, in many morphological characters, simply a larger version of the latter. In addition, *A. chlorolepis* is endemic to the higher altitudes within the range of the *A. divaricatus.* Both of these pieces of evidence support the autotetraploid origin of *A. chlorolepis.*

The relationships between the other taxa are not nearly as clear. In fact, there are at least two plausible origins for most of the species. For example, because it is found in the northern two-thirds of the range of *Aster divaricatus,* and because it shares inflorescence size and shape characters with *A. divaricatus,* it is possible that the hexaploid, *A. schreberi,* arose from *A. divaricatus* by means of autopolyploidy and subsequent backcrossing to the diploid.

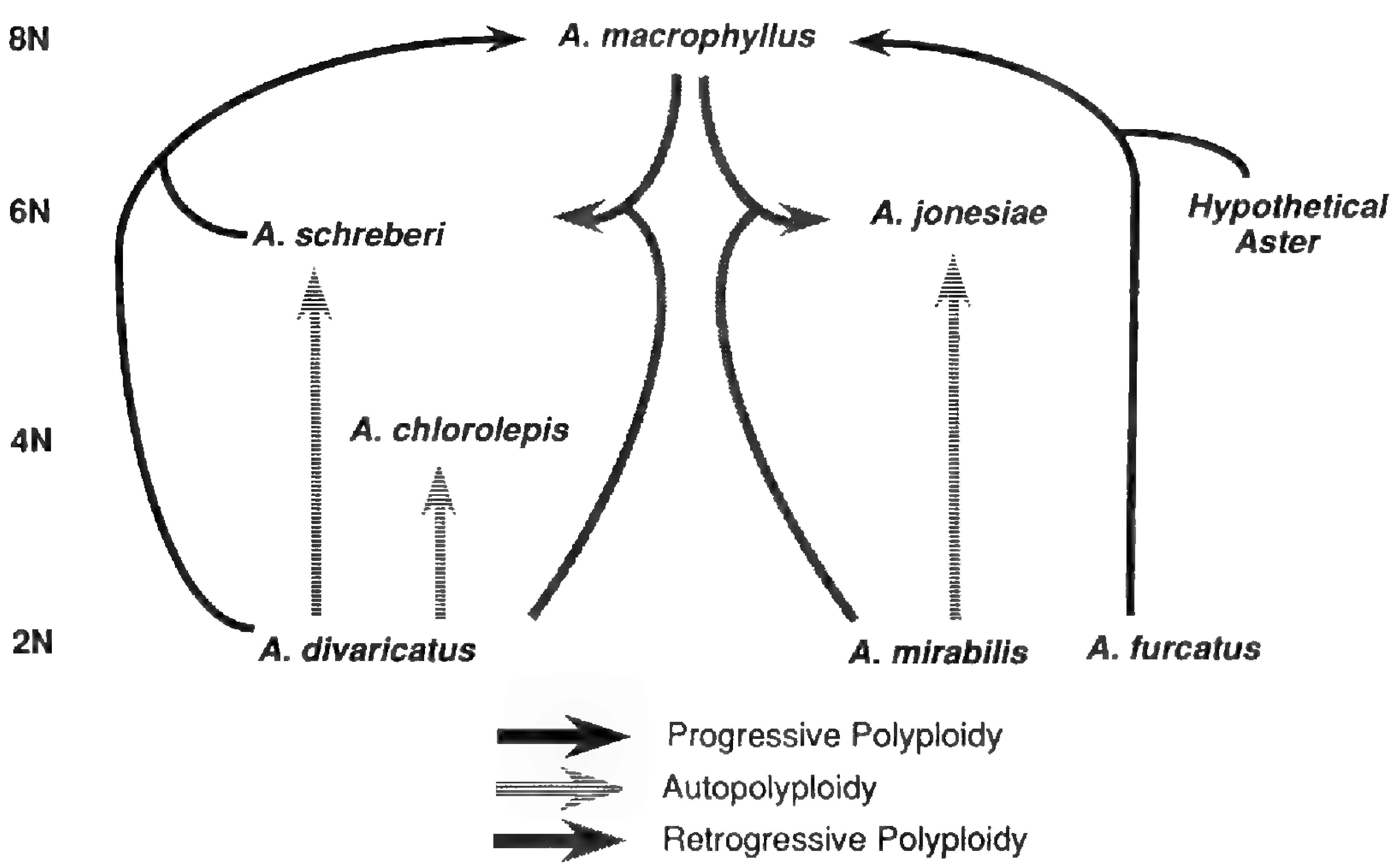

Figure 1. Possible ancestor - descendant relationships between species in *Aster* section *Biotia.* Arrows point from ancestors to descendants. Polyploid levels of the species are indicated at the left. Note that for some species, e.g., *Aster schreberi,* the information currently available does not strongly favor one mode of origin over the others.

On the other hand, plants of *Aster schreberi* are similar in size to *A. macrophyllus,* and they exhibit the same leaf shape, leaf toothing, and clonal colony formation as well. This similarity suggests that *A. schreberi* may have arisen by retrogressive polyploidy from a hybrid between *A. divaricatus* and *A. macrophyllus.* Retrogressive polyploidy as defined by Lamboy and Jones (1988) is: "the formation of a hybrid derivative from a successful cross between two species, one a high polyploid and the other a lower polyploid or diploid, resulting in a sexually reproducing species having a ploidy level intermediate between that of the two parents."

The other hexaploid in *Aster* section *Biotia, A. jonesiae,* has squarrose phyllaries and a caudiciform rhizome system, characteristics it shares with the diploid, *A. mirabilis,* but it has stem diameter, overall plant size, and basal and lower cauline leaves much like those of the octoploid, *A. macrophyllus.* Both *A. jonesiae* and *A. mirabilis* are native to the Piedmont of the southeastern United States, and *A. macrophyllus* grows close by in cool shaded habitats in the southern Appalachians. It is possible, therefore, that *A. jonesiae* arose either from *A. mirabilis* by autopolyploidy with backcrossing to the diploid or by retrogressive polyploidy from putative parents *A. mirabilis* and *A. macrophyllus.*

Morphology provides little information about the relationships of the diploids to one another. Geographic and ecological evidence suggests, though, that *Aster divaricatus* may be the oldest of the three diploids. This species is native to the eastern deciduous forest and possesses the most extensive range of the three species. In contrast, both *A. furcatus* and *A. mirabilis* have restricted ranges and occupy less stable habitats. The former is found in rocky places along watercourses, and the latter is native to the transition zone between southern Appalachian hardwoods and oak-pine forests. Before *A. divaricatus* can be accepted as the oldest of the diploids, however, additional evidence must be obtained.

Finally, the octoploid, *Aster macrophyllus,* may represent the endpoint of the increasing polyploid series: *A. divaricatus* to *A. chlorolepis* to *A. schreberi* to *A. macrophyllus,* since plant height, stem diameter, and cauline leaf size form an increasing series in this order. On the other hand, *A. macrophyllus* could be the allopolyploid derivative of a hybrid (e.g., between *A. furcatus* and some other *Aster* species), for *A. furcatus* and *A. macrophyllus* have been found historically in a number of the same locations in the midwest, and they both possess scabrous leaves, large capitula, and tall, thick stems.

Because morphology does not clarify the origins of and the relationships among species in *Aster* section *Biotia,* we conducted an electrophoretic analysis using isozymes of all members of the section to shed more light on their phenetic relationships. In addition to providing an answer to the fundamental question of what the genetic distances are between the taxa, analysis of electrophoretic data can help answer other questions of taxonomic interest, such as whether gene frequency data support the origin of *A. chlorolepis* from *A. divaricatus* by autopolyploidy. Such data may also throw light on three questions: did the two hexaploids, *A. jonesiae* and *A. schreberi,* originate by retrogressive polyploidy or via the more usual progressive polyploidy; from what parentage did *A. macrophyllus* arise; and how are the diploids related to one another?

The goals of the electrophoretic analysis of *Aster* isozymes were:

1. To obtain genetic distances between species and to construct phenograms from this information.

2. To determine whether genetic distances between putatively different species have numerical values that are usually found for different species, or whether they are in the range usually found for different populations of the same species.
3. To use unique alleles, if any, present in the diploids to assess ancestry of the polyploids, and to determine if they are likely to be auto- or allo-polyploids.
4. To examine genetic distances in order to find species that are particularly closely related, which may be evidence that they have diverged from one another relatively recently.

No published information is available on isozymes in *Aster.* Gottlieb (1981) analyzed seven taxa, two of which he called *Aster,* and five species of *Machaeranthera.* However, one species, *A. riparius,* has since been transferred to *Machaeranthera,* and the remaining species, *A. hydrophilus,* should probably also be transferred to *Machaeranthera,* or at the very least, should be taken out of *Aster.* The only previous numerical work on the phylogeny of members of the genus *Aster* was done by Jones and Young (1983), and their study, using morphological characters and chromosome numbers, assessed the phylogeny of North American supraspecific groups in the genus but did not examine phylogenies of species within any section.

MATERIALS AND METHODS

Living plants were obtained from populations in the eastern United States. Since the purpose of this study was to examine interspecific rather than intraspecific genetic relationships, and since the members of *Aster* section *Biotia* are native to most of the eastern United States, emphasis was placed on collecting specimens from as many localities throughout the entire geographic range of each species as possible, rather than on collecting many specimens from a single population. Results obtained by previous workers show that this procedure should give a reasonably accurate representation of the genetic variation in *Aster* species which are outcrossing (Jones, 1974; Lamboy, unpubl.), even though population information will not be available (Avise, 1975; Crawford, 1983).

Living plants were greenhouse-grown in Urbana, Illinois, and leaf material was collected on the day of grinding. Leaves were cut near the base of the petiole with a razor blade, transferred to plastic sandwich bags, and then placed on ice in a plastic cooler. All leaf material was ground within two hours of collection, although tests showed that material left overnight at 4°C before grinding showed no loss of enzyme activity. Two grams of leaf material, cut with scissors, were placed in a mortar with 5–8 times (by volume) liquid nitrogen, and ground by hand with a pestle. Before the powdered tissue was allowed to thaw, it was transferred to a test tube containing grinding buffer at 4°C consisting of: .029 M sodium tetraborate, .017 M sodium metabisulfite, .100 M sodium ascorbate, .016 M diethyldithiocarbamic acid, and .100 M potassium dihydrogen phosphate adjusted to pH 7.5. Five percent (w/v) PVP-40 and 1.0% (v/v) 2-mercaptoethanol were added to the buffer before use. The mixture was homogenized at maximum speed with a Polytron homogenizer, and the homogenate was transferred to plastic centrifuge tubes and centrifuged at 10,000 rpm for 10 minutes at 0°C. The supernatant was poured into microfuge tubes and stored at −100°C.

The extracts were thawed on ice and the liquid absorbed onto filter paper wicks. Enzyme separation was performed on 14% horizontal starch gels as described by Shaw and Prasad (1970). The following enzyme systems were used: triose phosphate isomerase (TPI) [E.C. 5.3.1.1], leucine amino peptidase (LAP) [3.4.11.1], phosphoglucomutase (PGM) [5.4.2.2], and phosphoglucoisomerase (PGI) [5.3.1.9], since these were the only ones which could be scored with confidence, although many other enzyme systems showed activity.

TPI, PGM, and LAP were resolved on a gel using a lithium-citrate buffer (Ridgway et al., 1970) and PGI was resolved using the citrate-morpholine buffer of Clayton and Tretiak (1972), modified according to Nickrent (1984, Ph.D. dissertation, Miami University, Oxford, Ohio).

In addition to the enzymes exhibiting bands of adequate intensity and resolution, the following enzyme systems were examined: acid phosphatase, aconitase, adenylate kinase, alcohol dehydrogenase, aldolase, cytochrome oxidase, diaphorase, esterase, fructose 1,6-diphosphatase, glyceraldehyde-3-phosphate dehydrogenase, glycerate-2-dehydrogenase, glucose-6-phosphate dehydrogenase, glutamate dehydrogenase, glutamate oxaloacetate transaminase, glutathione reductase, hexokinase, isocitrate dehydrogenase, maleate dehydrogenase, malic enzyme, menadione reductase, peroxidase, 6-phosphogluconate dehydrogenase, polyphenol oxidase, and shikimic acid dehydrogenase. Although most of these enzymes showed activity in extracts from some plants, because of lack of sufficient intensity, resolution, or repeatability, none of them was found suitable for analysis. Unusually high levels of phenolic compounds are almost certainly responsible for the loss of enzyme activity in these species of *Aster.*

Because of the difficulty in obtaining interpretable banding patterns for many of the enzymes listed, a number of compounds were added to the grinding buffer to try to improve resolution and intensity. Substances added to the grinding buffer included: .5 M ascorbate, bovine serum albumin, casein, cysteine, diethyldithiocarbamic acid, diethyldithiothrietol, dimethylsulfoxide, ethylenediamine tetraacetic acid, ethanol, glycerol, higher concentrations of metabisulfite, nicotinamide adenine dinucleotide, nicotinamide adenine dinucleotide phosphate, phenylmethylsulfonyl fluoride, polyethylene glycol, pyridoxine-5′-phosphate, sucrose, thiourea, and Tween 80 (a detergent). These additions were done using various 2^{p-k} fractional factorial designs (Box and Draper, 1987), which would have indicated if any of these substances was useful either alone or in combination. However, none of them improved resolution or intensity over that achieved with the grinding buffer recipe listed above.

Many other gel and electrode buffer combinations were used in an attempt to obtain repeatable and interpretable enzyme bands and to improve band resolution and intensity. None resolved the isozymes any better than those produced on gels prepared with the lithium-citrate or citrate-morpholine buffers. Similarly, use of tissue from the very youngest leaves did not significantly improve the results.

Enzyme staining protocols were derived from Soltis et al. (1983). For enzyme systems with two or more loci present on a gel, the fastest moving (most anodal) locus was designated as number one. Alleles at a locus were designated by capital letters, with A being the most anodally migrating allele. Allelic frequencies were estimated for the polyploids based on visual inspection of the intensity of band staining (Jorgensen, 1986; Nielsen, 1980) and analyzed phenetically using the program BIOSYS-1 (Swofford and Selander, 1981).

Because determination of gene frequencies for polyploids is not as straightforward as for diploids, a brief explanation on how gene frequencies were determined is necessary. Consider a banding pattern for TPI-1 (a dimer) for a specimen of the tetraploid, *A. chlorolepis,* where the intensities of evenly spaced bands from top (anode) to bottom (cathode) are approximately 1:2:4:4:4. Based on banding patterns from diploid homozygotes, the faintest band occurs at the position of allele A, the middle band is located at the position of allele B, and the lowest band at allele C. The simplest explanation for these band intensities at these positions is that there is one copy of allele A, one of allele B, and two of allele C. In this case, the actual band intensities would be 1:2:5:4:4, with the AC dimer occurring at the same position as the BB dimer.

Because no more than 4 different alleles were found for the dimeric enzymes TPI-1, TPI-2, and PGI-2, estimation of gene dosages were, even for the most complex patterns, not much more difficult to interpret than that described above. In every case, the simplest explanation that would account for the observed banding pattern was accepted as correct. Fortunately, the genetic distance measures of Nei (1972, 1978) and Rogers (1972) are not overly sensitive to small differences in gene frequencies, so that minor errors in estimating gene dosages do not change the resulting phenograms. In addition, the most variable enzyme, PGM-2, is a monomer, so that the determination of gene dosages for this enzyme is not confused by overlapping bands that represent different allelic combinations.

In order to determine gene frequencies for a species, it was assumed that each plant carries two copies of every gene for every copy of the diploid genome it possessed. Thus, for example, an octoploid plant must carry 8 copies of the PGM-2 gene, and the enzyme banding intensities must reflect this. The total number of PGM-2 genes in the sample of 44 *A. macrophyllus* plants that must be accounted for is then 8 times the number of individuals, that is, 8 × 44 = 352. Thus since allele G of PGM-2, for example, was found 4 times out of 352, it has a gene frequency of 4/352 × 100% = 1% (with rounding). Gene frequencies were computed similarly for other enzymes and other species. Since Nei's and Rogers's genetic distance measures depend only on gene frequencies, and not on ploidy level, these quantities were computed by the computer program BIOSYS-1 and used in the phenetic analyses.

Five assumptions are involved in determining gene frequencies as described above. The first two are that there are no null alleles in any of the taxa and no inactive loci in the polyploids. Null alleles cannot definitively be detected without crossing experiments, and these could not be conducted because Biotian asters will not bloom under our greenhouse conditions. The third and fourth assumptions are that all forms of an enzyme have the same enzyme activity and that all duplicate loci in the polyploids are homologous, thus allowing dosages to be estimated from banding intensity, ploidy level, and knowledge of enzyme quaternary structure. The fifth is that there have been no gene duplications in the polyploids above those resulting from polyploidy itself.

RESULTS AND DISCUSSION

Four enzyme systems representing seven presumed loci were analyzed: TPI-1, TPI-2, LAP, PGI-1, PGI-2, PGM-1 and PGM-2. The estimated allelic frequencies for alleles at these loci are shown in Table 1. Three alleles were found for TPI-1, TPI-2, and LAP, seven were found for PGM-2, and four were found for PGI-2. PGI-1 and PGM-1 were found to be monomorphic across all species in the section.

Two isozymes of TPI, PGM, and PGI were detected in diploid members of *Aster* section *Biotia.* This number is usually found for these enzymes (e.g., Gottlieb, 1982; Gottlieb et al., 1985). Only one isozyme of LAP was found. Previous workers reported either one or two loci for LAP (Bayer and Crawford, 1986; Crawford and Bayer, 1981; Crawford and Smith, 1984; Gottlieb et al., 1985; Heywood and Levin, 1984; Warwick and Gottlieb, 1985). Thus, none of the diploid members of *Aster* section *Biotia* appear to have duplicated loci, which, if found, might have been of help in assessing the ancestry of the polyploid taxa. Because of the method of computing gene frequencies in polyploids, it was not possible to determine if they possessed any duplicate loci not possessed by the diploids.

Since PGI, PGM, and TPI are known to be found both in the plastids and the cytosol in other plant taxa (Gottlieb, 1982), these are assumed to be their subcellular locations in members of *Aster* section *Biotia.* Since LAP is not known from plastids, this enzyme is probably cytosolic in these *Aster* species also.

When all species in the section are considered, a total of four loci was found to be fixed for a single allele. TPI-1 is fixed at allele C in *Aster mirabilis* and *A. jonesiae.* This finding is evidence

Table 1. Allelic frequencies for the seven species in *Aster* section *Biotia*. Species names are abbreviated using the first three letters of the specific epithet.

	Species						
Locus	div	fur	mir	chl	jon	sch	mac
TPI-1							
(N)	70	18	19	12	4	16	44
A	.057	.000	.000	.479	.000	.083	.108
B	.121	.639	.000	.104	.000	.250	.412
C	.822	.361	1.000	.417	1.000	.667	.480
TPI-2							
(N)	70	18	19	12	4	16	44
A	.250	.028	.237	.333	.625	.365	.324
B	.700	.972	.684	.667	.375	.635	.625
C	.050	.000	.079	.000	.000	.000	.051
LAP							
(N)	70	18	19	12	4	16	44
A	.100	.000	.000	.000	.000	.000	.023
B	.850	1.000	.684	.958	.500	.781	.920
C	.050	.000	.316	.042	.500	.219	.057
PGM-2							
(N)	70	18	19	12	4	16	44
A	.014	1.000	.000	.104	.000	.000	.088
B	.158	.000	.105	.396	.500	.281	.415
C	.021	.000	.000	.000	.000	.000	.006
D	.800	.000	.605	.500	.500	.719	.441
E	.000	.000	.290	.000	.000	.000	.028
F	.000	.000	.000	.000	.000	.000	.011
G	.007	.000	.000	.000	.000	.000	.011
PGI-2							
(N)	70	18	19	12	4	16	44
A	.164	.056	.000	.000	.000	.000	.074
B	.529	.944	.026	.500	.500	.281	.418
C	.300	.000	.974	.500	.500	.625	.494
D	.007	.000	.000	.000	.000	.094	.014

for a close relationship between the diploid, *A. mirabilis,* and the hexaploid, *A. jonesiae.* LAP is fixed at allele B and PGM-2 is fixed at allele A in *A. furcatus.* Since the B allele for LAP is the most common allele in all the species, no inference can be based on its fixation in *A. furcatus.* Allele A for PGM-2, however, is rare or absent in the other members of the section, which helps account for the relatively distant relationship of *A. furcatus* to the

Table 2. Mean unbiased heterozygosity and mean number of alleles per locus for species in *Aster* section *Biotia*. Results from the loci that are monomorphic across all species (PGI-1 and PGM-1) are included.

Species	Mean Unbiased Heterozygosity per Locus	Mean Number of Alleles per Locus
A. divaricatus	.281	2.9
A. furcatus	.091	1.4
A. mirabilis	.219	1.9
A. chlorolepis	.327	2.0
A. jonesiae	.321	1.6
A. schreberi	.327	2.0
A. macrophyllus	.353	3.1

rest of the species in the section. *Aster divaricatus, A. chlorolepis, A. schreberi* and *A. macrophyllus* were polymorphic for all loci examined.

The only allele unique to a species is PGM-2 allele F in *Aster macrophyllus,* and it is found at a very low frequency. It may represent an allele that was obtained by the octoploid species from some *Aster* species outside of the section, an allele that arose *de novo* in the species, or an allele present in the other species but that escaped detection owing to sampling variability.

Based on the values for mean unbiased heterozygosity per locus (Table 2), six of the Biotian asters are in the normal range of variability as compared to most other angiosperms, which have heterozygosity values in the range .20 to .35. The low heterozygosity value (.091) for *Aster furcatus* may be a consequence of widely separated populations and a relatively higher degree of self-compatibility (Les, pers. comm.).

Values for Nei's unbiased genetic identity and Rogers's genetic similarity were computed from gene frequencies and are displayed in Table 3. Phenograms constructed by the unweighted pair group method with arithmetic averages (Sneath and Sokal, 1973) using Nei's unbiased genetic identity measure (Figure 2) or Rogers's genetic similarity measure (Figure 3) show the phenetic relationships between the seven species in the group. In both figures, *Aster chlorolepis* and *A. macrophyllus* are grouped first, and then *A. divaricatus* and *A. schreberi* are joined. These two clusters are then united together to form the set consisting of the eastern North American deciduous forest species of *Aster* section *Biotia.*

Table 3. Matrix of genetic similarity and identity coefficients for species in *Aster* section *Biotia*. Above diagonal: Rogers's genetic similarity. Below diagonal: Nei's unbiased genetic identity.

Species	1	2	3	4	5	6	7
1 *A. divaricatus*	*****	.570	.746	.789	.715	.837	.809
2 *A. furcatus*	.669	*****	.397	.578	.385	.509	.625
3 *A. mirabilis*	.854	.448	*****	.663	.726	.785	.688
4 *A. chlorolepis*	.916	.700	.804	*****	.721	.813	.889
5 *A. jonesiae*	.895	.495	.894	.851	*****	.750	.727
6 *A. schreberi*	.959	.603	.936	.948	.947	*****	.849
7 *A. macrophyllus*	.924	.740	.825	.974	.868	.969	*****

Next, *Aster jonesiae* and *A. mirabilis* are joined to the four-species group, which is the only topological difference between the two figures. In Figure 2, *A. jonesiae* and *A. mirabilis* first are joined in a two-taxon cluster, which is united to the cluster of the four previous species. By contrast, in Figure 3, first *A. jonesiae* is joined into a five-species group, and a very short distance later, *A. mirabilis* is united with the previous five species. Although Figures 2 and 3 differ slightly in the clustering of *A. jonesiae* and *A. mirabilis,* both emphasize the close relationship between these two Piedmont species.

Finally, in both Figures 2 and 3, *Aster furcatus* is joined to the remaining six species at a relatively low level of genetic similarity.

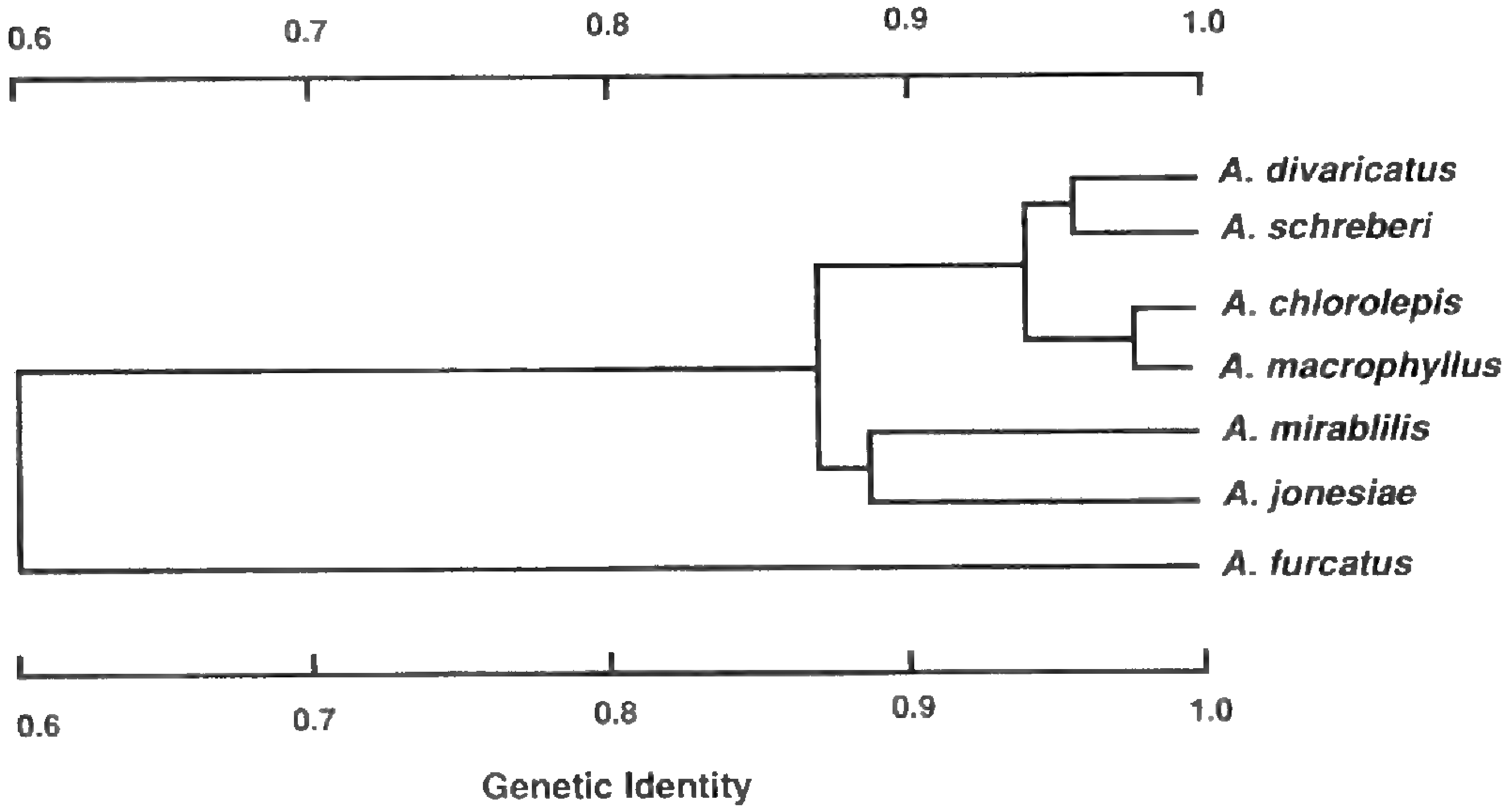

Figure 2. Cluster analysis using unweighted pair group method. Coefficient used: Nei's (1978) unbiased genetic identity. Abbreviations are as in Table 1.

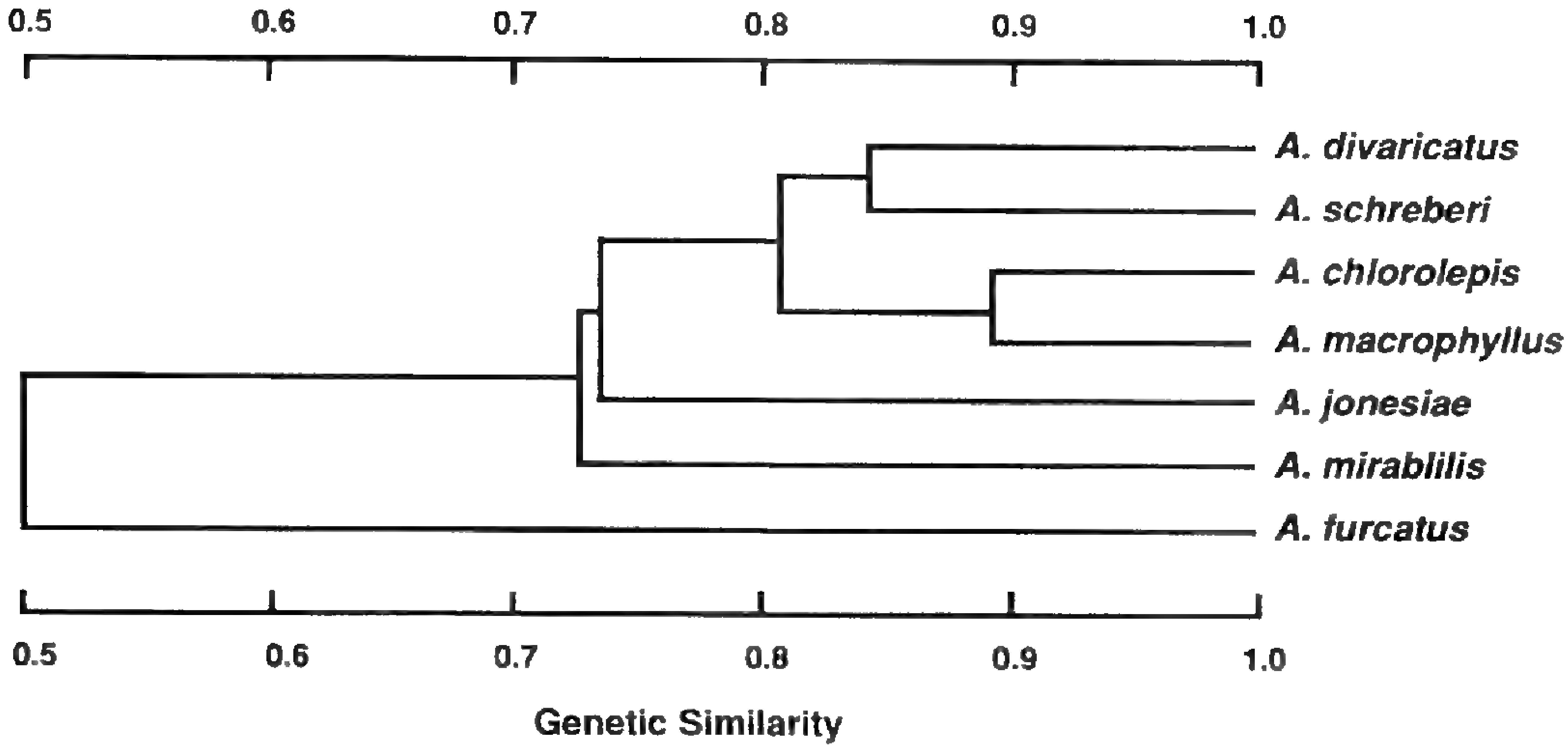

Figure 3. Cluster analysis using unweighted pair group method. Coefficient used: Rogers's (1972) genetic similarity. Abbreviations are as in Table 1.

Phenograms constructed using either weighted pair group clustering with arithmetic averages or complete linkage clustering (Sneath and Sokal, 1973) show the same topologies as those in Figures 2 and 3.

The relationships shown in Figures 2 and 3 are precisely those one would predict from phytogeographic information. *Aster divaricatus, A. chlorolepis, A. schreberi* and *A. macrophyllus* are native to eastern and central North America north of the mountains of Alabama, Georgia, and South Carolina. *Aster mirabilis* and *A. jonesiae* are restricted in range to the Piedmont of Alabama, Georgia, South Carolina, and North Carolina, and the single species, *A. furcatus,* is a midwestern endemic.

Previous isozyme studies by other workers have shown that conspecific populations usually have genetic identities of .90 and above (Crawford, 1983). When different species have genetic identities this high, they are often assumed to have diverged relatively recently. If species limits in *Aster* section *Biotia* were determined solely on the basis of the .90 criterion for conspecificity, *A. divaricatus, A. chlorolepis, A. schreberi,* and *A. macrophyllus* would be considered to be members of the same species (Figure 2). Because the morphologies and chromosome numbers of *A. divaricatus, A. chlorolepis, A. schreberi,* and *A. macrophyllus* differ, however, these taxa have been maintained as distinct (Lamboy, 1990, op. cit.). This interpretation is not without precedent. For example, Nickrent (1986) also found several pairs of *Arceuthobi-*

um species with genetic identities greater than .90, but he did not regard them as conspecific. The high values for the genetic identities of the four Biotian asters indicate, however, that these taxa may have diverged from an ancestral taxon relatively recently, perhaps since the last glaciation.

Lamboy (1991, at review) has argued that *Aster chlorolepis* is an autotetraploid derivative of *A. divaricatus.* The isozyme data support this conclusion in two ways. First, there is no evidence of the fixed heterozygosity in *A. chlorolepis* that would be expected in an allotetraploid. In addition, the species maintains at least 3 alleles at two loci, TPI-1, and PGM-2, and it shows both homozygous and heterozygous banding patterns. Finally, it has a greater heterozygosity than its putative progenitor (Table 3), which is what would be expected in an autopolyploid (Soltis and Rieseberg, 1986).

Lamboy and Jones (1988) hypothesized that *Aster jonesiae* arose by retrogressive polyploidy from a hybrid of *A. mirabilis* and *A. macrophyllus.* All plants of *A. jonesiae* examined display the predicted fixed heterozygosity of such an origin. *Aster jonesiae* and *A. mirabilis* are also the only two species fixed for allele C at TPI-1. There is, thus, some evidence supporting the hypothesis of origin by retrogressive polyploidy, but confirmation is desirable.

The suggestion that *Aster schreberi* arose by retrogressive polyploidy (Lamboy and Jones, 1988) from a hybrid of *A. divaricatus* and *A. macrophyllus* also is supported by the isozyme data. Although there is no evidence for the fixed heterozygosity expected in a taxon of allopolyploid origin (Soltis and Rieseberg, 1986), if *A. schreberi* or its hybrid progenitor originated independently several times, fixed heterozygosity might not be evident in the observed genotypes. Since the ranges of the putative ancestors, *A. macrophyllus* and *A. divaricatus,* overlap through much of New England, New York, Pennsylvania, Ohio, and Virginia (Lamboy, 1990, op. cit.), multiple origins of *A. schreberi* or its hybrid progenitor would not be unexpected. Furthermore, *A. schreberi* has its greatest genetic identity with *A. macrophyllus,* and its second greatest with *A. divaricatus,* and every allele found in *A. schreberi* is also found in both *A. divaricatus* and *A. macrophyllus.* Thus, the isozyme data provide substantial evidence supporting the origin of *A. schreberi* by retrogressive polyploidy.

Finally, the isozyme data are inconclusive concerning the derivation of the octoploid, *Aster macrophyllus.* Among the taxa examined, this species has the greatest genetic identity with *A. chlorolepis* and the second greatest with *A. schreberi*. One allele, E at PGM-2, present in low frequency, *A. macrophyllus* shares only with *A. mirabilis*. These inconsistent results leave the relationship and origins of *A. macrophyllus* obscure.

This study represents the first published information on isozymes in the genus *Aster*. It must be emphasized that because of the limited number of loci and small number of plants of some species, the conclusions reached cannot be considered definitive. Nevertheless, the electrophoretic data do corroborate some of the results obtained from chromosome numbers, morphological measurements, and phytogeographic information. Analysis of the gene frequencies of isozyme alleles in *Aster* species still holds great potential for answering taxonomic and phylogenetic questions in the genus, since it is the best method for obtaining genotype information on large numbers of individuals at a reasonable cost. If this potential is to be realized, however, the problem of loss of enzyme activity due to unusually high concentrations of phenolic compounds in *Aster* must be overcome.

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APPENDIX

Vouchers for Living Specimens Used in the Isozyme Analyses

All numbers are Lamboy collections unless otherwise noted. Numbers in parentheses indicate number of plants analyzed that belonged to the population from which the voucher plant was taken. All specimens are deposited at ILL.

Aster chlorolepis. **North Carolina:** Caldwell Co., *303, 305, 306,* Swain Co., *313, 315, 316, 317,* Yancey Co., *310, 430*; **Tennessee:** Carter Co., *426*; **Virginia:** Grayson Co., *415, 417.*

Aster divaricatus. **Alabama:** Marshall Co., *261, 262*; **Connecticut:** Fairfield Co., *170,* Litchfield Co., *246,* New Haven Co., *171, 176*; **Georgia:** Rabun Co., *319, 439*; **Kentucky:** Carter Co., *395, 396, 398*; **Massachusetts:** Berkshire Co., *181, 248, 249,* Bristol Co., *189,* Franklin Co., *254,* Norfolk Co., *190,* Worcester Co., *192*; **New Hampshire:** Cheshire Co., *201,* Rochester Co., *Jones 4338*; **New Jersey:** Warren Co., *161, 162*; **New York:** Cattaraugus Co., *239, 241,* Suffolk Co., *164, 167,* Ulster Co., *243*; **North Carolina:** Caldwell Co., *300, 302,* Henderson Co., *432, 433,* Jackson Co., *434, 435,* Macon Co., *438,* Swain Co., *322, Jones 3440,* Wilkes Co., *413,* Yancey Co., *307*; **Ohio:** Hocking Co., *380, 386, 389, 390, 393,* Jefferson Co., *74,* Vinton Co., *382,* **Pennsylvania:** Allegheny Co., *80,* Clarion Co., *126, 127, 129, 134, 138,* McKean Co., *222,* Westmoreland Co., *43, 47*; **Tennessee:** Carter Co., *424, 425,* **Vermont:** Windsor Co., *216*; **Virginia:** Giles Co., *411,* Grayson Co., *414, 422,* Page Co., *408,* Smyth Co., *418, 419, 420, 423*; **West Virginia:** Grant Co., *404,* Hardy Co., *406,* Pendelton Co., *402, 403,* Randolph Co., *399.*

Aster furcatus. **Illinois:** LaSalle Co., *4, 5, 6* (3), *443, 447, 448, 449, 450, Jones 6228* (2); **Indiana:** Warren Co., *444, 445, Jones 6524* (2); **Iowa:** Muscatine Co., *Watson s.n.* (2); **Wisconsin:** Fond du Lac Co., *224.*

Aster jonesiae. **Georgia:** Harris Co., *264, 265,* Morgan Co., *273, 274.*

Aster macrophyllus. **Connecticut:** Litchfield Co., *178*; **Massachusetts:** Franklin Co., *194,* Norfolk Co., *191,* Worcester Co., *193*; **Michigan:** Benzie Co., *156,* Delta Co., voucher lost, Grand Traverse Co., *Jones 5675* (2), Mason Co., *143, 154, 160, 442*; **New Hampshire:** Coos Co., *211,* Grafton Co., *213*; **New York:** Cattaraugus Co., *240, 242,* Essex Co., *220*; **North Carolina:** Henderson Co., *431,* Yancey Co., *309, 429*; **Ohio:** Hocking Co., *384, 387, 391, 392, 395*; **Pennsylvania:** Allegheny Co., *64,* Clarion Co., *119, 134,* Clearfield Co., *86,* Venango Co., *90, 94*; **Vermont:** Windsor Co., *217*; **Virginia:** Giles Co., *410, 412,* Page Co., *407, 409*; **West Virginia:** Greenbrier Co., *Jones 6036,* Pendleton Co., *401,* Randolph Co., *400*; **Wisconsin:** Fond du Lac Co., *225, 228,* Sauk Co., *17, 34,* Washington Co., *230.*

Aster mirabilis. **South Carolina:** Chester Co., *280, 281, 282, 283, 284, 285, 286, 288,* Lancaster Co., *289, 290, 293, 295, 297, 298, 440,* Richland Co., *Jones 6185* (4).

Aster schreberi. **Connecticut:** Hartford Co., *183*; **Illinois:** Peoria Co., *7* (2), *446, Ebinger 23678, Jones 6202*; **Kentucky:** Carter Co., *397*; **Massachusetts:** Berkshire Co., *247*; **New York:** Ulster Co., *245*; **Ohio:** Hocking Co., *381, 383, 388,* Morrow Co., *378, 379, 441*; **Vermont:** Bennington Co., *196.*

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TAXONOMY OF *VACCINIUM* SECTION *OXYCOCCOIDES* (ERICACEAE)

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ABSTRACT

The Appalachian *Vaccinium erythrocarpum* and the SE Asian *V. japonicum* are morphologically indistinct and share a similar chromosome number ($n = 12$). Their flavonoid profiles are also quite similar; however, the two taxa do show some difference in their capacity to accumulate derivatives of the two flavonols kaempferol and quercetin: *V. japonicum* accumulates both, while *V. erythrocarpum* accumulates only quercetin. Reciprocal crossing experiments between the taxa produce fertile hybrids. Therefore in the absence of a potential genetic barrier and no morphological gap, the reduction of these vicariads to subspecies is warranted. Consequently *V. erythrocarpum* subspecies *japonicum, comb. et stat. nov.* is proposed.

Key Words: *Vaccinium, Oxycoccoides,* taxonomy, flavonols, chromosome numbers, southeast Asia, southeast U.S.

INTRODUCTION

Taxa referred to *Vaccinium* section *Oxycoccoides* (Hooker f.) Sleumer share the following features: perennating buds covered by two partially fused prophylls; solitary flowers borne in leaf axils and set on nodding pedicels continuous with the calyx tube; corolla deeply 4-cleft; stamens eight, thecae awnless with long, slender tubules. Berry 4-locular, with each locule containing 20–25 ovules.

Currently section *Oxycoccoides* is comprised of two disjunct species, *Vaccinium erythrocarpum* Michx., a local endemic in the Appalachians of the southeastern U.S. (Wood, 1961; Vander Kloet, 1988) and *V. japonicum* Miq., widely distributed in the highlands of southern China, Formosa and Japan (Wood, 1961; Horikawa, 1972; Fang, 1986). *Vaccinium japonicum* consists of three varieties (Wood, 1961): var. *sinicum* (Nakai) Rehd. is restricted to China (Fang, 1986), var. *lasiostemon* Hayata to Formosa, and var. *japonicum* to Japan and Quelpaert Island (Wood, 1961). The only morphological difference between these vicariads is that the Appalachian material is usually somewhat more glandular-pubescent and robust than the Asian (Table 1; Sleumer, 1941; Vander Kloet, 1988). These differences are scarcely sufficient to warrant specific status, especially when one considers that *V.*

Table 1. Morphological comparison between selected attributes of the North American *Vaccinium erythrocarpum* and the Asian *V. japonicum*. Values given are means ± one standard deviation.

Character	*V. erythrocarpum*	*V. japonicum*
1. Plant height	30–150 (200) cm	(10) 20–60 (150)
2. Habit	rhizomatous (crown-forming)	rhizomatous (crown-forming)
3. Twigs	± terete	± terete
4. Twig indumentum	pubescent in lines	glabrous to pubescent
5. Leaf: width	23 ± 5 mm	19 ± 3 mm
6. Leaf: length	53 ± 10 mm	41 ± 9 mm
7. Leaf: margin	serrate	serrate
8. Leaf: blade	glandular beneath	± eglandular beneath
9. Corolla lobes	reflexed at anthesis	reflexed at anthesis
10. Filaments	pilose	pilose
11. Anther sac tubules	4 ± 1 mm long	4 ± 1 mm long
12. Pedicel length	8–15 mm	10–20 mm
13. Berry color	red, deep purple, black	red

japonicum var. *ciliare* Matsumura was established to accommodate the more glandular and pubescent Japanese material. Before combining these highly disjunct populations into a single species, however, their karyology, flavonoid chemistry, and ecology are described in some detail to evaluate their status.

MATERIALS AND METHODS

Collection data for the population samples analyzed are given in Table 2. In addition to leaf and twig collections, 20 to 30 ripe berries were also collected at each site. Berries were measured to the nearest millimeter. Seeds were washed from the berries, air dried, and the large, plump, brown seeds were separated from the small, pale or collapsed ones, and each batch was counted. From the plump seeds, 10 were randomly selected and weighed individually to .001 g on a Cahn Model 4100 electronic balance. Means and standard deviations were calculated for the seeds from each accession number and expressed as mg/100 seeds.

The seeds were either stored in sealed jars at 2°C for at least 6 months and then placed in pots on a 1:1 peat-sand mixture in a misting chamber in the greenhouse or germinated fresh on a 1:1 peat-sand mixture in a misting chamber. Stored seeds were germinated under 14 hours of light at 28 ± 5°C and 10 hours of

Table 2. Collection data for *Vaccinium* section *Oxycoccoides*. 1 = seed collections for crossability studies; 2 = analyzed for flavonoid constituents; 3 = chromosomes counted. msm = *meters supra mare* = meters above sea level.

V. erythrocarpum Michx. U.S.A. North Carolina: Avery Co.: Grandfather Mt. at 1100 msm. *Vander Kloet 134877* (1, 2); Haywood Co.: Water-rock Knob at 1462 msm. *Vander Kloet 11981, 21981* (1, 2, 3); Gaylord Stoney Tennent Mt. at 1510 msm. *Vander Kloet 61981, 71981, 81981* (1, 2, 3); Blue Ridge Parkway at Richland Balsam Gap, 1512 msm. *Vander Kloet 41981, 51981* (1, 2, 3).

V. japonicus Miq. JAPAN. Nagans Prefecture: Bandokoro, Minamia zumi-gun, 1300 msm. *Vander Kloet 218886* (2); Gifu Prefecture: Takayama, 919-7 Jwaicho, 1300 msm. *Vander Kloet 125886* (1, 2, 3); Mt. Sanpo-i-wa, 1200–1445 msm. *Vander Kloet 225856* (3); Kyoto Prefecture: Midorogaike pond, Sakyo-ku, Kyoto, 100 msm. *Vander Kloet 126886, 226886* (1, 2, 3).

darkness at 13 ± 2°C. Fresh seeds were germinated under a similar regime or at temperatures of 22 ± 3°C/5 ± 2°C. When the cotyledons emerged, pots were removed from the misting chamber, placed on greenhouse benches and watered daily, if necessary. Days to emergence of radicles, of cotyledons and of first leaves, and percent germination were recorded. Three months after germination, five or more vigorous seedlings were pricked off; each was set out in a 10 cm clay pot, and watered when necessary.

In late summer of the following year, all plants were transferred to coldframes and kept there until the following spring when they were returned to the greenhouse for cytogenetic studies and crossing trials.

A series of young flower buds from each population was fixed, stained and squashed following the procedure of Hall and Galletta (1971) so that their chromosome numbers could be determined. Remaining flower buds were allowed to develop on the plants; anthesis began in about 3 weeks. Initially a few flowers were selfed on all plants; subsequently reciprocal outcrosses were attempted within and between Japanese and Appalachian plants. All selfs and outcrosses were tagged to follow ovule development. Once each berry was ripe, the seeds were removed, counted, and sown directly so that the viability of the progeny could be determined.

Dried leaves from the following sources were analyzed for flavonoids: herbarium specimens (listed in the appendix); dried specimens of wild populations; and fresh material from both garden- and greenhouse-grown plants, including some of the hybrids described below. Plants were extracted with 80% methanol by soaking for several days. After a final wash with boiling 80% methanol, the extracts from individual plants were combined and evaporated to dryness under reduced pressure at 35°C; residues were then extracted with boiling water to remove their polar components. Extraction of the aqueous solutions with water-saturated n-butanol yielded the polyphenolic fractions. The n-butanol solutions were reduced to dryness under reduced pressure and the residues taken up in small volumes of methanol. The methanol solutions were applied to TLC plates (Polyamid 6.6, homemade) and chromatographed two-dimensionally in the solvent systems described by Wilkins and Bohm (1976). Spots were made visible by examination under UV light and by spraying with diphenylboric acid ethanolamine complex (.1% in 50% aqueous methanol) and examination under UV light. Identifications are based upon characteristic chromatographic and color behavior of the compounds involved using standards.

RESULTS

Chromosome counts were consistently diploid ($n = 12$). Thirty-four preparations were examined from which 11 clear counts were obtained, three from the Appalachians and eight from Japan. Morphology, length of the chromosome and genome sizes were quite similar to those described by Hall and Galletta (1971) for three other sections of *Vaccinium,* namely, sections *Cyanococcus* A. Gray, *Herpothamnus* (Small) Sleumer and *Oxycoccus* (Hill) Koch.

However, an error has crept into the literature. Bolkhovskikh et al. (1969), citing a report by Flory (1937) and repeated by Funabiki (1958), stated that *Hugeria japonica* (Miq.) Nakai, a synonym of *Vaccinium japonicum* Miq., has a diploid chromosome number of 14. But Flory (1937) reported only counts for the Polemoniaceae, not the Ericaceae, and this particular count refers to *Hugelia japonica* Benth. A recorded *lapsus linguae,* perhaps!

Selfing invariably failed, probably due to the same late acting incompatibility system that results in massive embryo abortion as has been reported by Vander Kloet (1991) for *V. corymbosum* L., but outcrossing was quite successful (Table 3). Seventy-five percent of the crosses attempted among the Appalachian plants were successful, producing 30 ± 11 seeds/berry; crosses among

Table 3. Comparative crossability between and among plants of *Vaccinium erythrocarpum* and *V. japonicum*. Values are means ± one standard deviation; data in parentheses from material collected in the wild.

Taxon	*V. erythrocarpum*		*V. erythrocarpum* × *V. japonicum*	*V. japonicum*	
Number of crosses	32		26	17	
Seed set (days)	59 ± 7		71 ± 10	58 ± 3	
Relative set success	75%		61%	86%	
First radicle emerges (days)	13 ± 1	(15 ± 1)	14 ± 1	18 ± 2	(16 ± 2)
First cotyledons (days)	24 ± 2	(24 ± 1)	25 ± 2	31 ± 4	(34 ± 6)
First true leaves (days)	33 ± 3	(34 ± 6)	35 ± 4	45 ± 5	(58 ± 10)
Seeds/berry	30 ± 11	(10 ± 7)	35 ± 8	35 ± 19	(24 ± 6)
Seed wt (mg/100 seeds)		(29 ± 10)			(23 ± 8)
Relative germination success	94%	(71%)	51%	80%	(14%)

the Japanese plants produced a similar number of seeds per berry, but berry set was 11% higher than in the Appalachian crosses. Similarly, crosses between these vicariads produced 35 ± 8 seeds/berry when fresh pollen was used. The use of pollen stored dry at −20°C for 6 months markedly reduced seed set (4 ± 5 seeds/berry). Storage was necessary because these vicariads display different phenologies in the Acadia greenhouse. The Japanese plants sometimes begin to bloom within a year after germinating and they continue to bloom sporadically throughout the year with only a minimal chilling period (about 20 hours at 0 to 2°C). The Appalachian plants, however, require about five years after germination before they will bloom; they also need eight months of chilling to break dormancy and then bloom only once for about three weeks in June. Nonetheless, the hybrids produced by crossing these disjunct taxa are as vigorous as plants from the intraspecific crosses and produce ample normal pollen which is indistinguishable from that of parental plants.

The lower seed set per berry observed in wild populations (Table 3) may be attributable to interflower selfing (Vander Kloet and Lyrene, 1987) and/or to few pollinators, since the floral display is never massive in these plants but rather diffuse and asynchronous. We have yet to observe an insect visit these flowers in the wild.

Seed germination and seedling development were quite good for all seed populations, both wild and greenhouse-grown, except for seed collected from *Vaccinium japonicum* in the wild (Table 3). The Japanese plants not only had berries that contained somewhat smaller seeds which weighed about 20% less than those of *V. erythrocarpum* (23 ± 8 mg/100 seeds for the former vs. 29 ± 10 mg/100 seeds for the latter), but these seeds also exhibited much poorer germination (14% success vs. 71% for *V. erythrocarpum*) and took longer to develop first true leaves as a seedling than *V. erythrocarpum* (58 ± 10 days vs. 34 ± 6 days). Even seed produced in the greenhouse from intraspecific crosses and which had much higher germination than the wild seed (80% vs. 14%) nevertheless took 12 days more to produce a seedling than *V. erythrocarpum.*

Some of these phenological differences in blooming, seed set and germination may be due to genetic drift since the populations are small and local, or to habitat selection against mesic forms in the Appalachians, or to a combination of both factors. *Vac-*

cinium japonicum occurs in mixed coniferous stands or beech forests from sea level to 2600 msm (*meters supra mare*) (Horikawa, 1972) while *V. erythrocarpum* occurs primarily in openings of red spruce, Fraser fir and yellow birch stands from 1500 to 1950 msm in the southern Appalachians (Busing et al., 1988).

The flavonoid profiles of the two species, and of their hybrids, are based upon the common flavonols kaempferol and quercetin in the form of their 3–0–glycosides, eriodictyol 7–0–glucoside and a variety of blue-fluorescing compounds that are likely derivatives of cinnamic acids.

The flavonoid pigment profiles for the two taxa show some difference in their capacities to accumulate derivatives of the two flavonols kaempferol and quercetin: *Vaccinium japonicum* accumulates both, while *V. erythrocarpum* accumulates only quercetin and its derivatives. The two taxa are further differentiated by the tendency of *V. japonicum* to make higher-order glycosides as well as monoglycosides, in contrast to the tendency of *V. erythrocarpum* to make principally monoglycosides.

Vaccinium erythrocarpum is characterized by comparatively large amounts of quercetin 3–0–glucoside (galactoside may also be present), 3–0–rhamnoside, 3–0–glucuronide and eriodictyol 7–0–glucoside. There were no kaempferol monoglycosides in this taxon and only faint traces of diglycosides in a few individuals. *Vaccinium japonicum,* on the other hand, exhibited both kaempferol and quercetin 3–0–monoglucosides (possibly galactosides as well) and 3–0–diglycosides. Likewise, a trace of quercetin 3–0–glucuronidae was indicated; eriodictyol 7–0–glucoside was present but not abundant.

The F_1 hybrids often (but not always) had complementary flavonoid profiles. This result was not entirely unexpected since some of the Japanese parents used in the crossing experiments were missing one or more flavonoids, such as eriodictyol 7–0–glucoside.

It is noteworthy that the variation observed in the flavonoid chemistry mimics the morphological variation. In SE Asia where the species is polymorphic, none of the plants had identical flavonoid profiles, but the monomorphic Appalachian plants all had similar flavonoid profiles.

All these data suggest that the Appalachian and the Asian taxa, although tertiary relicts *sensu* Wood (1972), are not distinct biological entities; indeed, the only qualitative difference observed in this study was the presence of kaempferol monoglycoside in *Vaccinium japonicum* and its absence in *V. erythrocarpum.* The remainder of the morphological and biological evidence, such as the ability to interbreed with no apparent loss of fertility in the hybrids and only minor quantitative differences in morphology, supports the notion of a single species with several ecotypes or biotypes. Since these ecotypes are quite disjunct, it might be useful to recognize them at the sub-specific level.

TAXONOMIC TREATMENT

Vaccinium section **Oxycoccoides** Hooker f. in Benth. et Hook. f., Gen. Pl. 2: 573. 1876.

V. subgenus *Oxycoccoides* (Hook. f.) Sleumer, Nat. Bot. Gart. Mus. Berlin-Dahlem 13: 111. 1936.
Oxycoccoides (Hook. f.) Nakai, Bot. Mag. Tokyo 31: 246. 1917.
Hugeria Small, Fl. S.E. U.S. 896. 1336. 1903.

Shrubs up to 3 m tall; main growth of the plant carried out by shoots other than those that bear flowers; buds composed of 2 partially-fused prophylls; leaves deciduous; flowers solitary in leaf axils borne toward the ends of shoots of the same season, set on nodding pedicels continuous with the calyx tube. Corolla deeply cleft, 4-merous; stamens 8, exerted at anthesis, awnless, with long tubules. Berry 4-locular, each locule with 20–25 ovules.

Rehder (1927) reported that in section *Oxycoccoides,* the calyx tube is articulated with the pedicel; Sleumer (1941) observed that the berry is 5-loculed and the corolla 5-merous; Palser (1961) has stated that the stamens have short awns. We have been unable to verify any of these observations in the specimens collected in the field or examined at A, GH, K, BM and NY.

Stevens (Taxonomic studies in the Ericaceae. Ph.D. thesis, University of Edinburgh, 1969) has observed that in section *Oxycoccoides* there is extensive lignification around the midrib bundle.

Section *Oxycoccoides* has a southeastern North American and eastern Asian distribution, a pattern first detected and described by A. Gray in 1860 for some 150 taxa of flowering plants, and usually explained in terms of a distribution that became disrupted by climatic changes or by migration connected with these changes. Wood (1961) regarded this section as a morphological intermediate between section *Myrtillus* and section *Oxycoccus.* The former has similar perennating buds, bears single flowers in the axils of the lower leaves on the vegetative shoots, and the calyx tube is continuous with the pedicel; section *Myrtillus* differs from section *Oxycoccoides* in that the flowers are 5-merous, have 10 awned stamens, and the corolla lobes are not reflexed at anthesis. Section *Oxycoccus* has a 4-merous flower, eight awnless stamens, and corolla lobes deeply cleft at anthesis, but it differs from section *Oxycoccoides* in that the calyx tube is articulated with the pedicel, the pedicels bear bracts, and the inflorescence is frequently reduced into a pseudo-raceme (especially in *V. oxycoccus*) and the testa is more than a single layer of cells thick (Vander Kloet, 1983).

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H. lasiostemon (Hayata) Maekawa, Bot. Mag. Tokyo 47: 617. 1933.
H. randaiensis (Hayata) Masamune, J. Soc. Trop. Agric. Taiwan 4: 301. 1932.
H. sinica (Nakai) Maekawa, Bot. Mag. Tokyo 47: 615. 1933.
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O. erythrocarpus (Michx.) Persoon, Syn. 1: 419. 1805.
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O. japonicus (Miq.) Nakai, Bot. Mag. Tokyo 31: 247. 1917.

KEY TO THE SUBSPECIES

A. Plants 60–150 cm high; leaves 53 ± 10 mm long; kaempferol monoglycoside absent; SE North America .... *V. erythrocarpum*
AA. Plants 30–60 cm high; leaves 41 ± 9 mm long; kaempferol monoglycoside present; SE Asia .... *V. japonicum*

Vaccinium erythrocarpum Michx. subspecies **erythrocarpum**

Shrubs (50) 80–150 (300) cm high, crown-forming or weakly rhizomatous; twigs of current season smooth, ± terete, pubescent in lines; leaves elliptical, ovate to oblong-lanceolate, deciduous, membranaceous, 40–70 mm long, 15–30 mm wide, glandular-pubescent beneath, green on both sides, margin serrulate; calyx and pedicel continuous, glabrous, calyx lobes 4, <1 mm long, pedicel up to 1.5 cm long with a pair of caducous basal bracteoles; corolla lobes 4, deeply reflexed at anthesis, white, pink, rarely red; stamens with the filaments pilose, the anther sacs awnless, tubules 3–5 mm long; pollen tetrads 33–37 μm in diameter. Berry red, deep purple or black (*f. nigrum* Allard), (6) 9–11 (15) mm in diameter; nutlet ca. 1 mm long. Chromosome number $n = 12$.

TYPE LOCALITY. High Mountains in northern Carolina. TYPE at *P.* Lectotypified by Vander Kloet (1989).

RANGE. Southeastern North America in the Appalachians at high elevations from West Virginia to northern Georgia. Several outlying populations occur in central Tennessee (Vander Kloet, 1988).

HABITAT. Wooded slopes, subalpine shrubbery, boggy areas, rocky slopes and thickets from (600) 1000–1950 msm. In the southern Appalachians, subspecies *erythrocarpum* frequently occurs in virgin spruce-fir forests (Busing et al., 1988) where it is associated with *Viburnum alnifolium* Marsh., *Rubus canadensis* L., and *Sambucus pubens* Michx. (Oosting and Billings, 1951).

Vaccinium erythrocarpum Mich. subspecies **japonicum** (Miq.) Vander Kloet, *comb. et stat. nov.*

var. *fauriei* Sleumer, Bot. Jahrb. 71: 490. 1941.
var. *ciliare* Matsumura in Nakai, Trees and Shrubs of Japan 2: 229. 1927.
var. *sinicum* (Nakai) Rehder, J. Arnold Arbor. 5: 56. 1924.
var. *lasiostemon* Hayata, J. Coll. Sci. Imp. Univ. Tokyo 30: 449. 1911.

Shrubs (15) 30–60 (150) cm high, crown-forming or weakly rhizomatous; twigs of the current season ± terete, usually glabrous, occasionally pubescent; leaves 15–55 mm long, 10–30 mm wide, usually eglandular and glabrous beneath, rarely pubescent and glandular; leaves and pedicels of flowering shoots occasionally very much reduced; berries red, 5–7 (10) mm in diameter. Chromosome number $n = 12$.

Using pedicel length, leaf shape and leaf margin, as well as blade-petiole indumentum, Maekawa (1933) divided this SE Asian population into four species. However, pedicel length is quite plastic, and consequently variation within a single clone is often of the same magnitude as that encountered between populations from different areas. This variation is especially true of those few plants that have pedicels which continue to elongate prior to, during, and after anthesis. The remaining diagnostic features cited by Maekawa are not constant and occur in various combinations. Whoever would accept two species here will eventually be led to accept four, then perhaps eight!

TYPE LOCALITY. Japan; TYPE at L! Von Siebold 102330. Herb. Ludg.-Bat 908. 265–275.

RANGE. Southeastern Asia; Japan; Quelpaert Island (Korea); Formosa (Taiwan) and southeastern China.

HABITAT. Coniferous woods, mixed coniferous woods, beech forests, subalpine shrubberies, sub-alpine grasslands, rocky slopes and thickets from sea level to 2500 msm.

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APPENDIX

Citation of herbarium specimens from which 3–6 leaves were removed so that their flavonoid constituents could be adduced.

U.S.A.: **Georgia,** Rabun County, 1951 *Duncan 12545* (ACAD); **Tennessee,** Sevier County, 1930 *Jennison S. M.* (GH); **West Virginia,** Munroe County, 1931 *Hunnewell 12018* (GH). JAPAN: **Uzen Province,** Hondo, 1914 *Wilson 7209* (A); **Aomori Prefecture,** Hakkodo, Yachionsen, 1976 *Yamazaki 1031* (A); **Isikawa Prefecture,** Yamanaka, Enuma-gun, 1955 *Muroi 23155* (A). CHINA: **Western Hupeh,** 1922 *Chun* (A); **Chekiang,** 1932 *Ho 1625* (A).

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HYMENOXYS HERBACEA (ASTERACEAE): AN ENDEMIC SPECIES OF THE GREAT LAKES REGION

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ABSTRACT

Hymenoxys herbacea (*comb. nov.*), a federally-listed, threatened species endemic to Illinois, Ohio, and Ontario, has been treated formerly as *H. acaulis* var. *glabra. Hymenoxys herbacea* is a self-incompatible aneuploid with $x = 14$, genetically and morphologically separable from *H. acaulis.* The nomenclatural history of this taxon is summarized.

Key Words: *Hymenoxys herbacea, Hymenoxys acaulis* var. *glabra,* new combination, endemic, aneuploid, Great Lakes region

Hymenoxys herbacea (E. L. Greene) Cusick [*comb. nov.* based on *Tetraneuris herbacea* E. L. Greene, Pittonia 3: 268, 1896] (Asteraceae) is a showy scapose perennial herb endemic to a limited area of the Great Lakes region. Three populations presently are extant, two in Ontario and one in Ottawa County, Ohio. It formerly grew in Tazewell and Will Counties, Illinois. A report from Mason County, Illinois is in error (Cusick and Burns, 1984; Sheviak, 1981; White and Maher, 1983). The species is known as Lakeside daisy after the town of Lakeside, Ohio, near the Ottawa County population (Weed, 1890).

This species is closely allied to *Hymenoxys acaulis* (Pursh) Parker which grows over a broad area of the western half of the Great Plains from Saskatchewan to Texas and west to California. The Great Lakes populations of *Hymenoxys herbacea* are disjunct from *H. acaulis* by 900 to 1400 km. Parker (1950) without comment reduced the Great Lakes plants to varietal status as *Hymenoxys acaulis* var. *glabra* (A. Gray) Parker.

DeMauro (M.S. thesis, Univ. of Illinois at Chicago, 1988), who investigated the genetics of Lakeside daisy populations in Illinois, Ontario, and Ohio, cast doubt on Parker's treatment. The Illinois plants used in her study were from the last remaining natural population in the state prior to its destruction in 1981. DeMauro found *Hymenoxys herbacea* to be a self-incompatible, reduced aneuploid with $x = 14$. The base number in *Hymenoxys* is $x = 15$ (Strother, 1966). *Hymenoxys acaulis* has been listed variously as $x = 14$, $x = 15$, and $x = 30$ (DeMauro, *op. cit.*).

Hymenoxys herbacea morphologically is distinguished from *H. acaulis* by a paucity of villous pubescence. This feature is most evident on the rosette leaves. Leaves of *H. herbacea* are deep green and sparsely pubescent, becoming glabrate with age; those of *H. acaulis* are dull green and densely and permanently cloaked with long, silky hairs.

The ancestors of *Hymenoxys herbacea* probably migrated from the western cordillera into the Great Lakes region during the Xerothermic interval about 8000 years B.P. This period marked the eastward expansion of many drought-tolerant western taxa, a phenomenon known as the prairie peninsula (Transeau, 1935; Webb et al., 1983). Lakeside daisy probably became physically and genetically isolated from its progeners when more humid weather conditions developed in the Midwest about 4000 B.P. Aneuploidy may have arisen independently in the Great Lakes populations or it may have originated in western populations of *Hymenoxys* that subsequently migrated eastward during the Xerothermic interval. Powell and Turner (1963) reported isolated $x = 14$ aneuploids of *Hymenoxys acaulis,* although they did not record which varieties of that taxon were sampled.

The nomenclatural background of *Hymenoxys herbacea* is summarized below:

Actinella scaposa Nutt. var. *glabra* A. Gray (Man. ed. 5: 263, 1867).
Tetraneuris herbacea E. L. Greene (Pittonia 3: 269, 1896).
Actinea herbacea (E. L. Greene) Robinson (Rhodora 10: 68, 1908).
Actinea scaposa (Pursh) Spreng. var. *glabra* (A. Gray) Cronquist (Rhodora 47: 403, 1945).
Hymenoxys acaulis (Pursh) Parker var. *glabra* (A. Gray) Parker (Madroño 10: 159, 1950).

Gray's 1867 epithet "*glabra*" cannot be used at the species rank since Shinners (Field and Lab 19: 80, 1951) used that adjective for another species of *Hymenoxys,* based upon Nuttall's *Actinella glabra* of 1841 (Trans. Amer. Philos. Soc. n.s. 7: 379). Nuttall's name is the basis for *Tetraneuris glabra* (Nuttall) E. L. Greene (Pittonia 3: 268, 1896). The confusion surrounding the epithet "*glabra*" is reflected in the high number of references which misattribute that adjective to Nuttall rather than Gray when referring to Lakeside daisy (Gleason and Cronquist, 1963; Mohlenbrock, 1975; Sheviak, 1981; Roberts and Cooperrider, 1982; Fisher, 1988).

Hymenoxys herbacea is listed, as *H. acaulis* var. *glabra,* as threatened in the United States (USFWS, 1988), and as endangered by the state of Ohio (ODNAP, 1990). The recognition of its rarity has spurred research into the biology and taxonomy of this Great Lakes endemic.

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BRYOPHYTES OF ALGIFIC TALUS SLOPES IN WISCONSIN'S DRIFTLESS AREA

John A. Christy and Thomas A. Meyer

ABSTRACT

Naturally refrigerated (algific) talus slopes provide microclimates suitable for disjunct or relict populations of plants and invertebrates. Of 39 species of bryophytes collected on four of Wisconsin's largest algific slopes, one-third were restricted to cold air vents. Distribution of species on these slopes appears to be influenced by perennially stable air temperatures and condensate occurring at outflow vents. The moss *Seligeria donniana* is new to Wisconsin.

Key Words: bryophytes, algific talus slopes, cold air drainage, Driftless Area, Wisconsin

INTRODUCTION

Algific talus slopes are characterized by the venting of frigid air through openings among talus debris, and the associated refrigeration of rocks and shallow soils on these slopes. The temperature of air issuing from vents on algific slopes is consistently colder than the 8–10°C reported for caves and springs in temperate latitudes (Poulson and White, 1969; Knudson and Hedges, 1973), indicating the presence of subterranean ice. During the growing season, vegetation and rocks surrounding outflow vents tend to be saturated with water condensed from the mixing of chilled vent air and warmer air above ground (Hayden, 1843; Conard, 1938).

In North America, algific slopes or their functional equivalents have been reported from Indiana (McKnight, 1986), Michigan (Miller and Vitt, 1970), New York (Miller, 1966), West Virginia (Hayden, 1843; Brooks, 1965; Core, 1968, 1975; Kercheval, 1986) and the Driftless Area of Illinois, Iowa, Minnesota and Wisconsin (Conard, 1938, 1952; Frest, 1981, 1983; Lammers, 1983; Roosa, 1984; McKnight, 1985). It is not clear whether taxa reported in other papers (Blagg, 1928; Conard, 1932a, 1932b) occurred on algific slopes, or slopes with only cool northerly exposure.

The algific slopes of the Midwest's Driftless Area have received much attention in recent years because of their relict populations of land snails and rare plants. Foremost among these is the federally-endangered Iowa Pleistocene snail, *Discus macclintocki* (Baker), once known only from ice-age loess deposits and thought to have been extinct. The rare snails *Vertigo occulta* Leonard and *V. hubrichti* Pilsbry, also relicts from the Pleistocene, inhabit the slopes along with disjunct populations of plants that include *Carex media* R. Br., *Ribes hudsonianum* Richards, *Rhamnus alnifolia* L'Her., *Mitella nuda* L., *Mertensia paniculata* (Ait.) G. Don. and the federally-listed threatened species *Aconitum noveboracense* Gray.

Bryophytes are reportedly abundant on algific slopes in the Driftless Area, but a comprehensive list of species has never been published. We sampled the bryoflora on slopes in Wisconsin to determine if any taxa had disjunct boreal affinities.

METHODS

Bryophytes were collected in May 1987 on four of Wisconsin's largest algific talus slopes, at Chase Creek and Glen Haven, in Grant County, Wisconsin. The slopes, situated on north-facing hillsides, varied in area from about 10 m^2 to 7500 m^2. Vegetation immediately surrounding the slopes was composed of second-growth mesic forest species, primarily sugar maple (*Acer saccharum* Marsh.), basswood (*Tilia americana* L.) and red oak (*Quercus borealis* Michx. f.), along with their attendant understory species.

At the time of our visit, ambient air temperature was 24°C, and temperatures at outflow vents ranged from 2–6°C. Faint jets of fog were visible at the vents, and air turbulence was great enough to stir vegetation immediately surrounding the openings.

Collections were limited to those substrates occurring within the perimeter of the slopes. Nomenclature follows Crum and Anderson (1981), Koponen (1968) and Stotler and Crandall-Stotler (1977). Voucher specimens were deposited at MIL.

RESULTS AND DISCUSSION

Thirty-nine species of bryophytes occurred on the four sites sampled (Table 1). Based on Bowers and Freckmann (1979), *Seligeria donniana* was new to Wisconsin, and *Brachythecium salebrosum, Bryhnia graminicolor, Encalypta procera* and *Mnium stellare* were new to Grant County.

All of the species of bryophytes that we found on algific slopes in Wisconsin occur also in non-algific habitats elsewhere in the four-state Driftless Area (Vitt, 1976; Peck, 1978; McCleary and

Table 1. Bryophytes of four algific talus slopes in Wisconsin. Slope and vent habitats include soil and rocks. Localities: 1 = Chase Creek, 2 = Glen Haven. Habitat: L = log, S = slope, V = cold air vent, * = disturbed soils.

Species	Locality	Habitat
LIVERWORTS		
Conocephalum conicum (L.) Lindb.	1	S*
Marchantia polymorpha L.	1	S*, V
Porella platyphylla (L.) Pfeiff.	1, 2	S, V
Preissia quadrata (Scop.) Nees	2	V
Tritomaria exsecta (Schrad.) Loeske	1	L
MOSSES		
Amblystegium varium (Hedw.) Lindb.	1	S
Anomodon attenuatus (Hedw.) Hueb.	1, 2	S, V
A. rostratus (Hedw.) Schimp.	1	S
Bartramia pomiformis Hedw.	1	S, V
Brachythecium oxycladon (Brid.) Jaeg. & Sauerb.	1, 2	V
B. salebrosum (Web. & Mohr) BSG	1	S
Bryhnia graminicolor (Brid.) Grout	1	V
Bryoerythrophyllum recurvirostrum (Hedw.) Chen	1, 2	V
Bryum capillare Hedw.	1	S*
B. pseudotriquetrum (Hedw.) Gaertn., Meyer & Scherb.	1, 2	S*
Campylium chrysophyllum (Brid.) J. Lange	2	V
Ceratodon purpureus (Hedw.) Brid.	1, 2	S*, V
Climacium americanum Brid.	1	V
Desmatodon obtusifolius (Schwaegr.) Schimp.	1	S*
Didymodon fallax (Hedw.) Zand.	1	S*, V
Encalypta procera Bruch	2	S
Entodon cladorrhizans (Hedw.) C. Muell.	1, 2	L, S
E. seductrix (Hedw.) C. Muell.	1	V
Eurhynchium hians (Hedw.) Sande-Lac.	1	S, V
Funaria hygrometrica Hedw.	1	S*
Leptobryum pyriforme (Hedw.) Wils.	1	S*
Mnium marginatum (With.) Brid. ex P.-Beauv.	2	V
M. stellare Hedw.	1	V
Plagiomnium cuspidatum (Hedw.) T. Kop.	1, 2	L, S, V
P. medium (BSG) T. Kop.	1	S, V
Platygyrium repens (Brid.) BSG	1	L
Pohlia wahlenbergii (Web. & Mohr) Andr.	1	V
Rhodobryum roseum (Hedw.) Limpr.	1, 2	L, V
Rhytidiadelphus triquetrus (Hedw.) Warnst.	1	V
Seligeria campylopoda Kindb. ex Macoun & Kindb.	1	V
S. donniana (Sm.) C. Muell.	1	V
Thuidium abietinum (Hedw.) BSG	2	V
T. delicatulum (Hedw.) BSG	1	S
T. recognitum (Hedw.) Lindb.	2	S

Redfearn, 1979; Horton, 1983). We did not find any species with substantial disjunct distributions, although several such taxa are known to occur on algific slopes in Iowa and Minnesota (D. G. Horton, pers. comm.).

Fourteen (36%) of the bryophytes found on the slopes occurred only at outflow vents, suggesting that the perennially cool and moist conditions found there provide ideal growing conditions. Large polsters of the more typically wetland-inhabiting *Climacium americanum, Marchantia polymorpha* and *Plagiomnium medium,* clustered at vents halfway up the algific slopes, gave the illusion of artesian springs on the hillside, although the only source of water was condensate from the jets of fog occurring at the openings.

The association of bryophytes occurring at cold air vents, coupled with the occurrence of populations of relict snails and rare vascular plants, make algific slopes unique geological and biotic communities. A description of the apparently more diverse bryoflora of algific slopes in Iowa and Minnesota would document the occurrence of disjunct or relic taxa, currently the subject of many recent anecdotal accounts.

T. J. Frest (pers. comm.) estimated that 80% of the slopes that existed in the Driftless Area before European settlement have been destroyed. It is fortunate that The Nature Conservancy and the states of Iowa and Wisconsin are moving to protect the best of those that remain. Global warming will pose new challenges in monitoring these communities.

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ECOLOGICAL ASPECTS OF *ARETHUSA BULBOSA*, *CALOPOGON TUBEROSUS*, AND *POGONIA OPHIOGLOSSOIDES* (ORCHIDACEAE) IN EASTERN NEWFOUNDLAND.

I. FLOWERING AND FRUITING PATTERNS

J. TODD BOLAND AND PETER J. SCOTT

ABSTRACT

Differences in reproductive ecology and floral characteristics were investigated in three sympatric species of peatland orchids. *Arethusa* produced the highest percentage of flowers but the lowest percentage of seed capsules while *Pogonia* showed the opposite pattern. *Calopogon* had an intermediate percentage of flowers and a low capsule set. The pollination biology of these three species is discussed.

Key Words: peatland orchids, *Arethusa, Calopogon, Pogonia,* floral biology, eastern Newfoundland

INTRODUCTION

Peatlands are a significant feature of Newfoundland and 18 of the 32 species (Scott, 1981) of native orchids are inhabitants of peatland environments (Pollett and Wells, 1980). *Arethusa bulbosa* L., *Calopogon tuberosus* (L.) BSP, and *Pogonia ophioglossoides* (L.) Ker were chosen for this study because they are sympatric and it is common to find all three species occurring on the same bog (Luer, 1975). The flowers of these species are specifically adapted for pollination by *Bombus* and in Newfoundland, these orchids may be visited by either *Bombus borealis* Kirby or *B. sandersoni* Franklin. *Arethusa* is pollinated by queen bees, *Calopogon* by workers, and *Pogonia* by both. These species have flowers of similar size and color with yellow-white brushes on their lips which strongly absorb ultraviolet light (Thien and Marcks, 1972). They have little or no perfume or nectar. Despite their similarities in floral characters and habitat, no hybrids have been detected in nature. Thien and Marcks (1972) determined that the major isolating mechanism is placement of pollinia on the bee's body. Due to differences in lengths of columns in the three species, *Pogonia* places its pollinia onto the bee's head, *Arethusa* onto the bee's thorax, and *Calopogon* onto the bee's abdomen. Since stigma location is directly below the anther on the column, placement of pollinia onto the bee will be in the area specific to being picked up by the stigma when the bee visits the next conspecific flower.

The study site chosen has a harsh climate in that cold, wet weather can occur at time of flowering. This study was undertaken to collect data for comparison with data from other parts of the species' ranges.

METHODS AND MATERIALS

Field work was conducted Jun.–Sept. 1988. Study sites were three peatland areas located about 40 km west of St. John's, Newfoundland in the vicinity of the Witless Bay Line (Site 1: elev. 216 m, 47°22′00″N, 53°02′51″W; site 2: elev. 231 m, 47°20′35″N, 52°59′14″W; and site 3: elev. 197 m, 47°20′19″N, 52°55′52″W). Site 1 and 3 are slope bogs while site 2 is a ribbed fen (classification according to Wells, 1981).

A 10 m^2 plot was delineated at each site and each plot was subdivided into 400 .5 m^2 quadrats. The number of *Arethusa, Calopogon,* and *Pogonia* plants was counted in each quadrat. The total number of flowers and seed capsules was also determined for each plot. When available, the floral characters of inflorescence height from substrate surface to the base of the pedicel, natural spread of the flower, length and width of the lip, and length of the column were determined for ten flowers each of *Arethusa* and *Pogonia* from each of the three plots. The flowers of *Calopogon* were similarly measured, but since these orchids have a multi-flowered inflorescence, the lowest flower on each of ten spikes was measured.

Percent flowering of each species was determined from the ratio of flowering plants to the total plants of that species in each plot. Percent capsule set was determined from the ratio of capsules to total flowers produced by a species.

Data were tested for normality using the procedure outlined in the *Minitab Reference Manual* (1988). Homogeneity of variance was determined using the F-test. The mean size of various floral characters was compared between sites using a pooled *t*-test. Statistical significance is taken to be at the 5% level.

RESULTS

The total number of plants, flowers, and seed capsules of each of the three orchid species in the 10 m^2 plots at each of the three sites is summarized in Table 1.

Table 1. Summary of the total number of plants, flowers and seed capsules of *Arethusa*, *Calopogon* and *Pogonia*.

	Arethusa			*Calopogon*			*Pogonia*		
Site No.	1	2	3	1	2	3	1	2	3
Plants	187	25	78	33	87	155	201	921	136
Plants with bloom	54	5	26	6	9	17	7	21	6
Seed capsules	7	1	4	1	2	3	2	6	2
% Flowering	28.9	20.0	33.3	18.2	10.3	11.0	3.5	2.3	4.4
% Capsules/flower	13.0	20.0	15.4	16.7	22.2	17.6	28.6	28.6	33.3

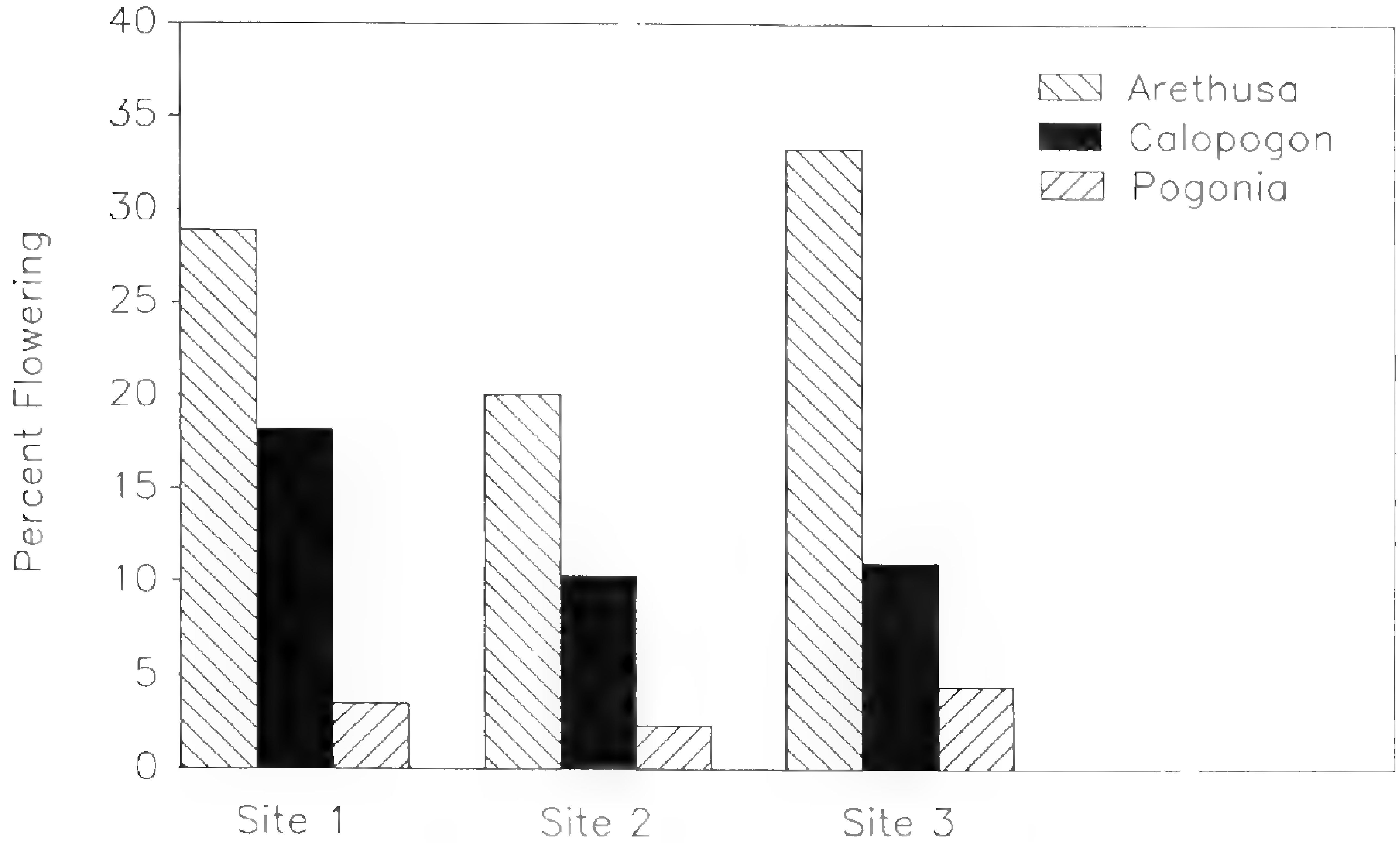

Figure 1. Percent flowering of *Arethusa, Calopogon,* and *Pogonia* from the three eastern Newfoundland sites.

The mean percent flower production for *Arethusa* was 27.4% (range = 20.0–33.3%), *Calopogon* 13.2% (range = 10.3–18.2%), and *Pogonia* 3.4% (range = 2.3–4.4%). The mean percent capsule set for those plants that flowered was: *Arethusa* 16.1% (range = 13.0–20.0%), *Calopogon* 18.8% (range = 16.7–22.2%), and *Pogonia* 30.2% (range = 28.6–33.3%). Figures 1 and 2 compare the percent flowering and capsule set by the three orchids.

Measurements of the various floral characters of the three species in Newfoundland were subjected to statistical analyses and were found to be comparable to those documented from the rest of North America (Correll, 1950; Thien and Marcks, 1972; Luer, 1975), except for inflorescence height, which in Newfoundland was at the lower end of the range of values.

DISCUSSION

Arethusa had the highest percentage of plants producing flowers with a mean of 27.4%, *Calopogon* had 13.2%, and *Pogonia* 3.4%. These values do not necessarily reflect typical flowering rates. The total number of flowers produced by these three species is quite variable from year to year. Firmage and Cole (1988) conducted a seven-year study on *Calopogon* in Maine. They found the total number of flowering plants on a single bog to vary from 101 to

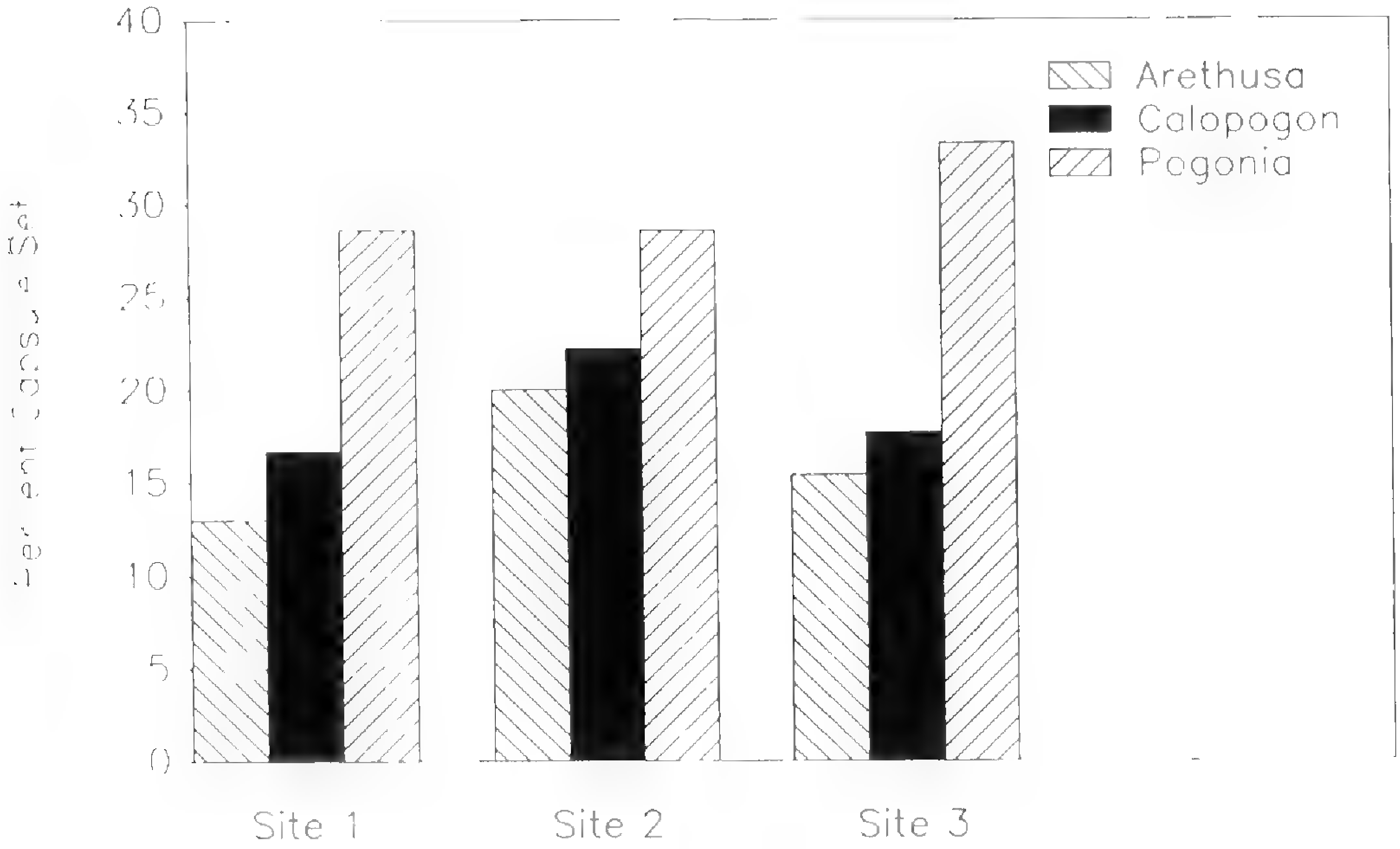

Figure 2. Percent capsule set by *Arethusa*, *Calopogon*, and *Pogonia* from the three eastern Newfoundland sites.

402. Case (1983) observed *Arethusa* on a particular bog for more than 30 years and found the number of blooming plants to fluctuate greatly. Case (1964) also noted that *Pogonia* may bloom abundantly in a particular bog one year but produce few flowers the next.

The mean percent capsule set was lowest for *Arethusa* (16.1%), a little higher for *Calopogon* (18.8%), and highest for *Pogonia* (30.1%). This pattern is opposite to the mean percent flower production. Thien and Marcks (1972) studied the same three species and, as in this study, found *Arethusa* to have the lowest percent capsule set (5%) among the three species. Firmage and Cole (1988) found *Calopogon* to have a range of 12–40% capsule set over a seven year period. Thien and Marcks (1972) found *Pogonia* capsule set to range from 10–100%. Some populations of *Pogonia* appear to be apomictic, hence the 100% capsule set (Thien and Marcks, 1972). *Arethusa* may have the lowest capsule set due to its time of anthesis (Case, 1983). *Arethusa* flowers earliest, in mid- to late June; *Calopogon* and *Pogonia* flower in July.

Despite these patterns, numbers of capsules produced by each of the three species are comparable. Among the three sites, *Arethusa* produced twelve capsules, *Calopogon* six, and *Pogonia* ten. Each species produces seed capsules of similar size (Luer, 1975), thus they should produce comparable numbers of seeds and have similar reproductive output. *Pogonia* produced fewer flowers than *Arethusa* or *Calopogon* yet was able to maintain its reproductive output at levels close to those of the other two species. Flowering is energetically expensive to a plant (Schwage, 1971). *Pogonia* can maintain its reproductive output with a minimal number of flowers and hence with a proportionately minimal expenditure of energy.

Overall, the number of seed capsules produced in these three orchids is quite low compared to other non-orchidaceous bog plants. Low capsule set is the norm for many northern species of orchids (Thien and Utech, 1960). The study species are pollinated by deceit, appearing to offer food while, in fact, offering little or none (Thien and Marcks, 1972). After visiting several flowers of a nectarless plant, a bee soon learns to identify and avoid these flowers; few visits by bees result in low pollination rates. *Calopogon* has several ways to reduce its chances of being quickly identified by the bees. This orchid is unscented; scent is used for close-range orientation, thus the bees are forced to rely on color to identify the flower (Thien and Marcks, 1972). This orchid, as well as the other two, has flowers which are randomly variable in color, from pale pink to deep magenta. Color variability may cause problems for the bees; after learning to avoid one shade of a species they then encounter other shades of that species (Heinrich, 1979).

Ability of bees to recognize a food source is especially problematic for low nectar-producing or nectarless plants which produce large numbers of flowers. *Arethusa* was in such a situation by producing the highest percentage of flowers of the three species. A concentration of low-nectar flowers in a small area allows potential pollinators to more quickly identify the flowers as non-rewarding; thus in future foraging, the pollinator will avoid those flowers. This avoidance may be another reason for the low percentage capsule set for *Arethusa.* Because *Pogonia* produced the fewest flowers, bees may not as quickly identify its flowers as being a poor food source.

Firmage and Cole (1988) suggested that *Calopogon* is pollinated by what Stoutamire (1967) called "chance pollination." The relatively large flowers with the ultraviolet pattern produced by pseudoanthers are attractive to bees. However, once visiting several flowers and finding no food reward, bees will avoid this species; any pollination which occurs during foraging is simply due to chance. The idea of "chance pollination" has been suggested by Melampy and Hayworth (1980) for *Isopyrum biternatum* L. (Ranunculaceae) and by Dafni (1983) for *Orchis caspia* Trautv. These species also lack food and are pollinated by deceit. If "chance pollination" occurs for *Calopogon,* it may equally apply to *Arethusa* and *Pogonia* since they too are pollinated by deceit.

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THE COMPOSITAE OF THE GUIANAS, I: HELIANTHEAE (HELIANTHEAE, TAGETEAE, COREOPSIDEAE)

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ABSTRACT

Approximately 200 species in the family Compositae have been collected in the Guianas (Guyana, Suriname, French Guiana), South America. Members of the tribe Heliantheae *s.l.* collected in the Guianas or expected there are listed, and a key to the genera is provided.

Key Words: floristics, Heliantheae, Compositae, Asteraceae, Guyana, Suriname, French Guiana, Guianas, South America

The *Flora of the Guianas* is a multinational effort by a consortium of the following botanical institutions: Botanischer Garten und Botanisches Museum Berlin-Dahlem, Berlin, Germany; Herbier, Centre O.R.S.T.O.M., Cayenne, French Guiana; Guyana National Herbarium, University of Guyana, Georgetown, Guyana; New York Botanical Garden, Bronx, New York, U.S.A.; National Museum of Suriname, University of Suriname, Paramaribo, Suriname; Museum National d'Histoire Naturelle, Laboratoire de Phanerogamie, Paris, France; Institute of Systematic Botany, Utrecht, The Netherlands (coordinator); U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. The goal of this international group, which began in 1983, is to produce a written account of the vegetation of Guyana, Suriname and French Guiana over a period of 20 years. Over 200 specialists are working on treatments of the seed plants, ferns, algae, bryophytes, and lichens. Several family treatments have been published, including the Chrysobalanaceae (Prance, 1986), Bromeliaceae-Tillandsioideae (Gouda, 1987), Verbenaceae (Jansen-Jacobs, 1988) and Burmanniaceae (Maas and Maas-van de Kamer, 1989) and others are in press, including the Poaceae (Judziewicz, in press) and Melastomataceae (Wurdack, in press).

Treatment of the Compositae is being coordinated out of the U.S. National Herbarium, under the auspices of the Smithsonian's "Biological Diversity of the Guianas Program." A preliminary list of species for the family has been assembled. While compiling this list several things became apparent: first, that there are far fewer composite species in the Guianas than in most other areas in the neotropics; second, in general, those Compositae in the Guianas are represented by few plant collections; third, many of the species expected in the Guianas have never been collected there, including many common species that have been collected from Venezuela, Trinidad, and/or northern Brazil. Finally, it will be many years before the various Compositae treatments are assembled and ready for publication. In order to facilitate studies of the flora, a list of the species and a key to the genera were deemed a good idea. Because of the size of the family, the list has been divided into tribes and will be published in three papers. The Heliantheae (to include the Heliantheae, Tageteae and Coreopsideae) with 35 genera and ca. 70 species and varieties are covered in this paper. The tribes Anthemideae, Astereae, Chicorieae, Cynareae, Mutisieae and Senecioneae will be included in the second paper and the Vernonieae and Eupatorieae in the third.

I have examined specimens from BRG, CAY, K, NY, P, U, and US (acronyms according to Holmgren et al., 1981). Most of the specimens in BRG, housed at the University of Guyana, were collected by G. S. Jenman, government botanist, Georgetown, Guyana, 1879–1902. The most complete set of Jenman collections, outside of BRG, are housed at NY and K, with less complete sets at a variety of other institutions. However, Jenman also collected many specimens of cultivated plants and most of these are found only at BRG.

Most members of the tribe Heliantheae that are found in the Guianas are weedy and are widespread in the neotropics. However, a few, such as *Ichthyothere granvillei* H. Robinson, *Ambrosia microcephala* DC., *Calea caleoides* (DC.) H. Robinson, and the species of *Reincourtia,* are found primarily in the Guianas. Most genera have one to three native species, the exceptions being *Acmella* (5 taxa), *Bidens* (4), *Calea* (7), and *Oyedaea* (4). The most commonly collected genus in the Heliantheae is *Clibadium.*

ARTIFICIAL KEY TO THE GENERA OF THE HELIANTHEAE OF THE GUIANAS

1. Leaves mostly alternate 2
  2. Leaves small and lobed, at least the lower ones deeply so, often finely dissected; heads less than 3 mm across . . 3
    3. Synflorescence a spike; pistillate and staminate florets

in separate heads, pistillate florets without corolla; achene tightly enclosed in an involucral bract .... *Ambrosia*

3. Synflorescence a much-branched panicle; pistillate and staminate florets in same head, pistillate florets with corolla; achene forming a disarticulating complex with two infertile disc florets and an involucral bract ... . *Parthenium*

2. Leaves large, sometimes lobed but never finely dissected; heads more than 3 mm across 4

4. Receptacle with spine-like setae; pappus of 5–10 squamellae; achenes wholly or partially covered with long stiff white hairs .... *Gaillardia*

4. Receptacle with bract-like pales; pappus of bristles, awns or absent; achenes without long stiff white hairs .. 5

5. Ray florets neuter and sterile; heads large, more than 2 cm in diameter 6

6. Peduncle fistulose; inner involucral bracts not cupping achene of ray floret; receptacle convex; pappus of 2 awns or absent; disc florets yellow .... *Tithonia*

6. Peduncle not fistulose; inner involucral bracts forming partial cup around achene of ray floret; receptacle distinctly conical; pappus a short crown or absent; disc florets purplish .... *Rudbeckia*

5. Ray florets pistillate and fertile, or absent; heads medium to small, less than 2 cm in diameter 7

7. Pappus of 2 awns; mature achenes broadly winged .... *Verbesina*

7. Pappus of 1–2 rows of numerous capillary bristles; mature achenes not winged ..... *Neurolaena*

1. Leaves mostly opposite (at least below) 8

8. Involucral bracts uniseriate and equal; leaves with raised oil glands 9

9. Involucral bracts united into a tube or cup ... *Tagetes*

9. Involucral bracts free or nearly so 10

10. Heads discoid; leaves petiolate, blades broadly ovate .... *Porophyllum*

10. Heads radiate; leaves sessile, blades linear or narrowly oblanceolate .... *Pectis*

8. Involucral bracts not uniseriate and equal; leaves without raised oil glands 11

11. Differentiated peripheral florets neuter and sterile, or absent 12

12. Heads eradiate 13

13. Pappus absent or apex of achene abruptly contracted, appearing peg-like; florets fewer than 25 per head 14

14. Apex of achene abruptly contracted, appearing peg-like; florets 2–6 per head; individual florets subtended but not surrounded by receptacular bracts; florets arranged in normal capitula; achene pericarp buff-colored or white .... *Eleutheranthera*

14. Pappus absent; florets 8–25 per head; individual florets surrounded by herbaceous bracts resembling an involucre; florets aggregated in dense clusters resembling secondary heads; achene pericarp dark .... *Lagascea*

13. Pappus of awns or bristles; numerous florets per head 15

15. Pappus of retrorsely barbed awns .... *Bidens pilosa*

15. Pappus of bristles, broad scales or smooth awns 16

16. Receptacle clearly conical 17

17. Shrub; leaves petiolate .... *Salmea*

17. Herb; leaves sessile .... *Spilanthes*

16. Receptacle convex 18

18. Florets yellow; achene with pappus of few to many persistent subulate scales .... *Calea*

18. Florets white; achene apex with a few easily deciduous bristles .... *Melanthera*

12. Heads radiate 19

19. Leaves compound, deeply lobed or finely dissected; pales flat 20
    20. Achenes elliptic in outline, 2-winged with pappus of 2 glabrate or antrorsely barbed awns . . . . *Coreopsis*
    20. Achenes linear in outline, wingless, with or without 1–6 retrorsely barbed awns 21
        21. Achenes apically contracted with thickened cap; heads large, the involucre more than 2 cm across; pappus absent or rudimentary . . . . *Dahlia*
        21. Achenes without thickened cap; heads smaller, the involucre mostly less than 2 cm across; pappus awns 1–6, well-developed or absent 22
            22. Achenes without a beak, the pappus of 1–6 retrorsely barbed awns; filaments glabrous; florets white or yellow . . . . *Bidens*
            22. Achenes with a long narrow beak, the pappus of 1–3 retrorsely barbed awns or absent; filaments hirsute; florets a variety of colors . . . . *Cosmos*
19. Leaves simple, if lobed, not deeply so; pales conduplicate, enfolding or strongly cupping the achene 23
    23. Ray florets white; pappus absent; pales of fruiting heads greatly exceeding the length of the achene and sometimes spinose at tip . . . . *Montanoa*
    23. Ray florets yellow or orange; pappus present; pales never greatly expanded at fruiting and without spinose tip 24
        24. Achenes dimorphic, the ray florets

with pappus of 3–4 awns and the disc florets with 2 awns; involucral bracts in several distinctly graded series .... *Oyedaea*

24. Achenes monomorphic, the pappus of 1–2 deciduous awns, or absent; involucral bracts in 2–3 subequal series 25
    - 25. Woody vine or clambering shrub; pales thickened at apex; leaves opposite; achenes round in cross-section, fleshy at maturity; pappus absent . ... *Wulffia*
    - 25. Annual or perennial herbs; pales not thickened; leaves usually alternate above and opposite below; achenes elliptical in cross-section, indurate; pappus of 2 deciduous awns ... . *Helianthus*

11. Differentiated peripheral florets pistillate and fertile 26
    - 26. Disc florets functionally male; pappus very reduced or absent 27
        - 27. Peripheral florets tubular, not forming well-developed ligules, 4-lobed 28
            - 28. Shrubs; ray florets 3–10; disc florets 8–12; involucral bracts 8–10 .... *Clibadium*
            - 28. Herbs; ray florets 1; disc florets 8–9; involucral bracts 4–6 ..... *Riencourtia*
        - 27. Peripheral florets forming well-developed ligules, apically rounded to 3-lobed 29
            - 29. Ray florets apically rounded, flared at base into an annular disc; achenes ovoid, notched at base .... *Unxia*
            - 29. Ray florets apically dentate to emarginate, without a basal annular disc; achenes obovoid, without notch at base 30

30. Inner involucral bracts closely enveloping the ray achenes and bearing spines, ridges, or lobes . . 31
    31. Achenes cuneate or oblong-fusiform, enclosing bract indurate, covered with long hooked spines; ray florets 5–8; disc florets 3–30, yellow . . . . *Acanthospermum*
    31. Achene ovoid, enclosing bracts becoming leathery, without spines; disc florets 3–5, green . . . . *Milleria*
30. Inner involucral bracts not enveloping the ray achenes and without spines, ridges or lobes 32
    32. Heads sessile; pappus absent; ray corollas with 3–4 lobes; achenes obovoid, never winged, plump, smooth or costate, glabrous . . . . *Ichthyothere*
    32. Heads pedicellate; pappus a crown of tissue or collar of short awns; ray corollas emarginate; achenes triquetrous, sometimes winged, flattened, smooth to tuberculate, puberulent . . . . *Baltimora*

26. Disc florets functionally hermaphroditic; pappus of scales, bristles or awns, or pappus absent 33
    33. Pales flat, hair-like or lacking, sometimes subtending but not enclosing the achene . . 34
        34. Pales hair-like, fimbrillate (easy to miss), not necessarily subtending disc florets . . . . *Eclipta*
        34. Pales flat and subtending disc achenes, or lacking 35
            35. Involucre of 3–4 series of imbricate

bracts; pappus of many subulate awns; shrubs .... *Calea*

35. Involucre bi-seriate; pappus of two stiff awns or a few fimbriate scales or ca. 20 lanceolate scales or absent; herbs 36
  36. Achenes dimorphic, disc achenes with 2–3 awns and ray achenes with prominent dentate lateral wings; heads inconspicuous, sessile in leaf axils .... *Synedrella*
  36. Achenes monomorphic, without awns or wings; heads conspicuous, in loose or congested clusters ...... *Galinsoga*

33. Pales loosely cupping, enveloping, or partially enclosing the disc achenes 37
  37. Involucral bracts with dark band along margin; ray corolla persistent on the achene .... *Zinnia*
  37. Involucral bracts without dark band; ray corolla deciduous from the achene 38
    38. Flowering branches covered with obvious, erect, multi-cellular, gland-tipped hairs .. *Sigesbeckia*
    38. Flowering branches without obvious gland-tipped hairs 39
      39. Pappus of plumose bristles; involucral bracts markedly graduate .... *Tridax*
      39. Pappus of scales or non-plumose bristles, or absent; involucral bracts subequal 40
        40. Annual herbs; receptacle clearly conical; achene apex with or without shoulders, the pappus of 1–10 soft bristles or absent .... *Acmella*

40. Perennial herbs or shrubs; receptacle flat or slightly convex; achene apex contracted, the pappus of minute fused scales sometimes with one or two short awns . . . . *Wedelia*

Species List

Compositae: Tribe Heliantheae

Acanthospermum

A. hispidum DC.
A. australe (Loefl.) Kuntze

Acmella

A. brachyglossa Cass.
A. ciliata (H.B.K.) Cass.
A. oppositifolia (Lam.) R. K. Jansen var. *oppositifolia*
***A. radicans* var. *debilis* (H.B.K.) R. K. Jansen
A. uliginosa (Sw.) Cass.

Ambrosia

**A. crithmifolia* DC. [Hort!]
***A. cumanensis* H.B.K.
A. microcephala DC.

Baltimora

B. geminata (Brandgee) Stuessy

Bidens

B. alba (L.) DC. var. *radiata* (Schultz Bip.) Ballard
B. cynapiifolia H.B.K.
B. pilosa L.
B. riparia H.B.K. var. *refracta* (Brandgee) O. E. Schultz

Calea

***C. berteriana* DC.
C. caleoides (DC.) H. Robinson
C. lucidivenia Gleason & Blake var. *lucidivenia*
var. *cardonae* Maguire & Wurdack
C. oliverii B. L. Robinson & Greenm.

C. prunifolia H.B.K.
C. solidaginea H.B.K. var. *deltophylla* (Cowan) Pruski & Urbatsch

Clibadium
C. armani Schultz Bip. ex Baker
C. surinamense L.
C. sylvestre (Aubl.) Baill.

Coreopsis
**C. drummondii* Torrey & Gray [Hort!]

Cosmos
**C. bipinnatus* Cav. [Hort!]
C. caudatus H.B.K.
**C. parviflorus* Pers. [Hort!]
C. sulphureus Cav.

Dahlia
**D.* sp. [Hort!]

Eclipta
E. prostrata (L.) L.

Eleutheranthera
E. ruderalis (Sw.) Schultz Bip.

Gaillardia
**G. pulchella* Foug. var. *lorenziana* Voss [Hort!]

Helianthus
H. annuus L. [Hort!]
**H. argyrophyllus* Torrey & Gray [Hort!]

Ichthyothere
I. davidsei H. Robinson
I. granvillei H. Robinson
I. terminalis (Sprague) Blake

Lagascea
***L. mollis* Cav.

Melanthera
**M. nivea* (L.) Small

Milleria
***M. quinqueflora* L.

Montanoa
**M. bipinnitifida* (Kunth) K. Koch [Hort!]

Neuroleana
N. lobata (L.) R. Br.

Oyedaea
O. rusbyi Blake
O. scaberrima (Benth.) Blake
***O. tepuiana* (Badillo) Pruski *in ed.*
***O. verbesinoides* DC.

Parthenium
P. hysterophorus L.

Pectis
P. elongata H.B.K. var. *elongata*
var. *floribunda* (A. Rich.) Keil
P. humifusa Sw.
***P. linifolia* L.

Porophyllum
P. ruderale (Jacq.) Cass.

Riencourtia
R. glomerata Cass.
R. pittieri Blake

Salmea
***S. scandens* DC.

Sigesbeckia
**S. orientalis* L. [Hort!]

Spilanthes
***S. urens* Jacq.

Synedrella
S. nodiflora (L.) Gaertn.

Tagetes
T. erecta L.

Tithonia
**T. diversifolia* (Hemsl.) A. Gray [Hort!]

Tridax
T. procumbens L.

Unxia
U. camphorata L. f.

Verbesina
***V. alata* L.
V. schomburgkii Schultz Bip.

Wedelia
W. calycina L. C. Rich in Pers. (or *W. caracasana* DC.)
W. fruticosa Jacq.
W. trilobata (L.) Hitchc.

Wulffia
W. baccata (L. f.) Kuntze
W. rubens Alexander

Zinnia
Z. elegans Jacq.
**Z. haageana* Regel. [Hort!]

* = No specimen present at US or NY. Specimen in BRG labeled with this name or a synonym.

** = Unknown from the Guianas but documented from neighboring regions, hence to be expected in the Guianas.

[Hort!] = specimen label contains information that collection was horticultural.

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VEGETATIVE AND SEXUAL REPRODUCTION IN THE RARE SEDGE, *CAREX POLYMORPHA* (CYPERACEAE)

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ABSTRACT

Carex polymorpha is a rare sedge of eastern North America, currently a candidate for Federal listing. Populations in Maine and Massachusetts were studied to establish a scientific basis for population monitoring, management, and protection. We examined potential and actual fecundity, and used pollination experiments to test hypotheses regarding breeding systems. Sexual reproductive characters were compared with the common species, *C. vestita*. Studies of vegetative reproduction of *C. polymorpha* included determination of rhizome growth patterns, above- and below-ground biomass, organ dimensions and dynamics of shoots in permanent plots.

Both vegetative growth and sexual reproduction appear to be correlated with canopy closure. Numbers of flowering shoots, flowers and seeds appear to be limited by light availability. Both the number of achenes and the percent seed set per flowering shoot are similar in *Carex polymorpha* and *C. vestita*. Density of vegetative shoots and of leaf and rhizome sizes are also correlated with canopy cover: biomass production appears to be limited by light levels. Shoot dynamics are correlated with light and microhabitat type. The least stable shoot populations are in disturbed, open sand sites, while shoot populations in undisturbed, open canopy sites have high turnover rates but stable sizes. These results suggest that canopy management may be critical to maintenance of vegetative and sexual reproduction in established populations of *Carex polymorpha*.

Key Words: *Carex,* rare species, reproductive biology, vegetative reproduction, Maine, Massachusetts

INTRODUCTION

Carex polymorpha Muhl. (section *Paniceae* G. Don) is a rare sedge with fewer than 30 extant populations distributed from Maine to West Virginia. It is listed as rare in each of the states in which it is known to occur or to have occurred. *Carex polymorpha* has been under review by the U.S. Fish and Wildlife Service for Federal listing since 1983 when it was placed in category 2, comprised of those taxa for which listing may be appropriate, but for which substantial data on biological vulnerability and threats are needed to ascertain their status. The primary goals of this study were to provide data on the life history and population dynamics of this rare sedge that would be of value in efforts to monitor populations and to develop recommendations for management and protection strategies.

Section *Paniceae* G. Don is a group of approximately 12 *Carex* species of Eurasia and North America. In North America this section includes the European adventive *Carex panicea* L. and several widely distributed species of neutral or calcareous habitats that are, however, listed as rare in several states (*C. livida* (Wahl.) Willd., WA, NY; *C. meadii* Dewey, NY; *C. tetanica* Schkuhr., IA; *C. vaginata* Boott, NY; *C. woodii* Dewey, IA). Other species included in section *Paniceae* are *C. biltmoreana* Mackenz., a rare southern Appalachian endemic of wet shaded cliffs in the Blue Ridge Mountains and also under consideration for Federal listing; *C. chapmanii* Steud., a coastal plain endemic occurring from Florida to North Carolina; and *C. californica* L. H. Bailey, a rare species occurring from northwestern California to Idaho. *Carex californica* appears to be the closest relative of *C. polymorpha.* It is morphologically very similar in all vegetative and most floral characters, and differs only in the shorter and non-oblique beak of the perigynium.

Preliminary observations of populations of *Carex polymorpha* in Maine, Massachusetts, New Hampshire, Rhode Island, and Pennsylvania led us to develop the hypothesis that variation in flowering, seed set and vegetative growth is correlated with canopy cover. To test these hypotheses, field observations of plants and experimental manipulations were performed at two sites in Maine and one in Massachusetts. Permanent plots were established to study shoot life history, density and turnover of shoots. Destructive sampling of additional plots provided data on vegetative growth patterns, meristem dynamics, and vegetative morphology. We estimated light levels using photographs to quantify canopy cover and compared canopy cover in areas which had, or lacked, flowering shoots.

Observations also suggested that recruitment via sexual reproduction is limited, and that vegetative reproduction may be the most important factor in maintenance of existing populations. To characterize reproductive biology in *Carex polymorpha,* we observed flowering phenology and dichogamy, and investigated fecundity, seed set, and breeding systems. Sutherland (1986) investigated correlations among environmental and life-history characteristics and fruit set in plants. He found that fruit set is always less than 100%, and attributed this reduction to pollinator limitation, lack of pollinator attraction, overproduction of flowers to compensate for variations in resource availability ("bet-hedging"), or selective abortion of embryos. We attempted to determine whether reduced seed set in *Carex polymorpha* was due to self-incompatibility, reduced pollen loads due to low air flows in shaded or brushy sites, or to "bet-hedging" and limited environmental resources by conducting experiments with controlled pollinations and comparing these results to open-pollinated plants in several habitats.

The final hypothesis tested was whether limited seed output is correlated with rarity in *Carex polymorpha.* We compared fecundity and seed set with a common species, *C. vestita* Willd. (section *Carex*). Although not phylogenetically closely related, *C. vestita* is morphologically similar, occurs sympatrically, and provides a useful congeneric comparison to test hypotheses on the causes of rarity of *C. polymorpha.*

MATERIALS AND METHODS

Study Sites

Studies of *Carex polymorpha* were conducted in three populations. Two were located in Falmouth Foreside, Cumberland County, Maine: the Borrow Pit site, an extensive area of former sand and gravel excavations with several vegetation types, and the Woods site, less than 2 km north of the Borrow Pit site, wooded and undisturbed. The third population was located in Duxbury, Plymouth County, Massachusetts, and grew on sand dikes of a former cranberry bog and in adjacent woods.

Comparative studies of *Carex vestita* were conducted at a population which grew in a power line right-of-way adjacent to a cemetery in Stoughton, Norfolk County, Massachusetts.

Flowering Phenology

Each site was visited weekly in May, 1988 to collect data on flowering phenology. The number of flowering shoots in each of five classes was recorded. These classes were defined as 1) not yet in flower, 2) in a female-only phase defined as having the stigmas white and exserted, 3) in a hermaphroditic phase defined as having both stigmas and anthers exserted, 4) in a male-only phase defined as having anthers dehiscing and stigmas brown and withered, and 5) flowering shoots that had ceased to flower. Additional observations were made at the Borrow Pit site to assess numbers of flowering and vegetative shoots in consecutive 20-cm wide × 100-cm long quadrats along three parallel transects. Each of these transects included areas of sand-vegetation edge, lightly shaded woods, and open sedge-dominated areas.

Fecundity

Female flower production (potential fecundity) was studied by counting the number of pistillate spikes and perigynia produced per flowering culm. For *Carex polymorpha,* 250 flowering culms were collected in mid-July 1988 from three subpopulations of the Maine Borrow Pit population. Of these, 50 culms were collected as a grab sample from an area in full sun (area 1), 100 from young woods collected along two 10-m transects (area 2), and 100 culms from the edge of a bog (area 3). For *C. vestita,* 100 culms were collected from a population along a utility line easement in Stoughton, Massachusetts. Seed set (actual fecundity) in both species was assessed by determining the number of mature achenes per flowering shoot. Percent seed set was calculated as the percent of perigynia containing mature achenes.

Breeding System

The breeding system of *Carex polymorpha* was investigated through experimental manipulation of plants at the Borrow Pit site in May, 1989. The subpopulation selected occurs in an open, relatively unshaded site where seed set would be expected to be high. This experiment was designed to determine whether the low seed set observed in 1988 was due to either self-incompatibility or to limited pollen dispersal in wooded sites.

Six treatments were used: 1) emasculated, 2) emasculated and bagged, 3) bagged, 4) emasculated, hand-pollinated with pollen from a different subpopulation, and bagged, 5) hand-pollinated with pollen from the same subpopulation, and 6) undisturbed controls. These treatments enabled us to determine whether plants were apomictic, self-compatible, or self-incompatible, and to isolate any effects due to emasculation or bagging. Ten replicates of each treatment were used. All pollinations were done on 21 May 1989, and bags were removed ten days later, after pollen release in the population had ceased, to allow normal achene development. The unequal number of replicates analyzed in the results is due to the death of some shoots due to grazing or manipulation. Plants were emasculated by manual removal of the terminal staminate spike or spikes prior to emergence of stigmas, and were bagged by enclosure of the entire flowering culm, prior to emergence of stigmas, in glassine photographic negative envelopes (3 cm × 17 cm) which were tied at the base. Hand-pollination was accomplished by removal of a staminate spike with dehiscent anthers from a donor plant, and brushing the anthers of this spike onto the exposed stigmas of the receptor plant until the stigmas were visibly yellow. All the experimental culms were harvested on 13 July 1989, and the total numbers of perigynia and mature achenes were determined.

Vegetative Morphology

Destructive sampling of rhizomes was performed at the two Maine sites in six 1 m^2 quadrats: two in the Falmouth Woods population designated Woods 1 and 2, three along the sand-vegetation edge at the Borrow Pit site designated Borrow Pit A 1, 2 and 3, and one in a partially wooded area of the Borrow Pit site with a dense herbaceous layer of *Carex polymorpha* designated Borrow Pit B. The purpose was to investigate patterns of rhizome growth and shoot production. Data recorded for each inter-shoot unit (consisting of one to several internodes between scale-leaves) included the length of the unit and dry weight per cm of the rhizome. Data recorded for each node included the number of meristems produced and the developmental fate of each meristem (vegetative shoot, flowering shoot, rhizome). Rhizome weight was determined for arbitrarily selected 20 mm lengths of excavated rhizomes cut distally to the terminal living shoot, dried at 60°C for 24 hours, and weighed to the nearest .0001 gram.

Vegetative morphology was examined by measuring lengths and widths of the longest leaf from arbitrarily selected shoots in the Woods and Borrow Pit populations in Maine to determine whether canopy cover affects above-ground biomass production.

Permanent Plots

Shoot turnover was investigated in permanent plots established at randomly selected intervals along a line transect through the longest axis of each population or subpopulation. Each permanent plot was 20 cm × 50 cm (.1 m^2) and marked at the four corners by bamboo stakes inserted into the substrate. A mapping frame with a transparent acrylic top and adjustable hanging plumb line was used to record shoot locations, with an accuracy of ±1 cm. Shoot locations were mapped in May, July, and September (the early, middle, and late growing season) in 1988 and 1989 for the Maine populations. Permanent plots in the Massachusetts population were sampled in May, July and September 1988 and May 1989. These data were used to determine recruitment and turnover rates of vegetative shoots within and between growing seasons in different microhabitats.

Six permanent plots were established at the Borrow Pit population, three each along two transects. One transect was placed at the boundary between open sand and a vegetated area (transect A), and all plants were growing in sand. The second transect was placed in an area with an open canopy (transect B) and a dense herbaceous layer dominated by *Carex polymorpha.* Three permanent plots were established along a transect in the Woods population. Nine permanent plots were established at the Duxbury, Massachusetts site. Three plots were located along a transect on the top of a dike (transect A), three plots were in an area with an open canopy and a dense herbaceous layer dominated by *C. polymorpha* (transect B), and three plots were located in pine forest with a dense canopy (transect C).

Canopy Cover

Photographs were taken of the canopy by placing a camera with a 28 mm wide-angle lens at 10 cm above the ground, facing upwards. Photographs were taken when the canopy was fully expanded, on 8 July 1988 in Maine and on 15 July 1988 in Massachusetts. A matrix of 100 evenly-spaced dots was placed on each photograph to estimate the percent of canopy cover, which is correlated with light levels (Piper, 1989). At the Borrow Pit site, photographs of the canopy were taken within and at the edge of a partially wooded area dominated by *Carex polymorpha.* At the Falmouth Woods site, photographs were taken at several locations within the population. At the Duxbury site, photos were taken in the wooded areas where only vegetative shoots were present as well as in the open areas at the foot of the dike and along the dike trail where both vegetative and flowering shoots were present.

RESULTS

Reproductive Biology

Flowering shoots comprise, on average, 1.5% of the total population of shoots in the Borrow Pit subpopulation sampled. Based on our observations, this figure is typical of populations in open or slightly shaded sites. In sites with a well-developed canopy, such as the Falmouth Woods site, flowering shoots comprise less than 1% of the total. In heavily shaded sites, such as portions of the Duxbury site, no flowering shoots may develop.

Plants of *Carex polymorpha* are protogynous. For an individual shoot, the initial pistillate phase has a duration of less than a week, the intermediate hermaphroditic phase has a duration of one to two days, and the terminal staminate phase lasts from one to several days. Although dichogamous, the overlap in flowering potentially permits self-pollination to occur.

Plants within and among populations exhibit considerable asynchrony in flowering. At the Maine sites, the Borrow Pit population initiated flowering earlier than the Woods population. The Borrow Pit population was predominantly in the hermaphroditic phase on 16 May 1988, at which date the Woods population had not begun to flower. A week later, on 24 May, flowering shoots at the Borrow Pit had ceased flowering or were in their terminal staminate stage while all shoots at the Woods population were in a staminate phase. This Woods population showed a high degree of synchrony and completed the entire flowering sequence in 8 days. At the Massachusetts population, flowering of different subpopulations was also asynchronous, and flowering occurred over a 12-day period from 8–19 May. Achenes were mature in both Maine and Massachusetts populations by 23 July, approximately eight weeks after flowering had ceased.

The number of pistillate spikes, as well as the number of perigynia produced per flowering shoot, varied among subpopulations of *Carex polymorpha* at the Borrow Pit site: shoots in area 3 had, at most, one pistillate spike and on average 16 perigynia per spike, while shoots in areas 1 and 2 had at least one pistillate spike and on average 32–40 perigynia per shoot (Table 1). This difference

Table 1. Female flower and fruit production of *Carex polymorpha* and *C. vestita* (data are the mean ± 1 SD).

Population	No. Pistillate Spikes	No. Perigynia	No. Achenes	% Seed Set
Borrow Pit (1)	1.3 ± 0.4	40.1 ± 17.0	30.1 ± 15.5	72.7 ± 20.8
Borrow Pit (2)	1.4 ± 0.5	32.1 ± 11.7*	1.2 ± 1.7*	4.5 ± 6.4
Borrow Pit (3)	1.0 ± 0.0	16.3 ± 7.1*	1.2 ± 1.9*	7.4 ± 0.1
C. vestita	1.9 ± 0.7	94.4 ± 37.5	6.4 ± 6.3	6.8 ± 6.2

* Means are not significantly different at $P < .1$ in Student's t comparisons; all other means were significantly different.

among subpopulations in potential fecundity appears to be correlated with shading and canopy closure. Shoots of *C. vestita* tended to have two pistillate spikes and, on average, 95 perigynia (Table 1).

Actual fecundity, measured as the number of achenes and the percentage of perigynia which produced mature achenes, varied significantly among subpopulations of *Carex polymorpha* and between the two species (Table 1). The open, relatively unshaded subpopulation 1 of *C. polymorpha* at the Borrow Pit site had a seed set of 72% and produced on average 30 achenes per pistillate spike. This number is significantly different from the two more shaded Maine subpopulations (2, 3), which produced fewer than two achenes per spike and had seed sets of less than 10%. All populations of *C. polymorpha* differed significantly from *C. vestita,* which produced from 0–25 mature achenes per flowering shoot with an average seed set of less than 7%.

Mature achenes were obtained in all experimental pollination treatments (Table 2). The highest percent seed set was observed

Table 2. Achene production in breeding system experiment (mean ± 1 SD). (See text for further explanation.)

Treatment*	*n*	Perigynia	Achenes	% Seed Set
1	9	52 ± 25	42 ± 22	78%
2	8	58 + 20	14 ± 13	30%
3	7	43 ± 17	22 ± 10	55%
4	9	55 ± 18	34 ± 13	62%
5	7	44 ± 18	31 ± 18	70%
6	7	46 ± 22	37 ± 17	79%

* 1 = emasculated, open-pollinated; 2 = emasculated and bagged; 3 = selfed (bagged); 4 = outcrossed (emasculated, hand-pollinated, bagged); 5 = hand-pollinated (emasculated, hand-pollinated); 6 = control.

for the open-pollinated plants in treatments 1, 5 and 6. These seed set rates (> 70%) are comparable to those found for plants in open habitats, demonstrating that emasculation or hand-pollination have no discernable effects on seed set. The somewhat lower seed set figures for treatments 3 and 4 show no difference between donor pollen from the same plant or a different clone, but suggest that seed set was somewhat limited by bagging. The low seed set for treatment 2, in which plants were expected to set no seed if sexual and to have a significant seed set if apomictic, is puzzling. However, we found that although spikes are fundamentally unisexual, the majority of pistillate spikes developed a few inconspicuous staminate flowers at their tip which were not noticed and therefore not removed by emasculation. The presence of some pollen within the pollen exclusion bags in treatment 2 from these few anthers could explain the low level of seed set in this treatment testing for apomixis. This experiment for apomixis is thus not conclusive, but results are consistent with the hypothesis that *Carex polymorpha* is self-compatible and not apomictic.

Vegetative Morphology

Growth in the clonal species *Carex polymorpha* is sympodial, and occurs in the following sequence. The apical meristem of a rhizome turns upward and develops into a vegetative shoot which persists for a single growing season. During the growing season, axillary meristems form at the base of this shoot; these meristems may develop into elongate rhizomes which initiate further vegetative spread, or may develop into short ascending rhizomes which form either vegetative or flowering shoots. Individual leafy shoots persist for only a single growing season. This form of sympodial growth produces a pattern of either single, isolated shoots if all meristem growth is of elongate rhizomes, or may produce a pattern of tightly clustered shoots if most meristem growth is of short, ascending rhizomes.

The pattern of rhizome growth was investigated in the 6 quadrats that were excavated. By tracing rhizomes for their entire length in these quadrats, we found that relatively few shoots in any given square meter belonged to the same clone. Rhizomes are capable of continued growth for several meters, and rhizomes from several different directions converge and intermingle in a

Table 3. Comparison of rhizome inter-shoot unit lengths and meristem number among samples of *Carex polymorpha* in Maine.

Site	Quadrat	*n*	Mean Rhizome Length (cm) ± SEM	Mean Number of Meristems	Canopy Cover
Woods	1	144	5.078^{c} ± 0.484	1.243^{b}	closed
	2	370	6.304^{c} ± 0.389	1.372^{b}	closed
Borrow Pit A	1	22	13.855^{a,b} + 2.445	1.567^{b}	open
	2	38	15.850^{a} ± 1.752	2.721^{a}	open
	3	86	11.506^{b} ± 1.418	2.372^{a}	open
Borrow Pit B	1	74	3.920^{c} ± 0.393	1.107^{b}	closed

^{a,b,c} Differences between means were assessed using Student-Newman-Keul's *a posteriori* test in an ANOVA of comparisons by site. Differences among means with different group letters were significant at $P < .0001$. Means with the same letter were not significantly different. SEM = standard error of the mean.

single area. This growth pattern indicates that competition among different genets may be occurring at a high level in populations of *Carex polymorpha* that consist of more than one genet. Intact rhizome systems were excavated that had up to 14 nodes. Analysis of the branching pattern, based on our observations regarding shoot growth and differentiation, indicate that ramets may remain connected to the parent rhizome for at least 8, and perhaps as long as 10 years, based on the observation that a single node is produced per year at this site.

Rhizome inter-shoot unit lengths differed significantly among these sites (Table 3) and when sites were grouped according to canopy types. Rhizome inter-shoot lengths in the Woods and Borrow Pit B quadrats averaged 4–6 cm, but reached 11–14 cm in an open sand quadrat at the Borrow Pit site. Average inter-shoot length in closed canopy sites is 5.70 cm, while average internode length in open canopy sites is 12.99 cm. Analysis of variance showed this difference to be significant at $P < .0001$, $F = 92.68$.

The weights of rhizome segments differed between the Woods and Borrow Pit sand quadrats. The average rhizome dry weight (2 cm segment) for plants in the Borrow Pit quadrat was .0755 g, while average weight from plants in the Woods site was .0407 g. Student's t-test ($df = 44$) found this difference to be significant at $P < .1$, $t = 1.7939$ (the lower significance level of $P = .1$ was chosen due to the restricted amount of material available).

Leaf production and dimensions were studied in arbitrarily selected vegetative shoots from closed-canopy (Woods) and open (Borrow Pit) sites. Although there was some difference in the mean leaf number (Borrow Pit = 8.57 ± 1.94, $n = 21$; Woods = 6.95 ± 1.09, $n = 22$), the means were not significantly different according to Student's *t*-test ($t = .652$, $P < .1$). Lengths of the longest leaf of each shoot were also compared. Mean leaf lengths were somewhat different (Borrow Pit = 478.7 ± 80.7 mm, Woods = 430.3 ± 64.1 cm), but not significantly so ($t = .336$, $P < .1$). Leaf widths are significantly different between the shaded Woods and open Borrow Pit sites, with the Woods population having leaves on average 2.45 ± .72 mm wide, and the Borrow Pit population leaves 5.41 ± 1.12 mm wide ($t = 2.227$, $P < .05$). The narrower leaf width in the shaded site may result from limited resources available to support vegetative growth.

The average number of meristems produced per node was greater for plants growing in open sites ($\bar{x} = 2.31$, range 0–9) than in closed-canopy sites ($\bar{x} = 1.31$, range 0–5) based on an analysis of variance ($F = 59.12$, $P < .0001$). However, there were significant variations within the open sand site (BP-B), in which one replicate quadrat was found to be more similar to the Woods site. This variability may indicate that the open sandy quadrats were not located in a homogeneous environment, or may indicate that canopy effects are not the sole explanation for differences in rhizome meristem production.

Permanent Plots

Density of shoots in the permanent plots was correlated with canopy cover. Those plots with high shoot density (≥ 200 shoots/m^2) were the Borrow Pit transect B (BP plots 4–6) and the similar Duxbury transect B (Table 4). These relatively unshaded sites had shoot densities ranging from 170 to 390 shoots/m^2. Two sets of plots, the Duxbury dike transect A and Falmouth Woods, were in more shaded areas and had intermediate shoot densities (100 to 200 shoots per m^2). Two sites had very low shoot densities (< 100 shoots/m^2). Duxbury transect C occurred in heavily shaded woods. Borrow Pit transect A (BP plots 1–3) was comparable to the intermediate density sites in shading, but occurred in a microsite with very sandy soil of potentially lower quality to plant growth due to lower water and/or nutrient availability.

Shoot turnover in the permanent plots, measured as the rate of persistence of individual shoots during a growing season, appeared to be correlated to canopy closure. In the forested sites (Falmouth Woods, Duxbury C) nearly all shoots present at the beginning of a growing season persisted through the season, and few or no new shoots were initiated (Table 4). Shoot density is lowest in these populations as well. Several plots (Borrow Pit 4–6, Duxbury B) had high rates of shoot turnover, with as little as 50% of the total shoot population persisting through a growing season (Table 4). The total shoot number in each of these plots tended to remain approximately the same at each sampling date as well as throughout the growing season despite turnover of 20–40% of the shoots; it is clear that these sites with high turnover also had the highest shoot density.

Most sites and plots exhibited little change in total number of shoots from year to year, although minor fluctuations were common. Three plots, Duxbury A-1, Borrow Pit 1 and 2 showed increases of up to 100% from year 1 to year 2 of the study (Table 4). One plot, Borrow Pit 3, showed a decline of 50% in this period. These data indicate that the vegetation-sand edge is a very dynamic region, in which the population may expand rapidly, suffer high levels of shoot mortality, or both.

Canopy Cover

Results from the measurement of canopy closure are not sufficiently precise, nor were a sufficient number of replicate measurements taken to provide adequate statistical precision to their analysis. The two populations with substantial numbers of flowering shoots (Borrow Pit B and Duxbury A) had, on average, less than 50% canopy cover above patches of flowering shoots: at the Borrow Pit, the median was 42% (range 9–69%); at Duxbury the median was 30% (range 15–65%). Areas within these populations where only vegetative shoots were present had substantially higher canopy cover, with median values above 80%. Two populations which had low levels of flowering, Falmouth Woods and Duxbury B, had canopy cover of approximately 65–80% above both flowering shoots and vegetative shoots. The population that had no flowering, Duxbury C, had a median canopy cover of 82%.

A correlation between canopy cover and flowering frequency is strongly suggested. Canopy cover of less than 50% appears to

Table 4. Within-year shoot turnover* and changes in shoot numbers for *Carex polymorpha*.

Quadrat		Date						Annual Turnover
		5/88	7/88	9/88	5/89	7/89	9/89	
Duxbury A-1	Shoot number	4	6	5	16	—	—	
	% Turnover	—	0	33	—	—	—	
	% Change	—	+50	−16	—	—	—	+120
A-2	Shoot number	24	25	26	24	—	—	
	% Turnover	—	8	48	—	—	—	
	% Change	—	+4	+4	—	—	—	0
A-3	Shoot number	16	18	15	16	—	—	
	% Turnover	—	0	17	—	—	—	
	% Change	—	+13	−17	—	—	—	0
B-1	Shoot number	38	27	37	34	—	—	
	% Turnover	—	58	7	—	—	—	
	% Change	—	−29	+37	—	—	—	−40
B-2	Shoot number	23	27	28	25	—	—	
	% Turnover	—	39	7	—	—	—	
	% Change	—	+17	+4	—	—	—	+20
B-3	Shoot number	36	37	37	39	—	—	
	% Turnover	—	8	16	—	—	—	
	% Change	—	+3	0	—	—	—	+30
C-1	Shoot number	4	4	4	4	—	—	
	% Turnover	—	0	0	—	—	—	
	% Change	—	0	0	—	—	—	0
C-2	Shoot number	4	4	5	5	—	—	
	% Turnover	—	0	0	—	—	—	
	% Change	—	0	+25	—	—	—	+10

Table 4. Continued.

Quadrat			Date						Annual Turnover
			5/88	7/88	9/88	5/89	7/89	9/89	
	C-3	Shoot number	4	5	5	3	—	—	
		% Turnover	—	0	20	—	—	—	
		% Change	—	+25	0	—	—	—	−10
Maine**	BP-1	Shoot number	10	10	11	8	8	6	
		% Turnover	—	0	0	—	0	25	
		% Change	—	0	+10	—	0	−25	
	BP-2	Total shoots	2	2	2	5	7	6	
		% Turnover	—	0	0	—	0	14	
		% Change	—	0	0	—	+40	−14	
	BP-3	Total shoots	4	4	4	6	6	5	
		% Turnover	—	0	0	—	0	17	
		% Change	—	0	0	—	0	−17	
	BP-4	Total shoots	19	17	18	17	24	20	
		% Turnover	—	11	0	—	0	21	
		% Change	—	−11	+6	—	+42	−17	
	BP-5	Total shoots	32	31	28	26	32	27	
		% Turnover	—	38	29	—	0	22	
		% Change	—	−3	−10	—	+23	−16	
	BP-6	Total shoots	19	17	17	13	13	13	
		% Turnover	—	11	18	—	0	8	
		% Change	—	−11	0	—	0	0	

Table 4. Continued.

Quadrat		Date 5/88	 7/88	 9/88	 5/89	 7/89	 9/89	Annual Turnover
FW-1	Total shoots	19	14	12	13	14	—	
	% Turnover	—	26	36	—	0	—	
	% Change	—	−26	−14	—	+8	—	
FW-2	Total shoots	10	11	12	12	12	9	
	% Turnover	—	0	0	—	0	25	
	% Change	—	+10	+9	—	0	−25	
FW-3	Total shoots	6	6	4	5	5	5	
	% Turnover	—	17	33	—	0	0	
	% Change	—	0	−33	—	0	0	

* Percent turnover is calculated as number of shoots persisting between sampling dates divided by the total number of shoots on the previous sampling date. Percent change is calculated as the difference in total shoot number on two successive sampling dates, divided by the total number of shoots on the earlier sampling date.

** BP = Borrow Pit; FW = Falmouth Woods.

promote flowering, while the canopy cover between 50 and 80% inhibits flowering, although environmental factors other than light may be important in regulation of flowering within this range of light levels. Canopy cover greater than 80% appears to inhibit flowering completely.

DISCUSSION

Sexual reproduction in *Carex polymorpha* is potentially resource-limited at each stage of reproduction. Production of flowering shoots may be initially limited primarily by light levels which reduce allocation of resources to flowering. Light, measured by canopy closure, further limits the number of pistillate spikes and perigynia produced by each flowering shoot. Finally, resources may limit the number of achenes which mature. The net result is lack of sexual reproduction in severely shaded habitats, negligible seed set in less shaded sites, and high levels of seed set only in the most open sites.

Flowering shoots form, on average, 1.5% of the total population of shoots. Based on our observations, this ratio is typical of populations in favorable conditions such as open or slightly shaded sites. In sites with a well-developed canopy, flowering shoots form less than 1% of the population, or may be entirely absent. Piper (1989) found that microsite variation in light had a strong influence on flowering in *Smilacina,* due to the increase in shoot size with increased light.

This correlation between canopy cover and flowering frequency is supported by our study of canopy closure. The highest incidence of flowering in *Carex polymorpha* occurred where the canopy cover was less than 50%, and decreased to zero in areas where the canopy cover was greater than 80%.

In populations with high numbers of flowering shoots, reproductive success may be limited by the number of pistillate spikes and the number of perigynia produced per flowering shoot. Differences among subpopulations in potential fecundity (the number of female flowers produced) also appeared to be correlated with shading and canopy closure, with the highest potential fecundity in the most open sites.

Reproduction is further limited by seed-set. Although the number of perigynia determines potential fecundity, actual fecundity is measured as the number of achenes which mature, and ranges from 72% in open areas to less than 10% in areas with higher canopy cover. These figures are comparable to the average fruit-set for self-compatible monoecious species, for herbaceous perennials, for temperate species, for species with "cheap fruits," and for wind-pollinated plants (Sutherland 1986). *Carex polymorpha* may be placed in all of these categories.

Seed set is not reduced because of self-incompatibility in *Carex polymorpha.* The controlled breeding experiment showed that seed set rates for hand-pollinated plants are comparable to those for open-pollinated plants in the most favorable open habitats. These results were not conclusive due to unexpected low levels of self-pollen available to bagged inflorescences, but support the hypothesis that *C. polymorpha* is self-compatible and not apomictic, and that in open habitats fecundity is not limited by pollen availability. These results indicate that the low actual fecundity appears to be due to embryo abortion controlled by extrinsic environmental factors, such as resource limitation. Based on experience with controlled crosses in other species of *Carex,* we expect that the perigynia would not expand and no early embryo development would take place in unpollinated perigynia. Since the majority of perigynia on open-pollinated plants in shaded sites were fully developed with aborted embryos, we assumed in this species that where seed set is low, embryos abort due to resource limitation in this species.

Resource limitation of sexual reproduction reduces the potential for establishment of new individuals within existing populations. If light is the limiting resource, existing populations in severely shaded or wooded sites are incapable of expansion by sexual reproduction. Recruitment of new individuals can only occur in those populations where light levels are sufficiently high to trigger the production of flowering shoots and to allow the plants to allocate sufficient resources to developing achenes. By extension, only those populations which occur in open sites can produce propagules which may disperse, colonize new sites, and establish new populations. Recruitment of new individuals by seed may be rare in *Carex* in general, particularly in established populations. Bernard (1975, 1976) reported that no seedlings of either *C. rostrata* Stokes or *C. lacustris* Willd. were seen in several years of study. Callaghan (1976) also never observed seedlings of *C. bigelowii* Torrey. Our observations, including those of the senior author over the past 15 years, confirm this.

Reproductive biology of *Carex polymorpha* is similar to that of a wide range of other species characterized as "stress-tolerant competitors" (Grime, 1979), and does not appear to be correlated with the distribution or frequency of this species. Many long-lived herbaceous perennials are capable of extensive vegetative growth, and allocate resources to sexual reproduction only under favorable environmental circumstances. This strategy allows plants to compete successfully in established sites for limited resources such as space, light, nutrients, or water.

Comparisons were made to the common *Carex vestita* to determine whether reproductive characteristics of *C. polymorpha* are correlated with its rarity. *Carex vestita* had a significantly higher potential fecundity but a lower seed set; on average, shoots produced fewer than 7 achenes, with an average seed set of 6.8%. This species, even in open, apparently favorable habitats, has an actual fecundity which is lower than that of *C. polymorpha* in similar favorable sites. Fritz-Sheridan (1988) found a similar result for the rare *Erythronium grandiflorum* Pursh var. *candidum* (Piper) Abrams in comparison to the common var. *grandiflorum*. These results indicate that, although sexual reproduction in *C. polymorpha* is resource limited, there is no real difference from common or widely distributed species. Reduced sexual reproduction, measured here by number of flowering shoots, potential and actual fecundity, does not appear to be a cause of rarity in *C. polymorpha*.

The mode of vegetative reproduction in *Carex polymorpha* is similar to that of most rhizomatous species of *Carex*. This species has a sympodial growth form, in which a module consists of a rhizome and a terminal shoot which produces roots at nodes and which has buds in the axils of basal scale-leaves. Rhizomes may be horizontal and long, or short and vertical. This growth form produces a pattern of clusters of connected shoots produced by short rhizomes, dispersed at the ends of long rhizome segments. This sympodial growth form is typical of most *Carex* species investigated (Kershaw, 1962; Bernard, 1975, 1976; Noble et al., 1979; Callaghan, 1976; Schmid, 1984; Bedford et al., 1988) as well as other monocots such as *Smilacina stellata* (L.) Desf., *S. racemosa* (L.) Desf., and *Streptopus roseus* Michx. (Antos, 1988; Piper, 1989), and was illustrated by Bernard (1975).

This growth pattern can be described as producing "K-selected genets" which are long-lived and produce large stands, but for which new genets are infrequently formed. However, shoots can be described as "r-selected modules" (Schmid, 1984) which are short-lived and produced rapidly and continuously. This pattern may also conform to the "stress-tolerant competitor" model of Grime (1979). This growth form has many ecological advantages; the potential of clones to spread by vegetative growth into different microsites buffers clones against disturbance and death. Clones, or their fragments, have the potential to take advantage of different microsite conditions, and to distribute resources between more- and less-favorable microsites. Nutrients and/or photoassimilates may be translocated from ramets in high-quality microsites to lower-quality sites, and may even out the patchy distribution of resources in forested sites. Studies of several other *Carex* species (Kershaw, 1962; Bedford et al., 1988) also found that rhizomes from several genets converged in each apparent clump or tuft of shoots. This convergence is presumably due to the ability of rhizome growth and shoot production to respond to and exploit resource gradients. Noble et al. (1979) showed that nutrient levels were correlated with development of dormant buds into shoots, allowing genets to exploit favorable microsites.

Rhizome persistence, rhizome lengths, and shoot dynamics of *Carex polymorpha* are similar to those found in other species of *Carex*. Rhizome continuity among shoot systems has been estimated at 7 to 12 years (Callaghan, 1976; Noble et al., 1979). Although Bedford et al. (1988) found horizontal rhizomes up to 60 cm long in *C. lasiocarpa* Ehrh., Noble et al. (1979) found that plants in favorable conditions produced rhizomes 11–16 cm long, while plants in less favorable sites produced shorter rhizomes 5–7 cm long. These results correspond with results for *C. polymorpha.*

Noble et al. (1979) described five phases which could be observed in populations of *Carex arenaria* L. The juvenile phase, at the leading edge of the clone, had a low density; the adolescent phase consisted of high shoot density (near the carrying capacity), but of vegetative shoots only; the mature phases had a similar shoot density, but with abundant flowering shoots. In the senile and slack phases, shoot density declined. Similar phases can be described for *C. polymorpha.* The juvenile phases, at vegetation-sand boundaries, have a low shoot density as found for the Borrow Pit A permanent plots. The adolescent and mature phases, typified by the Borrow Pit B plots and by Duxbury A and B plots, have high shoot densities and high levels of flowering. Senile phases, with reduced density and no flowering, are typified by the forested areas of the Duxbury C and Falmouth Woods populations.

Turnover of shoots in *Carex polymorpha* is similar to patterns of shoot demography found in other species of *Carex*. Most studies have found a continuous emergence of new ramets, and new shoots present at all sampling dates (Bernard, 1976; Noble et al., 1979; Bedford et al., 1988). These studies also found the number of shoots present at any one time were constant over the growing season, despite considerable turnover. Noble et al. (1979) found that the highest death rate of shoots occurred at the same time as the highest birth rate, as we found for *C. polymorpha.* He hypothesized that this correlation could be due to the production of new shoots causing the death of older shoots, or that the death of old shoots allows the growth of new shoots.

Shoot density and dynamics are correlated with habitat conditions; densities and turnover are correlated, with the highest turnover rates associated with the highest densities. Shoot density and dynamics can be useful in predicting the health and stage of the population. Maximum densities occur in the most favorable microsites, and represent the "adolescent" or "mature" phases of clonal growth according to the model of Noble et al. (1979). Low densities occur in the least favorable sites and "senile" phase of growth, and are correlated with very low shoot turnover rates. Callaghan (1976) suggested that shoot turnover and the number of shoots in a population correlated with habitat quality, and that both were higher in high-quality sites. Our data suggest that low densities also occur in the "juvenile" advancing edge of the population where they are correlated with high turnover rates.

Results and observations from this study of the population biology of *Carex polymorpha* should enable rare-species managers to make informed decisions regarding habitat management and long-term monitoring goals. We have found that *Carex polymorpha* appears to be somewhat tolerant of frequent, low-level disturbance, judging by its occurrence and even vigor on the edges of dirt roads, dikes, trails, railroad embankments and utility rights-of-way which are regularly cleared of at least some vegetation. Such disturbance may reduce the shading effects of taller vegetation.

It is likely that *Carex polymorpha* is adapted to, or has been characteristic of, habitats with frequent fires. The typical habitats in which we have found *C. polymorpha* have sandy, low-nutrient soils and tend to become very dry in late summer. These are habitats which are susceptible to fire, and which have canopy species (oaks, pitch pine) known to be fire-tolerant. Fires would reduce density of the canopy and increase the amount of light available to *C. polymorpha* for growth and reproduction, and may function to remove the litter layer that may inhibit seed germination. The underground rhizomes and meristems of *C. polymorpha* could survive a cool ground-fire and rapidly re-sprout. This conjecture is partially supported by our observations of the vigorous re-growth of *C. vestita* following a grass fire at the study site, as well as the similarity of its reproductive biology to that of *C. polymorpha.*

The development of modern concepts of rarity was recently presented by Fiedler (1986) in a review of historic and recent literature. She discussed the "age and area" hypotheses, which argued that rare species were either young species not yet dispersed to their potential range, or old, relict species reduced to a few sites. The concept of competition became integrated into this hypothesis, and many have argued that rare species are unable to compete successfully and expand into new sites. Stebbins (1980) and others have concluded that rare species are represented by a single or few genotypes, biotypes, or ecotypes, and are poor competitors. It is clear as we investigate the biology, evolutionary and recent history, and demographic patterns of rare species, that there is no single explanation for rarity. Rabinowitz et al. (1986) recognized seven types of rare species based on distribution, habitat specificity, and population sizes. Although this system enables rare species to be classified, it is also clear that it is inadequate to explain the complexity of rarity, and the individualistic nature of rare species.

Carex polymorpha has a moderately broad geographic distribution, a somewhat restricted habitat specificity, and large population sizes. These characteristics place it between two of Rabinowitz's classes of rare species, those with a narrow geographic range, broad habitat range, and large population and those with a wide geographic range, narrow habitat specificity, and large populations. The first group is hypothesized to have substantial ecological plasticity and a wide tolerance for environmental variation, but limited dispersal abilities which restrict their movement into new sites (i.e., may be genetically variable but reproductively limited). The second group is hypothesized to have already sampled a wide range of sites, and to have achieved successful colonization only on those rare, suitable patches (i.e., may be genetically depauperate but reproductively successful).

The geographic distribution of *Carex polymorpha* provides some support for membership in the latter group; that it has colonized sites from Maine to Virginia indicates that many other sites have probably been "sampled" by propagules which have not successfully established populations. However, we can identify no unique habitat requirements for this species. *Carex polymorpha* has been shown to consist of a large number of genotypes and ecotypes (Standley and Dudley, unpubl. data), and does not fit the model of a genetically depauperate rare species. In this paper, we examine the hypothesis that limited reproductive potential, resulting in a reduced ability to colonize new sites or successfully compete when established, is a cause of rarity in *C. polymorpha.*

Threats to *Carex polymorpha* are substantial. Fewer than 30 extant populations are known to occur. Although the locations of these are known to regulatory agencies and The Nature Conservancy, few state laws or regulations are available that provide protection to this rare species. *Carex polymorpha* generally grows in upland habitats or in buffer zones to wetlands—areas that are generally not protected from development by Federal or state wetland protection statutes. The sandy substrates preferred by this species have, and continue to be, altered by sand and gravel removal operations. Several populations occur on railroad or utility rights of way or easements where vegetation management through use of herbicides may pose a threat. Unless placed under protective ownership, all localities must be regarded as under severe risk of development or alteration that would eliminate habitat suitable for *C. polymorpha.* Even within protected areas, habitat management may be necessary to maintain optimal conditions for vegetative growth and sexual reproduction necessary for the long-term viability of this species.

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COASTAL-PLAIN PLANTS IN INLAND NOVA SCOTIA

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ABSTRACT

Kejimkujik National Park lies near the headwaters of the Mersey River, in the center of southwestern Nova Scotia on the Atlantic Upland. Lakes and streams are numerous; in this glaciated area, granite, slate and greywacke areas are represented, along with numerous drumlins. Distributions of coastal-plain plants in this protected area are discussed. Maps of *Hydrocotyle umbellata* L. and *Cephalanthus occidentalis* L. are given as examples of plants that are rare or unknown in the Tusket River valley.

Key Words: coastal-plain flora, inland location, Kejimkujik National Park, Nova Scotia

The existence of a southern or coastal-plain flora in southwestern Nova Scotia has long been known. The presence of many species, rare or unknown elsewhere in Canada, was documented by M. L. Fernald and members of the Gray Herbarium Expedition (Fernald, 1921, 1922). Their explorations were mainly near the coast of Yarmouth and Shelburne Counties and, in particular, along the Tusket River system in Yarmouth County. Much of this area has now been lost to urban development or submerged as a result of hydro dam development.

Further studies in Yarmouth County have been carried out during the last few years and an ecological reserve for several of the rarer plants has been established further up the Tusket River at Wilsons Lake (Keddy, 1985). However, very little attention has been paid to presence of a southern flora towards the center of the province. C. A. Weatherby spent two weeks in the Ponhook region of Queens County, a region of lakes and bogs draining into the Medway River southeast of Lake Kejimkujik (Weatherby, 1942). Here, he found additional stations for *Lophiola americana* (Pursh) Wood. and the only known station in Canada for *Lachnanthes tinctoria* (Walt.) Ell.

The Mersey River system, running parallel to the Medway River to the east, contains wetlands supporting diverse coastal plain communities. Most of this watershed is protected inside Kejimkujik National Park, established in 1969. This is a region of stream, lakes and bogs. The park is located around the junction of Digby, Queens and Annapolis Counties, 50 miles (80 km) from the Tusket Valley in Yarmouth Co. and 40 miles (65 km) from the Atlantic coast at a level of 300 feet (95 meters) above sea level.

This area is over halfway up the slope of the Southern Upland of the province (Roland, 1982) and is approximately 25 miles (40 km) in diameter, with an area of 145 square miles (385 sq km). Its largest lake is Lake Kejimkujik, six miles long (nearly 10 km) and about six miles wide (Resource Atlas and Description, 1976).

The area was glaciated from the northwest so that many of the lakes and their shores are very rocky. The eastern side of the park has many drumlins which form rounded hills and several of the islands in the lake. The western half is formed predominantly from granite and greywacke and contains only small lakes and ponds. Only Lake Kejimkujik is margined by any considerable sandy beaches. Peaty shores are evident in many protected coves of Lake Kejimkujik and are well developed at the eastern end of the second largest lake of the park, Lake Peskowesk (Roland, 1982).

Forests occupy over 50 percent of the land area and of these, about three-quarters are of mixed stands; logging and frequent fires have largely resulted in a young second-growth forest. The coastal-plain plants are restricted almost entirely to margins of the lakes and streams.

Acer rubrum L. is the most common tree behind the beaches, with some beech and oak on the drumlins. In addition to the ever-present *Pteridium aquilinum* (L.) Kuhn and *Comptonia peregrina* (L.) Coult., the shrubby understory usually contains *Gaylussacia dumosa* (Andr.) T. & G. and *Hamamelis virginiana* L. *Toxicodendron radicans* Ktze. ssp. *radicans* is found in most of the low areas and *Woodwardia virginica* (L.) Sm. often flourishes near the bogs.

The aquatic vegetation has coastal-plain elements; the most abundant plant in shallow water is *Nymphoides cordata* (Ell.) Fern. Bladderworts are less conspicuous, but of the eight species found in the park, four are typically coastal-plain. *Utricularia purpurea* Walt. is the most abundant and luxuriant, often covering the bottom in shallow water. *Utricularia radiata* small occurs only during late summer, when flowering scapes are occasionally present in many of the deeper lakes. *Utricularia subulata* L., more properly a land plant, is common around the lakes, varying from plants the size of pinheads to ones with forking stems several centimeters high. *Utricularia gibba* L. is a rare coastal-plain plant in Nova Scotia which blooms regularly in the quaking margin of Grafton Lake (Maher et al., 1978).

Along the lake shores, *Euthamia galetorum* (Greene) Friesner is usually abundant and even invades areas of shallow water. *Panicum virgatum* L. var. *spissum* Linder is common on the upper edges of the beaches, especially in sandy or gravelly areas; *Decodon verticillatus* (L.) Ell. is found as scattered populations in the western part of the park. More widespread *Juncus militaris* Bigel. often forms pure colonies extending out into the deeper water, and *Spartina pectinata* Link is sometimes present on the rocky shores (Stanley et al., 1973).

Following is a list of plants typical of southwestern Nova Scotia, many of them unknown elsewhere in Canada; scientific names and their authorities are those given in Gray's Manual (Fernald, 1950).

Lycopodium inundatum L. var. *bigelovii* Tuckerm. Common on peaty margin of Lake Peskowesk; many intermediate forms are present in an abandoned mill-pond near the west end of Lake Peskowesk.

Dryopteris simulata Davenp. Scattered colonies near the lakes and streams.

Woodwardia areolata (L.) Moore. One station at the northern end of Little Red Lake (Stanley et al., 1973); present also near Sand Lake outside the park, very local in southwestern Nova Scotia, while *W. virginica* is abundant.

Glyceria obtusa (Muhl.) Trin. Scattered in peaty areas and bogs near the lakes; found elsewhere in a few locations in southwestern New Brunswick.

Panicum dichotomiflorum Michx. var. *puritanorum* Svenson. Several locations on sandy beaches of Lake Kejimkujik; plants small and prostrate.

Panicum virgatum L. var. *spissum* Linder. Common, often in large pure stands on sand beaches.

Panicum longifolium Torr. Peaty beaches, more common westward in the park and along the lower Mersey River.

Panicum spretum Schultes. Scattered throughout lake margins, its tall height permits it to compete with other grasses.

Cyperus dentatus Torr. Rare on sand beaches around Lake Kejimkujik; the only species of *Cyperus* present in southwestern Nova Scotia.

Rhynchospora capitellata (Michx.) Vahl. Common on the lake shore, along with forma *discutiens* (C. B. Clarke) Gale.

Carex bullata Schkuhr. Widespread in meadows and edges of bogs.

Xyris caroliniana Walt., or its northern segregate. Common on many of the beaches; variable in character.

Smilax rotundifolia L. Small patches on the edges of the lakes or streams; rarely luxuriant, but commonly present (Figure 2).

Sisyrinchium atlanticum Bickn. Common beach-species, and the principal *Sisyrinchium* in the park.

Toxicodendron (*Rhus*) *radicans.* Ktze. ssp. *radicans.* Common. All the poison ivy shows some of the characteristics of ssp. *radicans.* Vine-like growth is seen only along streams to the west.

Ilex glabra (L.) Gray. Common around the lakes in the southern third of the park.

Hypericum virginicum L. var. *fraseri.* (Spach) Fern., is the common taxon near the drumlin area, while the typical var. *virginicum* becomes more abundant westward.

Rhexia virginica L. Common, especially on the damp sand beaches.

Decodon verticillatus (L.) Ell. var. *laevigatus* T. & G. Very rare in slate areas, more common westward, and very common around Mud Lake. In some of the lakes, plants of this species grow in shallow water. The plants are all of the northern variety with the lower leaf-surface glabrous.

Hydrocotyle umbellata L. (Figure 1). Scattered on the east side of Kejimkujik Lake, with isolated stations across the lake at Jeremy Bay and several kilometers away in a cove on George Lake. (Roland, 1980). The plants can survive in a meter of water with leaves floating at the surface; during a year of low water the species rapidly spreads and flowers on the wet mud.

Utricularia subulata L. This typical coastal-plain plant is common on peaty lake-beaches. It varies from plants the size of pinheads to branching plants several centimeters tall.

Utricularia radiata Small. Difficult to find, these delicate plants are conspicuous only when flowering scapes are present. Scattered in five lakes, floating in deep water.

Utricularia gibba L. Common at the board-walk, Grafton L., and at Mud Lake, growing on wet mud.

Utricularia purpurea Walt. Common and often luxuriant. It often forms a pure growth on the bottom of shallow lakes; rarely seen in flower.

Cephalanthus occidentalis L. In muck or alluvial soil in the

Figure 1. Southwestern Nova Scotia, showing location of Kejimkujik National Park. Below, outline of the park with locations of *Hydrocotyle umbellata* indicated with dots.

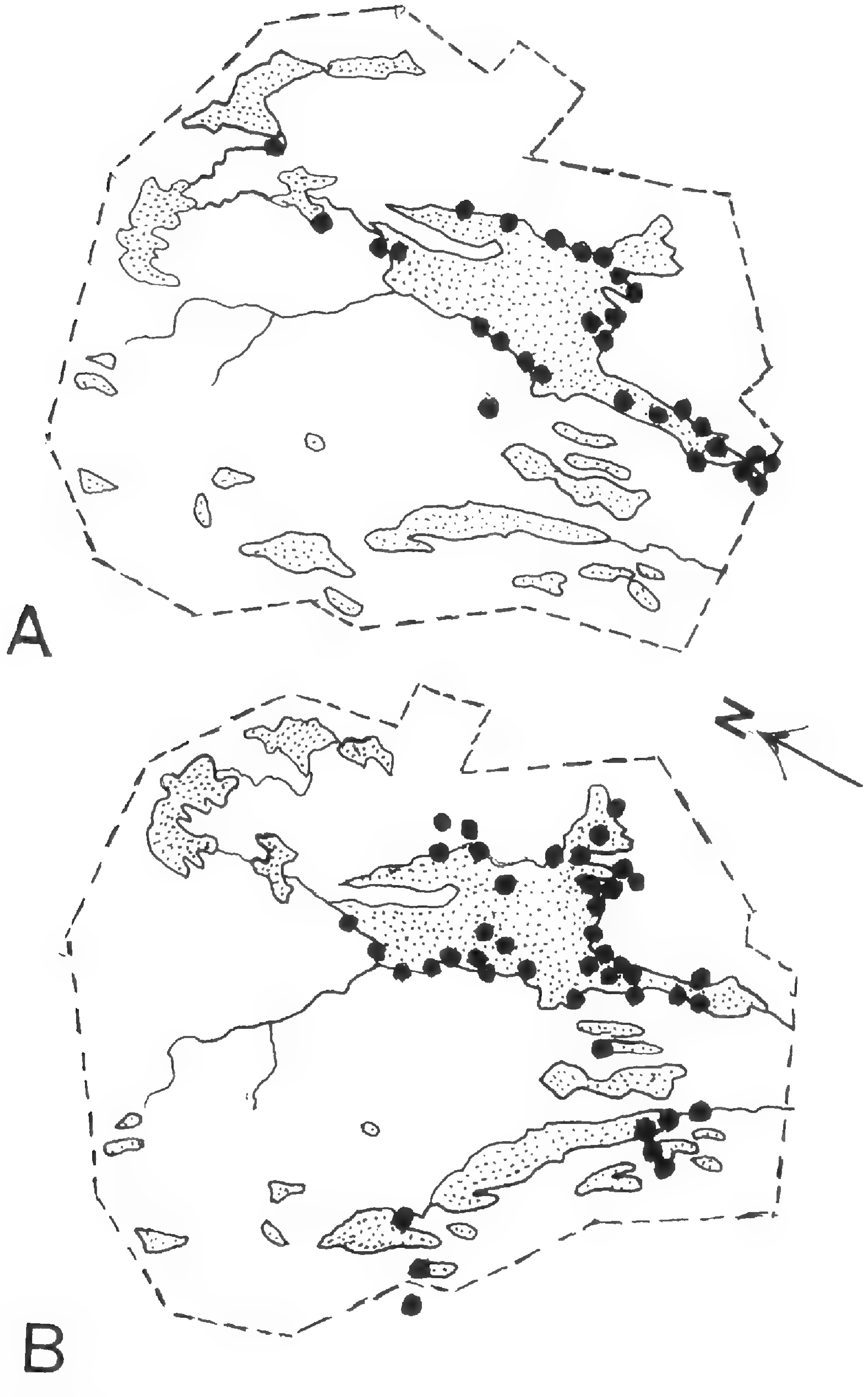

Figure 2. Kejimkujik National Park. **A.** Distribution of buttonbush, *Cephalanthus occidentalis*; **B.** Distribution of *Smilax rotundifolia*.

eastern area around Lake Kejimkujik and down the Mersey River (Figure 2), plants small and heavily browsed by deer.

Euthamia galetorum (Greene) Friesner. One of the most common and typical park-species found on every beach, and at times covers mud-flats in shallow water. Plants are usually tall and narrow with small inflorescences, occasionally with numerous branches more typical of *Euthamia tenuifolia* Pursh.

DISCUSSION

The above records represent, in many cases, extensions of range northeastward towards the interior of Nova Scotia. Most of these species are found along the eastern side and the islands of Lake Kejimkujik, where ample beaches occur and the underlying rock is slate. *Hydrocotyle umbellata,* one of the rare plants of the Tusket River system, only occurs scattered along this eastern slaty shore. A few species, e.g., *Decodon verticillatus,* are more common westward in the granitic and greywacke areas. The southeastern section of the park thus contains a good representation of the southwestern coastal plain flora, in an area which will be protected from any great disturbance in the future.

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RHODORA, Vol. 93, No. 875, pp. 299–300, 1991

NEW ENGLAND NOTE

DISCOVERY OF *EUPATORIUM LEUCOLEPIS* VAR. *NOVAEANGLIAE* IN BARNSTABLE COUNTY, MASSACHUSETTS

Mario J. DiGregorio

ABSTRACT

In 1989, *Eupatorium leucolepis* var. *novaeangliae* was discovered growing on the northeast shoreline of North (Big) Hog pond in Sandwich, Barnstable County, Massachusetts. This record is the first for the species in Barnstable County, and represents the easternmost site in its range.

Key Words: *Eupatorium leucolepis* var. *novaeangliae*, endemic, endangered, coastal plain kettle pondshores, Barnstable County, Massachusetts

In August 1989, *Eupatorium leucolepis* (DC.) T. & G. var. *novaeangliae* Fern., New England boneset, was discovered by the writer along the upper margin of the northeast shore of North (sometimes known as "Big") Hog Pond in Sandwich, Massachusetts. Specimens are deposited with the Massachusetts Natural Heritage and Endangered Species Program in Boston and at NEBC.

This discovery represents the first documented occurrence of the species in Barnstable County and is an eastern range extension. Previously, it was restricted to fifteen stations in Plymouth County, Massachusetts and Washington and Newport Counties in Rhode Island. It is endemic to southern New England and is listed as Endangered by the Massachusetts Natural Heritage and Endangered Species Program; it is also a candidate for federal listing under the Endangered Species Act (B. A. Sorrie, pers. comm.).

New England boneset or thoroughwort is a stiffly erect member of the Asteraceae, standing .5–1.3 m in height. The sessile leaves are narrow (.8–2 cm) and sharply toothed, with a pilose undersurface; flowers occur in flat-topped corymbs with three to seven whitish flowers in each head. It differs from *Eupatorium leucolepis* var. *leucolepis* in its more northerly range and in having much broader and more sharply toothed leaves which taper to an acute tip (Crow, 1982). The variety is illustrated on the cover of *Rhodora,* Vol. 90, 1988.

Eupatorium leucolepis var. *novaeangliae* grows in the uppermost shore margins of coastal plain kettle ponds, where it is adapted to the sandy, gravelly-peaty soils found abutting and underlying these nutrient-poor, acidic bodies of water. Depending on the fluctuating water table, this and associated kettle-pond species may flourish during periods of low water or may lie dormant or grow vegetatively without flowering during high water years (MNHESP, 1988). This sporadic dormancy/flowering periodicity may account for such a large population as the one reported here going unnoticed for so long.

A population of 220 stems was located at the Hog Pond station in 1989, with a slight increase to 225 found in August of 1990. Associated species found with the Hog Pond colony included *Eupatorium perfoliatum* L., *Rhexia virginica* L., *Solidago tenuifolia* Pursh, *Coreopsis rosea* Nutt., *Gratiola aurea* Muhl., *Crotalaria sagittalis* L., *Polygonum puritanorum* Fern. and *Linum intercursum* Bickn.

New England thoroughwort's habitat has been impacted in recent years by pondshore development, septic system leachate with concomitant nutrient loading, and off-road recreational vehicle rutting. Four historical locations apparently have been extirpated due to habitat destruction, and a fifth, the type station in Lakeville, Plymouth County, Massachusetts, nearly so (Crow, 1982; Sorrie, 1987).

ACKNOWLEDGMENT

I thank Bruce Sorrie of MNHESP for information used in this article.

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RHODORA, Vol. 93, No. 875, pp. 301, 1991

BOOK REVIEW

John M. Kingsbury. 1988. *200 Conspicuous, Unusual, or Economically Important Tropical Plants of the Caribbean.* Pp. 225; 748 illust.; indexed. ISBN 0–9612610–2–1. Available from Bullbrier Press, 10 Snyder Heights, Ithaca, NY 14850. (Soft cover, $20.00)

This beautifully illustrated little book is an excellent guide to rapid identification of the more commonly encountered flowering trees, shrubs and vines of the islands in and around the Caribbean Sea. It includes both native and exotic species, and shows them in the full panoply of their floral, vegetational and ecological contributions to the landscape. Descriptions are on the left side of each double page, and illustrations of that plant are on the right. The book is useful throughout the tropics worldwide where people have been engaged in horticulture, because these ornamentals have been introduced freely from one native area into essentially all others with like growing conditions.

Plants selected for inclusion are clearly recognizable, and for the most part include as well close-up photographs of flowers, fruits and other unusual features such as bizarre leaves, stems and roots which often aid in identification. I detected only two errors; one of the pictures attributed to the mistletoe *Phoradendron* is of a fruiting branch of *Dendropemon,* and *Tillandsia recurvata,* the ball moss of the islands, is misidentified as *T. usneoides,* the Spanish Moss common along our moist Gulf coasts.

The book is well worth taking along as a reliable field companion for anyone interested in learning to identify the often startlingly beautiful major components of the flora found at our southern doorsteps. It also serves as a marvelous recall device when relating one's plant discoveries to other friends not fortunate enough to have been there with you.

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RHODORA, Vol. 93, No. 875, pp. 302, 1991

BOOK REVIEW

John M. Kingsbury. 1991. *Columbus as a Botanist.* Reprinted with color illustrations from The Cornell Plantations Quarterly; 30 pages. Available from Bullbrier Press, 10 Snyder Heights, Ithaca, NY 14850. (Soft cover, $2.50 plus 75 cents for delivery and handling.)

In January 1990, WGBH-TV duplicated Christopher Columbus' voyage of exploration from San Salvador to Cuba, to Haiti, and the Dominican Republic for part of an upcoming series commemorating the 500th anniversary of Columbus' discovery of the New World. The author of this booklet participated in that cruise aboard the *SSV Westward* to address the questions of what plants (species) Columbus sought, what he found, and what he thought he found, and to deduce from the original logged descriptions something about Columbus the man. The clues which the author scrutinizes, along with his reasoning as to what plant Columbus was describing in each instance, gives us a fascinating glance into what it meant to be having this truly "first encounter" with the native Caribbean food, fiber and medicinal plants used by the original inhabitants.

In view of the upcoming attention to be paid to this earliest of chapters in American botanical history, it can be recommended that the short time needed to read this elegant work will be well spent, both for its own sake and for the information it imparts on the importance of plants and their values in assuring the early colonization of the New World.

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RHODORA, Vol. 93, No. 875, pp. 303, 1991

NOTICE OF PUBLICATION

Angelo, Ray. 1990. *Concord Area Trees and Shrubs.* Museum of Comparative Zoology. Harvard University. Cambridge, MA. Copies may be ordered by writing to: Publications Department, Museum of Comparative Zoology, 26 Oxford Street, Cambridge, MA 02138. ($10; checks payable to Museum of Comparative Zoology.)

This guide to the woody plants in the vicinity of Concord, Massachusetts was produced for Harvard's Concord Field Station. It is a revision and combination of the author's two previous guides, *Concord Area Trees* and *Concord Area Shrubs,* in a larger 8½″ × 11″ spiral-bound format. The 118-page volume is illustrated with many leaf prints and line drawings. Almost all of the woody species likely to be encountered in the wild in eastern Massachusetts are included.

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THE NEW ENGLAND BOTANICAL CLUB

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Cover Illustration

Diapensia lapponica L. ssp. *lapponica.* Found on the higher mountains of northern New England, this Arctic circumpolar early-blooming tussock plant is a rare disjunct to New England. Original artwork by Josephine Ewing.

Rhodora

JOURNAL OF THE
NEW ENGLAND BOTANICAL CLUB

Vol. 93 October 1991 No. 876

RHODORA, Vol. 93, No. 876, pp. 307–321, 1991

VEGETATION PATTERNS AND BASIN MORPHOMETRY OF A NEW ENGLAND MOAT BOG

Glenn H. Motzkin and William A. Patterson III

ABSTRACT

We describe the relationships between vegetation patterns, depth of sediment accumulation, and distance to shore in Arcadia Bog, a small moat bog in Belchertown, Massachusetts. A Fringe Moat community occurs primarily where sediment depths are 0–2 m and at 0–10 m from shore. Shrub Thickets are least restricted in their distribution, occurring at 0–30 m from shore above 0–10 m of sediment. The true bog community (Dwarf Tree/Shrub) is divided into two types—Tamarack/Spruce centered at 15–25 m from shore above 7–11 m of sediment and Spruce/Tamarack at the deeper, more distant central portion of the basin (20–40 m from shore, 10–13 m depth). This community is uncommon in central Massachusetts. Variations in surface-water pH suggest that the distributions of at least some species may be influenced by nutrient availability. Additional studies would be required to determine the relationship between physiographic location and water chemistry and flow, the ecological factors most likely controlling vegetation patterns in Arcadia Bog.

Key Words: wetlands, moat bogs, vegetation classification, ordination, central Massachusetts

INTRODUCTION

Much of the literature of peatlands relates to northern mires of types that, except for Maine, are not widespread in northeastern United States. A number of authors have described the vegetation patterns of peat bog-lake systems (Vitt and Slack, 1975; Dunlop, 1987; Damman and French, 1987), but few satisfactory interpretations of the factors responsible for vegetation distribution in these peatlands have been developed. This study was undertaken to determine the relationship between vegetation patterns and physiographic characteristics of Arcadia Bog, a small moat bog (*sensu* Damman and French, 1987) in central Massachusetts. An understanding of this relationship could be helpful in identifying fundamental environmental factors controlling vegetation patterns within bogs of this type.

Early investigations of bogs focused on the influence of hydrarch succession on vegetation patterns (Clements, 1916) and the importance of physical factors as they affect basin filling and bog-margin development (Shaw, 1902). Although plant succession may influence current vegetation patterns (Swan and Gill, 1970), vegetation zonation in peat bogs may remain fairly stable in the absence of changes in hydrology (Damman and French, 1987). In such instances, chemical and hydrologic factors may be significant in determining vegetation patterns. Kratz and Dewitt (1986) described the processes influencing peat accumulation in bogs similar to Arcadia Bog, but they did not discuss implications for vegetation patterns. Damman and French (1987), drawing on the work of Damman (1978), Ivanov (1981), Ingram (1984) and others, indicated that water chemistry and water levels control vegetation patterns in peat bogs. In field work reported here, we examine the relationship between vegetation zones and basin morphometry (depth of organic sediments and distance to shore); it is useful to determine the relationship between vegetation zonation and basin morphometry because factors influencing vegetation development may vary predictably with location within a bog.

GENERAL SITE DESCRIPTION

Arcadia Bog is southeast of Arcadia Lake in Belchertown, Massachusetts [southeastern corner of the Belchertown Quadrangle (U.S.G.S. 7.5 min. series, no. N4215)]. The bog and nearby kettle-hole lakes lie in an area underlain by glaciofluvial deposits (mostly sand and gravel) with a general southwestern drainage pattern. These kettle-hole depressions overlie the Eastern Border Fault that separates the Connecticut Valley sedimentary formations (of Mesozoic age) from the Pelham Hills metamorphic formations (primarily gneiss and schist of Paleozoic age) (Caggiano, 1978, Ph.D. Dissertation, University of Massachusetts, Amherst). Drainage along the Eastern Border Fault may influence the hydrologic regime of the entire area, including the kettle-hole basins

(Motts and O'Brien, 1981). Large springs are reported in Arcadia Lake and other nearby lakes.

Stone and Borns (1986) suggested that deglaciation of central Massachusetts occurred as early as 14,000 to 15,000 B.P., although ice blocks apparently remained buried in the till and outwash after general glacial retreat. The presence of a deep-lying layer of forest floor material [including a white spruce (*Picea glauca* (Moench) Voss) cone recovered from 13 m below the surface] indicates that the ice block forming Arcadia Bog remained intact while vegetation colonized the soil above. Stratigraphy of a sediment core which we obtained indicated that after the ice block melted, the depression accumulated approximately 7 m of lake sediments; above these limnic sediments are 6 m of peat. Abundant *Ambrosia* (ragweed) pollen in the surface 25 cm suggests that this material was deposited since 1750 A.D., shortly after Belchertown was settled by Europeans.

Arcadia Bog has no channeled water inlet or outflow. Outflow from the basin may have been altered by the construction of a road on the south side of the bog, but we see little evidence that this construction substantially altered bog hydrology. Current water levels seem to reflect groundwater levels and the seasonal and periodic balance between precipitation and evapotransporation. The eastern edge of the bog is bordered by a steep slope, and the bog has a small watershed area with a ratio of the area of the watershed to the surface area of the bog of 1.3:1. Available plant nutrients in the bog are probably limited primarily to those being carried by inflowing water (from spring snowmelt, groundwater, and precipitation), to those entering in leaf fall from the upland or as dry fallout from the atmosphere, and to those made available by biotic agents (e.g., nitrogen fixation by blue-green algae, and "scavaging" by insectivorous plants such as *Sarracenia purpurea* L. and *Drosera rotundifolia* L.). A small section of the northern portion of the basin has been filled with refuse and is now overgrown with vegetation typical of disturbed areas in the surrounding uplands. We estimated the volume of fill to be 640 m^3, about 2% of the bog's total volume of approx. 30,960 m^3.

METHODS

A north–south baseline was established through the eastern part of the bog in 1985. East–west transects were established at 5 m intervals along this baseline. Depth probings were made with steel

Table 1. Vascular plant species list for Arcadia Bog, Belchertown, Massachusetts. Primary community affiliations are indicated for non-woody species.

Non-woody Species

- *Bidens* sp. (Moat)
- *Calla palustris* L. (several)
- *Carex canescens* L. (Moat/Shrub Thicket)
- *Carex stricta* Lam. (Moat)
- *Carex trisperma* Dewey (Dwarf Tree/Shrub)
- *Drosera rotundifolia* L. (Dwarf Tree/Shrub)
- *Eriophorum* sp. (Dwarf Tree/Shrub)
- *Triadenum virginicum* (L.) Raf. (Moat)
- *Lycopus* sp. (Moat)
- *Osmunda cinnamomea* L. (Moat)
- *Peltandra virginica* (L.) Kunth (several)
- *Sarracenia purpurea* L. (Dwarf Tree/Shrub)
- *Symplocarpus foetidus* (L.) Nutt. (rare)
- *Typha latifolia* L. (Moat)

Woody Species

- *Acer rubrum* L.
- *Betula populifolia* Marsh.
- *Cephalanthus occidentalis* L.
- *Chamaedaphne calyculata* (L.) Moench
- *Decodon verticillatus* (L.) Ell.
- *Gaylussacia baccata* (Wang.) K. Koch
- *Ilex verticillata* (L.) Gray
- *Kalmia angustifolia* L.
- *Kalmia polifolia* Wang.
- *Larix laricina* (DuRoi) K. Koch
- *Lyonia ligustrina* (L.) DC
- *Nemopanthus mucronatus* (L.) Trel.
- *Nyssa sylvatica* Marsh.
- *Picea mariana* (Mill.) BSP
- *Pinus rigida* Mill.
- *Pinus strobus* L.
- *Pyrus arbutifolia* (L.) Ell.
- *Rhododendron viscosum* (L.) Torr.
- *Rhus vernix* L.
- *Sambucus canadensis* L.
- *Vaccinium corymbosum* L.
- *Vaccinium oxycoccos* L.
- *Vitis* sp.

rods at sample points 5 m apart along the east–west lines. Each sample point served as the center of a circular plot of 2 m radius on which a relevé (Mueller-Dombois and Ellenberg, 1974) was sampled. Cover was estimated by assigning each woody species to one of the following cover classes: <1%; 1–5%; 5–25% 25–50%; and 75–100%. The average height of the dominant vegetation on the plot was also recorded. Sediment probing for the entire bog and vegetation sampling on the southern two-thirds of the bog were completed in February, 1986. Vegetation sampling of the northern portion of the bog was completed in March, 1987. Transect work was completed during the winter because of the difficulty associated with traversing the bog mat, much of which "floats," and the potential for damaging the vegetation in the process of carrying heavy equipment along closely spaced transects during the growing season. The bog was visited several times during the spring and summer of 1986 to record presence of herbaceous and low-lying species that were not evident during the dormant season surveys (Table 1). All but two of the 14 non-woody species we recorded appear to be largely restricted to vegetation types defined through analysis of the relevé data. On December 10, 1987 a portable meter was used to record pH values at a number of sample points in each of the vegetation zones identified from analyses of the vegetation data. Taxonomic nomenclature follows Gleason and Cronquist (1963).

An objective of our analysis was the delineation and evaluation of vegetation patterns in Arcadia Bog—patterns that are subjectively obvious but for which there exists no quantification with respect to vegetation structure, species composition or basin morphometry. Vegetation data generated from the relevés were analyzed using AGGLOM, a modification of Orloci's (1967) optimal agglomeration-polythetic clustering (classification) method, and DECORANA, a detrended correspondence analysis (DCA) ordination program (Gauch, 1982).

RESULTS

A bathymetric map (Figure 1) was developed for the bog, with 1 m contour intervals extrapolated between pairs of the 220 sample points on the grid. For mapping purposes, we assumed that the bog surface was level at approximately 100 m above sea level. Much of the bog mat floats, however, and its absolute height undoubtedly varies with seasonal changes in water level. We have not measured the extent of this variation.

Analysis of relevé data with AGGLOM defined five major groups or "clusters." Standardized and absolute Euclidian distance coefficients were used and produced similar groupings. Our interpretation is based upon the absolute distance analysis because it better utilizes our estimates of species cover. Community similarity indices were calculated to evaluate the similarity among vegetation groupings identified by cluster analysis (Table 2). We calculated three separate indices: Jaccard's which emphasizes species presence and total numbers of species; Sorensen's, which is similar to Jaccard's but places greater emphasis on species that recur in two communities than on those that are unique to one or another; and Spatz's, which incorporates an estimate of species abundances (Mueller-Dombois and Ellenberg, 1974). Two veg-

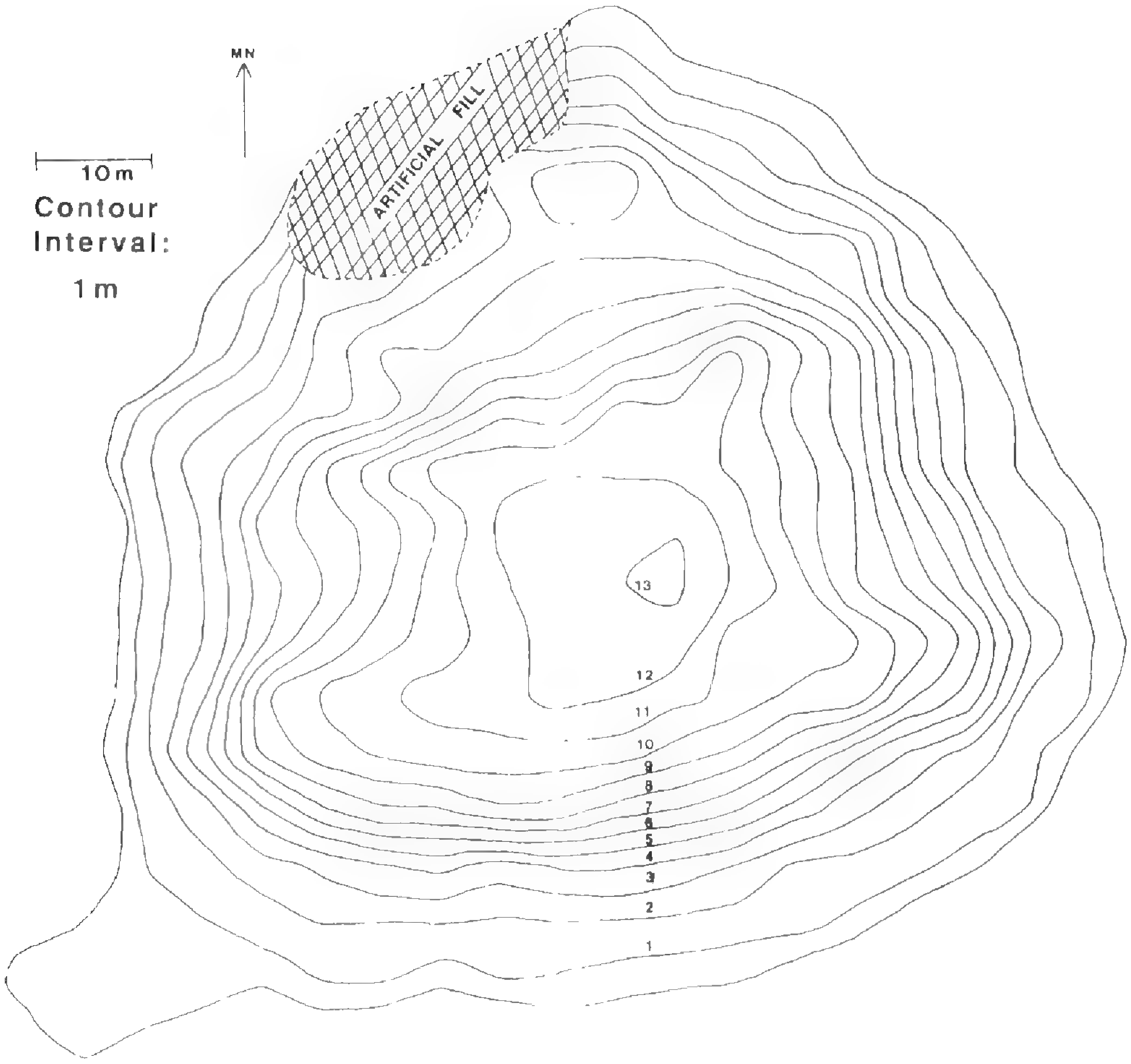


Figure 1. Bathymetric map of Arcadia Bog.

etation groups (IA2 and IB1) distinguished by cluster analysis have almost identical similarity indices (SI's) when compared with the other groups and have the highest SI's when compared with each other; in addition, they are not significantly different with respect to sediment depth or distance to shore. Therefore, we considered these two groups to be part of one broad Shrub Thicket group in defining vegetation communities and mapping their distributions on the bog.

Plotting DCA results revealed that for the first and second axes a number of sample points were high or low on the first axis and were strongly correlated with a defined cluster grouping (Figure 2). The Fringe Moat and Dwarf Tree/Shrub plots were removed, and the remaining Shrub Thicket and undefined plots were included in a second ordination according to the method of Peet (1980). This procedure facilitated a more detailed ordination of

Table 2. Similarity indices for vegetation groups identified by cluster analysis. [$I.S._J$ = Jaccard's Index of Similarity; $I.S._S$ = Sorensen's Index of Similarity; $I.S._{Sp}$ = Spatz's Index of Similarity (after Mueller-Dombois and Ellenberg, 1974)].

Group Number (original groups defined by AGGLOM)	Similarity Index		
	$I.S._J$	$I.S._S$	$I.S._{Sp}$
II vs. IB2	81.8	90.0	.38
II vs. IB1	69.2	81.8	.27
II vs. IA2	66.7	80.0	.21
II vs. IA1	50.0	66.7	.11
IB2 vs. IB1	84.6	91.7	.27
IB2 vs. IA2	83.3	90.9	.27
IB2 vs. IA1	64.3	78.3	.18
IB1 vs. IA2	84.6	91.7	.49
IB1 vs. IA1	78.6	88.0	.33
IA2 vs. IA1	64.3	78.3	.23
(After combining groups IA2 and IB1, with community designations in parentheses)			
II (Spruce/Tamarack) vs. IB2 (Tamarack/Spruce)	81.8	90.0	.38
II (Spruce/Tamarack) vs. IA2/IB1 (Shrub Thicket)	69.2	81.8	.24
II (Spruce/Tamarack) vs. IA1 (Fringe Moat)	50.0	66.7	.11
IB2 (Tamarack/Spruce) vs. IA2/IB1 (Shrub Thicket)	84.6	91.7	.27
IB2 (Tamarack/Spruce) vs. IA1 (Fringe Moat)	64.3	78.3	.18
IA2/IB1 (Shrub Thicket) vs. IA1 (Fringe Moat)	78.6	88.0	.28

similar plots, including the identification of additional Fringe Moat and Dwarf Tree/Shrub points (Figure 3).

Four vegetation communities and two transition zones defined by cluster analysis and DCA are as follows:

GROUP IA1—FRINGE MOAT COMMUNITY. Plots classified in this vegetation group have much standing water, only scattered, sparse vegetation, and occur at 0–2 m depth and 0–10 m distances to shore. Characteristic species include *Pyrus arbutifolia, Acer rubrum, Ilex verticillata, Decodon verticillatus, Rhododendron viscosum* and *Vaccinium corymbosum.* Absent are *Picea mariana, Larix laricina, Kalmia polifolia, Gaylussacia baccata* and *Pinus strobus.* See Table 1 for authorities of all plant names used in this paper.

TRANSITION ZONE 1 (TZ–1). This zone is intermediate between the Fringe Moat and Shrub Thicket. It has substantially

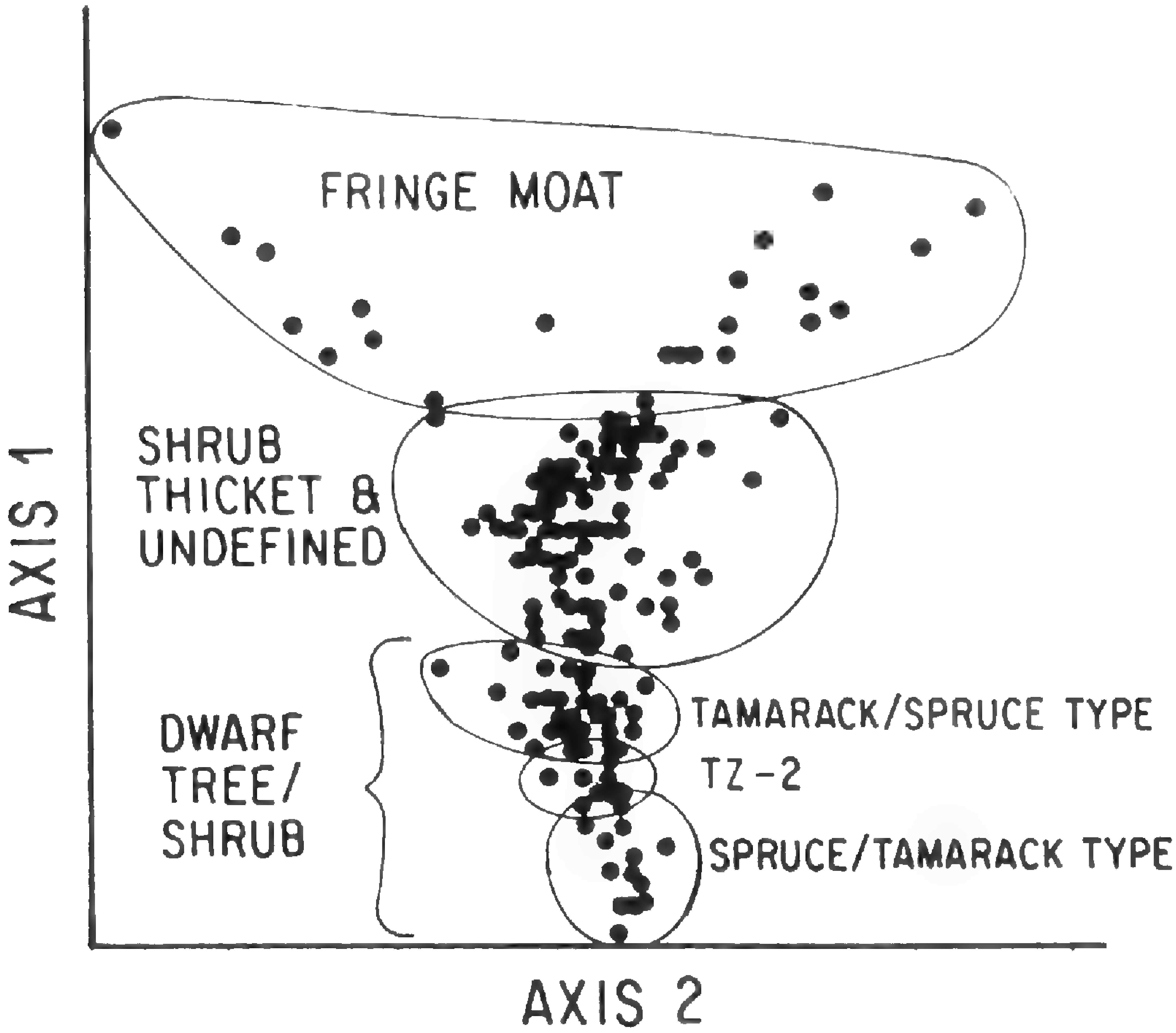


Figure 2. First ordination of relevé data from Arcadia Bog on the first two DCA axes showing the occurrence of sample plots which are related (along axis 1) to groupings identified by cluster analysis.

less *Kalmia angustifolia* than the Fringe Moat and no *Ilex verticillata,* but more *Lyonia, Pinus strobus, Acer rubrum,* and *Decodon.* There is less *Kalmia polifolia* and *Chamaedaphne* compared to the Shrub Thicket, and no *Picea, Larix* or *Gaylussacia.* Like the Fringe Moat, it has more *Pyrus* than the Shrub Thicket.

Group IA2/IB1—Shrub Thicket Community. This community is characterized by tall, dense shrubs and little open water. Plots extend across a wide range of depths (0–10 m) and distances to shore (0–30 m). *Rhododendron* and *Vaccinium* are the dominant plants, with *Pyrus, Gaylussacia, Kalmia angustifolia, Chamaedaphne* and *Larix* scattered throughout with low cover values. Absent are *Picea, Kalmia polifolia, Acer, Ilex* and *Decodon.*

Group IB2—Dwarf Tree/Shrub Community (Tamarack/Spruce type). Plots in this community have a continuous cover

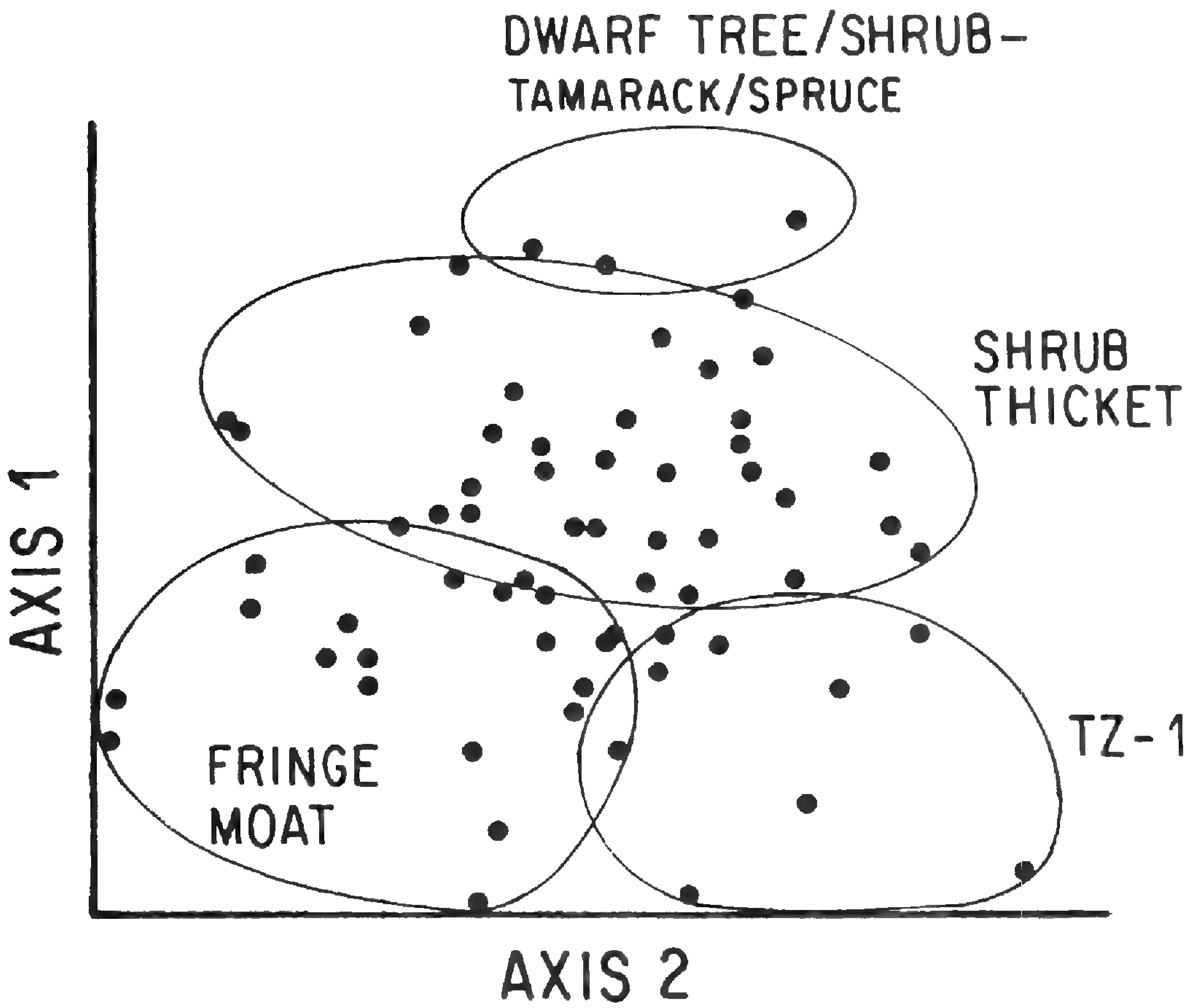


Figure 3. Second ordination of relevé data from Arcadia Bog, with Fringe Moat and Dwarf Tree/Shrub plots removed. Polygons encircle plots grouped as indicated by cluster analysis.

of *Sphagnum* spp., with areas of tall *Larix* (up to 5 m) and clustered *Picea.* The zone occurs at distances of 15–25 m from shore and at depths of 7–11 m. *Picea, Larix, Rhododendron, Vaccinium, Gaylussacia, Kalmia angustifolia* and *Chamaedaphne* are widespread in this vegetation group, with *K. polifolia* also present. Absent are *Pyrus, Acer rubrum, Decodon* and *Ilex.*

TRANSITION ZONE 2 (TZ-2). This zone has less *Larix, Kalmia angustifolia,* and *Pyrus* than the Tamarack/Spruce type and no *P. strobus.* It has less *Kalmia angustifolia* but more *Lyonia, Gaylussacia,* and *Acer rubrum* than the Spruce/Tamarack type.

GROUP II—DWARF TREE/SHRUB COMMUNITY (SPRUCE/TAMARACK type). This community occupies the central-most section of the bog. *Picea* attains its greatest frequency and cover here, as does *Kalmia polifolia.* This zone occurs primarily at depths of 10–13 m, 20–40 m from shore. *Picea, Larix, Chamaedaphne,*

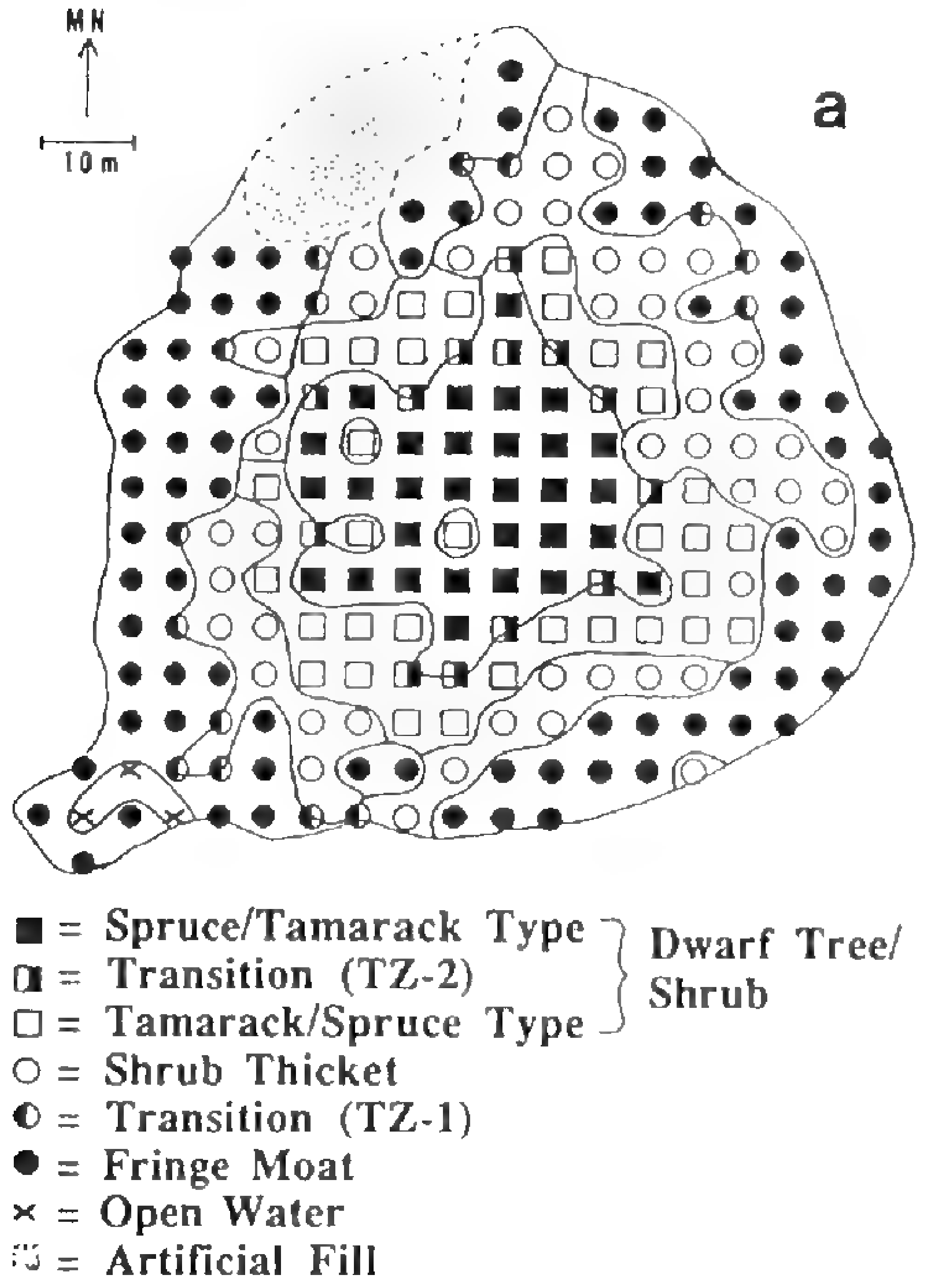
Table 3. Percent constancy within vegetation communities for woody species occurring in 217 relevés in Arcadia Bog (FrMo = Fringe Moat, ShTh = Shrub Thicket, T/S = Tamarack/Spruce, S/T = Spruce/Tamarack, TZ = transition zone).

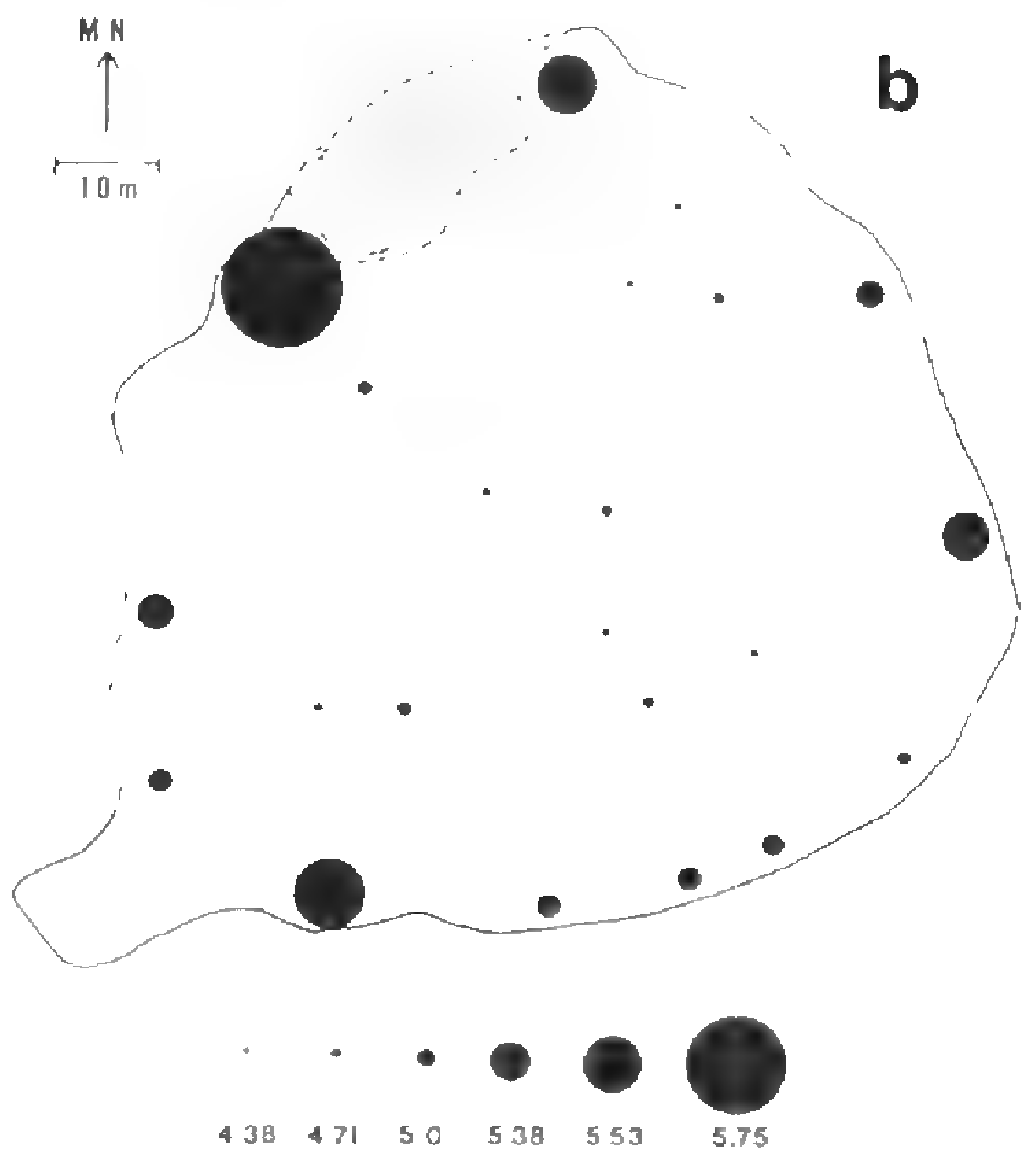
Species (see Table 1 for authorities)	Vegetation Community					
	FrMo	TZ-1	ShTh	T/S	TZ-2	S/T
Picea mariana	.0	.0	32.2	84.9	92.3	100.0
Larix laricina	4.94	.0	31.1	63.6	38.5	40.0
Rhododendron viscosum	75.3	100.0	97.8	81.8	76.9	73.3
Vaccinium corymbosum	91.4	80.0	100.0	100.0	84.6	73.3
Kalmia angustifolia	42.0	13.3	77.8	63.6	46.2	80.0
Kalmia polifolia	.0	6.67	20.0	72.7	84.6	83.3
Chamaedaphne calyculata	21.0	13.3	75.6	90.0	92.3	96.7
Lyonia ligustrina	2.47	20.0	13.3	24.2	23.1	3.33
Pyrus arbutifolia	72.8	86.7	48.9	18.2	7.69	.0
Gaylussacia baccata	.0	.0	46.9	78.8	76.9	50.0
Pinus strobus	12.4	40.0	48.9	18.2	.0	.0
Acer rubrum	12.4	40.0	31.1	12.1	15.4	.0
Decodon verticillatus	6.17	20.0	.0	.0	.0	.0
Ilex verticillata	16.1	.0	2.22	.0	.0	.0
Vitis sp.	4.94	.0	.0	.0	.0	.0
Cephalanthus occidentalis	3.70	.0	2.22	.0	.0	.0
Nemopanthus mucronatus	1.23	.0	.0	.0	.0	.0
Betula populifolia	2.47	.0	6.67	.0	.0	.0
Salix sp.	1.23	.0	.0	.0	.0	.0
Rhus vernix	1.23	6.67	6.67	.0	7.69	.0
Total Relevés in Community Type	81	15	45	33	13	30

Kalmia polifolia, Rhododendron, Vaccinium, Gaylussacia, and *Kalmia angustifolia* are the main taxa present in this vegetation group, with a marked absence of *Pyrus, Pinus strobus, Acer rubrum, Decodon* and *Ilex.*

The vegetation map (Figure 4a) was drawn using the results of the species ordination. Percent constancies for species within the six communities are presented in Table 3.

Canopy heights decline from the edge of the bog inward, with those at the center differing significantly from those in the Fringe Moat and Shrub Thicket zones (Table 4). The tallest trees in the bog are tamarack, which reach 6–8 m in the Shrub Thicket zone and about 5 m in the more central areas. A few black spruce within 10 or so meters of the edge of the bog reach 4–5 m, but





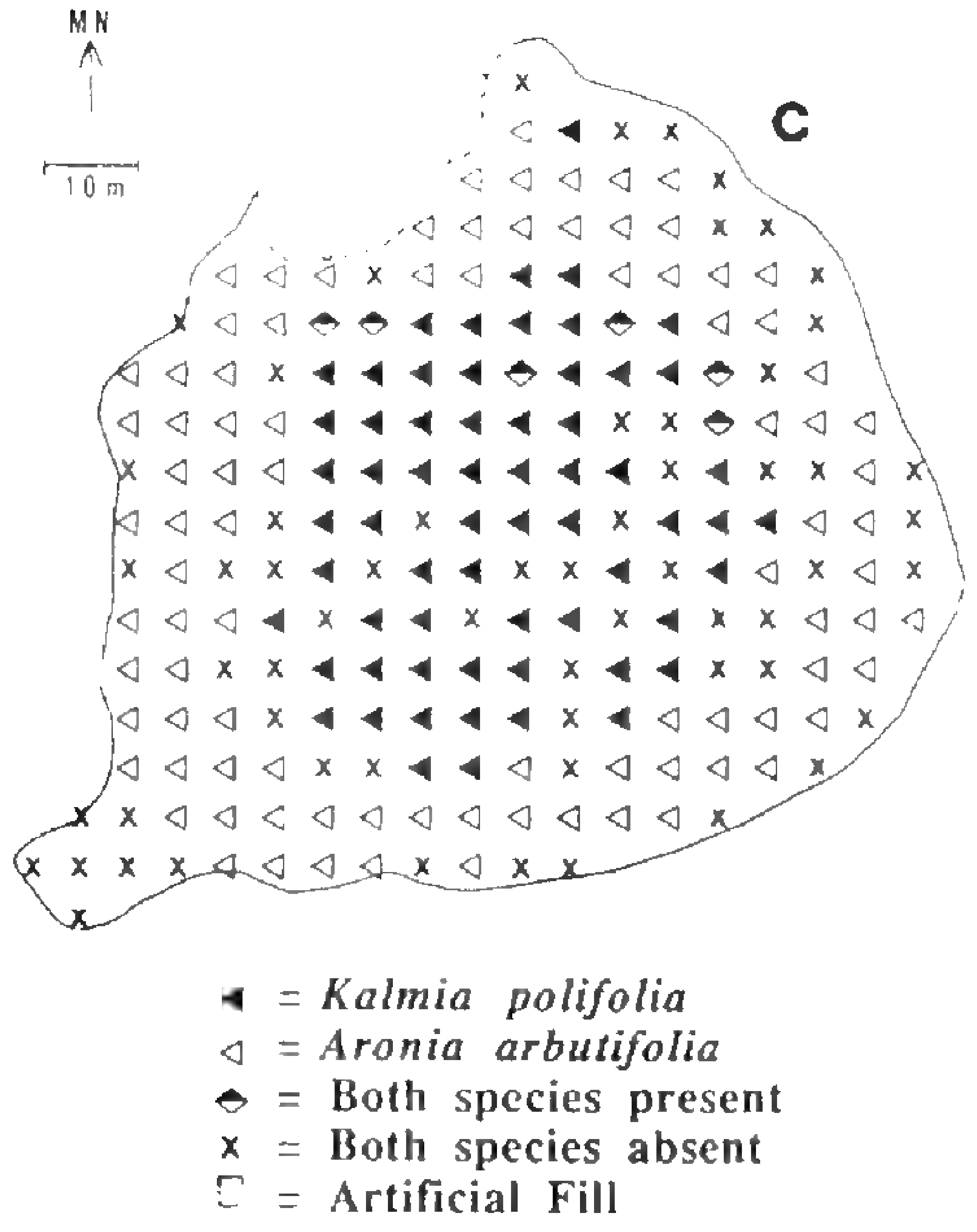


Figure 4a. Vegetation map for Arcadia Bog based upon the results of detrended correspondence analysis.

Figure 4b. Arcadia Bog pH values on December 10, 1987 for 22 sample points.

Figure 4c. Arcadia Bog distribution map of *Kalmia polifolia* and *Pyrus arbutifolia.*

none in the center exceeds 2.8 m. Most plants in the Dwarf Tree/ Shrub community are a meter or less in height. Spruce were generally too small to age by coring, but we did section five stems growing in the central portion of the bog. There is a weak rela-

Table 4. Canopy heights by vegetation community type based on relevé data. Means followed by the same superscript are significantly different ($P < .05$). Data were unavailable for some relevés.

Vegetation Community	Number of Relevé's	Mean Height (m)	Range (m)
Fringe Moat	69	2.36^{a}	.60–3.50
TZ-1 (FrMo-ShTh)	13	2.42^{b}	1.10–4.00
Shrub Thicket	45	2.00^{ac}	.80–3.50
Tamarack/Spruce	29	1.50^{abcd}	.40–3.50
TZ-2 (T/S-S/T)	12	1.26^{abc}	.60–2.40
Spruce/Tamarack	30	1.04^{abcd}	.25–1.75

tionship between age and height ($r = .72$). Most stems taller than 1 m contain at least a few female cones and many stems smaller than 0.5 m appear chlorotic and in poor health. Dead spruce in the bog are generally 1–2 m in height.

Figure 5 presents the four vegetation groups and two transition zones discussed above as a function of depth and distance to shore. The Fringe Moat is generally restricted to the shallow portions of the bog which lie close to shore (mean depth = 1.4 m; mean distance to shore = 4.2 m). The Shrub Thicket occurs across a broad range of sediment depths (0–10 m) and distances to shore (mean depth = 4.2 m; mean distance to shore = 11.1 m). The Tamarack/Spruce type occupies the deeper portions of the bog with mean depths of 8.5 m and an average distance to shore of 20 m. Finally, the Spruce/Tamarack type is found in the section of the bog with the greatest accumulation of sediment (mean depth = 11.4 m) lying farthest from shore (mean distance to shore = 30.1 m). Chi-square tests comparing the number of sample points for each zone occurring at a particular depth indicate that there is a significant difference between the four primary groups ($P < .05$). The Tamarack/Spruce type has, in addition to widely scattered tamarack up to 5 m in height, fewer spruce than the Spruce/Tamarack type.

DISCUSSION

There is a clear relationship between vegetation zones, depth of sediment and distance to shore in Arcadia Bog. The vegetation patterns observed are similar to those described by Damman and

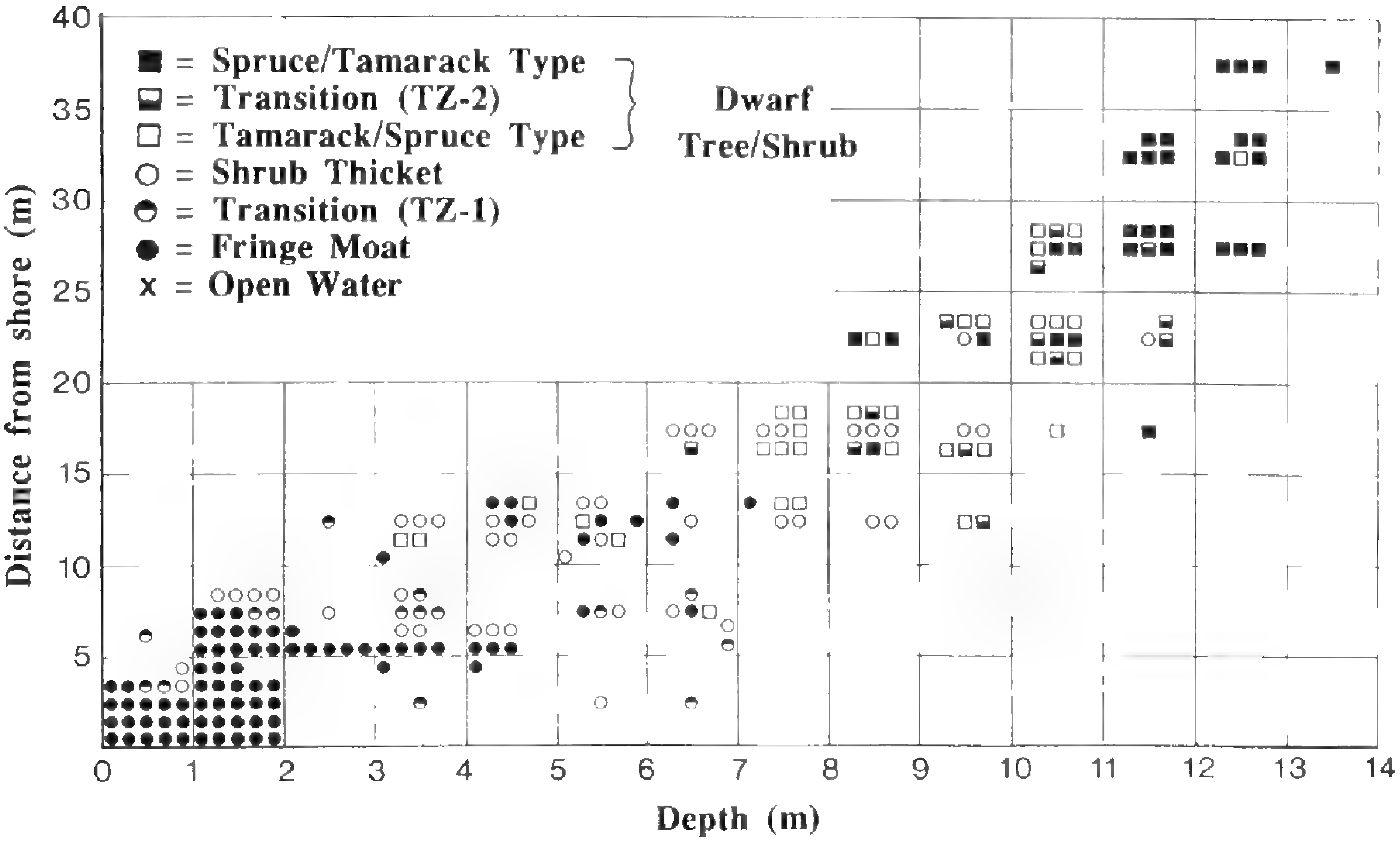


Figure 5. Distribution of vegetation plots by community and depth and distance to shore.

French (1987) as typical of moat bogs. A notable addition in Arcadia Bog is the well-developed Dwarf Tree/Shrub community in the center. The presence of a dwarf spruce community thus may reflect increasingly nutrient-poor conditions toward the center of the bog. Of interest is the presence in the moat fringe of certain species (*Typha* and others) more typical of eutrophic, marsh-like conditions. This association is not uncommon in moat-fringed bogs, which may occur in regions of large periodic (i.e., seasonal, annual or otherwise) water table fluctuations (Buell and Buell, 1975). The development of moat-fringed bogs is generally not well understood (Damman and French, 1987), although a number of hypotheses have been posed (MacMillan, 1894; Shaw, 1902; Buell and Buell, 1975).

Cluster analysis and DCA produced similar results; both identify Fringe Moat and central Dwarf Tree/Shrub communities (including, in the latter, Spruce/Tamarack and Tamarack/Spruce types). Classifying individual relevés using dendrograms generated by cluster analysis is sometimes difficult, however, since sample points which are similar in species composition and abundance may fall into separate clusters. Although these clusters (i.e., vegetation groups) may appear as distinct entities in the dendrogram, they may actually represent zones of transitional vegetation between truly distinct groups. Transition zones are to be expected because vegetation patterns reflect the differential responses of individual species to environmental gradients (Gleason, 1926; Whittaker, 1967). The results of DCA thus more accurately represent the gradational nature of vegetation variation than do cluster analysis results.

The distribution patterns of *Pyrus arbutifolia* (L.) Ell. and *Kalmia polifolia* are noteworthy. These species occur widely throughout the bog, but they co-occur in only six of 159 plots on which one of them occurs (Figure 4c). In Massachusetts *Pyrus arbutifolia* is most commonly found in swamps and at the edges of lakes, whereas *Kalmia polifolia* is generally restricted to nutrient-poor bog environments (Emerson, 1850). Their distributions at Arcadia Bog reflect these regional patterns, with *Pyrus* occurring principally near the bog margin and *Kalmia* occurring in the more central areas with lower pH values, suggesting that nutrient availability may be an important factor influencing the distribution of at least three species.

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A REVISION OF *ACONOGONON* (= *POLYGONUM* SECT. *ACONOGONON*, POLYGONACEAE) IN NORTH AMERICA

Suk-Pyo Hong

ABSTRACT

An account with keys, illustrations, and distribution maps of the three species of North American *Aconogonon* (= *Polygonum* sect. *Aconogonon*) is given. Epidermal anatomy of the leaf and pollen morphology are also briefly studied. One new variety, *A. phytolaccifolium* var. *glabrum* S.-P. Hong, is described. Two new combinations proposed are *A. hultenianum* var. *lapathifolium* (Cham. & Schlechtend.) S.-P. Hong and *A. davisiae* var. *glabrum* (Jones) S.-P. Hong. Two species names are relegated to synonymy. A neotype for *A. hultenianum* var. *lapathifolium* (Cham. & Schlechtend.) S.-P. Hong, and a lectotype for *A. davisiae* (Brewer ex A. Gray) Soják are selected.

Key Words: Polygonaceae, *Aconogonon*, *Polygonum* sect. *Aconogonon*, epidermal anatomy, pollen morphology, taxonomy, distribution, North America

INTRODUCTION

This paper presents a taxonomic revision, including information on epidermal anatomy of leaves and on the pollen morphology of the three North American species of *Aconogonon* (Meisn.) Reichb. (= *Polygonum* sect. *Aconogonon*). This account forms an extension of a revision of this genus in the Himalayas and adjacent regions (Hong, in prep.), and is part of a world-wide taxonomic revision of the genus.

Aconogonon has been treated as a separate genus or as a section under allied genera (cf. Haraldson, 1978; Ronse Decraene and Akeroyd, 1988). However, the genus can be separated from allied genera in the tribe Persicariae Dum. by its very uniform pollen type (Hedberg, 1946; Hong and Lee, 1983; Hong and Hedberg, 1990), a morphologically distinctive inflorescence, some anatomical features (Haraldson, 1978), and its seed anatomy (cf. Marek, 1954, 1958). Recently, Ronse Decraene and Akeroyd (1988) delimited the *Polygonum sensu lato* group on the basis of microcharacters of the floral parts. While treating *Aconogonon* as a section under the genus *Persicaria* Mill., they agreed that some microcharacters in the *Aconogonon* group provide distinctions from the other sections. The generic limits have been accepted by many authors (Hedberg, 1946; Hara, 1966, 1982; Haraldson, 1978; Wilson, 1988), and many modern floras use *Aconogonon* as a generic name (Hara, 1966, 1982; Grierson and Long, 1983; Polunin and Stainton, 1984; Tzvelev, 1987; Stainton, 1988; Hong, 1990). In this treatment I consider *Aconogonon* a natural group and recognize it as a separate genus.

Polygonum polystachyum Wallich ex Meisn., which has been introduced into North America, has sometimes been brought to *Aconogonon.* But the pollen grains of this species, like those of *Polygonum pinetorum* Hemsly from SW China, clearly belong to the *Persicaria* type (cf. Hong and Hedberg, 1990), and both those species should be brought to the genus *Persicaria,* although their inflorescences show some similarities to those in *Aconogonon.* Therefore, *P. polystachyum* is excluded from the present study. Recently Král (1985) created a new genus (*Rubrivena*) for *P. polystachyum,* but I do not agree to that. The distinctness between *Aconogonon, Persicaria* and *Koenigia* L. will be further discussed in a later paper (Hong, in prep.).

MATERIALS AND METHODS

This study is mainly based on herbarium specimens. The following herbaria have been consulted: A, ALA, BM, CAN, GH, JEPS, K, MO, MU, NY, S, UBC, UC, UPS, US, WS and WTU (abbreviations according to Holmgren et al., 1981). In all, about 700 collections were examined for this study.

Epidermal structures were investigated using cuticular membrane preparations. The macerating mixture used was Jeffrey's solution (equal parts 10% chromic acid and concentrated nitric acid). After about 24 hours in the mixture, the leaf samples were transferred to water in a Petri dish, washed with a camel's hair brush, then stained in 1% safranin. Most measurements were made on dry material, but floral parts were measured using boiled material. Pollen studies were made on acetolyzed samples mounted in glycerin jelly and sealed with paraffin, according to the standard method (Erdtman, 1960). Scanning electron microscope examinations were made, both on acetolyzed pollen and untreated herbarium material of leaf parts, coated with Au/Pd. Scanning electron microscope (SEM) studies were made with a Jeol JSM-35 instrument.

The terminology follows Stearn (1983) in general morphology,

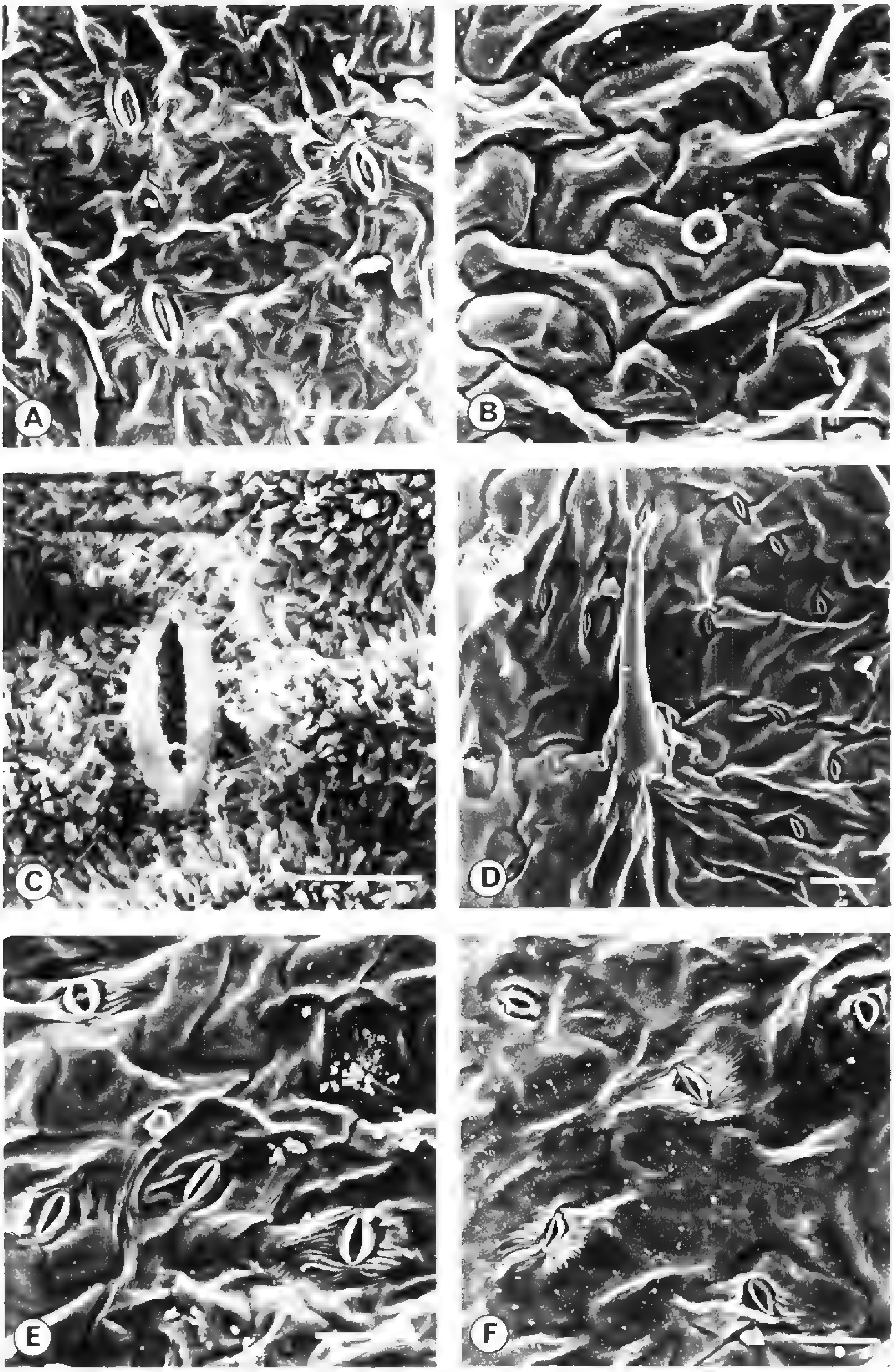

Figure 1. SEM photographs of details of leaf epidermis in North American *Aconogonon* spp. **A.** Stomata in abaxial side, showing slightly striate cuticula (*A. hultenianum* var. *lapathifolium, Batten 87-3*). **B.** Stomata absent in adaxial side (*A. hultenianum* var. *lapathifolium, Batten 87-3*). **C.** Stomata with dense wax crystals in abaxial side (*A. davisiae* var. *davisiae, Mastrogiuseppe 4713*). **D.** Scat-

Wilkinson (1979) in leaf epidermal anatomy, and Erdtman (1966), and Hong and Hedberg (1990) in palynology. A complete list of all specimens studied has been prepared separately and is on deposit at UPS.

RESULTS

Leaf Epidermal Anatomy

In *Aconogonon phytolaccifolium* (Meisn. ex Small) Rydb. and *A. davisiae* (Brewer ex A. Gray) Soják the leaves have stomata on both surfaces (amphistomatic); the stomata are usually anisocytic and anomocytic, and 30–34 × 18–22 μm. The stomata of *A. phytolaccifolium* are slightly larger than those of the other species. In *Aconogonon hultenianum* (Yurtz.) Tzvel. stomata are present only on the abaxial leaf surface (leaves are hypostomatic); the stomata are usually anomocytic, and ca. 30 × 20 μm (Figures 1A and 1B). Wax crystals in the form of rods and filaments (type b, group 2 of Wilkinson, 1979), showing a dense mass of individual rods nearly perpendicular to the surface, were observed on both sides of leaves of some *A. davisiae* specimens (Figure 1C). The cuticula is mostly striate on both sides of the leaves of *A. phytolaccifolium* (Figures 1E and 1F) and slightly striate on the abaxial side of the leaves in *A. hultenianum* (Figure 1A). In *A. davisiae* cuticular striation is apparently absent on both sides of the leaves (Figure 1D).

On both upper and lower leaf surfaces of *Aconogonon hultenianum* and *A. phytolaccifolium,* there are depressions containing peltate, glandular trichomes (Figure 1B). Taxonomically, epidermal structures proved of only limited diagnostic value.

Pollen Morphology

The pollen morphology of two North American species had previously been studied, but only by light microscope (Hedberg, 1946). In the present study, pollen morphology of these species

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tered stomata with trichome in adaxial side (*A. davisiae* var. *davisiae, Gillett 310*). **E.** Stomata with striate cuticula in abaxial side (*A. phytolaccifolium* var. *phytolaccifolium, Henderson 5653*). **F.** Stomata with striate cuticula in adaxial side (*A. phytolaccifolium* var. *phytolaccifolium, Henderson 5653*). Further explanations in the text. Scale bars: A–B, D–F = 50 μm; C = 10 μm.

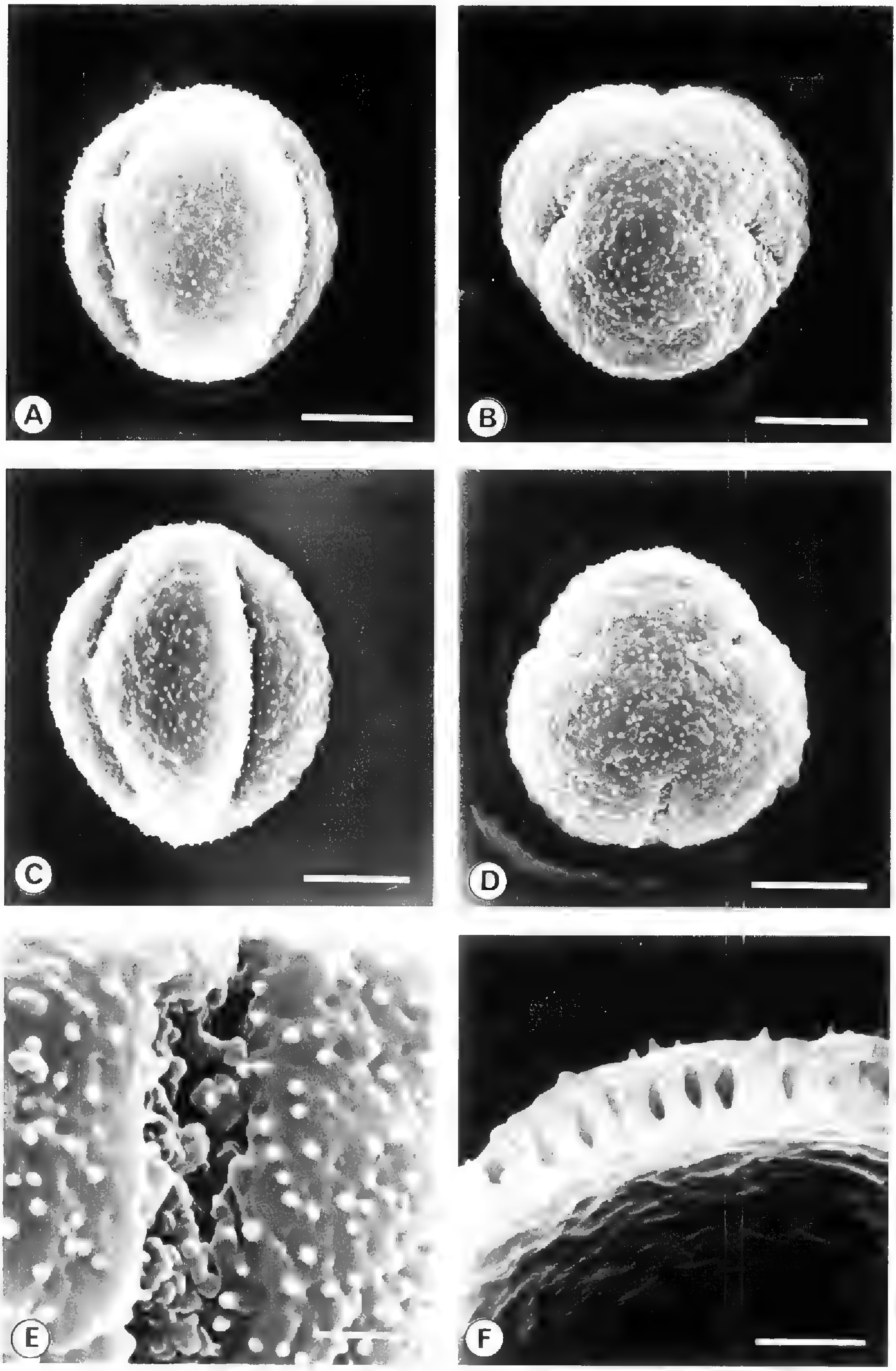

Figure 2. SEM photographs of acetolyzed pollen grains of North American *Aconogonon* spp. **A.** Equatorial view (*A. hultenianum* var. *hultenianum*, *Porsild 347*). **B.** Polar view (*A. phytolaccifolium* var. *phytolaccifolium*, *Steward & Steward 6792*). **C.** Equatorial view (*A. davisiae* var. *davisiae*, *Gillett 310*). **D.** Polar view

is re-evaluated using the SEM. Pollen grains of the North American species can be described as follows: Pollen grains 3-colpate, mostly prolate-spheroidal, rarely spherical or prolate (Figures 2A and 2C). P (polar axis) = 27.6–31.2 μm (the pollen grains of *Aconogonon hultenianum* are slightly smaller than those of the other species), E (equatorial diameter) = 24.8–27.3 μm, P/E = 1.1–1.3. Amb circular (Figures 2B and 2D). Colpi 19.0–20.6 μm, quite narrow. Exine 2.6–3.6 μm thick, sometimes slightly thinner at the equator (in *A. hultenianum* the exine is slightly thicker than that of the other species). Exine structure tectate, punctate or somewhat foveolate with scattered microspinules, the surface often slightly irregularly bulging (Figure 2E). Columellae regularly distributed, more or less densely packed (Figure 2F).

TAXONOMIC TREATMENT

Aconogonon (Meisn.) Reichb., Handb. Nat. Pflanzensyst. 236. 1837 ["*Aconogonum* (Meisn.)"]. *Polygonum* sect. *Aconogonon* Meisn., Prodr. Polygon. 43 & 55. 1826. *Polygonum* subgen. *Aconogonon* (Meisn.) Small, Mem. Dept. Bot. Columbia Coll. 1: 20. 1895. *Polygonum* sect. *Aconogonum* (Meisn.) Aschers. & Graebn., Synop. Mitteleurop. Fl. 840. 1913 ("*Acontogonum*"). *Persicaria* sect. *Aconogonon* (Meisn.) H. Gross, Bull. Géogr. Bot. 23: 27. 1913. *Aconopogon* Nakai ex Mori, Enumer. Pl. Cor. 129. 1922, *orth. mut.* TYPE: *Aconogonon divaricatum* (L.) Nakai ex Mori (= *Polygonum divaricatum* L.), designated by Roberty & Vautier, Boissiera 10: 40. 1964.

Polygonum **Polygonum* L., Sp. Pl. 362. 1753, *pro parte*.

Gononcus Raf., Fl. tellur. 3: 16. 1837 ("1836"). TYPE: *Gononcus undulatus* Raf. (fide Farr et al., Index Nom. Gen. 1: 738. 1979).

Pleuropteropyrum H. Gross, Bull. Géor. Bot. 23: 7. 1913. TYPE: *Pleuropteropyrum weyrichii* (Fr. Schmidt) Gross (= *Polygonum weyrichii* Fr. Schmidt), designated by Roberty & Vautier, Boissiera 10: 53. 1964.

Ampelygonum Lindl., Bot. Reg. 63. 1838, *pro parte*.

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(*A. davisiae* var. *davisiae, Heller 12614*). **E.** Surface pattern (*A. phytolaccifolium* var. *phytolaccifolium, Steward & Steward 6792*). **F.** Fractured exine (*A. davisiae* var. *davisiae, Gillett 310*). Scale bars: A–D = 10 μm; E–F = 5 μm.

Mostly erect herbaceous perennials, 10–150 (–200) cm tall; stem terete to slightly angular, simple or somewhat branched, rarely zigzag, glabrous to pubescent; rhizomatous, often forming thick, elongated woody stocks rooting adventitiously; leaves alternate, mostly cauline, simple, sessile to long-petioled, margin usually entire or sometimes slightly undulate, usually ciliate or scabrous, rarely smooth without hairs, blades narrow lanceolate to ovate, acute to long-acuminate or rarely obtuse at the apex, with rounded or truncate, sometimes cuneate bases; ochrea membranous, funnel-shaped, easily torn, often keeping the tubular shape, glabrous to pubescent, marginal cilia absent; inflorescences terminal, subterminal or sometimes also axillary, small fascicles borne singly, or in short axillary racemes or much branched panicles; flowers usually perfect, or pseudohermaphroditic (female or male part poorly developed), on pedicels subtended by ochrea-like small hyaline bracts (ochreolae), articulate or sometimes unjointed; tepals 5, fused for one-fourth or one-fifth of their length, creamy or greenish or yellowish white, subequal or sometimes unequal (3 larger segments, 2 smaller segments), usually glabrous, ovate to obovate, sometimes spathulate, usually rounded or blunt at the apex, persistent, usually enclosing the achene at maturity, venation of usually 3–5 veins arising from the base; stamens 8, usually included, inserted at the base of the tepals in one or two whorls; filaments filiform, glabrous; anther dorsifixed with 2 longitudinal slits; pollen usually 3-colpate, mostly spheroidal to subprolate; amb usually circular; exine tectate, foveolate or punctate with scattered microspinules; ovary one, unilocular, triangular; style 3-partite, glabrous; stigma capitate; embryo accumbent, usually rounded; achene trigonous or sometimes winged, often ovoid to oval, shiny, smooth, yellowish or darkish brown.

The genus has approximately 25–30 species, which are distributed in the Himalayas, the Far East (China, Japan, Korea, etc.) and U.S.S.R., with one species extending to southeastern Europe and three species occurring in North America. The center of diversity of the genus is in the Himalayas and adjacent regions, which have many endemic species (Hong, in prep.).

Soják (1974) defined three sections within the genus *Aconogonon*: *Aconogonon, Smallia* Soják, and *Knorringia* (Czukav.) Soják. According to Soják, two species (*A. newberryi, A. davisiae*) from North America belong to the section *Smallia,* while the remaining species (*A. hultenianum, A. phytolaccifolium*) belong to sect. *Aconogonon.*

Tzvelev (1987) defined four sections in his preliminary Far East U.S.S.R. Flora: *Aconogonon, Fagopyroides* Tzvel., *Hultenia* Tzvel., *Pleuropteropyrum* (H. Gross) Tzvel. Section *Hultenia* Tzvel. was described on the basis of a North American species, *Aconogonon hultenianum.* Tzvelev (1987) raised sect. *Knorringia* to the rank of genus. This genus does not fit in the tribe Persicariae Dum.; it has been transferred to the tribe Coccolobeae Dum. *emend.* Haraldson, and its generic independence substantiated by Hong (1989). Prior to completing a revision of the genus, I will withhold judgement on infrageneric classifications of North American *Aconogonon.* Therefore, neither Soják's (1974) nor Tzvelev's (1987) infrageneric classifications are applied here.

KEY TO THE NORTH AMERICAN SPECIES OF *ACONOGONON*

1. Plant usually 10–40 cm tall; inflorescences of short, 3–4-flowered terminal racemes or fascicles in leaf axils; leaves oblong-ovate or ovate, rarely broadly lanceolate to oblong, up to 9 cm long, subsessile or sessile, or with petioles up to 15 mm long; achenes not winged .... **3.** *A. davisiae*
1. Plant usually (50) 60–120 (–200) cm tall; inflorescences much-branched panicles, terminal or subterminal, sometimes also axillary; leaves ovate to lanceolate or narrowly lanceolate, more than 9 cm long, petioled; achenes winged 2
    2. Achenes 2.6–3.2 (–3.5) mm long, with three thin, membranous wing-like structures, mostly included or slightly exserted from the tepals at maturity; inflorescences much-branched, with copious flowers, mostly terminal with only bracteate panicles, rarely a few axillary ones; peduncles pubescent; pedicels 0.5–0.9 mm long in articulate ones .... **1.** *A. hultenianum*
    2. Achenes 3.8–7.0 mm long, three-angled with three hard, wing-like structures, half or one-third exserted from the tepals; inflorescences terminal, subterminal and often axillary, leafy to merely bracteate, loose panicles; peduncles glabrous; pedicels (0.9) 1.0–1.7 mm long in articulate ones .... **2.** *A. phytolaccifolium*

1. **Aconogonon hultenianum** (Yurtz.) Tzvel., Novit. Syst. Plant Vasc. 24: 77. 1987.

Perennial herb, 50–150 cm tall; stem simple or with few branches, erect, glabrous to densely and retrorsely hairy, 3–14 mm in diameter; leaves cauline, narrowly lanceolate to ovate, 5.0–19.5 × 2.0–8.0 cm, long-acuminate, rarely short-acuminate, with rounded-obtuse, rarely subcordate or truncate base, glabrous to pubescent on both sides; margin entire or slightly undulate, ciliate or rarely smooth; petiole glabrous to pubescent, 0.8–3.5 (4.0) mm long; ochrea 1.0–2.2 cm long, membranous, pilose to glabrescent, easily torn; inflorescences usually terminal, sometimes also axillary, with many flowers, panicles leafy to leafless; peduncles pubescent, very rarely glabrous; pedicels glabrous, 0.5–0.9 mm long (in fruit up to 1.9 mm), articulate; flowers hermaphroditic; tepals unequal or sometimes subequal, deeply incised, creamy white, obovate, 1.9–3.8 × 0.9–1.7 mm long; stamens included; filaments (0.5) 0.6–1.0 mm long; anthers ca. 0.3 mm long; ovary ovate; style ca. 0.3 mm long (including stigma); stigma capitate, ca. 0.1 mm in diameter; achene with three very thin, membranous wings, normally ovate, pale brownish or greyish brown, shiny, 2.6–3.8 × 1.4–2.0 mm, included or slightly exserted above the tepals.

Aconogonon hultenianum is related to *A. tripterocarpum* (A. Gray) Hara from E Siberia, but differs in its ovate-lanceolate and larger leaves, pubescent ochreae and peduncles, much-branched panicles with many flowers, larger tepal lobes, by having the fruits held erect, and by its much smaller and thin-membranous winged achenes. *Aconogonon hultenianum* may be confused with *A. phytolaccifolium,* although they are not closely related. *A. hultenianum* can be distinguished from *A. phytolaccifolium* by its smaller achenes with thin membranous wall structure, and by its much branched panicle with pubescent peduncle, many flowers and somewhat shorter pedicels.

KEY TO THE VARIETIES OF *ACONOGONON HULTENIANUM*

1. Leaves glabrous on both sides; stem usually glabrous, rarely with a few hairs below the nodes . . **1a.** var. *hultenianum*
1. Leaves pubescent on both sides; stem usually retrorsely hairy. . . . . **1b.** var. *lapathifolium*

1a. **Aconogonon hultenianum** (Yurtz.) Tzvel. var. **hultenianum.** *Polygonum alaskanum* ssp. *hultenianum* Yurtz., Bot. Zurn. 59: 1452. 1974. *Aconogonon alaskanum* ssp. *hultenianum* (Yurtz.) Soják, Čas. Nár. Muz. (Prague). 150: 137. 1982. TYPE: Alaska, Fairbanks area, roadside, College Road, near Ft. Caribou, 64°50′N, 147°50′W, July 16, 1962, *N. L. Simmerman 147* (HOLOTYPE: LE, not seen; ISOTYPE: GH!). [Nomenclatural Note: This species has previously generally been called *Aconogonon alaskanum* (Small) Wight, but the basionym of this, *Polygonum alpinum* var. *alaskanum* Small (1895) is superfluous, as an earlier legitimate name, *P. alpinum* var. *lapathifolium* Cham. & Schlechtend., was cited in synonymy (*see also* Kartesz and Gandhi, 1990). The only other name available for the species as circumscribed here is *A. hultenianum* (Yurtz.) Tzvel.]

Polygonum alaskanum var. *glabrescens* Hultén, Lunds Univ. Årsskr. N. F. Avd. 2. Bd 40 (no. 1). 4: 612. 1944. TYPE: U.S.A., Alaska, Bonanza Creek, June 19, 1924, *Eastwood 298* (HOLOTYPE: GH!; ISOTYPES: CAN!, UC!: 2 sheets, US!).

P. alaskanum var. *laevimarginatum* Porsild, *nom. tant.* [Note: Porsild (1943, 1951) recognized this variety in the Mackenzie Delta area, and even designated a type collection (*Porsild 7295,* in CAN, GH, S). It seems, however, that the name was never validly published.]

Stem usually glabrous or rarely with a few hairs below the nodes; leaves ovate to narrowly lanceolate, 6.0–17.0 (19.5) × 2.1–7.0 (8.0) cm, glabrous on both sides, entire, ciliate or sometimes smooth at the margin; petiole glabrous or glabrescent, 0.8–2.5 mm long; peduncle usually pubescent mainly at nodes. Chromosome number: $2n = 20$ (Bowden, 1966).

ILLUSTRATIONS. Figure 2A (pollen); Figure 3 (map).

REMARK. Two collections, *Macoun 91284* and *Sims 6057* from Yukon, are totally glabrous.

ECOLOGY AND DISTRIBUTION. Common in moist hillsides, waste places, stream banks, sandy lake shores, and on talus slopes above tree-line. It is often associated with *Calamagrostis, Salix* and *Luzula* spp. Var. *hultenianum* is distributed in Alaska, in the United States and in the Yukon Territory and western part of the Northwest Territories of Canada (Figure 3). The known altitudinal range is 250–1700 m.

USE. The young stems and leaves are edible and provide an acceptable substitute for fresh rhubarb (Porsild and Cody, 1980: 262).

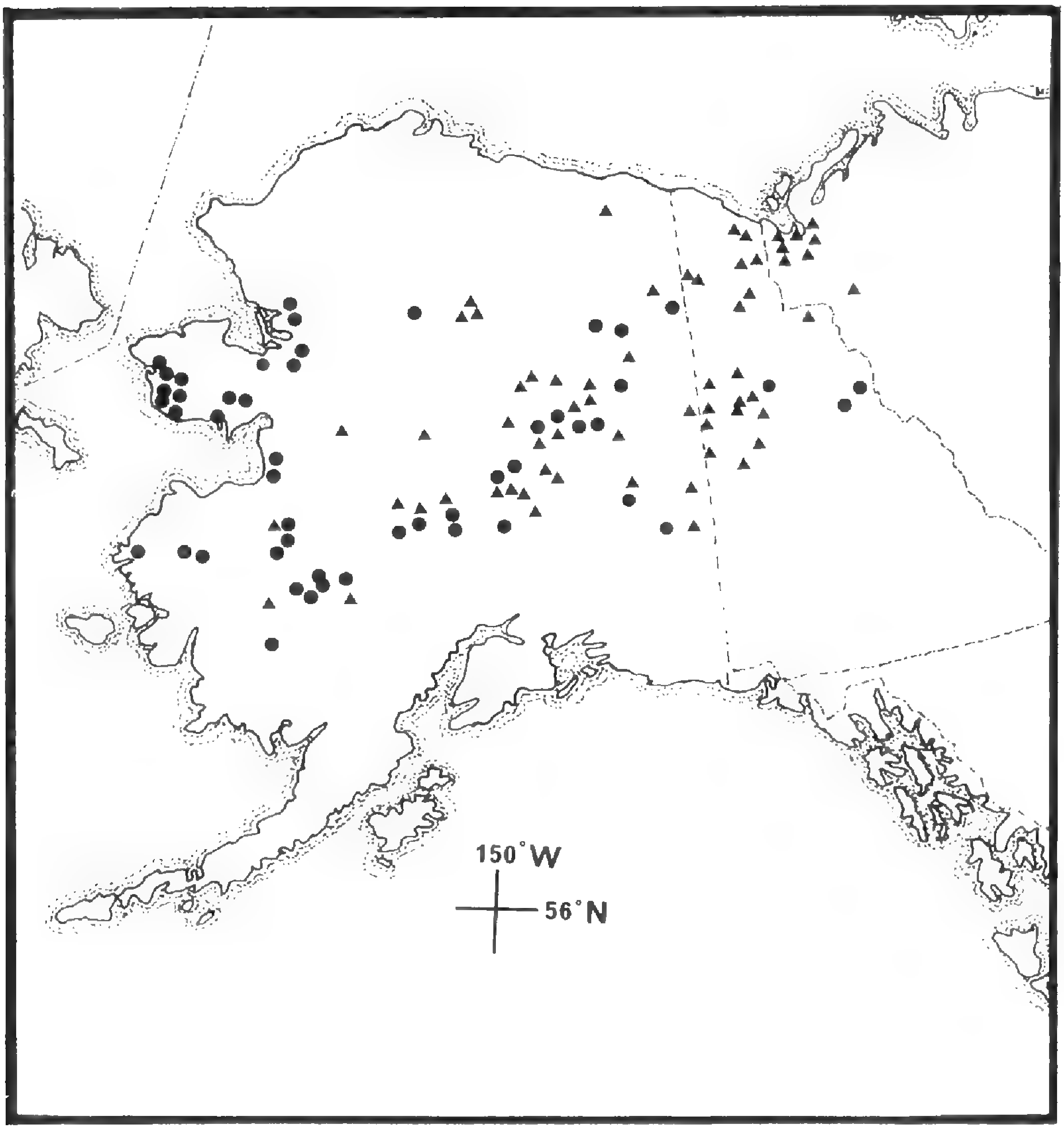


Figure 3. Known distribution of *Aconogonon hultenianum* var. *hultenianum* (▲) and var. *lapathifolium* (●).

Representative specimens. CANADA. **Northwest Territories:** Lower Mackenzie River Distr., Mts. Conoe Lake, W of Aklavik, *Hultén s.n.* (A: 2 sheets, S); ibid., East branch, *Porsild 7295* (CAN, GH, S); ca. 3 miles E of Mackenzie River East Channel, *Sims 6053* (UBC). **Yukon Territory:** Dawson, *Anderson 1589* (NY); *Calder & Billard 3729* (GH, MO); the Yukon Valley, 2 miles below Sheep Creek, *Collier 158* (US); Klondike River, *Gorman 1161* (CAN, NY, S, US); N of Bonanza Creek, *Macoun 91284* (CAN, NY); Rampart House, *Loan 501* (UC); Ogilvie Mts., along Dempster Rd., *Porsild 347* (CAN, GH, UBC); vicinity of camp on Henry Creek, 61°47′N, 138°50′W, *Raup et al. 13515* (A, CAN); N side of Bell River, First terrace, at Lapierre House, 67°23′N, 136°56′W, *Welsh & Rigby 12218* (CAN, NY).

UNITED STATES. **Alaska:** Livengood, *Anderson 8989* (GH); Circle, *Bayne Beanchamp Exped. 53* (UC); SE of Northway on Alaska Hwy., *Dempster 1291* (UC); Mt. McKinley Nat'l Park Station, *Dixon 54* (UC, US); vicinity of Wonder Lake, 63°27′N, 150°50′W, *Viereck 1594* (GH, S), *Nelson & Nelson 3871* (GH, MO, NY, UC, US); Kuskokwim River Drainage, Canoe Mt., *Drury 1863* (CAN, GH); Yukon Valley, near Poston, Forty Mile Creek, *Funston 154* (GH, K, MO, NY, S, US); Red Rock Campground, W of Central, 65°30′N, 145°W, *Harms 2759* (GH); N of Fairbanks, at summit of Roundhouse, *Harshberger s.n.* (US); Hot Springs on the Tanana River, *Hitchcock s.n.* (US); Yukon River, 30 miles above Nulats, *Hollich s.n.* (NY); Koyukuk River, Middle Fork, Bettles, *Jordal 2452* (S, US); Rampart, *Jones 45* (US: 2 sheets); N of Fairbanks, *Purer 7609* (US); Valley of Alatna River, ca. 20 miles above the mouth, *Mendenhall s.n.* (US); between Yukon River and Nation River, 65° to 65°30′N, 141° to 142°W, *Mertie 8* (US); Kokrines Mts., N side of divide towards Melozitna River, *Porsild & Porsild 722* (CAN, S, GH); S side of Tanana River Valley, 63°45′N, 138°43′W, *Raup & Raup 12672* (A, CAN, S, UBC); N slopes of Nutzotin Mts., 63°23′N, 143°45′W, *Raup & Raup 12789* (A, CAN, S); NW of McGrath, in the Upper Kuskokwim Valley, *Scamman 1838* (GH); Lower Yerrick Creek, *Spetzman 790* (US); 28 miles S of Delta Junction, along the Delta River, *Taylor et al. 19202* (NY).

1b. **A. hultenianum** var. **lapathifolium** (Cham. & Schlechtend.) S.-P. Hong *comb. nov. Polygonum alpinum* var. *lapathifolium* Cham. & Schlechtend., Linnaea 3: 38, 1828. *P. polymorphum* var. *lapathifolium* (Cham. & Schlechtend.) Ledebour, Fl. Ross. 3: 518. 1850, *nom. illegit.* TYPE: Alaska, Bering Strait, Kotzebue's Sound, not dated, *Chamisso and Beechey s.n.* (NEOTYPE: K!, designated here). [Note: The original type localities of *Polygonum alpinum* var. *lapathifolium* are Chamisso Is. and Eschscholtz Bay in Alaska. However, I failed to trace any original material in B and LE. The neotype is from the same area as the original material and was cited by Hooker (1840) as *P. alpinum* var. *lapathifolium*.]

Polygonum alpinum var. *alaskanum* Small, Mem. Dept. Bot. Columb. Coll. 1: 33. 1895, *nom. illegit. P. alaskanum* (Small) Wight ex Hultén, Lunds Univ. Årsskr. N. F. Avd. 2. Bd 40 (no. 1). 4: 610. 1944, *nom. illegit. P. alpinum* spp. *alaskanum* (Small) Welsh, Great Basin Natur. 28:154. 1968, *nom. illegit.*

P. polymorphum sensu J. Macoun, Cat. Canad. Pl. 3: 412. 1886, non Ledebour, Fl. Ross 3: 518. 1850.

Aconogonon phytolaccifolium sensu Sharples, Alas. Wild. Fl. 4. 1938, non Rydberg, Fl. Rocky Mts. 238. 1917.

Stem pubescent with mostly retrorse hairs; leaves lanceolate to narrowly lanceolate, 5.0–16.8 × 2.0–6.0 cm, pubescent on both sides, entire, ciliate; petiole pubescent, 0.8–3.5 (4.0) cm long; peduncle densely pubescent. Chromosome number: $2n = 20$ (cf. Bowden, 1966; Dawe and Murray, 1979).

ILLUSTRATIONS. Anderson, 1959: 223, plate 18, Figure 394; Polunin, 1959: 156; Hultén 1968: 386; Porsild and Cody 1980:

265, Figure 399. All are *sub nomine Polygonum alaskanum.* Figures 1A and 1B (epidermal anatomy); Figure 3 (map).

ECOLOGY AND DISTRIBUTION. *A. hultenianum* var. *lapathifolium* occurs on montane slopes above the treeline, steep hillsides, steep cut banks or on sandy loam of rivers. Known from Alaska in the United States and in the Yukon Territory of Canada (Figure 3). According to Scoggan (1978) this variety may occur in the mountains of British Columbia in Canada, but no collections from that area are known to me. It was also reported from Chukotskiy peninsula in the U.S.S.R. by Tzvelev (1989), but I have not seen material from this area. The known altitudinal range is 100–1300 m.

VERNACULAR NAMES. 'Miner's greens,' 'Wild rhubarb' in Alaska.

REPRESENTATIVE SPECIMENS. CANADA. **Yukon Territory:** Canol Rd., SE slopes of Mt. Sheldon, *Porsild & Breitung 11719* (GH, NY, S, UC, US); 10 miles SW of Macmillan Pass, 63°12'N, 130°07'W, *Coly & Brigham 20544* (UBC).

UNITED STATES. **Alaska:** Anvik, *Chapman 12* (GH); Aniak Region, 61°37'N, 159°30'W, *Drury 1437* (GH); Kuskokwim River Drainage Basin, *Drury 1753* (GH), *Layden 52* (US); Morainic till near Farewell Lake, *Drury 2433* (GH); Limestone Mts., SE of Farewell, 62°28'N, 153°50'W, *Drury 2821* (GH); 16 miles W of Nome, *Flett 1574* (US); between Cook Inlet and the Tanana River, *Glenn s.n.* (US); Noorvik, on the Kobuk River, *Scamann 6345* (GH); Upper Kobuk River, Selby Lake, *Hultén s.n.* (A: 4 sheets, S); Norton Sound, vicinity of Unalakleet, *Johnston & Palmer 48* (GH, US); Rocky Point, *Mason s.n.* (K, S: 2 sheets, UC); Kuskokorin Valley, *Meimann s.n.* (GH); McKinley Nat'l Park, N end of Wonder Lake, *Mexia 2163* (GH, MO, NY, S, UC, WTU); Buckland River, *Miller 55c* (US), *Palmer 209* (GH, US); Circle Hot Springs near Steese Hwy. ca. 138 miles N of Fairbanks, *Scamann 151* (GH); Bering Strait, Teller, on Port Clarence, *Scamman 5470* (GH); vicinity of Port Clarence, bank of Tuksuk Channel, *Walpole 1606* (US); near Mary's Igloo, *Walpole 1647* (US); near Fairbanks, *Batten 87-3* (ALA, UPS).

2. **Aconogonon phytolaccifolium** (Meisn. ex Small) Rydb., Fl. Rocky Mts. 238. 1917.

Perennial herb, 70–150 cm tall, sometimes up to 200 cm high; stem simple or usually branched above, erect, usually glabrous or sometimes pubescent, rarely only in the lower part; roots thick, large and somewhat woody, sometimes more than 5 cm in diameter; leaves cauline, lanceolate to ovate-lanceolate, 5.0–15.0 × 1.4–7.5 cm, acute or acuminate, often obtuse at the apex, more or less rounded at the base, entire, ciliate or scabrous, sometimes totally hairless, often with revolute margins, usually glabrous to weakly hairy, sometimes densely pubescent on both sides; petiole glabrous to pubescent, 0.5–3.0 (3.7) mm long, upper leaves usually subsessile; ochrea roughly 1–3 cm long, membranous, usually pubescent, sometimes totally glabrous or pubescent only following veins, easily torn; inflorescences usually terminal, subterminal and axillary, leafless to leafy-bracteate with a few branched panicles; peduncles glabrous; pedicels glabrous, articulate or often non-articulate in fruit, (0.9) 1.0–1.7 mm long in articulate ones, (1.6) 1.9–3.5 mm long in non-articulate ones; flowers usually hermaphroditic, rarely pseudo-hermaphroditic (usually stamens poorly developed); tepals usually subequal, ovate to obovate, 2.2–3.2 × 0.9–1.8 mm long (up to 3.8 mm in fruit); filaments 0.8–1.2 (1.7) mm long; anthers 0.3–0.4 mm long; ovary ovate, trigonous, styles ca. 0.4 (0.5) mm long (including stigma); achenes three-angled with three hard, wing-like structures, ovoid, mostly yellowish-brown, smooth, shiny, 3.8–7.0 mm long, usually half- or one-third exserted from the tepals.

As Hitchcock et al. (1964: 161) mentioned, in a high proportion of the collections from Idaho, Montana, eastern Oregon, and parts of Nevada, plants are glabrous to glabrescent throughout and the pedicel is usually non-articulate. On the other hand, most of the collections from California and Washington have a tendency towards pubescent, more ovate leaves and often articulated pedicels.

Kongar (1973) described *Polygonum smallii* on the basis of the size of achenes, presence/absence of a jointed pedicel in the fruiting stage, and leaf shape. His treatment is not followed here, since these characters show continuous intergradation. In some collections (e.g., *Baker 1379, Eastwood 1878, Morris 1038, Tracy 12921*), specimens are slightly smaller, and the triquetrous shape of the achenes is less pronounced. The pedicel is not always jointed at the middle or beneath the tepals. *P. smallii,* therefore, is treated as a synonym of *Aconogonon phytolaccifolium.*

In North America *Aconogonon phytolaccifolium* has been confused with the Asian species *A. alpinum* (All.) Schur. The two species are similar in general morphology, but the former differs from the latter in its usually much broader leaves, much shorter petiole, its loose panicles, in having half or one-third of the achene exserted from the tepals, and its triquetrous, three hard, wing-like structures, brownish, shiny achene. One deviating group is here recognized as a taxonomic variety.

KEY TO THE VARIETIES OF *ACONOGONON PHYTOLACCIFOLIUM*

1\. Plants glabrescent to pubescent; leaf margin always ciliate . . . . **2a.** var. *phytolaccifolium*
1\. Plants totally glabrous throughout; leaf margin eciliate, often somewhat revolute . . . . **2b.** var. *glabrum*

2a. **Aconogonon phytolaccifolium** (Meisn. ex Small) Rydb. var. **phytolaccifolium.** *Polygonum phytolaccifolium* Meisn. ex Small (as "*phytolaccaefolium*"), Bull. Torrey Bot. Club 19: 360. 1892. Type: U.S.A., California, without date, *Cuming 229* (Holotype: NY, photo!; isotype: NY, photo!).

Polygonum smallii Kongar, Bot. Zurn. SSSR 57: 1337. 1973, *syn. nov. Aconogonom smallii* (Kongar) Soják, Čas. Nár. Mus. 150: 137. 1982. Type: U.S.A., Idaho, Valley Co., granite slopes of Gold Fork Lookout Payette Nat. Sawtooth Mts., 8000′, July 9, 1937, *Thompson 13744* (Holotype: LE!; isotypes: GH!, NY!, S!, UC!: 2 sheets, WTU!).

Polygonum polymorphum var. *foliosum* R. Keller, Bull. Soc. Bot. Belg. 30: 49. 1891. *P. alpinum* var. *foliosum* (R. Keller) Small, Bull. Torrey Bot. Club 19: 360. 1892. Type: U.S.A., Washington, Mt. Adams, August 1882, *Ph. J. Howell s.n.* (?Isosyntypes: MO! NY!: 3 sheets, US!, WTU!).

P. alpinum auct. Amer., non All., Misc. Taur. 5: 94. 1773.

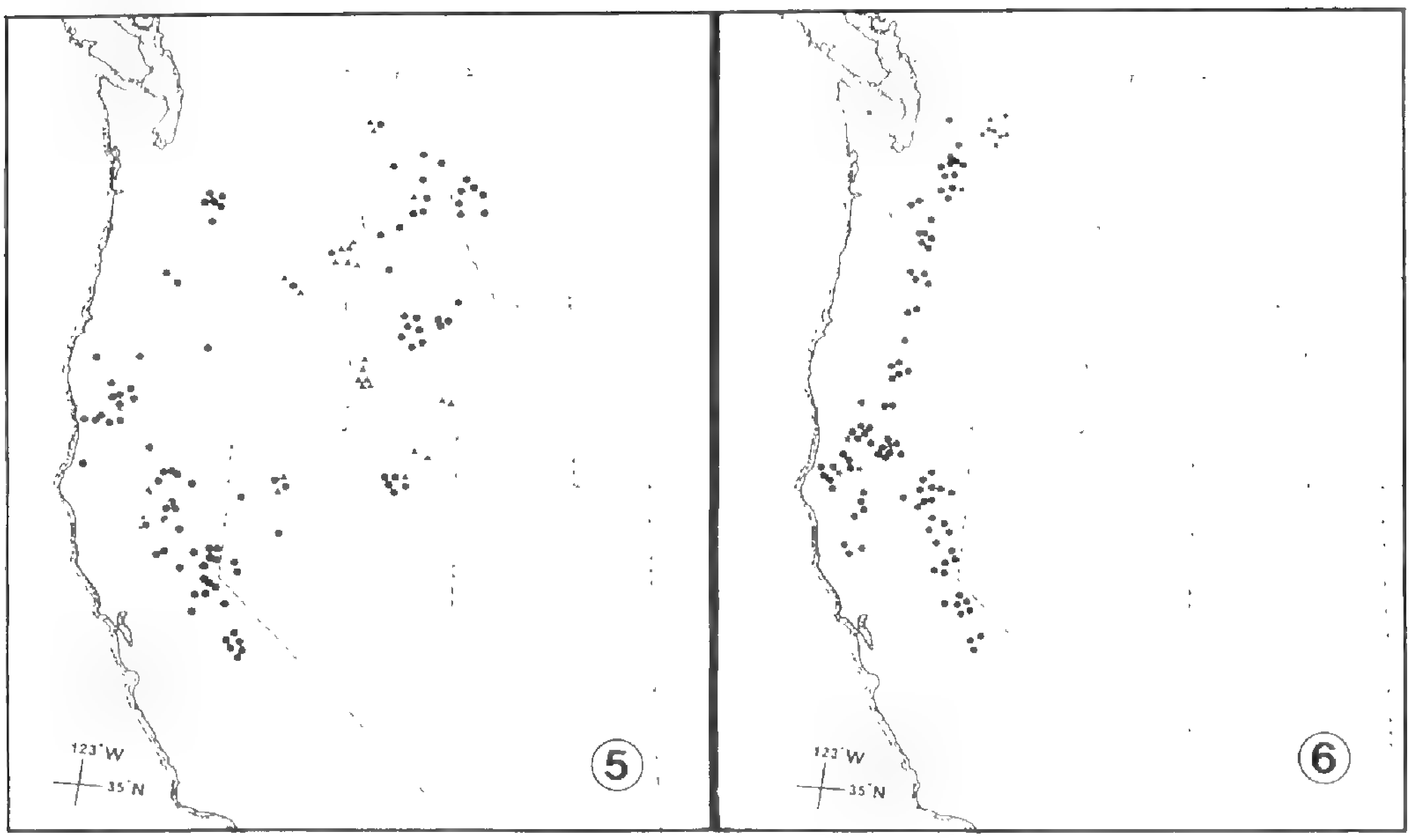
P. polymorphum auct. Amer., non Ledeb., Fl. Ross. 4: 521. 1850.

Stem glabrous to pubescent; leaves 5.0–15.0 (19.0) × 1.4–7.4 cm, ciliate or scabrous, usually glabrescent to pubescent on both sides; petiole glabrous to pubescent, 0.4–2.5 (–3.7) cm long; ochreae usually glabrescent to pubescent, sometimes hairy only on the veins, easily torn, 1–3 cm long; pedicels usually articulate, or sometimes not forming articulation, 0.9–1.8 mm long (in articulate ones), 2.2–3.5 mm long (in non-articulate ones).

Illustrations. Small, 1895: 35, plate 4; Abrams, 1944: 64, Figure 1467; Hitchcock et al., 1964: 164. All are *sub nomine Polygonum phytolaccifolium.* Figures 1E and 1F (epidermal anatomy); Figures 2B and 2E (pollen); Figure 5 (map).

Ecology and distribution. Var. *phytolaccifolium* grows on moist or sometimes dry rocky granitic slopes; it is common in alpine meadows, and sometimes along streams or in wet spots. It is associated with *Stipa occidentalis* Thurb. ex Wats, *Abies magnifica* Murr., and *Pinus contorta* Dougl. ex Loud. It occurs in Washington, Idaho, Montana, Oregon, California and Nevada in the United States (Figure 5). The known altitudinal range is 1200–3100 m.

Figure 4. Holotype specimen (GH) of *Aconogonon phytolaccifolium* var. *glabrum.*



Figures 5 and 6. Known distribution of *Aconogonon* in North America. **5.** *A. phytolaccifolium* var. *phytolaccifolium* (●) and var. *glabrum* (▲). **6.** *A. davisiae* var. *davisiae* (●) and var. *glabrum* (★).

VERNACULAR NAME. It is called 'Ragweed' by the cattleman (fide *Alexander & Kellogg 5808*).

REPRESENTATIVE SPECIMENS. UNITED STATES. **California:** Alpine Co.: without precise locality, *Hansen s.n.* (UC). Amador Co.: Silver Lake, *Hansen 314* (K, MO, UC). Butte Co.: Jonesville, *Copeland 628* (GH, K, MO, MU, NY, S, UC); bank of a stream at Chaparral, *Heller 15278* (MO: 2 sheets, NY, S, UC, US, WTU). Del Norte Co.: Siskiyou Mts., Indian Creek, *Jepson 18565* (JEPS). Eldorado Co.: Tahoe Tavern, *Blake 10306* (GH); Pyramid Peak, *Hall & Chandler 4758* (UC). Humboldt Co.: Grouse Mt., *Tracy 12921* (GH, UC). Nevada Co.: Donner Lake towards Donner Pass, *Heller 7123* (GH, MO, NY, UC, US); Soda Springs, *Jones 2613* (BM). Placer Co.: Mt. Lincoln, south of Summit Valley, *Heller 12934* (GH, MO, NY, UC); near Donner Pass, *Torrey 425* (GH). Plumas Co.: Lassen Peak, *Austin 154* (MO, UC, US); Morgans Springs, *Eastwood 1878* (GH, NY, UC). Sierra Co.: North Fork Yuba River, Pioneer Road Station, *Jepson 16797* (JEPS: 2 sheets). Siskiyou Co.: Marble Mts., Paradise Lake, *Alexander & Kellogg 5808* (K, US, WTU); E side of Hancock Lake, *Oettinger 437* (UC). Tuolumne Co.: Yosemite Valley, *Abrams 4678* (GH, NY), *Brewer 1670* (GH, US). **Idaho:** Adams Co.: Black Lake, Weiser, *Christ 8703* (NY). Blaine Co.: Sawtooth Primitive Area, NW of Alturas Lake, Alpine Creek, *Hitchcock & Muhlick 10445* (NY, WTU). Boise Co.: Pilot Peak, ca. 10 miles SW of Lowman, *Hitchcock & Muhlick 9913* (GH, NY, UC, WTU). Custer Co.: Mt. Heybuon, Sawtooth Range, *Thompson 13668* (MO, NY, US, WTU). Elmore Co.: Trinity Mts., above Big Trinity Lake, *Baker 11183* (NY); Trinity Lake, ca. 10 miles W of Featherville, *Hitchcock & Muhlick 10397* (NY, UC, WTU); near Big Roaring River Lake, 20 miles N of Pine, *Meyer & Meyer 2274* (MO, NY, S, UC). Idaho Co.: Selway Mts., Fog Mt. Saddle, *Baker 15297* (NY, WTU). Kootenai Co.: Wiesner's Peak, *Sandberg 662* (GH, K, NY, US). Shoshone Co.: Bullion, along Idaho State Line, *Baker 13447* (NY, WTU). Valley Co.: NW of McCall, Payette Lakes, E slope of Mt.

Brundage, *Baker 10276* (NY, WTU); E side of Divide between Warm Lake and Cascade, *Hitchcock & Muhlick 14032* (NY, UC, WTU). **Montana:** Granite Co.: Burnt Fork Trail, Skalkaho Rd., *Hitchcock & Muhlick 14491* (NY, WTU). Mineral Co.: above Hoodoo Pass, *Mooar 13839* (NY). Ravalli Co.: Bitterroot Mts., 1 mile E of St. Mary's Peak, *Hitchcock & Muhlick 15301* (MO, NY, UC, WTU). **Nevada:** Elko Co.: Ruby Range, S ridge above Island Lake, *Maguire & Holmgren 22604* (GH, NY); Ruby Mts., Verdi Peak, *Mills & Beach 1589* (UC). Ormby Co.: Clear Creek Canyon, *Baker 1379* (GH, MO, NY, UC, US). Washoe Co.: Crason Range, Ophir Creek, *Pinzl 3781* (NY). **Oregon:** Baker Co.: Wallowa Mts., near Cornucopia, *Thompson 13324* (GH, NY, UC: 2 sheets, US, WTU). Grant Co.: Blue Mts., John Day Valley, *Henderson 5653* (GH, MO). Josephine Co.: 3 miles E of Oregon Cave, on Lake Mt. trail, *Hitchcock & Martin 5132* (GH, UC, WTU), *Thompson 12442* (GH, NY, UC, US, WTU: 2 sheets). Lane Co.: below Fairview Lookout, *Powell s.n.* (UC, WTU). Linn Co.: Tombstone Prairie, *Steward & Steward 6792* (GH, S). Wallowa Co.: Aneroid Lake Trail, *Kruckeberg 2261* (NY, S, UC, WTU). **Washington:** Klickitat Co.: Cascade Mts., White Salmon, *Lloyd s.n.* (NY). Yakima Co.: Mt. Adams, *Howell 1546* (US); ibid., Wodan's Vale, *Suksdorf 6366* (GH, MO, NY, WTU); Mt. Paddo, *Suksdorf 6851* (GH), *1414* (NY).

2b. **Aconogonon phytolaccifolium** (Meisn. ex Small) Rydb. var. **glabrum** S.-P. Hong *var. nov.* TYPE: United States, Oregon, Wallowa Mts., 7–8000′, July 16, 1900, *Cusick 2442* (HOLOTYPE: GH!; ISOTYPES: JEPS!, K!, MO!, NY!, US!).

Plerumque formae typicae similis sed planta omnino glaberrima differt.

Stem totally glabrous; leaves 5.4–12.5 × 1.6–4.8 cm, usually obtuse, more or less revolute, eciliate, totally glabrous on both sides; petiole 0.5–1.2 (1.6) cm long, glabrous; ochrea totally glabrous, 1.0–2.2 cm long. Pedicels usually non-articulate, very rarely articulate, (1.1) 1.6–3.2 mm long; achene 4.8–6.1 (7.0) × 2.8–4.2 (4.5) mm.

ILLUSTRATIONS. Figure 4 (holotype); Figure 5 (map).

ECOLOGY AND DISTRIBUTION. Usually in sandy patches, in dry or sometimes moist rocky slopes, often associated with *Abies lasiocarpa* (Hook.) Nutt., and *Picea engelmannii* Parry ex Engelm. Var. *glabrum* is distributed in Idaho, Nevada, and Oregon in the United States. Only one collection (*Grinnell s.n.* in JEPS) is known so far from California (Figure 5). The known altitudinal range is 1800–3350 m.

USE. In Oregon, this plant is eaten by sheep apparently in preference to the grass (*fide Shear 1765*).

REPRESENTATIVE SPECIMENS. UNITED STATES. **California:** Tehama Co.: Brokeoff Mt., *Grinnell s.n.* (JEPS). **Idaho:** Adams Co.: 3 miles S of Goose Lake, *Baker 11719* (NY, WTU). Benewah Co.: St. Joe Baldy, *Christ 5010* (NY). Blaine Co.: above W side of Alturas Lake, *Cronquist 2625* (GH); Coeur d'Alene Mts., *Leiberg 1195* (GH, K, MO, NY, UC). Idaho Co.: Seven Devils Mts., Seven Devils Camp, *Baker 12015* (NY, WTU); Bitterroot Mts., Lora Trail Road, near Rocky Ridge Lookout, *Sharsmith 4054* (GH, MO, NY, S, UC). Owyhee Co.: near headwaters of Sawpit Creek, ca. 3 miles SW of Silver City, *Baker 7895* (NY); Silver City, *Macbride 430* (GH, NY, UC, US, WTU); 45 miles E of Pierce, along Lolo Trail Rd. to Powell, *Hitchcock & Muhlick 21915* (NY, UC, WTU). Shoshone Co.: Grizzly Peak, *Christ 3595* (NY); 2–3 miles W of Quarles Peak, *Wilson 213* (GH, MO, UC). **Nevada:** Elko Co.: Angel Lake, ca. 13 miles SW of Wells, *Morris 1038* (GH, NY); Ruby Mts., S slope Lamoille Canyon, opposite Ranger Station, *Train 4563* (NY, UC); E Humboldt Mts., *Watson 1071* (GH: 2 sheets, NY, US). **Oregon:** Grant Co.: Blue Mts., divide S of Anthony Lakes, *Hitchcock 19708* (UC, WTU). Union Co.: Cove Mts., Cove-Minam trail, *Cusick 3737* (WTU). Wallowa Co.: Wallowa Mts., Hudsonian Lake Basin, at edge of Mirror Lake, *Constance & Jacobs 1334* (UC, WTU); 6 miles above Wallowa Lake, *Shear 1765* (US); Imnaha Nat'l Forest, Stanley Range, *Sampson & Pearson 135* (US).

3. **Aconogonon davisiae** (Brewer ex A. Gray) Soják, Preslia 46: 151. 1974.

Perennial herb, 12–42 (50) cm tall; stems usually several, simple to freely branched, mostly erect, slightly angular, pubescent with soft or sometimes scabrous hairs to glabrous; leaves broadly or rarely narrowly lanceolate to oblong, oblong-ovate or ovate, 2.1–7.5 (9.7) × 1.0–5.0 cm, sometimes sublustrous on both sides, especially in glabrous specimens, acute or sometimes obtuse at the apex, usually truncate or rarely cordate at the base, entire, ciliate or scabrous at the margin and glabrous to pubescent on both sides; petiole glabrous to pubescent, 0.3–15 mm long, upper leaves often sessile; ochrea 0.3–2.0 (3.0) cm long, tubular, membranous, glabrous to pubescent, usually remaining tubular, sometimes torn; inflorescences short axillary racemes bearing few flowers; peduncles usually glabrous; pedicels glabrous, usually articulate, 0.5–1.9 (2.4) mm long, usually slightly longer in fruiting condition; flowers normally hermaphroditic, rarely pseudohermaphroditic (stamens poorly developed); tepals usually subequal or rarely unequal, the 3 outer ones slightly larger than the inner 2, greenish to pinkish white, oblong-oval to obovate, usually obtuse, 2.0–4.3 × 1.0–2.4 mm; venation of usually 3–4 (5) veins arising from the bases with 2–5 secondary ramifications; stamens 8 (9), included; filaments (0.2) 0.5–1.3 mm long; anthers 0.3–0.7 mm long; ovary ovate, trigonous; style 0.3–0.6 (0.9) mm long (including stigma); achene ovoid or narrowly ovoid, yellowish brown, smooth and more or less shiny, 4.5–6.0 (8.3) mm long, one-third to one-half exserted from the tepals.

Small (1894) distinguished *Aconogonon davisiae* (as *Polygonum davisiae*) from *A. newberryi* (as *P. newberryi*) on the basis of the length of inflorescence and some other minor characters (petioled or sessile/subsessile leaves, leaf shape, etc.), including their different distributions. Many local floras (e.g., Abrams, 1944; Munz, 1959; Hitchcock et al., 1964) of North America followed this treatment of Small (1894, 1895). After careful investigation, however, the diagnostic characters given appear unreliable. No absolute morphological discontinuities exist in any of these characters. Therefore, it seems necessary to treat *A. newberryi* as a synonym of *A. davisiae.* Two taxonomic varieties are recognized here, distinguished by the presence or absence of indumentum.

KEY TO THE VARIETIES OF *ACONOGONON DAVISIAE*

1. Plants pubescent, rarely glabrescent . . . . **3a.** var. *davisiae*
1. Plants totally glabrous throughout . . . . **3b.** var. *glabrum*

3a. **Aconogonon davisiae** (Brewer ex A. Gray) Soják var. **davisiae.** *Polygonum davisiae* Brewer ex A. Gray, Proc. Amer. Acad. Arts 8: 399. 1873. TYPE: U.S.A., California, Sierra Nevada, Alpine Co., Carson Pass, 8200′, August 16, 1863, *Brewer 2105* (LECTOTYPE: GH!, selected here; ISOLECTOTYPES: K!, UC!: 2 sheets, US!).

Polygonum newberryi Small, Bull. Torrey Bot. Club 21: 170. 1894, *syn. nov. Aconogonon newberryi* (Small) Soják, Preslia 46: 151. 1974. TYPE: U.S.A., Oregon, Cascade Mts., at Crater Pass, 7000′, growing in scoria near the snow line, September 1, 1856, *Newberryi s.n.* (HOLOTYPE: NY!).

Stem mostly pubescent, rarely glabrous; leaves 2.1–7.5 × 1.1–5.0 cm, usually acute, rarely obtuse, usually rounded or slightly truncate at the base, entire, ciliate or scabrous at the margin, usually rough or soft hairy on both sides, or sometimes glabrescent; petiole usually pubescent, rarely glabrescent, 0.3–17.0 (22.0) mm long, usually sessile or subsessile in the upper leaves; ochrea 0.4–2.0 cm long, pubescent or rarely glabrescent; pedicels 0.5–1.7 (2.4) mm long; tepals 2.1–4.3 × 1.1–2.2 mm; filaments (0.5) 0.8–1.3 mm long; anthers 0.3–0.5 (0.7) mm long; achenes 3.2–5.8 (8.3) mm long. Chromosome number unknown.

ILLUSTRATIONS. Small, 1895: 37, 39, plate 5, *sub nomine Polygonum newberryi,* plate 6, *sub nomine Polygonum davisiae*; Abrams, 1944: 64, Figure 1468, *sub nomine P. newberryi,* Figure 1469, *sub nomine P. davisiae*; Hitchcock et al., 1964: 162, *sub nomine P. newberryi.* Figures 1C and 1D (epidermal anatomy); Figures 2C, 2D and 2F (pollen); Figure 6 (map).

ECOLOGY AND DISTRIBUTION. *A. davisiae* var. *davisiae* is common in steep subalpine slopes, or on volcanic fell fields with large lava blocks. It is often associated with *Abies lasiocarpa* (Hook.) Nutt., *Eriogonum* spp., *Pinus albicaulis* Engelm., *Lupinus* spp., and *Tsuga mertensiana* (Bong.) Carr. This taxon occurs from Washington through Oregon to California in the United States (Figure 6). The known altitudinal range is 1200–3050 m.

REPRESENTATIVE SPECIMENS. UNITED STATES. **California:** Alpine Co.: Big Tree Road, Silver Valley, *Brewer 1955* (UC: 2 sheets, US); Carson Pass, *Mason 12353* (GH, JEPS, K, MO, NY: 2 sheets, UC); Wood Lake region, above Winnemucca Lake, *Peirson 12800* (UC); Markleville, *Yates 3966* (UC). Butte Co.: Jonesville, *Copeland 629* (GH, K, MO, NY, S, UC, US, WTU). Colusa Co.: Snow Mt., West Peak and Cirque, *Heekard & Hickman 5983* (JEPS). El Dorado Co.: above Lois Lake, Rockbound Valley, Wilderness Area, *Robbins 1795* (GH, UC). Humboldt Co.: Trinity Summit, *Davy & Blasdale 5806* (UC); Slamon Summit, *Tracy 14383* (GH, UC). Lake Co.: Snow Mt., West Peak, *Munz 22307* (NY). Lassen Co.: Mt. Dyer, *Austin s.n.* (NY, US). Mariposa Co.: Shasta, *Congdon s.n.* (UC). Mendocino-Teham Co.: Anthony Peak, *Eastwood & Howell 9855* (UC). Nevada Co.: 1 mile N of Castle Peak, *French 523* (UC). Northern Lake Co.: Mt. Hull, *Hall 9537* (UC). Placer Co.: Truckee, *Bolt 194* (UC). Plumas Co.: Lassen Forest, Lost Creek, *Eggleston 7564* (GH, NY, US); N of Engelmine, *Stebbins & Jenkins 2248* (GH, UC). Shasta Co.: Lassen Volcanic Nat'l Park, summit area of Lassen Peak, *Gillett 310* (GH, S, UC, WTU), *Balls 9081* (BM, S); near the head of Little Hot Spring Valley, *Heller 18282* (MO, NY). Sierra Co.: ½ mile above upper Tamarack Lake, *Kruckeberg 3682* (NY, WTU). Siskiyou Co.: E of Mt. Shasta Ski Bowl Lodge, *Terrell & Holmberg 4190* (US); Mt. Fork, Hoolly Creek, *Butler 187* (UC); Spirit Lake, *Howell 14897* (UC); along Squaw Valley Creek meadows, *Cooke 17664* (MU); Mt. Eddy, *Heller 13429* (NY, US, WTU); S slope of Mt. Shasta, *Turesson & Alm 484* (S, UPS: 2 sheets). Tehama Co.: South Yolla Bolly Mt., Middle Eel-Yolla Bolly Primitive Area, *Munz 16935* (NY, WTU). Trinity Co.: Twinto Thompson Park, *Alexander & Kellogg 300* (UC); Salmon Mts., above Union Lake, *Hall 8691* (UC); ca. 15 miles N of Helena at Papoose Lake, *Spellenberg 5012* (NY). Tuolumne Co.: Dardanelles, *Howden 112* (UC). **Oregon:** Clackamas Co.: S slope of Mt. Hood, 1 mile above Timberline Lodge, *Rossbach 174* (UC). Deschutes Co.: N of North Sister Mts., near MacKenzie Pass, *Hitchcock & Martin 4871* (GH, MO, NY, UC, WTU). Hood River Co.: E slope of Mt. Hood, *Kruckeberg 3997* (NY, WTU). Jackson Co.: Siskiyou Mts., Ashland Peak, *Thompson 12339* (GH, NY, UC, US WTU). Josephine Co.: near summit of Lake Mt., *Baker & Ruhle 331* (NY, WTU). Klamath Co.: Crater Lake Nat'l Park, *Heller 12614* (GH, MO, NY, UC, US, WTU: 2 sheets), *Irvine 515* (BM); Mt. Hood, *Thompson 12299* (GH, NY, UC; 2 sheets, US), *Moldenke 7150* (NY), *Ripley & Barneby 9531*

(NY: 2 sheets), *Mastrogiuseppe 4713* (WS). Marion Co.: on ridge above Jefferson Park, Skyline Trail to Mt. Jefferson, *Dennis & Smith 2256* (GH, NY, WTU); 4 miles S of Mt. Jefferson, *Nelson 2871* (GH). Yakima Co.: Yakima Region, Cascade Mts., *Brandegee, 14873* (MO). **Washington:** Klickitat Co.: without precise locality, *Suksdorf s.n.* (BM, NY). Lewis Co.: Mt. Rainier, *Piper 2112* (GH: 2 sheets, NY, US); Mt. Burroughs, *Jones 10346* (GH, NY). Pierce Co.: Mt. Rainier, *Evans 10603* (MU), *Grant 124* (US); above Goat Pass, *Thompson 11081* (GH, MO, US, WTU: 2 sheets). Skarmania Co.: Mt. St. Helens, *Coville 766* (US). Snohomish Co.: near Twin Lakes, *Broadbent s.n.* (WTU). Yakima Co.: Mt. Adams, *Thompson 11166* (GH, NY, US, WTU); Cascade Mts., near Chinook Pass, *Thompson 15142* (GH, MO, NY: 2 sheets, S, UC, US, WTU); Mt. Goat, *Allen 127* (GH, K, MO, NY, UC, US: 2 sheets); west side of Mt. Peddo, *Suksdorf 6367* (GH, MO, NY, WTU).

3b. **Aconogonon davisiae** (Brewer ex A. Gray) Soják var. **glabrum** (Jones) S.-P. Hong *comb. nov.* *Polygonum newberryi* var. *glabrum* Jones, Rhodora 40: 359. 1938. TYPE: U.S.A., Washington, Olympic Mts., Seven Lakes basin, without date, *Jones 8322* (HOLOTYPE: GH!; ISOTYPE: WTU!).

Stem entirely glabrous; leaves 2.4–5.8 × 1.2–3.2 cm long, sublustrous on both sides, usually acute, rarely more or less obtuse, usually rounded, rarely truncate at the base, entirely glabrous on both sides including the margin; petiole glabrous 0.5–15.0 mm long; ochrea 0.8–1.5 cm long, glabrous; pedicels 0.6–1.4 mm long; tepals 2.9–3.6 × 1.0–2.0 mm; filaments 0.3–1.0 mm long; anthers 0.3–0.5 mm long. Chromosome number $2n = 20$ (information from the label of Kruckeberg, collection *5039*).

ILLUSTRATIONS. Hitchcock et al., 1964: 162, *sub nomine Polygonum newberryi* var. *glabrum.* Figure 6 (map).

ECOLOGY AND DISTRIBUTION. *Aconogonon davisiae* var. *glabrum* grows on open rocky mountain sides, talus slopes or at the edges of raw serpentine outcrops. This variety is associated with *Pinus albicaulis* Engelm. and *Abies lasiocarpa* (Hook.) Nutt. It is distributed from Washington (Chelan Co., Clallam Co. and Kittitas Co.) and northern California, and probably in Oregon as well; however, I have seen no collections from Oregon so far (Figure 6). The known altitudinal range is 1050–2150 m.

REPRESENTATIVE SPECIMENS. UNITED STATES. **California:** Siskiyou Co.: Caribou Lake, Salmon-Trinity Alps Primitive Area, *Wiggins 13540* (NY, UC). Trinity Co.: bordering headwaters of Deer Creek, in shadow of Granite Peak, on trail to Deer Lake, *Kruckeberg 3758* (NY). **Washington:** Chelan Co.: Mt. Stuart region, *Thompson 5830* (GH, MO, WTU). Clallam Co.: Olympic Mts., Bogachiel Ridge, headwaters of the Hoh River, *Rollins & Chambers 2703* (GH, UC, US). Kittitas Co.: Mt. Stuart region, near head of Beverly Creek, *Thompson 8760* (GH, MO, NY, UC, US, WTU); Trail to Ingalls Lake, above N Fork Teanaway River, *Kruckeberg 5039* (UC).

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FOREST HISTORY AND COMPOSITION OF HALFWAY POND ISLAND, PLYMOUTH COUNTY, MASSACHUSETTS

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ABSTRACT

The forest on a 6 hectare island in Halfway Pond is dominated by *Fagus grandifolia, Tsuga canadensis* and *Pinus strobus.* This composition contrasts with the vegetation around the pond, which is predominantly *Pinus rigida* and *Quercus ilicifolia.* Most large trees on the island are 150–200 years old, with a few 300-year-old *Nyssa sylvatica.* Growth ring analyses indicate that a hurricane in 1944 was the most significant disturbance event in the last 130–150 years. Additional evidence suggests that the present composition and structure of the island forest reflect selective logging of large trees in the 18th and early 19th centuries.

Comparisons of the island's flora with fossil pollen spectra from nearby sites (Patterson and Backman, 1988) suggest that the distinctive vegetation on Halfway Pond Island has been maintained for centuries and is not representative of regional pre-settlement forests, which were predominantly white pine and oak. Fire has probably always been less frequent on the island than on the surrounding landscape, a factor that would account for these differences in composition.

Key Words: 1944 hurricane, fire, forest history, fossil pollen, southeastern Massachusetts

INTRODUCTION

The unusual natural history of Halfway Pond Island (Plymouth County, Massachusetts) has been locally recognized for many decades. Tall forests of beech (*Fagus grandifolia* Ehrh.), hemlock (*Tsuga canadensis* (L.) Carr.), and white pine (*Pinus strobus* L.) that cover the 6 hectare island stand in sharp contrast to the pitch pines (*Pinus rigida* Mill.) and scrub oaks (*Quercus ilicifolia* Wang.) of the pine barrens around the pond. These differences have led to claims that the island "contains what is believed to be one of the oldest forests remaining in Massachusetts" (Nature Conservancy, 1982). Several reports describe the flora and fauna of the island (Lloyd-Evans, 1975; Richardson, 1976, *see* reference below). The site was acquired by The Nature Conservancy in 1978, and has been proposed for designation as a National Natural Landmark (Worley, 1980, *see* reference below).

Richardson (1976 unpubl. rpt., National Park Service) considered the island to be "an undisturbed representation of the original forest type" found in the surrounding Myles Standish pine barrens. This pre-settlement vegetation was extensively modified by agricultural land clearance, logging and fires (Patterson and Backman, 1988). Worley (1980 unpubl. rpt., National Park Service) questioned the characterization of the island's vegetation as unspoiled and pristine, pointing out cut stumps as evidence of past disturbance.

This study reconstructs the recent forest history of Halfway Pond Island through analyses of forest composition, structure, age and growth rates. In particular, I sought to determine whether the forest was an old-growth remnant of the pre-settlement vegetation of this region.

STUDY AREA

Halfway Pond Island is located in the center of Halfway Pond, a 110 ha kettlehole pond at the eastern edge of Myles Standish State Forest (Lat. 41°51′N, Long. 70°37′W). Most of the island is less than 2 m above water level, although a 5-m-high ridge runs along the south end (Figure 1). The soils are typically coarse and well-drained, characteristic of the glacial outwash that covers much of this area. About a hectare of the island is very close to pond level, and has swampy, poorly drained conditions.

The pond lies within the pitch pine-oak vegetation type (Westveld et al., 1956) characteristic of much of southeastern Massachusetts. The island is heavily forested, primarily by more mesic taxa such as beech and hemlock; the understory is generally open, with a sparse herbaceous layer. A dense shrub stratum occurs primarily only in the swamp.

METHODS

Forest composition was described from 8 east-west cross island transects. Each transect was separated from adjacent transects by 50 m. Point-centered quarter (PCQ) sampling of trees >10 cm dbh (diameter at breast height) was carried out at 10 m intervals along each transect. The dbh, distance, and species of the nearest tree in each of the four quarters was recorded (Cottam and Curtis, 1956). The frequency of understory species was measured by placing a 1-m-square quadrat at each point and recording the presence of all species within.

Forest history and age determinations were made by examining growth rings on increment cores collected from selected trees throughout the island (Figure 1). One core from each of 56 trees of 10 different species had been collected in 1981 by Ian Worley. This study used Worley's cores, supplemented by the maps and field notes that accompanied them, but all interpretations and analyses are my own. Cross-dating of these increment cores between trees on the island was generally possible for only a few decades before the present. With only one core per tree, I was unable to date most cores precisely through periods of suppressed growth, vague rings, and other growth irregularities.

Age determinations were made by counting to the innermost visible ring, estimating the number of additional rings to the center of the tree based on growth rates of the innermost rings, and adding a further correction (usually 8–25 years) for growth to the height at which the tree was cored. These two corrections introduce some uncertainty in age estimates for many specimens, although I judge that most ages are accurate to within ±15 years.

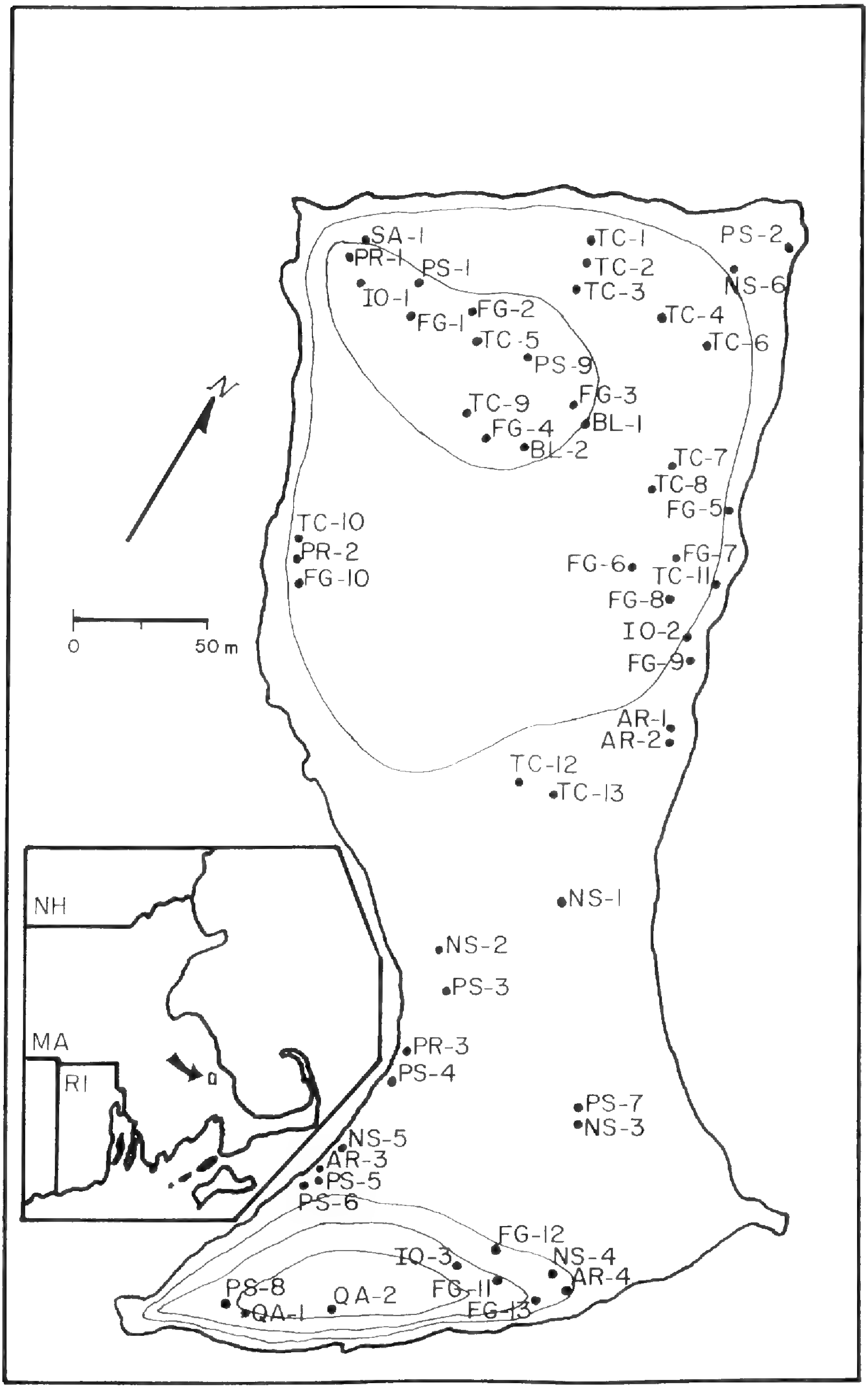
RESULTS

Forest Composition

Of the 16 tree species recorded on Halfway Pond Island, 12 were encountered at the 59 PCQ sampling points (Table 1). Other tree species which have been reported on the island include *Betula lenta* L., *B. populifolia* Marsh., *Prunus serotina* Ehrh. and *Quercus rubra* L.

The dominance of beech in the forest is emphasized in the frequency, density, basal area, and importance values of trees (Table 1). Beech ranks first in all four measures for trees >10 cm dbh. Evidence of beech-bark disease (*Nectria coccinea* var. *saginata* Lohman, Watson & Ayers) is present on some of the larger trees. Hemlock, red maple (*Acer rubrum* L.), white pine, tupelo (*Nyssa sylvatica* Marsh.) and yellow birch (*Betula lutea* Michx. f.) are the other dominant taxa, collectively comprising 95% of the basal area. In the understory, only *Clethra alnifolia* L. and *Maianthemum canadense* Desf. occurred frequently; they were found in 11 and 15 percent of the quadrats, respectively.

No data were collected to quantify dead and down wood. However, fallen snags, broken tops, and conspicuous tip-up mounds from uprooted trees attest to a history of windstorm damage,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TC-4
TC-6
TC-9
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IO-3
NS-4
AR-4
PS-8
QA-1
QA-2
FG-11
FG-13

Table 1. Summary of point-centered quarter data for all trees >10 cm dbh.

Species	Frequency	Density (trees/ha)	Basal Area (m/ha)	Relative Frequency	Relative Density	Relative Cover	Importance Value
Tsuga canadensis	58	124	8.67	22.5	22.9	28.5	73.9
Fagus grandifolia	76	205	11.37	29.8	37.7	37.4	104.9
Pinus strobus	20	35	4.13	7.9	6.4	13.6	27.9
Acer rubrum	32	62	2.04	12.8	11.4	6.8	31.0
Nyssa sylvatica	31	53	1.79	11.9	9.8	5.9	27.6
Betula lutea	15	32	.87	5.9	5.9	2.9	14.7
Ilex opaca	3	5	.06	1.3	.8	.2	2.3
Pinus rigida	3	5	.47	1.3	.8	1.6	3.7
Quercus alba	3	5	.18	1.3	.8	.6	2.7
Quercus velutina	5	7	.65	2.0	1.3	2.1	5.4
Sassafras albidum	7	9	.18	2.6	1.7	.6	4.9
Hamamelis virginiana	2	2	.03	.7	.4	.1	1.2
Overall		544	30.44				

especially to larger trees on the island. The northerly orientation of many fallen trees and mounds indicate that south winds account for much of this damage. The presence of occasional sawn stumps and logs of various sizes suggest that some wood has been removed from the island.

Age and Growth of Trees

Tabulations of age estimates and sizes for the 56 cored trees indicate that the oldest trees on the island are not the largest (Table 2). Two tupelos (NS-1, NS-6) had diameters of 48 and 62 cm and were estimated to have germinated in the late 1600's. Several other tupelos of similar sizes occur on the island and probably are also around 300 years old.

A gnarled, 15-m-tall white oak (*Quercus alba* L.) along the south ridge was the third oldest tree, dating back to the early 1700's (QA-1). The oldest beech, which also occurs on this ridge, is a stout, stunted tree about 180 years old (FG-12). Other beeches

←

Figure 1. Topographic map of Halfway Pond Island, showing the approximate locations of the 56 cored trees. Contour interval is 2 meters. Species and age information are on individual trees listed in Table 3. Abbreviations are first letters of genus and species.

Table 2. Summary data of cored trees. Locations mapped in Figure 1. The approximate uncertainty in the germination date estimates can be determined by combining the number of years added to estimate the pith date and the estimated age at coring height. Species are coded by first letters of genus and species from Table 1.

ID Code	Diameter (cm) From Core	Diameter (cm) From Tree	Coring Height (cm)	Innermost Ring	Estimated Pith Date	Core Height Age	Germination Date
FG-1	45.4	47.5	51	1843	1838	15	1823
FG-2	35.0	41.7	48	1867	1862	15	1847
FG-3	31.0	31.5	36	1934	1930	10	1920
FG-4	35.0	38.1	46	1909	1909	14	1895
FG-5	48.8	64.5	38	<1878	1850	11	1839
FG-6	>46	42.9	43	1862	1855	13	1842
FG-7	29.4	32.3	61	1873	1860	18	1842
FG-8	30.0	25.4	30	1927	1900	9	1891
FG-9	36.0	59.9	56	1858	?	17	<1841
FG-10	53.2	55.9	61	1851	1840	18	1833
FG-11	39.0	41.7	46	1847	1845	14	1831
FG-12	32.6	43.2	132	1869	1850	40	1810
FG-13	51.4	51.3	51	1852	1842	15	1827
TC-1	52.8	56.6	61	1854	1830	18	1812
TC-2	25.4	25.7	38	1851	1830	11	1819
TC-3	17.6	15.7	30	1934	1930	9	1921
TC-4	68.4	71.6	38	1831	1815	11	1804
TC-5	29.4	37.6	36	1868	1860	11	1849
TC-6	66.4	69.9	61	1851	1830	18	1812
TC-7	22.8	25.4	30	1921	1921	9	1912
TC-8	14	13.7	30	1946	1946	9	1937
TC-9	44	59.7	46	1873	1860	14	1846
TC-10	64	71.9	91	1816	1800	30	1770
TC-11	40.8	46.5	38	1848	1843	11	1832
TC-12	64.8	70.1	66	1813	1805	20	1785
TC-13	>74.6	N.R.	N.R.	1827	≪1820?	20?	<1800
PS-1	60	72.6	61	1874	1860	10	1850
PS-2	62	76.2	46	<1873	1860	8	1852
PS-3	73.6	89.4	74	1860	1850	13	1837
PS-4	66	68.1	61	1836	1830	10	1820
PS-5	44	58.4	51	1851	1845	9	1836
PS-6	49	50.3	51	1864	1860	9	1851
PS-7	39.4	55.4	71	1850	1835	12	1823
PS-8	63	71.6	51	1858	1850	9	1841
PS-9	43	48.3	46	1950	1950	8	1942
PR-1	43.6	45.7	38	1839	1837	10	1827
PR-2	48	51.8	61	1848	1845	18	1835
PR-3	68	67.6	61	1824	1818	18	1800
IO-1	24	24.9	46	1862	1858	15	1843

Table 2. Continued.

ID Code	Diameter (cm) From Core	Diameter (cm) From Tree	Coring Height (cm)	Innermost Ring	Estimated Pith Date	Core Height Age	Germination Date
IO-2	26	N.R.	N.R.	1854	1848	8	<1840
IO-3	12	12.7	36	1914	1914	12	1902
QA-1	54	68.6	61	1773	1740	20	1720
QA-2	51	62.0	91	1849	1830	28	1802
NS-1	42	48.5	74	1735	1720	26	1694
NS-2	55.0	48.0	56	1850	1842	20	1822
NS-3	21.0	28.4	61	1854	1845	22	1823
NS-4	22.0	33.3	46	1870	1860	17	1843
NS-5	27.6	33.8	41	1873	1860	16	1844
NS-6	62.0	62.5	46	1691	1687	17	1670
SA-1	27.4	35.6	36	1860	1860	15	1845
BL-1	9.7	10.2	10	1956	1956	4	1952
BL-2	18.4	17.8	5	1946	1945	2	1943
AR-1	18.8	24.4	30	1949	1949	8	1941
AR-2	17.0	21.6	30	1948	1945	8	1937
AR-3	40.0	38.6	51	1837	1832	14	1818
AR-4	30.0	33.8	51	1860	1854	14	1840

exceeding 50 cm in diameter are not uncommon on the island. Individuals 40–60 cm dbh were usually 150–160 years old. The tallest trees, estimated to be 25–30 m, are the hemlocks and white pines. The oldest hemlocks appear to have germinated in the late 1700's (TC-10, TC-12, TC-13). White pines grow faster than the hemlocks, and none was found that became established before 1820. The largest pine was 89.4 at a height of .75 m, but was only about 150 years old (PS-3).

As with white pines and beeches, ages estimated from ring counts of large individuals of other species, including pitch pine, holly (*Ilex opaca* Ait.), sassafras (*Sassafras albidum* (Nutt.) Nees) and red maple, all yielded germination dates between 1800 and 1850 (Table 2).

DISCUSSION

Four types of information were used to identify the nature and date of disturbance events in the history of the Halfway Pond Island forest: 1) historical records, 2) field evidence in the form of tip-up mounds, uprooted or snapped trees, sawn logs and stumps, 3) inferences based on forest composition, size, age, and structure, and 4) changes in growth rates of trees determined from increment cores.

Historical Records

Steinway (1967) provided information regarding some of the earliest disturbance on the island. "Halfway Pond . . . has an island where large pine trees used to grow untouched by the forest fires that periodically ravaged the surrounding land. These trees were much prized in the 17th and 18th centuries for masts, and many were cut for the King's Navy as well as for local shipbuilders along the seacoast. The island . . . was once heavily wooded by beech, spruce, hemlock, and pine of immense size. The hurricane of 1938 took its toll of the virgin forest. Some of the fallen trees were lumbered and eventually 90 cords of firewood were taken off over the ice."

Allen (1981 unpubl. rpt., The Nature Conservancy) provided additional information regarding the recent storms. Trees in the area of the shrub swamp were "thought to have been damaged in 1938, while the trees at the northeast corner of the island and in the small clearing [near the north end] are thought to have been felled in 1944." She goes on to suggest that the 90 cords of wood, largely from downed trees, were removed following the 1944 hurricane.

Photographs provided by LeBaron Briggs documented the extensive damage from the September 14–15, 1944 storm, a hurricane whose path crossed almost directly over the pond. Photographs dated March, 1946 show extensive piles of wood cut to firewood dimensions stacked against many of the trees; another photograph shows a large pile of saw logs approximately 7 m long stacked along the shoreline.

Effects of the 1944 Hurricane

Evidence from the forest appears largely to confirm and augment these historical accounts. Steinway's (1967) description of large beech, hemlock, and, presumably, white pine continues to characterize the present dominant tree species, although her inclusion of spruce is doubtful. Tip-up mounds and fallen logs with

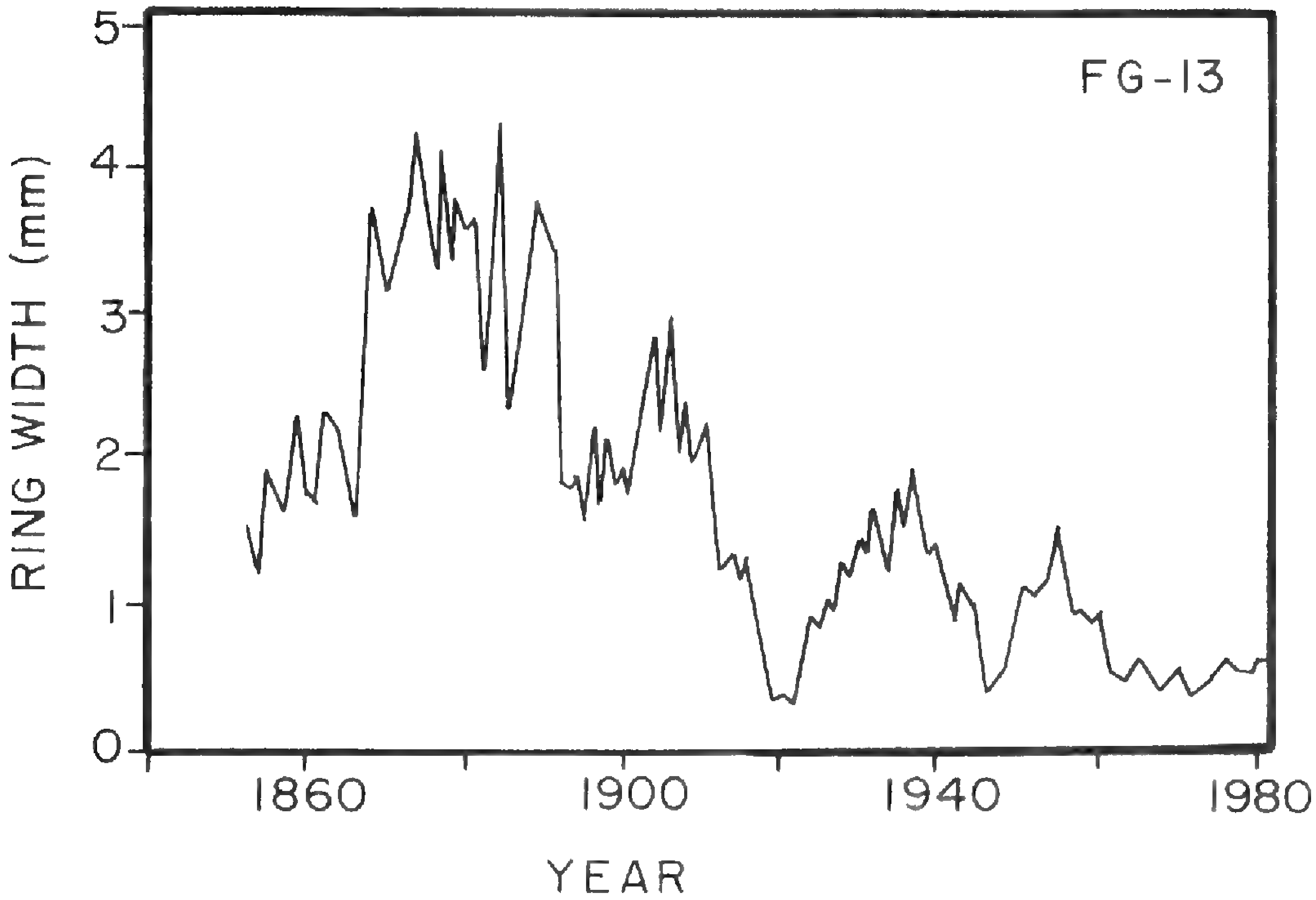

Figure 2. Ring widths from a beech tree, core FG-13, illustrating periods of suppressed growth beginning in 1945 and 1918, and a period of growth release about 1865.

an orientation of 350–360° occur frequently throughout much of the island. The condition of these features is generally in accord with a storm event dating 40–50 years ago. Sawn logs, and stumps often with a northward lean, also suggest salvaging of tipped and fallen trees followed this event.

Two opposite effects were noted among trees that survived the 1944 hurricane. A sharp reduction in the width of the 1945 ring, often followed by 3 to 7 additional narrow rings, was present among many white pines, hemlocks, beeches and some red maples, but only among individuals whose diameter in 1944 was >35–40 cm (Figure 2). Trees of this size probably were at, or emergent from, the canopy at the time of the storm and would have been the most likely individuals to suffer extensive breakage of limbs and snapping of roots due to excessive swaying. This damage would have resulted in a reduction in photosynthetic area and/or nutrient/water uptake, causing the observed reduction in growth.

An opposite effect was noted in trees whose diameter at the time was <15 cm (Figure 3). A large increase in growth, beginning in 1945, occurred among many of these small trees. The radial growth of hemlocks increased 4–8 times, and that of beeches as

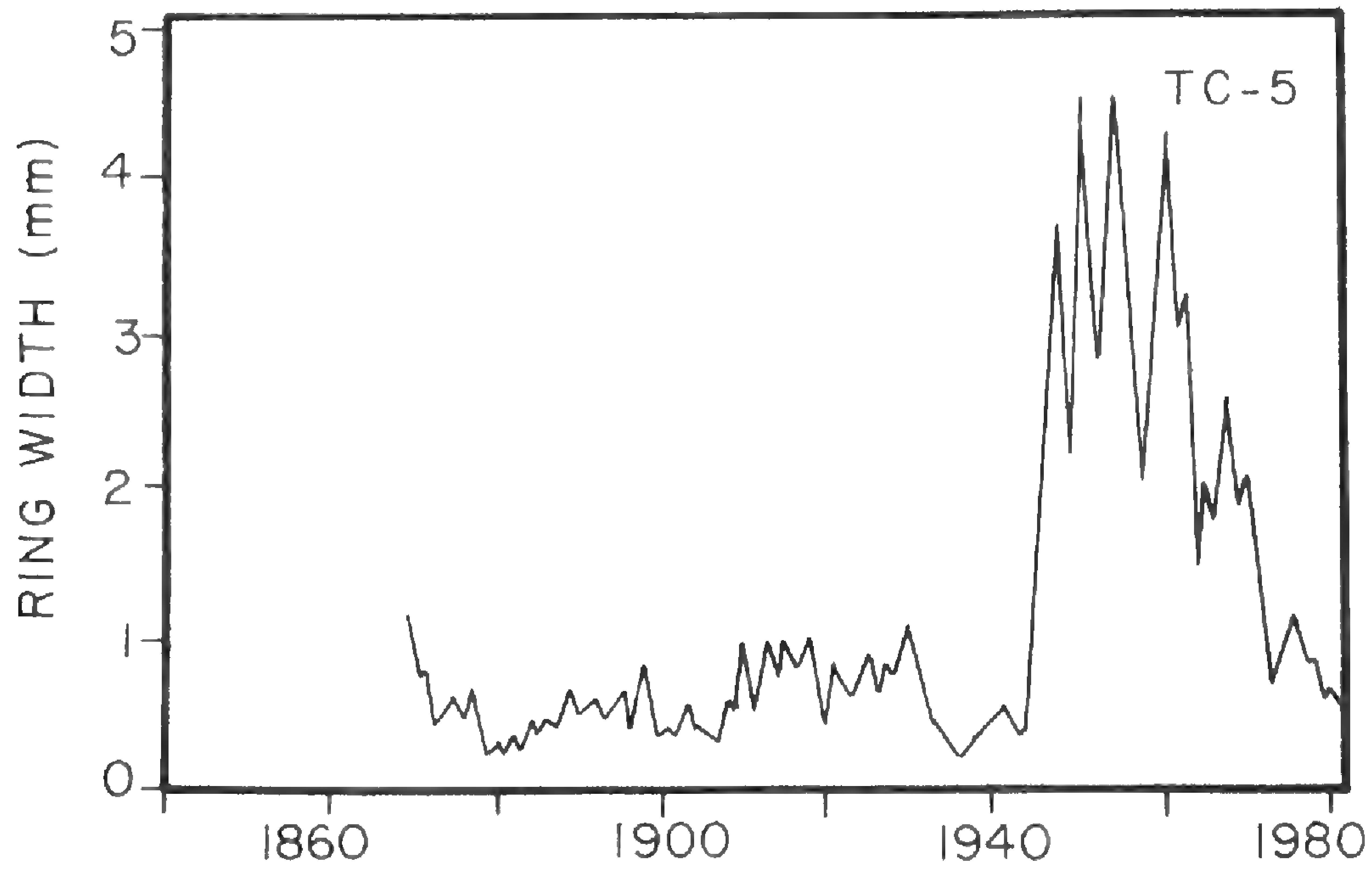

Figure 3. Ring widths from a hemlock tree, core TC-5, showing released growth following the 1944 hurricane.

much as 10–20 times the rate prior to 1944. Size rather than age appeared to be the factor that determined which trees would respond in this manner. Trees up to 100 years old that had been suppressed in the forest understory exhibited the same type of increase as younger individuals.

These abrupt changes in growth rates in 1945 were observed on 31 of the 56 individuals cored throughout the island. This pattern indicates that although historical reports of concentrated damage at the north end of the island may be accurate, ecologically significant impacts on both canopy and understory trees were widespread. The presence of saplings dating to the mid-1940's suggests that the 1944 hurricane also produced some regeneration on mineral soil exposed by upturned root systems.

Pre-1944 Disturbance Events

All cores were examined for growth ring patterns similar to those produced by the 1944 storm in order to determine the frequency of such occurrences in this forest. No effects could be seen in the cores that indicated significant effects from the 1938 hurricane. I suggest that this storm had relatively little impact on the island as a whole. Three other possible storm events were noted. Six large white pines show a significant reduction in growth beginning in 1955, and continuing for 2–7 years. Two hurricanes (Carol and Edna) passed through southern New England in August and September, 1954 and may have caused some damage to these trees.

Twelve trees, especially several beeches at the south end of the island, show pronounced growth reductions for 4–10 years beginning about 1918 (Figure 2), perhaps resulting from a large storm passing along the east coast on September 17–18, 1917 (Ludlum, 1986). A possible third event occurred about 1865, when 5 trees show a marked increase in growth that persisted for several decades (Figure 2). These were small trees at that time, and may have been released by a blowdown or logging that removed nearby individuals that had been suppressing their growth. From these results, it appears likely that the 1944 hurricane produced the greatest effects of any single storm on the island during at least the last 130–150 years.

Several lines of evidence suggest that some factor(s) removed large trees in the early- to mid-1800's, creating a relatively open forest at that time. First, only 6 of the cored trees germinated prior to 1800—3 hemlocks, 2 tupelos and a white oak. The scarcity of hemlocks exceeding 180 years old suggests that hemlock may have been selectively removed. Hemlock can live to 400–500 years, and the presence of much older tupelos suggests that a catastrophic disturbance did not destroy the entire forest during the period 175–300 years ago. Second, all the large white pines date from the first half of the 19th century. This species grows best in relatively open forest conditions, and all of the pines exhibit the extremely high growth rates typical of trees growing in the open. Third, the average growth rates of hemlocks and beeches during the mid-1800's, when they were young trees, are 3 to 6 times greater than comparable young trees growing in the forest 50 years later. This much higher growth rate is likely due to higher light levels in an open forest during the mid-1800's. Finally, the absence of old yellow birch, a species found as young trees growing on tip-up mounds in canopy gaps on the island today, may indicate that a different disturbance mechanism produced the open forest at that time.

Evidence suggests that the logging of large pines in the 17th and 18th centuries, cited by Steinway (1967), may have continued into the early 19th century and included large hemlocks and other merchantable species. Smaller, less valuable species such as tupelo, and gnarled trees such as the oak and beech along the exposed south ridge, were probably left uncut and account for the presence of older individuals of these species today.

The abundance of tip-up mounds throughout much of the island is another striking contrast with the landscape surrounding the pond. Although mounds cannot be used to date windthrow events precisely, they collectively indicate the importance of this type of disturbance among large trees. This difference with the terrain around the pond is further evidence for a long history of different vegetation and land use on the island, where trees reached sizes capable of producing large mounds when they fell.

I found no charred logs or fire scars on any trees on the island. Significant differences should occur in the abundance of charcoal in soils from on and off the island. Fires that may have started on the island probably were of low intensity, given the moister conditions and general lack of surface fuels, and would have little impact on the vegetation.

Comparisons with Pre-settlement Forests

Although documentation of these past disturbances to the island's forest challenge representations of the flora as "virgin," these data alone do not refute the possibility that this forest is similar in composition to the pre-European settlement vegetation. Fossil pollen studies of two ponds 5–8 km from Halfway Pond suggest that pre-settlement forests were dominated by oak and white pine (Patterson and Backman, 1988). Additional important species in the pollen record included hickory, beech, hemlock, and elm.

Comparisons of the present Halfway Pond Island vegetation with the pre-settlement record reconstructed from fossil pollen reveal important differences (Table 3). The percentages of beech, hemlock, red maple, tupelo, and yellow birch are considerably higher than represented by the pollen record, even when differential pollen productivity is taken into account. Similarly, black and white oak are much less abundant than would be expected if the island's vegetation were representative of pre-settlement forests. These differences suggest that the island's forests may have contrasted with surrounding areas even prior to European settlement.

Patterson and Backman (1988) suggested that occasional fires

Table 3. Comparison of Halfway Pond Island forest composition and pre-settlement forest taxa from fossil pollen.

Species	Island Trees*	Pre-settlement Pollen**
Fagus grandifolia	37.4	2–5
Tsuga canadensis	28.5	<5
Pinus strobus	13.6	20–25
Acer rubrum	6.8	<1
Nyssa sylvatica	5.9	<3
Betula lutea	2.9	0
Quercus spp.	2.7	30–40
Pinus rigida	1.6	<5
Carya spp.	0	<5
Ulmus spp.	0	<3

* Relative percent basal area of dominant island trees (from Table 1).

** Approximate percentages of arboreal pollen taxa prior to about 1700 A.D. (from Figures 3 and 4, Patterson and Backman, 1988).

were important in maintaining the pre-colonial pine-oak forests around the pond. Fires peripheral to the pond appear to have held succession at an earlier stage than on the island, where a more mesic, later successional vegetation developed because of less frequent fires and moister conditions. Thus large individuals of fire intolerant species such as hemlock and beech occurred more frequently on the island.

Around the pond, the scrub oak-pitch pine barrens were encouraged by colonial settlement, land clearance and a probable increase in more intense fires. These activities further increased the contrast between the island's forest and the surrounding landscape. Selective logging of merchantable timber on the island prior to 1850, as well as occasional storms, have allowed early successional species, especially white pine and red maple, to remain important components in the forest. Thus the vegetation today is not an undisturbed, old-growth stand, similar in composition to the regional pre-settlement forests. Rather, it is a product of both human and natural events imposed on a site that has remained free of fire to a much greater extent than any of the surrounding forests.

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LOST FARM
HUMMOCK POND ROAD
NANTUCKET, MA 02554

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FLORA OF THE MONOMOY ISLANDS CHATHAM, MASSACHUSETTS

J. P. LORTIE, B. A. SORRIE, AND D. W. HOLT

ABSTRACT

The flora of the Monomoy Islands has been sporadically investigated from 1932 to 1989. Previous plant species lists and herbarium vouchers were reviewed and compared to floral inventories during 1981, 1983, 1984, 1985, and 1989. A master plant list was then developed that noted the abundance and general distribution of each plant species, as well as possible misidentifications from previous studies.

Key Words: barrier beach flora, Monomoy National Wildlife Refuge, Massachusetts

INTRODUCTION

The Monomoy Islands are part of the 1317 ha Monomoy National Wildlife Refuge, administered by the U.S. Fish and Wildlife Service. The refuge, which includes North Monomoy Island (North Island), South Monomoy Island (South Island), and portions of Morris Island, is located at the "elbow" of Cape Cod in the town of Chatham, MA, and extends south 13 km into Nantucket Sound (Figure 1). New islands accreting west of this area, up to a declaration of taking line in Nantucket Sound, will also become part of the refuge. These barrier islands were created by the littoral drift of unconsolidated glacial deposits from the sea cliffs of Eastham and Wellfleet (Giese, 1981).

The Monomoy Islands are part of the extremely dynamic outer coast of Cape Cod that is continually modified by wave, wind, and tidal action. Over hundreds of years these islands have evolved from a submerged sandbar to an extension of the mainland. This barrier island system contained distinctive arcuate dune ridges on the downdrift portion of the system (southern South Island) and erosional features updrift, during our study period. These included dune scarping and washover fans on North Island (Leatherman, 1979). The southern third of South Island has been slowly increasing in size. However, the North Island and the northern portion of the south Isalnd have undergone some major changes during the last 200 years (Giese, 1981).

The Inward Point and Hospital Pond areas (Figure 1) have changed considerably since the mid-nineteen sixties when Moul

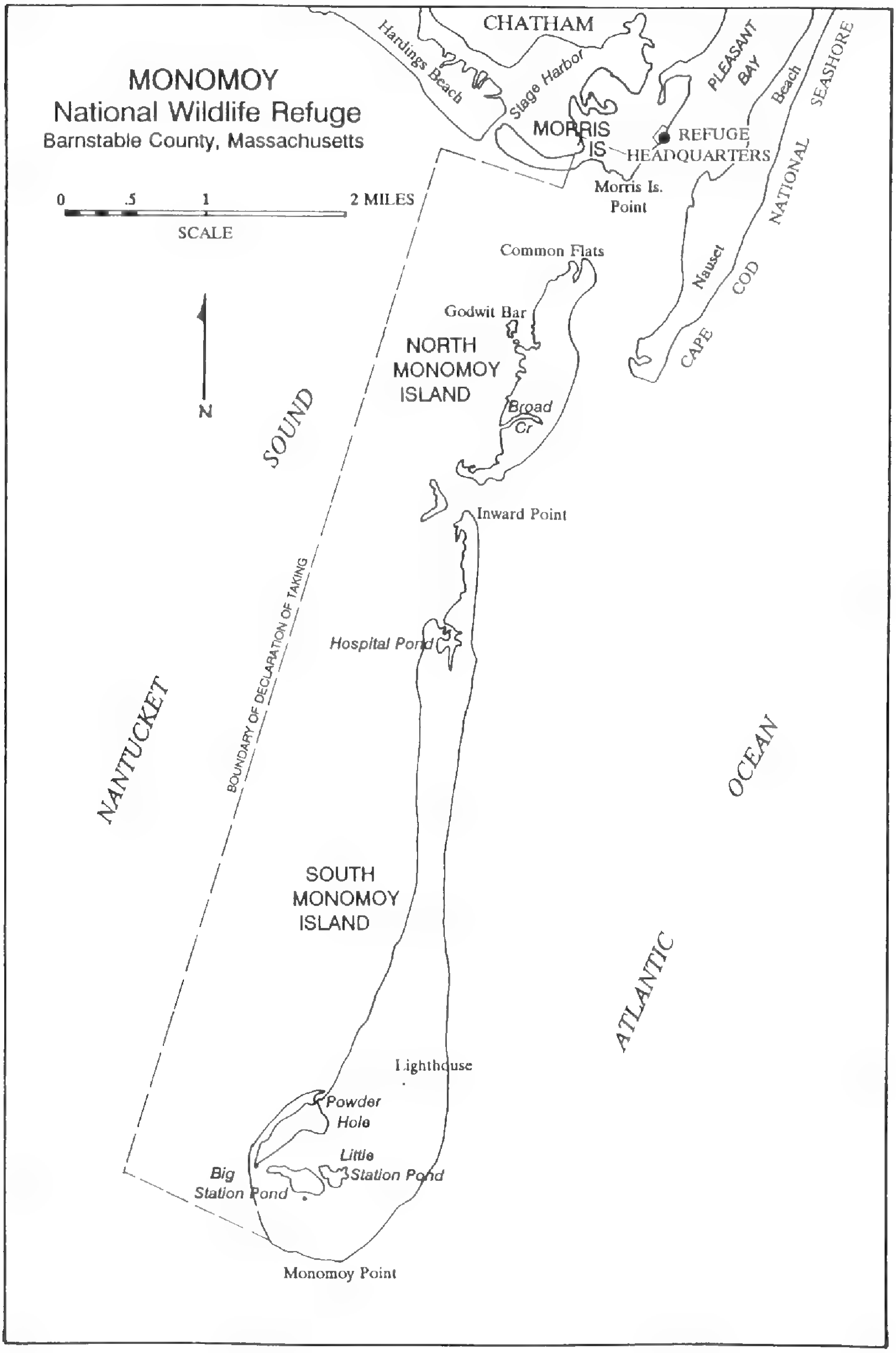

Figure 1. Monomoy National Wildlife Refuge, Chatham, Massachusetts.

(1969) was investigating Monomoy's flora. He reported that the most mature vegetation of the island (there was only one island then) was located in these areas, including a large freshwater marsh. The surrounding thickets than contained examples of most of the island's vegetation. A powerful northeast storm washed over this area in 1978 and destroyed almost all of the freshwater marsh and woody thickets. Surging waters from the storm cut a channel through the island into Nantucket Sound which persists today.

South Island contains many natural and several man-made fresh and brackish-water ponds, which vary in size from 1 ha to 27 ha. The plant communities on this island are much more diverse than those of North Island. According to the Cowardin et al. (1979) wetlands classification system the islands contain 322 ha in marine systems, 11 ha in lacustrine systems, 44 ha in palustrine systems, and 143 ha in estaurine systems. There are an additional 709 ha of drier habitat, consisting of primary and secondary dunes.

The flora of the Monomoy Islands has been reported on a number of times from 1954 to the present (Cross and Cross, 1954 unpubl. list; Bailey, 1965; Moul, 1969; Massachusetts Audubon Society, 1972; Schrot, 1985). The earliest Monomoy specimen of which we are aware dates from 1932. No specimens are available as vouchers for species listed in the 1954 and 1965 reports, but we have examined all of those of Moul (at SPWH) and those of the Massachesetts Audubon Society (collected by H. K. Svenson and W. Bailey, at NEBC).

Our objectives are to summarize all previous investigations, describe the vegetation of the islands during the summers of 1981, 1983, 1984, and 1985, and compile a master plant list. We feel that the synthesis of previous and current floristic work is important for three reasons: 1) to gather into one publication material which is now scattered and in some cases unavailable; 2) to provide a basis for future comparative work in a dynamic ecosystem; and 3) to document the flora as it currently exists as an aid to future management decisions. As Moul (1969) indicated, the flora of islands changes with time; new species appear, others disappear, and the distribution and abundance of each species varies. Our list contains species we documented from 1981 to 1989, species which were reported in previous years that may still occur but were not found during our survey, and taxa which represent possible misidentifications from other investigations.

Morris Island has been excluded from consideration, due to its direct connection to the mainland and the large number of mainland species found there. Our list more than doubles the number of species listed by Moul (1969), heretofore the most accessible reference on Monomoy's flora.

METHODS

The Monomoy Islands were surveyed during the summers of 1981, 1983, 1984, and 1985. A few additional species were documented in a brief visit to North Island, 1989. Broad vegetational community types were identified on both islands and then transected as completely as possible on foot by criss-crossing through each area. Special attention was given to unusual habitats as sources of overlooked species. Areas surrounding the South Island ponds contained the greatest plant diversity, therefore more time was spent examining them. Each community type was inventoried at least once each month from May to September during 1983 and 1984. Sampling occurred less frequently in 1981 and 1985. Herbarium vouchers were collected and deposited in the personal herbarium of J. Lortie. Vouchers were collected for approximately sixty percent of the species on the Master Plant List.

In the Master Plant List, the dates 1954, 1965, 1969, and 1972 refer to previous workers' lists, unless otherwise stated. The date 1985 includes observations by Schrot (1985) as well as the current authors. In order to reduce confusion and enhance direct comparisons among the various species lists, nomenclature used in the Master Plant List is that of Fernald (1950).

Plant species lists from previous botanical investigations were obtained from literature searches and supplemented by data extracted from the herbarium of the New England Botanical Club (NEBC), the Gray Herbarium (GH), and the G. M. Gray Herbarium at the Marine Biological Laboratory (SPWH). The 1954 unpublished plant list by S. G. Cross and C. E. Cross was provided by Marcia G. Norman.

Each species on the Master Plant List was accorded one of the following designations: cultivated, rare, occasional, common, or abundant (Table 1). The general habitat of each plant species was listed by broad plant community types including: beaches and sandspits, primary dunes, secondary dunes, salt marshes, permanent ponds, seasonal ponds, and bogs.

Table 1. Plant species status designations and definitions.

Designation	Definition
Cultivated	Planted by humans
Rare	Observed on the islands less than five times
Occasional	Occurs locally, not expected to be seen in a day trip
Common	Expected to be seen in a day trip
Abundant	Occurs throughout a major portion of the islands

Beaches and sandspits included sparsely vegetated areas occurring from mean high water inland up to primary and secondary dunes and/or salt marshes. These areas were greatly influenced by wind, wave, and tidal action, and were the most dynamic community type on the islands. Washover areas were included in this community.

The easternmost dune complex on the islands is regarded as primary dune. These areas were mainly modified by storm surges and aeolian erosion. Secondary dune areas included all inner or western dunes and contained several plant community types. Major secondary dune modifications included aeolian erosion and nesting herring gulls (*Larus argentatus*) and great black-backed gulls (*Larus marinus*).

Salt marsh communities included tidal flats and drainage channels, and regularly and irregularly flooded marsh. The daily tidal cycle, flooding range, and sediment transport determined the distribution of this community type on the islands.

Permanent ponds were defined as continually flooded, open and semi-open water bodies. These ponds did not dry up during the summer, whereas seasonal ponds usually did. Seasonal ponds included cranberry swales, wet marshy swales, and wet thickets. Precipitation and storm surges were the dominant modifiers of permanent and seasonal ponds. High seas, usually associated with severe storms, can erode primary dunes and flood some seasonal ponds, an occurrence observed in 1983 and 1984. Low wet areas dominated by sphagnum moss are regarded as bogs; these areas did not dry up during the summer.

PLANT COMMUNITY DESCRIPTIONS

The eastern beaches and sandspits on both islands contained the youngest plant communities. These area were sparsely populated with *Cakile edentula* (Bigel.) Hook., *Solidago sempervirens* L. and *Xanthium strumarium* L. The western beaches, which were protected from the open ocean, contained a more developed plant community. In these areas, besides the above mentioned species, *Lathyrus japonicus* Willd., *Atriplex arenaria* Nutt., *Salsola kali* L. and *Arenaria peploides* L. predominated. Following the blizzard of 1978 that split Monomoy Island in two, extensive new sandspits formed at the Inward Point area (Figure 1). *Ammophila breviligulata* Fern. was slowly colonizing portions of these spits that were above mean high water.

The dominant plant on both islands was *Ammophila breviligulata* Fern., which covered almost all of the primary dunes and a substantial portion of the secondary dunes. Common associates of *Ammophila* in the primary dunes were *Solidago sempervirens* L., *Chrysopsis falcata* (Pursh) Ell., and *Lathyrus japonicus* Willd. Owing to the dynamic nature of these barrier islands, many of the primary dunes on North Island and the northern third of South Island were actually secondary dunes at one time. Erosion of the outer primary dune resulted in these areas becoming the easternmost dune system. Therefore some of these areas contained species characteristic of secondary dunes, including *Myrica pensylvanica* Loisel., *Prunus maritima* Marsh., and *Rosa rugosa* Thunb.

The secondary dune system supports the most extensive community on the islands. Relatively stable areas within *Ammophila breviligulata* communities supported thickets of *Myrica pensylvanica, Rosa rugosa, Rhus radicans* L. and *Prunus maritima.* A large portion of this dune system north and south of the lighthouse was dominated by *Hudsonia tomentosa* Nutt., *Lechea maritima* Leggett and a lichen (*Cladonia* sp.). These gently undulating areas are called "moors" by some Cape Codders.

Nesting gulls occupied approximately sixty percent of the secondary dune habitat on both islands during our study. Gulls within these colonies created large areas of disturbed sandy soil mixed with droppings and uneaten animal matter, suitable for many adventive and weedy species. Black-crowned night-herons (*Nycticorax nycticorax*) and snowy egrets (*Egretta thula*) nested in dense colonies on *Salix bebbiana* Sarg.; concentrations of their droppings apparently killed some of these shrubs. Other animals affecting vegetation in the secondary dune community were white-tailed deer (*Odocoileus virginianus*) and muskrats (*Ondatra zi-*

bethica). These two species foraged extensively on herbaceous vegetation located in transition zones between wetland and secondary dune systems. White-tailed deer appeared to favor *Rhus radicans* in the early spring before other vegetation leafed out. The first clumps of sedges and rushes to green up in the spring were readily consumed by the deer in 1983 and 1984.

The extensive salt marshes of the North Island and northern South Island were dominated by *Spartina alterniflora* Loisel. and *S. patens* (Ait.) Muhl. Common associates included *Distichlis spicata* L., *Juncus gerardi* Loisel., *Triglochin maritima* L. and *Limonium carolinianum* (Walt.) Britt. *Spartina alterniflora, Zostera marina* L. and *Ruppia martima* L. grew in the tidal creeks. Members of the genera *Salicornia* and *Suaeda* grew in the shallow salt pannes throughout the marshes, as well as on flats exposed at low tide.

All the permanent ponds occurred on the southern half of South Island, the oldest and most stable portion of the Monomoy Islands. Big and Little Station Ponds and the Lighthouse Ponds were surrounded by thickets of *Myrica pensylvanica, Prunus maritima, Rhus radicans* and *Salix bebbiana*. Beneath the thickets was a carpet of *Ptilimnium capillaceum* (Michx.) Raf., *Galium trifidum* L. and *Thelypteris palustris* (L.) Gray. The Lighthouse Ponds also contained extensive stands of *Typha angustifolia* L., the only freshwater marsh habitat on the islands. Aquatic vegetation in the ponds included *Potamogeton pectinatus* L., *P. perfoliatus* L. var. *bupleuroides* (Fern.) Farw., *Ceratophyllum demersum* L., *Spirodela polyrhiza* (L.) Schleid. and *Nymphaea odorata* Ait. Along the pond margins grew *Cyperus filicinus* Vahl, *Iris versicolor* L., *Polygonum hydropiperoides* Michx., *Teucrium canadense* L. and *Scutellaria epilobiifolia* A. Hamilton. Associated with these species was a wide array of herbs dependent on low water levels during summer and fall.

The many seasonal ponds and wet depressions contained lush borders of *Eleocharis halophila* Fern. & Brack., *Carex atlantica* Bailey, *Juncus effusus* L. and *Iris versicolor* L. On the gentle slopes surrounding the seasonal ponds *Rhus radicans, Myrica pensylvanica, Thelypteris palustris* and *Teucrium canadense* grew. The seasonal ponds on the northern half of South Island were surrounded by *Salix bebbiana, Prunus maritima* and *Vaccinium corymbosum* L. These areas were flooded by storm surges during the winters of 1983 and 1984, and contained a less diverse plant population than seasonal ponds not subjected to inundation by salt water.

The southern third of South Island contained a number of small bogs dominated by *Sphagnum* sp., *Carex canescens* L., *Eriophorum virginicum* L. and *Vaccinium macrocarpon* Ait. Occasionally found with these species were *Drosera rotundifolia* L. and *Pogonia ophioglossoides* (L.) Ker; *Lyonia ligustrina* (L.) DC, *Myrica pensylvanica* and *Prunus maritima* surrounded the bogs. Collectively these bogs, seasonal ponds, and wet depressions, with their variability in soil moisture and organic content, provided habitat for a large diversity of plant species. Many of the islands' rarities occurred in or near them, including *Habenaria lacera* (Michx.) Lodd., *Gaylussacia baccata* (Wang.) K. Koch, *Equisetum arvense* L., *Ophioglossum vulgatum* L. and *Linum striatum* Walt.

Human impact on the plant communities decreased significantly after 1972 when off-road vehicles were banned on the islands. Only two seasonal cabins remained on South Island in 1986. All other cabins were removed when life-tenancy permits expired, but the surrounding cultivated vegetation was left. *Pinus thunbergii* Parl., *Elaeagnus umbellata* Thunb., *Pyrus communis* L. and *P. malus* L. were examples of surviving cultivated and/or introduced plants found during our study. The Monomoy Islands have a rich and interesting history of human settlement and abandonment, a detailed account of which can be found in a publication prepared by the Massachusetts Audubon Society (1972).

MASTER PLANT LIST

Pteridophyta

EQUISETACEAE

Equisetum arvense L.—Rare. Recorded in 1984. Seasonal ponds.

LYCOPODIACEAE

Lycopodium inundatum L.—Occasional. Recorded in 1965, 1972. Bogs. All *L. inundatum* records probably refer to the var. *bigelovii,* common in southeastern Massachusetts. We were unable to locate any populations of the nominate variety.

Lycopodium inundatum L. var. *bigelovii* Tuckerm.—Occasional. Recorded in 1969, 1981, 1984. Bogs and seasonal ponds. Moul's specimens were cited (1969) as nominate *L. inundatum,* but clearly belong to var. *bigelovii.*

OPHIOGLOSSACEAE

Ophioglossum vulgatum L.—Rare. Discovered in 1966 by R. Chandler near Big Station Pond, photographed by BAS in 1972 and not recorded since.

OSMUNDACEAE

Osmunda regalis L.—Common. Recorded in 1954, 1965, 1972, 1984. Ponds and seasonal ponds.

Osmunda cinnamomea L.—Common. Recorded in 1965, 1969, 1972, 1981, 1983, 1984. Ponds, seasonal ponds and bogs.

POLYPODIACEAE

Onoclea sensibilis L.—Common. Recorded in 1965, 1969, 1972, 1983, 1984. Ponds and seasonal ponds.

Dryopteris thelypteris (L.) Gray var. *pubescens* (Lawson) Nakai—Abundant. Recorded in 1954, 1965, 1969, 1972, 1981, 1983, 1984. Ponds, seasonal ponds and bogs.

Dryopteris spinulosa (O. F. Muell. Watt var. *intermedia* (Muhl.) Underw. [= *Dryopteris austriaca* (Jacq.) Woyner var. *intermedia* (Muhl.) Morton]—Rare. Recorded in 1965, 1972. Unknown location.

Gymnospermae

PINACEAE

Pinus resinosa Ait.—Cultivated. Recorded in 1965. Unknown location.

Pinus sylvestris L.—Cultivated. Recorded in 1969. Secondary dunes near Inward Point.

Pinus rigida Mill.—Occasional. Recorded in 1954, 1965, 1969, 1972, 1983, 1984. Secondary dunes.

Pinus thunbergii Parl.—Cultivated. Recorded in 1965, 1972, 1984. Secondary dunes.

Juniperus virginiana L.—Occasional. Recorded in 1969, 1984. Seconary dunes. Some plants may have been cultivated.

Angiospermae — Monocotyledoneae

TYPHACEA

Typha angustifolia L.—Abundant. Recorded in 1954, 1965, 1969, 1972, 1983, 1984. Ponds and seasonal ponds.

ZOSTERACEAE

Zostera marina L. var. *stenophylla* Aschers. & Graebn.—Abundant. Recorded in 1954, 1965, 1972, 1984. Tidal mudflats.

Potamogeton pectinatus L.—Abundant. Recorded in 1954, 1965, 1972, 1984. Ponds.

Potamogeton crispus L.—Recorded in 1965, 1972. May have been mistaken for *P. perfoliatus* var. *bupleuroides*. Ponds.

Potamogeton perfoliatus L. var. *bupleuroides* (Fern.) Farw.—Common. Recorded in 1983, 1984. Ponds.

Ruppia maritima L.—Occasional. Recorded in 1969, 1984. Tidal creeks and pools.

JUNCAGINACEAE

Triglochin maritima L.—Abundant. Recorded in 1969, 1984. Salt marshes.

GRAMINEAE

Bromus tectorum L.—Occasional. Recorded in 1965, 1969, 1972, 1984. Secondary dunes.

Bromus commutatus Schrad.—Rare. Recorded in 1984. Border of bog.

Festuca rubra L.—Common. Recorded in 1954, 1965, 1969, 1972, 1983, 1984. Secondary dunes, salt marshes and seasonal ponds.

Puccinellia maritima (Hudson) Parl.—Rare. Recorded in 1989. Salt marsh on North Monomoy.

Eragrostis pilosa L. Beauv.—Recorded in 1972. Unknown location.

Distichlis spicata L. Greene—Common. Recorded in 1965, 1972, 1984. Salt marshes.

Phragmites communis Trin.—Common. Recorded in 1969, 1972, 1983, 1984. Ponds and seasonal ponds.

Agropyron pungens (Pers.) R. & S.—Common. Recorded in 1954, 1965, 1969, 1972, 1983, 1984. Borders of salt marshes and secondary dunes.

Agropyron repens (L.) Beauv.—Occasional. Recorded in 1984. Secondary dunes.

Elymus virginicus L. var. *halophilus* (Bickn.) Wieg.—Rare. Recorded in 1969. Border of salt marsh, Inward Point. Moul collected two specimens; both prove to be *Agropyron pungens,* so the genus *Elymus* remains unrecorded for the Monomoy Islands.

Aira caryophyllea L.—Rare. Recorded in 1972. Unknown location.

Danthonia spicata (L.) Beauv.—Rare. Recorded in 1983. Secondary dunes.

Ammophila breviligulata Fern.—Abundant. Recorded in 1965, 1969, 1972, 1981, 1984. Primary and secondary dunes.

Agrostis alba L. var. *palustris* (Huds.) Pers.—Common. Recorded in 1954, 1969, 1972, 1984. Secondary dunes, seasonal ponds and borders of salt marshes.

Agrostis tenuis Sibth.—Occasional. Recorded in 1965, 1972. Unknown location.

Agrostis hyemalis (Walt.) BSP.—Occasional. Recorded in 1965, 1969, 1972. Unknown location. This and the following species are often considered to be part of one variable species. Moul's specimen, although cited (1969) as *A. scabra,* appears to be *A. hyemalis* due to its small spikelets.

Agrostis scabra Willd.—Occasional. Recorded in 1983, 1984. Seasonal ponds.

Spartina alterniflora Loisel.—Abundant. Recorded in 1965, 1969, 1972, 1984. Salt marshes and tidal mudflats.

Spartina patens (Ait.) Muhl.—Abundant. Recorded in 1965, 1969, 1972, 1984. Salt marshes.

Leersia oryzoides (L.) Sw.—Rare. Recorded in 1965, 1972. Unknown location.

Digitaria sanguinalis (L.) Scop.—Rare. Recorded in 1972, 1984. Secondary dunes and seasonal ponds.

Panicum dichotomiflorum Michx.—Occasional. Recorded in 1972. Borders of salt flats and permanent ponds.

Panicum virgatum L. Abundant.—Recorded in 1965, 1969, 1972, 1983, 1984. Secondary dunes, ponds, and seasonal ponds. Specimens examined are var. *spissum* Linder.

Panicum meridionale Ashe—Common. Recorded in 1972, 1984. Secondary dunes and seasonal ponds.

Panicum lanuginosum Ell. var. *implicatum* (Scribn.) Fern.—Recorded in 1954, 1965, 1972, 1984. Secondary dunes and seasonal ponds.

Panicum clandestinum L.—Rare. Recorded in 1984. Secondary dunes.

Andropogon scoparius Michx.—Common. Recorded in 1965, 1972, 1983, 1984. Secondary dunes.

Andropogon virginicus L. var. *virginicus*—Occasional. Recorded in 1984. Seasonal ponds.

Andropogon virginicus L. var. *abbreviatus* (Hack.) Fern. & Griscom—Occasional. Recorded in 1972, 1981, 1984. Bogs and seasonal ponds.

CYPERACEAE

Cyperus diandrus Torr.—Recorded in 1986. Borders of permanent ponds. Specimen at SPWH collected by Buckley and Hendrickson.

Cyperus filicinus Vahl—Occasional. Recorded in 1965, 1972, 1981, 1984. Borders of permanent ponds and seasonal ponds.

Cyperus strigosus L.—Occasional. Recorded in 1983, 1984. Seasonal ponds and secondary dunes.

Cyperus Grayi Torr.—Occasional. Recorded in 1965, 1969, 1972, 1983, 1984. Secondary dunes.

Cyperus filiculmis Vahl—Occasional. Recorded in 1972, 1984. Secondary dunes.

Eleocharis parvula (R. & S.) Link—Common. Recorded in 1954, 1965, 1969, 1972, 1981, 1984. Permanent and seasonal ponds.

Eleocharis palustris (L.) R. & S.—Recorded in 1954, 1965. Unknown location. Possibly mistaken for *E. halophila*; *E. palustris* prefers strictly fresh water.

Eleocharis halophila Fern. & Brack.—Common. Recorded in 1954, 1965, 1969, 1972, 1981, 1983, 1984. Ponds and seasonal ponds. Also collected in 1986 by Buckley (SPWH).

Eleocharis tenuis (Willd.) Schultes—Rare. Recorded in 1984. Bogs. Possibly *E. elliptica* Kunth.; no specimen was preserved.

Scirpus americanus Pers.—Common. Recorded in 1954, 1965, 1969, 1972, 1983, 1984. Ponds and seasonal ponds.

Scirpus validus Vahl—Occasional. Recorded in 1954, 1965, 1972, 1983, 1984. Seasonal ponds.

Scirpus acutus Muhl.—Recorded in 1965, 1972. Unknown location. Possibly mistaken for *S. validus,* the common species of southeastern Massachusetts; no specimen has been found.

Scirpus robustus Pursh—Rare. Recorded in 1965, 1972. Unknown location. These records are based on a specimen from "salt marsh, Morris Island, Chatham," 28 August 1928, *Fernald 824* (NEBC). However, this species is expected to occur on Monomoy and perhaps did so at the Inward Point marshes.

Scirpus maritimus L.—Rare. Recorded in 1954, 1965, 1972. Unknown location. Probably refers to *S. maritimus* var. *fernaldi* (Bickn.) Beetle, also known as *S. novae-angliae* Britt., or to *S. paludosus.* True *S. maritimus* is a European waif unknown in Massachusetts.

Scirpus paludosus Nelson—Recorded in 1938 from "borders of pools, Monomoy, Chatham," *Seymour 5137* (NEBC).

Scirpus cyperinus (L.) Kunth—Common. Recorded in 1954, 1965, 1969, 1972, 1983, 1984. Seasonal ponds.

Eriophorum virginicum L.—Occasional. Recorded in 1965, 1969, 1972, 1981, 1983, 1984. Bogs.

Rhynchospora capitellata (Michx.) Vahl—Occasional. Recorded in 1972, 1981, 1983, 1984. Seasonal ponds and bogs.

Carex canescens L.—Occasional. Recorded in 1972, 1984. Bogs and seasonal ponds.

Carex atlantica Bailey—Occasional. Recorded in 1984. Seasonal ponds.

Carex seorsa Howe—Recorded in 1972. Unknown location. This record is based on a specimen from "wet mossy woods at edge of cedar swamp, Monomoy, Chatham," 19 June 1932, *Weatherby 6164* (NEBC). Since Monomoy has not supported a cedar swamp, we believe that the label is in error and that the specimen was likely collected on the mainland in Chatham.

Carex scoparia Schkuhr—Recorded in 1965, 1972. Unknown location.

Carex albolutescens Schwein.—Occasional. Recorded in 1984. Seasonal ponds and bogs.

Carex longii Mackenz.—Occasional. Recorded in 1969. Seasonal ponds. *C. longii* is now included in *C. albolutescens.*

Carex silicea Olney—Common. Recorded in 1954, 1965, 1972, 1984. Primary and secondary dunes.

Carex hormathodes Fern.—Occasional. Recorded in 1984. Seasonal ponds.

Carex debilis Michx. var. *rudgei* Bailey—Rare. Last recorded in 1972. Thickets near landing, Inward Point. May no longer occur due to loss of habitat.

Carex livida (Wahlenb.) Willd.—Recorded in 1965. Unknown location. Probably a misidentification; *C. livida* inhabits calcareous fens.

Carex comosa Boott—Rare. Recorded in 1969, 1972. Seasonal ponds.

Carex lurida Wahlenb.—Occasional. Recorded in 1984. Seasonal ponds and bogs.

LEMNACEAE

Spirodela polyrhiza (L.) Schleid.—Common. Recorded in 1972, 1984. Permanent and seasonal ponds.

JUNCACEAE

Juncus bufonius L. var. *halophilus* Buchenau and Fern.—Occasional. Recorded in 1972, 1983, 1984. Permanent and seasonal ponds.

Juncus gerardi Loisel.—Abundant. Recorded in 1954, 1965, 1969, 1972, 1984. Salt marshes.

Juncus tenuis Willd.—Rare. Recorded in 1972. Brick pavement at lighthouse.

Juncus dichotomus Ell.—Common. Recorded in 1965, 1972, 1981, 1984. Seasonal ponds.

Juncus greenei Oakes and Tuckerm.—Common. Recorded in 1965, 1969, 1972, 1983, 1984. Secondary dunes and seasonal ponds.

Juncus effusus L.—Abundant. Recorded in 1954, 1965, 1969, 1972, 1984. Permanent ponds and seasonal ponds.

Juncus balticus Willd.—Occasional. Recorded in 1972. Seasonal ponds and salt marshes.

Juncus canadensis J. Gay—Occasional. Recorded in 1965, 1972, 1984. Seasonal ponds.

Juncus subcaudatus (Engelm.) Coville and Blake—Occasional. Recorded in 1965, 1972, 1984. Seasonal ponds.

Juncus acuminatus Michx.—Common. Recorded in 1954, 1965, 1969, 1983, 1985. Seasonal ponds.

Juncus articulatus L.—Rare. Recorded in 1972. Seasonal ponds.

Luzula multiflora (Retz.) LeJeune—Rare. Recorded in 1984. Seasonal ponds.

LILIACEAE

Smilacina stellata (L.) Desf.—Rare. Last recorded in 1969. Thickets at Inward Point. May no longer occur because the habitat at Inward Point was destroyed in 1978.

Smilax rotundifolia L.—Rare. Last recorded in 1972. Thickets at Inward Point. May no longer occur because the habitat at Inward Point was destroyed in 1978.

IRIDACEAE

Sisyrichium angustifolium Mill.—Occasional. Recorded in 1954, 1965, 1969, 1972, 1984. Seasonal ponds.

Iris prismatica Pursh—Rare. Recorded in 1984. Seasonal ponds.

Iris versicolor L.—Abundant. Recorded in 1954, 1965, 1969, 1972, 1984. Permanent ponds, seasonal ponds and bogs.

ORCHIDACEAE

Habenaria lacera (Michx.) Lodd.—Rare. Recorded in 1981, 1984. Bogs.

Pogonia ophioglossoides (L.) Ker—Occasional. Recorded in 1954, 1965, 1969, 1972, 1981, 1984. Seasonal ponds and bogs.

Spiranthes cernua (L.) Richard—Occasional. Recorded in 1965, 1972, 1981, 1984. Seasonal ponds and bogs.

Dicotyledoneae

SALICACEAE

Salix nigra Marsh.—Rare. Recorded in 1984. Seasonal ponds.

Salix bebbiana Sarg.—Common. Recorded in 1965, 1972, 1984. Seasonal ponds.

Salix discolor Muhl.—Recorded in 1965, 1969, 1972. Seasonal ponds and adjacent thickets. There are two specimens at SPWH: "thickets in hollow of dunes between Inward Point and Lighthouse."

MYRICACEAE

Myrica pensylvanica Loisel.—Abundant. Recorded in 1954, 1965, 1969, 1972, 1981, 1983, 1984. Secondary dunes and seasonal ponds.

Myrica gale L.—Rare. Recorded in 1981. Permanent ponds.

BETULACEAE

Betula populifolia Marsh.—Rare. Recorded in 1984. Seasonal ponds.

FAGACEAE

Quercus ilicifolia Wang.—Rare. Recorded in 1965, 1972. Unknown location. May no longer occur because the habitat at Inward Point was destroyed in 1978.

POLYGONACEAE

Rumex crispus L.—Common. Recorded in 1954, 1965, 1969, 1972, 1984. Seasonal ponds and secondary dunes.

Rumex maritumus L. var. *fueginus* (Phil.) Dusen—Occasional. Recorded in 1938 (*Seymour 5140,* NEBC), 1969 (Moul, SPWH), 1981, 1984. Permanent ponds.

Rumex acetosella L.—Abundant. Recorded in 1954, 1965, 1969, 1972, 1984. Permanent ponds and seasonal ponds.

Polygonum glaucum Nutt.—Rare. Recorded in 1965, 1972, 1985. Beach at south end of South Island.

Polygonum pensylvanicum L. var. *nesophilum* Fern.—Occasional. Recorded in 1969. Seasonal ponds. Moul's collection (at SPWH) proves to be this little known and geographically restricted taxon. In addition, F. C. Seymour collected this same variety on Monomoy in 1938 (NEBC).

Polygonum persicaria L.—Recorded in 1965, 1972. Seasonal ponds.

Polygonum punctatum Ell. var. *leptostachyum* (Meisn.) Small—Common. Recorded in 1965, 1969, 1972, 1983, 1984. Seasonal ponds.

Polygonum hydropiperoides Michx.—Abundant. Recorded in 1965, 1972, 1984. Permanent ponds and seasonal ponds.

Polygonum scandens L.—Occasional. Recorded in 1954, 1965, 1972, 1984. Seasonal ponds.

Polygonella articulata (L.) Meisn.—Occasional. Recorded in 1965, 1972, 1984. Secondary dunes and seasonal ponds.

CHENOPODIACEAE

Bassia hirsuta (L.) Aschers.—Recorded in 1965, 1969, 1972. Unknown location. Normally inhabits upper borders of salt marshes. A specimen originally determined by Moul as *Suaeda maritima* is this species: "Area #3. Edge of salt marsh. (Inward Point)" (SPWH).

Chenopodium graveolens Lag. & Rodr.—Recorded in 1965. Unknown location. Probably mistaken for *C. carinatum* R. Br., which occurs in waste places and beaches in southeastern Cape Cod.

Atriplex patula L. var. *hastata* (L.) Gray—Common. Recorded in 1954, 1965, 1969, 1972, 1984. Secondary dunes and beaches.

Atriplex arenaria Nutt.—Common. Recorded in 1954, 1965, 1969, 1972, 1984. Secondary dunes, beaches and borders of salt marshes.

Salicornia bigelovii Torr.—Occasional. Recorded in 1969, 1972, 1984. Salt marshes.

Salicornia europaea L.—Common. Recorded in 1954, 1969, 1972, 1984. Salt marshes.

Salicornia virginica L.—Occasional. Recorded in 1965, 1969, 1972, 1984. Salt marshes.

Suaeda maritima (L.) Dumort.—Common. Recorded in 1954, 1965, 1972, 1984. Salt marshes.

Suaeda richii Fern.—Occasional. Recorded in 1965, 1972, 1981. Tidal salt flats.

Suaeda americana (Pers.) Fern.—Rare. Recorded in 1971, 1989. Tidal salt flats south of Inward Point. Specimen at NEBC. In 1989 this species was found to be numerous on a salt flat at the south end of North Island.

Suaeda linearis (Ell.) Moq.—Rare. Recorded in 1965. Unknown location.

Salsola kali L.—Common. Recorded in 1965, 1969, 1972, 1983, 1984. Beaches, sandspits and borders of salt marshes.

PHYTOLACCACEAE

Phytolacca americana L.—Occasional. Recorded in 1965, 1969, 1972, 1983, 1984. Seasonal ponds.

AIZOACEAE

Mollugo verticillata L.—Occasional. Recorded in 1965, 1972, 1981, 1983, 1984. Secondary dunes, permanent ponds and seasonal ponds.

CARYOPHYLLACEAE

Spergularia marina (L.) Griseb.—Occasional. Recorded in 1969, 1980, 1984. Salt marshes and tidal sand flats.

Arenaria peploides L.—Common. Recorded in 1954, 1965, 1969, 1972, 1983, 1984. Beaches and borders of salt marshes.

Stellaria media (L.) Cyrillo—Occasional. Recorded in 1984. Secondary dunes.

Cerastium vulgatum L.—Occasional. Recorded in 1965, 1972, 1984. Secondary dunes.

Dianthus armeria L.—Rare. Recorded in 1969. Thickets by seasonal ponds.

CERATOPHYLLACEAE

Ceratophyllum demersum L.—Common. Recorded in 1965, 1972, 1984. Permanent ponds.

NYMPHAEACEAE

Nymphaea odorata Ait.—Common. Recorded in 1965, 1969, 1972, 1983, 1984. Permanent ponds.

PAPAVERACEAE

Glaucium flavum Crantz—Rare. Recorded in 1985. Secondary dunes.

CRUCIFERAE

Draba verna L.—Occasional. Recorded in 1972, 1984. Secondary dunes.

Lepidium campestre (L.) R. Br.—Occasional. Recorded in 1965, 1972, 1984. Secondary dunes.

Lepidium virginicum L.—Common. Recorded in 1954, 1965, 1969, 1972, 1984. Secondary dunes.

Cakile edentula (Bigel.) Hook.—Common. Recorded in 1954, 1965, 1969, 1972, 1983, 1984. Beaches and primary dunes.

Raphanus raphanistrum L.—Occasional. Recorded in 1984. Secondary dunes.

Barbarea vulgaris R. Br.—Occasional. Recorded in 1984. Secondary dunes and seasonal ponds.

DROSERACEAE

Drosera rotundifolia L.—Occasional. Recorded in 1965, 1969, 1972, 1981, 1983, 1984. Bogs.

ROSACEAE

Spiraea tomentosa L.—Common. Recorded in 1954, 1965, 1969, 1972, 1981, 1983, 1984. Seasonal ponds.

Pyrus communis L.—Cultivated. Recorded in 1984. Secondary dunes. Represented by a single tree.

Pyrus malus L.—Cultivated. Recorded in 1984. Secondary dunes. Represented by two trees.

Pyrus arbutifolia (L.) L. f.—Rare. Recorded in 1965, 1972, 1984. Secondary dunes and seasonal ponds.

Pyrus melanocarpa (Michx.) Willd.—Recorded in 1972. Thickets at Inward Point landing place. This species has been considered a variety of *P. arbutifolia*; the specimen at NEBC has black fruits of the former and hairy leaves of the latter.

Amelanchier canadensis (L.) Medic.—Occasional. Recorded in 1965, 1969, 1972, 1984. Secondary dunes and seasonal ponds. In 1969 Moul cited *A. laevis* Wieg. from Monomoy; the specimen is *A. canadensis.*

Amelanchier laevis Wieg.—Recorded in 1969. Secondary dunes in thickets. Mistaken for *A. canadensis.*

Potentilla norvegica L.—Occasional. Recorded in 1972, 1981, 1984. Seasonal ponds.

Potentilla simplex Michx.—Occasional. Recorded in 1984. Seasonal ponds.

Potentilla egedei Wormsk. var. *groenlandica* (Tratt.) Polunin—Rare. Recorded in 1969. Salt marshes at Inward Point. May not occur anymore because the habitat where it occurred was destroyed in 1978.

Rubus idaeus L. var. *strigosus* (Michx.) Maxim.—Occasional. Recorded in 1965, 1969, 1972, 1984. Secondary dunes.

Rubus hispidus L.—Common. Recorded in 1965, 1969, 1972, 1984. Secondary dunes.

Rubus pensilvanicus Poir.—Occasional. Recorded in 1965, 1972, 1984. Secondary dunes.

Rosa nitida Willd.—Recorded in 1969. Secondary dunes. Misidentification of *R. virginiana*; *R. nitida* is a species of northern bogs and swamps.

Rosa virginiana Mill.—Occasional. Recorded in 1954, 1969, 1984. Secondary dunes. This is the common species of coastal thickets in southeastern Massachusetts. Moul's *Rosa nitida* Willd. and *R. carolina* L. were misidentifications of *R. virginiana* (specimens at SPWH).

Rosa palustris Marsh.—Recorded in 1954. Unknown location. Possible misidentification of *R. virginiana.*

Rosa carolina L.—Rare. Recorded in 1969. Secondary dunes. Misidentification of *R. virginiana.*

Rosa rugosa Thunb.—Common. Recorded in 1954, 1965, 1969, 1972, 1984. Secondary dunes.

Prunus maritima Marsh.—Common. Recorded in 1954, 1965, 1969, 1972, 1984. Secondary dunes.

Prunus persica (L.) Batsch—Cultivated. Recorded in 1969. Hedge by abandoned house in secondary dunes.

Prunus serotina Ehrh.—Occasional. Recorded in 1965, 1969, 1972, 1983, 1984. Secondary dunes.

LEGUMINOSAE

Trifolium arvense L.—Recorded in 1965, 1972. Unknown location.

Trifolium repens L.—Recorded in 1965, 1972. Unknown location.

Trifolium agrarium L.—Recorded in 1954. Unknown location.

Lathyrus japonicus Willd.—Abundant. Recorded in 1954, 1965, 1969, 1972, 1984. Primary and secondary dunes, and borders of salt marshes.

LINACEAE

Linum striatum Walt. var. *multijugum* Fern.—Occasional. Recorded in 1981, 1983, 1984. Seasonal ponds and bogs.

OXALIDACEAE

Oxalis stricta L.—Rare. Recorded in 1984. Seasonal ponds.

EUPHORBIACEAE

Euphorbia cyparissias L.—Rare. Recorded in 1984. Secondary dunes.

Euphorbia polygonifolia L.—Common. Recorded in 1965, 1969, 1972, 1983, 1984. Secondary dunes, beaches, and sandspits.

CALLITRICHACEAE

Callitriche stagnalis Scop.—Recorded in 1965. Possible misidentification, prefers running waters; *C. heterophylla* Pursh is the expected species of brackish and muddy shores.

ANACARDIACEAE

Rhus radicans L.—Abundant. Recorded in 1965, 1969, 1972, 1983, 1984. Primary and secondary dunes.

AQUIFOLIACEAE

Ilex opaca Ait.—Cultivated. Recorded in 1984. Secondary dunes. Represented by two small trees growing next to the lighthouse.

Ilex verticillata (L.) Gray—Occasional. Recorded in 1965, 1969, 1972, 1984. Secondary dunes and seasonal ponds.

Ilex laevigata (Pursh) Gray—Recorded in 1954. Unknown location. Probably mistaken for *I. verticillata*; preferred habitat is red maple and Atlantic white cedar swamps.

MALVACEAE

Hibiscus palustris L.—Common. Recorded in 1965, 1972, 1983, 1984. Permanent and seasonal ponds.

GUTTIFERAE

Hypericum boreale (Britt.) Bickn.—Common. Recorded in 1965, 1969, 1972, 1981, 1983, 1984. Permanent and seasonal ponds.

Hypericum canadense L.—Rare. Recorded in 1965, 1972, 1981. Permanent ponds.

Hypericum virginicum L.—Abundant. Recorded in 1954, 1965, 1969, 1972, 1981, 1984. Permanent and seasonal ponds.

CISTACEAE

Hudsonia tomentosa Nutt.—Abundant. Recorded in 1954, 1965, 1969, 1972, 1981, 1983, 1984. Secondary dunes.

Lechea villosa Ell.—Occasional. Recorded in 1954, 1965, 1972, 1983, 1984. Secondary dunes.

Lechea maritima Leggett—Common. Recorded in 1965, 1969, 1972, 1984. Secondary dunes.

VIOLACEAE

Viola pallens (Banks) Brainerd—Recorded in 1965, 1972. Unknown location.

Viola lanceolata L.—Occasional. Recorded in 1965, 1969, 1972, 1981, 1984. Permanent ponds, seasonal ponds and bogs.

ELAEAGNACEAE

Elaeagnus umbellata Thunb.—Cultivated. Recorded in 1984. Secondary dunes.

LYTHRACEAE

Decodon verticillatus (L.) Ell.—Common. Recorded in 1965, 1972, 1984. Permanent and seasonal ponds.

Lythrum salicaria L.—Rare. Recorded in 1972. Unknown location.

ONAGRACEAE

Ludwigia palustris (L.) Ell. var. *americana* (DC.) Fern. & Griscom—Common. Recorded in 1965, 1969, 1972, 1981, 1983, 1984. Permanent and seasonal ponds.

Epilobium leptophyllum Raf.—Occasional. Recorded in 1965, 1972, 1984. Seasonal ponds and bogs. Also collected in 1938 by F. C. Seymour (NEBC).

Epilobium glandulosum Lehm. var. *adenocaulon* (Haussk.) Fern.—Occasional. Recorded in 1965, 1972, 1983, 1984. Seasonal ponds. Also collected in 1938 by F. C. Seymour (NEBC).

Oenothera biennis L.—Occasional. Recorded in 1954, 1965, 1972. Primary and secondary dunes. Some of these may refer to *O. parviflora,* the common species of maritime habitats.

Oenothera parviflora L.—Common. Recorded in 1984. Primary and secondary dunes.

Oenothera perennis L.—Occasional. Recorded in 1984. Secondary dunes.

UMBELLIFERAE

Ptilimnium capillaceum (Michx.) Raf.—Abundant. Recorded in 1954, 1965, 1969, 1972, 1981, 1983, 1984. Permanent and seasonal ponds.

Ligusticum scothicum L.—Occasional. Recorded in 1954, 1965, 1972, 1984. Secondary dunes and upper borders of salt marshes.

Daucus carota L.—Rare. Recorded in 1954, 1965, 1969, 1972. Secondary dunes.

CLETHRACEAE

Clethra alnifolia L.—Occasional. Recorded in 1965, 1972, 1984. Secondary dunes and seasonal ponds.

ERICACEAE

Kalmia angustifolia L.—Occasional. Recorded in 1954, 1984. Seasonal ponds and bogs.

Lyonia ligustrina (L.) DC.—Occasional. Recorded in 1965, 1969, 1972, 1984. Wet thickets in secondary dunes and bogs.

Arctostaphylos uva-ursi (L.) Spreng.—Recorded in 1954. Unknown location. May no longer occur.

Gaylussacia baccata (Wang.) K. Koch—Rare. Recorded in 1984. Borders of bogs.

Vaccinium corymbosum L.—Occasional. Recorded in 1965, 1969, 1972, 1984. Seasonal ponds and bogs.

Vaccinium angustifolium Ait.—Borders of thickets. Dune top, center of island. Inward Point, Area #3. 1 August 1966, *Moul, Hough, & Fairbrothers 66-138* (SPWH). This species was omitted by Moul (1969).

Vaccinium oxycoccos L.—Recorded in 1965. Bogs. Probably mistaken for narrow-leaved plants of *V. macrocarpon.*

Vaccinium macrocarpon Ait.—Occasional. Recorded in 1954, 1965, 1969, 1972, 1983, 1984. Seasonal ponds and bogs.

PRIMULACEAE

Lysimachia terrestris (L.) BSP.—Occasional. Recorded in 1954, 1965, 1972, 1984. Seasonal ponds.

Trientalis borealis Raf.—Rare. Recorded in 1965, 1969, 1972. Thickets in secondary dunes and seasonal ponds.

PLUMBAGINACEAE

Limonium carolinianum (Walt.) Britt.—Recorded in 1965, 1969, 1972. Salt marshes. Moul's (1969) specimens are immature and identification cannot be confirmed to taxon.

Limonium nashii Small—Abundant. Recorded in 1984. Salt marshes. Recent taxonomy places *L. Nashii* within *L. carolinianum*. Past *L. carolinianum* records probably refer to *L. nashii,* the taxon with hairy calyx tubes which is the overwhelmingly more common taxon in Massachusetts.

GENTIANACEAE

Bartonia virginica (L.) BSP.—Rare. Recorded in 1972, 1981. Bogs and seasonal ponds.

Bartonia paniculata (Michx.) Muhl.—Recorded in 1965. Possibly mistaken for *B. virginica*; prefers red maple and Atlantic white cedar swamps.

ASCLEPIADACEAE

Asclepias incarnata L. var. *pulchra* (Ehrh.) Pers.—Occasional. Recorded in 1984. Permanent and seasonal ponds.

CONVOLVULACEAE

Convolvulus sepium L.—Common. Recorded in 1965, 1972, 1984. Secondary dunes.

Cuscuta compacta Juss.—Occasional. Recorded in 1984. Secondary dunes.

LABIATAE

Teucrium canadense L.—Abundant. Recorded in 1965, 1969, 1972, 1983, 1984. Permanent and seasonal ponds.

Scutellaria epilobiifolia A. Hamilton—Common. Recorded in 1965, 1969, 1972, 1984. Permanent and seasonal ponds.

Scutellaria × *churchilliana* Fern.—Very common. Area #2. Lighthouse area. Edge of a fresh water pond. *Moul 65-99* (SPWH), 26 Jul 1965. Originally identified as *S. epilobiifolia,* this specimen is actually a hybrid of *S. epilobiifolia* and *S. lateriflora.*

Stachys palustris L.—Recorded in 1954. Unknown location. Possibly mistaken for *Teucrium canadense*; *S. palustris* prefers nutrient-rich marshes and river meadows.

Lycopus virginicus L.—Rare. Recorded in 1965, 1972. Permanent and seasonal ponds.

Lycopus uniflorus Michx.—Common. Recorded in 1954, 1965, 1972, 1984. Permanent and seasonal ponds.

Lycopus americanus Muhl.—Common. Recorded in 1965, 1969, 1972, 1983, 1984. Permanent and seasonal ponds.

SOLANACEAE

Solanum dulcamara L.—Occasional. Recorded in 1965, 1984. Secondary dunes.

Solanum americanum Mill.—Occasional. Recorded in 1972, 1984. Secondary dunes.

Lycopersicum esculentum Mill.—Rare. Recorded in 1984. Secondary dunes.

SCROPHULARIACEAE

Verbascum thapsus L.—Occasional. Recorded in 1965, 1969, 1972, 1984. Secondary dunes.

Linaria vulgaris Hill—Occasional. Recorded in 1969, 1984. Secondary dunes.

Linaria canadensis (L.) Dumont—Common. Recorded in 1954, 1965, 1969, 1972, 1983, 1984. Primary and secondary dunes and seasonal ponds.

Limosella subulata Ives—Common. Recorded in 1981, 1983, 1984, 1985. Permanent ponds.

Lindernia anagallidea (Michx.) Pennell—Occasional. Recorded in 1972, 1983, 1984. Permanent and seasonal ponds.

Veronica arvensis L.—Rare. Recorded in 1984. Secondary dunes.

Gerardia purpurea L.—Common. Recorded in 1981, 1984. Permanent and seasonal ponds.

PLANTAGINACEAE

Plantago major L.—Rare. Recorded in 1972. Seasonal pond. The specimen at NEBC appears to be var. *scopulorum* Fries & Broberg, the expected taxon of saline environments.

Plantago oliganthos E. & S.—Occasional. Recorded in 1965, 1969, 1972, 1984. Salt marshes.

Plantago lanceolata L.—Occasional. Recorded in 1972, 1984. Secondary dunes.

RUBIACEAE

Galium palustre L.—Recorded in 1954, 1965. Permanent and seasonal ponds. Possibly mistaken for *G. trifidum.*

Galium trifidum L.—Abundant. Recorded in 1969, 1972, 1984. Permanent and seasonal ponds. Moul's specimen, cited in his 1969 paper as *G. palustre,* has been annotated to *G. trifidum.*

CAPRIFOLIACEAE

Lonicera Morrowi Gray—Rare. Recorded in 1984. Secondary dunes.

Viburnum dentatum L.—Occasional. Recorded in 1965, 1969, 1972. Moist thickets in secondary dunes and seasonal ponds.

Viburnum recognitum Fern.—Occasional. Recorded in 1984. Seconary dunes and seasonal ponds.

CUCURBITACEAE

Cucurbita pepo L.—Rare. Recorded in 1989. Disturbed low sand ridge in salt marsh, North Monomoy.

COMPOSITAE

Eupatorium dubium Willd.—Occasional. Recorded in 1984. Seasonal ponds.

Eupatorium perfoliatum L.—Rare. Recorded in 1954, 1965, 1972. Seasonal ponds.

Chrysopsis falcata (Pursh) Ell.—Abundant. Recorded in 1954, 1965, 1969, 1972, 1981, 1983, 1984. Primary and secondary dunes.

Solidago sempervirens L.—Abundant. Recorded in 1954, 1965, 1969, 1972, 1983, 1984. Primary and secondary dunes.

Solidago rugosa Ait.—Rare. Recorded in 1965, 1972. Unknown location.

Solidago graminifolia (L.) Salisb.—Common. Recorded in 1954, 1965, 1972, 1984. Secondary dunes.

Solidago tenuifolia Pursh—Common. Recorded in 1969, 1972, 1981, 1984. Secondary dunes and seasonal ponds.

Aster pilosus Willd. var. *demotus* Blake—Rare. Recorded in 1965. Unknown location.

Aster ericoides L.—Rare. Recorded in 1965. Unknown location.

Aster dumosus L.—Rare. Recorded in 1972, 1981. Seasonal ponds.

Aster novi-belgii L.—Occasional. Recorded in 1972, 1981, 1984. Secondary dunes and seasonal ponds.

Aster linariifolius L.—Occasional. Recorded in 1965, 1972, 1984. Secondary dunes.

Aster subulatus Michx.—Occasional. Recorded in 1972, 1984. Salt marshes.

Erigeron canadensis L.—Rare. Recorded in 1954, 1981. Secondary dunes.

Erigeron pusillus Nutt.—Common. Recorded in 1972, 1981, 1984. Secondary dunes.

Baccharis halimifolia L.—Common. Recorded in 1969, 1972, 1984. Secondary dunes and borders of salt marshes.

Pluchea purpurascens (Sw.) DC.—Common. Recorded in 1965, 1969, 1972, 1983, 1984. Secondary dunes, seasonal ponds and borders of salt marshes.

Anaphalis margaritacea (L.) C. B. Clarke—Recorded in 1954, 1965, 1972. Unknown location.

Gnaphalium obtusifolium L.—Common. Recorded in 1965, 1969, 1972, 1983, 1984. Secondary dunes.

Iva frutescens L.—Occasional. Recorded in 1984. Borders of salt marshes.

Ambrosia artemisiifolia L.—Occasional. Recorded in 1954, 1965, 1972, 1984. Secondary dunes.

Xanthium chinense Mill.—Recorded in 1954. Unknown location. See *X. strumarium.*

Xanthium marina—Recorded in 1954. Unknown location. See *X. strumarium.*

Xanthium strumarium L.—Common. Recorded in 1965, 1972, 1984. Beaches, sandspits, and primary and secondary dunes. *Xanthium marina, X. chinense,* and *X. echinatum* are included in *X. strumarium* by current taxonomists.

Xanthium echinatum Murr.—Recorded in 1969. Primary and secondary dunes. See *X. strumarium.*

Bidens cernua L.—Common. Recorded in 1984. Permanent and seasonal ponds.

Bidens tripartita L.—Recorded in 1972. Unknown location. Probably mistaken for *B. frondosa,* the common species of moist pond shores in southeastern Massachusetts.

Bidens frondosa L.—Occasional. Recorded in 1954, 1965, 1972. Seasonal ponds.

Achillea millefolium L.—Occasional. Recorded in 1965, 1969, 1972, 1984. Secondary dunes.

Chrysanthemum leucanthemum L.—Rare. Recorded in 1954, 1965, 1972. Unknown location.

Artemesia caudata Michx.—Occasional. Recorded in 1954, 1965, 1969, 1972, 1984. Secondary dunes.

Artemesia stelleriana Bess.—Common. Recorded in 1954, 1965, 1969, 1972, 1984. Primary and secondary dunes. Also collected in 1932 by C. A. Weatherby (GH).

Erechtites hieracifolia (L.) Raf.—Rare. Recorded in 1965, 1969, 1972, 1984. Secondary dunes and borders of salt marshes.

Senecio vulgaris L.—Rare. Recorded in 1984. Secondary dunes.

Cirsium vulgare (Savi) Tenore—Common. Recorded in 1965, 1969, 1972, 1984. Secondary dunes.

Cirsium arvense (L.) Scop.—Rare. Recorded in 1954. Unknown location.

Cichorium intybus L.—Rare. Recorded in 1972. Secondary dunes.

Hypochoeris radicata L.—Occasional. Recorded in 1965, 1972, 1984. Secondary dunes and seasonal ponds.

Taraxacum officinale Weber—Occasional. Recorded in 1965, 1972, 1984. Secondary dunes.

Sonchus arvensis L.—Rare. Recorded in 1981, 1984. Secondary dunes and borders of permanent and seasonal ponds.

Sonchus asper (L.) Hill—Occasional. Recorded in 1965, 1969, 1972, 1984. Secondary dunes.

Lactuca canadensis L. var. *latifolia* Ktze.—Occasional. Recorded in 1965, 1972, 1984. Secondary dunes.

Lactuca biennis (Moench) Fern.—Rare. Recorded in 1973 by BAS. Secondary dunes.

Hieracium florentinum All.—Common. Recorded in 1984. Secondary dunes.

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ADDITIONS TO THE FLORA OF WASHINGTON COUNTY, MAINE

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ABSTRACT

The continued increase of logging roads makes interior Washington County, Maine, more readily accessible to the botanist. Ten species are reported for the first time from Washington County, including eight native species, one introduced species, and one hybrid. Several of these species are considered rare in Maine. Sawtelle Heath in Baileyville (Woodland) is suggested for further study.

Key Words: Range extensions, Washington County, Maine

During the summers of 1988, 1989 and 1990, we conducted botanical field work for analysis of alternative routes for a proposed transmission line from New Brunswick to Bangor, Maine. Botanical work carried out in interior eastern Maine in Aroostook, Penobscot, Hancock, and Washington Counties.

Recent and ongoing construction of logging haul roads throughout the interior portions of Washington and Hancock Counties to service the forest products industry has greatly enhanced access to a large area previously not well botanized. The Stud Mill Road, a private thoroughfare from Baileyville (Woodland) to Milford, provides ready access to many unorganized townships as well as interesting botanizing. It is not surprising, therefore, that additions to the known flora of the area were discovered. Even so, several stations for conspicuous, if uncommon, species were found in historically botanized and accessible areas near Woodland and Princeton.

To our knowledge, the species mentioned below have not previously been recorded from Washington County. None is listed in *The Revised Check-list of Vascular Plants of Maine* (Richards, Hyland, and Eastman, 1983). Records of the Critical Areas Program of the State Planning Office have been checked for those species on *Maine's List of Rare, Threatened, or Endangered Species* (Dibble et al., 1989). Voucher specimens have been variously distributed as noted in individual accounts.

Equisetum variegatum Schleich.

Variegated scouring-rush, *Equisetum variegatum,* was collected twice in Washington County. It is abundant on disturbed soil of a recently logged area west of Grand Falls Road, ca. six miles north of Woodland, Baileyville Township (*Gilman 89044,* MAINE, VT); and occasional in a ditch along a logging road, ca. one mile north of the Stud Mill Road west of Huntley Brook, Plantation 21 (*Gilman 89137,* MAINE, VT). This species appears to be colonizing suitable habitats in eastern Maine at a rapid rate; it was additionally collected from roadside ditches and beneath powerlines in Penobscot, Aroostook, and Hancock Counties, and was observed at several sites along the Stud Mill Road.

Cystopteris bulbifera (L.) Bernh.

A large population of the calciphilic bulblet bladder-fern, *Cystopteris bulbifera,* occurs along a vernal stream that is a tributary of Big Wallamatogue Stream, ca. 1500 feet south of the Stud Mill Road in Township 27 (T27 ED BPP) (*Gilman 89012,* MAINE, VT). Associated with *Cystopteris* were *Adiantum pedatum* L. and *Athyrium thelypteroides* (Michx.) Desv., both uncommon in eastern Maine.

Polystichum × potteri Barrington

The wholly anomalous presence of the hybrid holly fern, *Polystichum × potteri,* in a lowland and wetland situation, a northern white cedar swamp in Township 27 (T27 ED BPP), is remarkable. A single large, vigorous plant was observed at an elevation of 270 feet, ca. 2000 feet north of the Stud Mill Road, one mile west of Clifford Stream (*Gilman 89054,* VT). The hybrid is normally montane, usually being found on rich slopes below talus (Barrington, 1986). One parent, *Polystichum acrostichoides* (Michx.) Schott, is common in the area; the other parent, *Polystichum braunii* (Spenner) Fee, has not been recorded from Washington County and was not observed in the area. It is typically a species of mountainous terrain, although it is reported from relatively low elevations in Nova Scotia (Roland and Smith, 1969).

Cypripedium reginae Walt.

Two populations of showy lady's-slipper, *Cypripedium reginae,* were discovered under northern white cedar: along the southeast end of Sawtelle Heath in Baileyville, ca. six miles north of Woodland (*Gilman 89055,* MAINE), and on the north side of Pocomoonshine Mountain, Princeton (*Gilman 89046,* MAINE). Both stations are comprised of large clumps as well as scattered individuals. Closely associated with this species, as elsewhere in the northeast, is alder-leaved buckthorn, *Rhamnus alnifolia* L'Her.

Malaxis brachypoda (Gray) Fern.

White adder's-mouth, *Malaxis brachypoda,* has historically been considered rare in Maine, and throughout its range (Eastman and Gawler, 1985). A single individual was observed in Township 27 (T27 ED BPP), growing with small patches of *Cystopteris bulbifera* as noted above (*Gilman 89100* [photograph], MAINE). Case (1987) remarked that its habitat is wet, limy soil where competing vegetation is not well established, as is the condition at this station.

Goodyera pubescens (Willd.) R. Br.

A small population of downy rattlesnake plantain, *Goodyera pubescens* was found on Seavey Ridge in Plantation 21 (*Gilman 88167,* MAINE). This population is more than sixty miles from currently known stations in the Penobscot River valley. A group of eight to ten rosettes occurs in a beech-hemlock grove, ca. 300 feet north of the Stud Mill Road. Hinds (1986) reported that this species was once collected in New Brunswick but has not been seen there since 1888; it is possible that this station represents the easternmost population of this orchid, which is frequent or common in more southern locations.

Betula pumila L.

Dwarf birch, *Betula pumila,* was found on Sawtelle Heath near Grand Falls Road in Baileyville. Most of this peatland is a coalesced dome heath (*sensu* Worley, 1980) dominated by sphagnum and ericaceous shrubs. Wetter areas around the perimeter support a greater diversity of species, including a tiny population of *Betula pumila* (*Gilman 88150,* MAINE, VT). Only three small shrubs were observed in spite of an extensive search. No other calciphilic species were noted on the bog mat, although several occur in the cedar swamps along the southern edge of the heath.

Pyrola asarifolia Michx.

One such calciphilic species (referred to above) is *Pyrola asarifolia.* A large population (several hundred stems) exists here, associated with *Osmunda regalis* L., *Osmunda cinnamomea* L., *Toxicodendron rydbergii* (Small) Greene, *Mitella nuda* L., and other common species (*Gilman 89046,* MAINE). *Pyrola asarifolia* has not previously been recorded from Washington County.

The *Cypripedium, Betula,* and *Pyrola* which occur at Sawtelle Heath may fairly be regarded as extensions or outliers of the flora of eastern Aroostook County, which is typically calciphilic and boreal. Several other such species, not new to Washington County, occur here as well, including *Cypripedium calceolus* L. (*Gilman 89042,* MAINE) and *Carex vaginata* Tausch. The entire Sawtelle Heath complex of wetlands, which includes northern white cedar swamps, raised heath, lagg, pools, and kettlehole bogs, may be recommended for further investigation.

Vicia sepium L. and **Gnaphalium sylvaticum** L.

Other species not previously recorded from Washington County but not rare in Maine include: *Vicia sepium,* adventive in fields along the St. Croix River and roadsides, Calais (*Gilman 89041,* MAINE, VT); and *Gnaphalium sylvaticum,* occasional and apparently adventive on an old logging road, ca. one half mile east of Huntley Brook, Plantation 21 (*Gilman 88168,* VT).

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DISCOVERY OF *JUNCUS VASEYI* (JUNCACEAE) IN VERMONT

PETER F. ZIKA

ABSTRACT

Juncus vaseyi is an addition to the native flora of Vermont. A small population is vulnerable to human activities and natural succession in the Lake Champlain Valley of northwestern Vermont. It is recommended for state endangered species status.

Key Words: endangered species, *Juncus vaseyi,* Biosphere Reserve, Lake Champlain, Vermont

Juncus vaseyi Engelm., Vasey's rush, occurs across Canada and the northern United States. A new station in Vermont fills a gap in the southeastern limit of its range between Maine (Fernald, 1950; Bean et al., 1966), New York (unvouchered reports, Fernald, 1904; Clemants, 1990), and Michigan (Voss, 1972).

Juncus vaseyi is both rare and cryptic, and not surprisingly, there are no prior records in Vermont (Seymour, 1969, 1982; Atwood et al., 1973). In nature the plants are large but inconspicuous, resembling at a distance the abundant pasture rush, *Juncus effusus* L. The writer visited the Ferrisburg site several times before noticing *J. vaseyi* mixed among *J. effusus.*

A small population of *Juncus vaseyi* (*Zika 10886* NY, VT) was discovered in a damp meadow along an ephemeral watercourse at an elevation of 110 feet on a bluff overlooking Button Bay, Lake Champlain. The poorly drained soil conceals the bedrock, which according to Doll (1961) is either Ordovician calcareous shale (Stony Point formation) or limestone (Hortonville formation). The habitat is dominated by a diversity of native monocots with a scattering of weedy forbs and invading shrubs, including *Calamagrostis canadensis* (Michx.) Beauv., *Carex annectens* (Bickn.) Bickn., *C. buxbaumii* Wahlemb., *C. conoidea* Schkuhr ex Willd., *C. lanuginosa* Michx., *C. scoparia* Schkuhr ex Willd., *C. tenera* Dewey, *Chrysanthemum leucanthemum* L., *Cornus foemina* Mill. ssp. *racemosa* (Lam.) J. Wils., *Fragaria virginiana* Mill., *Galium* sp., *Juncus dudleyi* Wieg., *J. effusus* L., *Panicum boreale* Nash., *Poa pratensis* L., *Ranunculus acris* L., and *Stellaria graminea* L.

The station is located adjacent to a campground in Button Bay State Park, Ferrisburg, Addison Co. The park is within the Champlain-Adirondack Biosphere Reserve. Among the rare species documented in the park are some state threatened or endangered species (Thompson, 1989), including *Carex buxbaumii* (Zika, 1988), *Cypripedium arietinum* R. Br., *Pterospora andromedea* Nutt. (*No collector cited s.n.* NY), and *Sporobolus asper* (Zika, 1990). *Sporobolus asper* is rare across New England (Rawinski et al., 1989). Despite repeated searches, *P. andromedea* has not been seen since 1892 at Button Bay and is believed extirpated from the park. *Carex buxbaumii* inhabits the same wet meadow as *Juncus vaseyi.*

The *Juncus vaseyi–Carex buxbaumii* habitat appears to be a fragmented remnant of an extensive seasonal wetland dominated by native monocots. The site was altered by agriculture before it became a park. Trees were removed and the watercourse was partially channelized in an apparently unsuccessful attempt to dry out the meadows, which were mowed regularly. The park filled part of the wet meadows to install roads and campsites, eliminating considerable habitat and further altering the hydrology of the site. Shrubs are now invading the meadow.

Why is *Juncus vaseyi* rare at the site? Most of the available habitat was altered by farming or by construction activities when the park was developing facilities. Why is Vasey's rush rare regionally? This is the first report for the Champlain Valley of New York and Vermont. Presumably *J. vaseyi,* an early successional species, was quite rare prior to European settlement in this heavily forested area. It would have been restricted to damp natural openings, perhaps abandoned beaver meadows or wetlands in recently burned pine stands in the Champlain Valley. The absence of prior records implies it was always rare. Presumably increases in available habitat (agricultural clearings) were offset by increased competition from introduced hay species, draining, or dispersal and recruitment difficulties at the southern limit of the species range. Champlain Valley wetlands continue to be altered by agriculture and development, further limiting the available habitat.

The *Juncus vaseyi* population is threatened by possible expansion of facilities in this popular park. Natural succession is also a threat to the small and vulnerable station. The apparent extirpation of *Pterospora andromedea* from Button Bay emphasizes the need for legal protection and careful management of botanical resources in the state park. *Juncus vaseyi* is recommended for state endangered species status (10 V. S. A. Chapter 123).

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NEW ENGLAND NOTE

THE FIRST REPORT OF *AGROSTIS EXARATA* VAR. *MONOLEPSIS* (POACEAE) IN NEW ENGLAND

Peter F. Zika

Spike bent, *Agrostis exarata* Trin., is a western grass. Hitchcock and Chase (1971) showed its native range as extending from Alberta, Nebraska, Texas and Mexico west to the Pacific states, including Alaska. *Agrostis exarata* var. *monolepsis* (Torr.) A. S. Hitchc. is distinguished from other infraspecific taxa by the presence of a prominent bent awn on the lemma. Hitchcock and Cronquist (1973) noted its range is much more restricted than that of the nominate variety, extending from southern British Columbia to southern California, and sporadically east to Nevada and Idaho. An adventive colony of *A. exarata* var. *monolepsis* was discovered in Vermont in 1982. The species is not mentioned in the standard references for the region, and is apparently the first New England record.

The spike bent population is restricted to clearings along the access road at the southwestern end of Wallingford Pond, elev. ca. 2200 feet, Green Mountain National Forest, town of Wallingford, Rutland County, Vermont. The specimen (*Zika 6579* VT) was misidentified as *Agrostis canina* L. until recently. The two taxa may be distinguished in fruit by the following key:

Glumes 2 mm long; panicle branches loose and spreading . . . . *Agrostis canina*
Glumes 2.5–4 mm long; panicle branches appressed-ascending . . . . *Agrostis exarata* var. *monolepsis*

How *Agrostis exarata* arrived on a remote jeep road in Wallingford is unknown, but presumably a motor vehicle was involved. In the Pacific Northwest, *A. exarata* is somewhat weedy and occasionally grows on the margins of dirt roads in damp places.

A 1968 collection (*Wood s.n.* VT) labeled *Agrostis exarata* from "experimental land," Burlington, Chittenden Co., Vermont proved to be *A. gigantea* Roth.

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NEW ENGLAND NOTE

NEW SITE FOR *CORNUS FLORIDA* (CORNACEAE) IN MAINE

Charles Cormier

On November 24, 1990, my brother and I discovered a stand of *Cornus florida* L., the flowering dogwood, on Second Hill, in York, Maine, one mile northeast of Mt. Agamenticus. Mt. Agamenticus is the only historical site for naturally-occurring *C. florida* in Maine. The two former stands that existed here were discovered by Dr. Anne Perkins in 1936. A search by Dr. Perkins and Professor Hyland in 1954 revealed that both stands had been destroyed by construction and the building of a road. In 1973, one tree was found near the above-mentioned road by L. M. Eastman; it was observed by the author during the summer of 1990. The station at Second Hill is noteworthy owing to the fact that it is now the only known naturally-occurring stand of *C. florida* in the state (*see* Perkins, 1955; Eastman, 1976).

This species, a common understory tree of eastern North America, reaches the northeasternmost limit of its distribution at these sites. A report from Fayette Ridge, Maine, near Winthrop, has never produced a voucher specimen and is most likely erroneous.

The stand on Second Hill is located on the south side at about 165 m (500 ft.) above sea level, and consists of twelve trees four to five m in height, each about 7.5 cm in diameter at four feet above ground level (DBH). The site, about .5 acre, is dry rocky woods which also supports *Quercus alba* L., *Q. rubra* L., *Q. prinus* L., *Carya ovata* (Mill.) K. Koch, *Pinus strobus* L., *Tsuga canadensis* (L.) Carr, and *Ostrya virginiana* (Mill.) K. Koch. A voucher specimen has been deposited at MAINE.

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New scientific names are in **bold face**

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