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EFFECT OF ACHENE MORPHOLOGY AND MASS ON GERMINATION AND SEEDLING GROWTH OF *BOLTONIA DECURRENS* (ASTERACEAE), A THREATENED FLOODPLAIN SPECIES

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ABSTRACT. *Boltonia decurrens* (Asteraceae), a plant species endemic to the Illinois River Valley, is threatened with extinction. Alterations of the hydrologic regime of the river have resulted in habitat loss and population decline. Lack of information about the complex life cycle of this species frustrates efforts to develop an effective recovery plan. An essential part of any recovery plan is an understanding of seed germination, seedling recruitment, and early growth, and how each contributes to the maintenance of a population. In *B. decurrens*, the dimorphic achenes have different masses and may provide different dispersal mechanisms. This study examined the effect of achene morphology and mass on seed germination and early seedling growth of *B. decurrens* under controlled environmental conditions. There was no difference in timing of germination of disk and ray achenes in *B. decurrens*; however, there was a distinct difference in early growth of seedlings derived from disk versus ray achenes and from larger ray achenes compared to smaller ones. Disk achenes, which produced seedlings with more leaf area during the first 10–15 days, may provide a competitive advantage over those produced by ray achenes. Since leaf area and photosynthetic rates are closely correlated, seedlings with more leaf area early in their development may also be more competitive with seedlings of other species.

Key Words: dimorphic seeds, germination, seedling growth, seed size, threatened species, floodplain, *Boltonia*

Boltonia decurrens (Torr. & A. Gray) A. Wood (Asteraceae) is an herbaceous perennial whose distribution is restricted to the Illinois River floodplain (Torrey and Gray 1841; U.S. Fish and Wildlife Service 1990). The species is on the Federal List of threatened species (U.S. Fish and Wildlife Service 1988), and is currently listed as a Species of Concern in Missouri (Missouri

Department of Conservation 1999) and as Threatened in Illinois (Herkert 1991). Inflorescences are borne on panicles and produce prolific numbers of dimorphic achenes (Smith and Keevin 1998). Additionally, vegetative ramets that overwinter and reproduce sexually the following year are produced at the base of the senescing flowering plants each fall (Redmond 1993; Smith 1991; Smith et al. 1998). Despite these reproductive strategies, the construction of levees and navigation dams along the Illinois River have resulted in habitat loss and a decline in population size and number (Schwegman and Nyboer 1985; Smith et al. 1998; U.S. Fish and Wildlife Service 1990).

Dissimilarities in seed morphology within plant taxa may contribute to different dispersal and germination patterns as well as different growth and fitness of the resulting plants (Banovetz and Scheiner 1992; Zhang 1993). Disk flowers of *Boltonia decurrens* produce flattened, heart-shaped achenes that are characterized by a pappus of two bristles. Disk achenes average 1.8 mm in length and 1.3 mm in width with an average mass of 0.1 mg (Smith and Keevin 1998). Achenes produced from ray flowers are smaller and wedge-shaped, possessing a distinct third side, and they have greatly reduced bristles. Ray achenes average 1.3 mm in length and 0.9 mm in width, and they average 0.05 mg in mass (Smith and Keevin 1998). The increased surface area/mass ratio of the disk achenes provides greater buoyancy and allows them to float for extended periods of time (> 30 days; Smith and Keevin 1998), and this may facilitate the establishment of remote populations after flood waters recede. The wedge-shaped ray achenes do not float and may contribute to the maintenance of the species at or near an extant population (Smith and Keevin 1998; Smith et al. 1998).

Germination and early seedling development are the most critical stages in the life cycle of a plant (Harper et al. 1970), and any variation in achene morphology or mass that could affect germination or early growth could also influence the establishment of new populations or the maintenance of extant populations. Although germination studies have been conducted on *Boltonia decurrens* (Baskin and Baskin 1988; Smith and Keevin 1998; Smith et al. 1995), little is known of germination patterns or seedling growth specific to achene morphology or mass. The present study examines the effect of achene morphology and mass on germination and early seedling growth.

MATERIALS AND METHODS

Achenes were collected from West Alton, St. Charles County, Missouri (lat. 38°52′06″N, long. 90°12′22″W) and maintained at 5°C for two years before the initiation of this study. Size classes of each achene morphology were differentiated by sorting through a series of screens with mesh sizes of 0.841 mm, 0.595 mm, and 0.420 mm, followed by manual segregation of each morphological type using a stereoscope. The largest size class ($>$ 0.841 mm) contained predominantly disk achenes (D1); the smallest ($>$ 0.420 mm but $<$ 0.595 mm) contained mature ray achenes (R3) and a very small proportion of immature or nonviable disk achenes (lacking a visible embryo). Both mature disk and ray achenes (D2 and R2) were represented in the intermediate size class ($>$ 0.595 mm but $<$ 0.841 mm). Seeds with evidence of herbivory, or apparently nonviable (no visible embryo), were discarded. Otherwise, seeds were selected randomly to minimize possible sampling bias. Each of the ten replicates consisted of 25 disk and 25 ray achenes in each of two size classes, for a total of 1000 achenes. Dry mass was recorded for each sample of 25 seeds, and a mass : size correlation was calculated.

Since the achenes require light for germination (Baskin and Baskin 1988; Smith and Keevin 1998), they were germinated in 10 cm square pots on the surface of a commercial, peat-based growing medium in a Sherer CEL-25 7HL environmental chamber at 20°C and 200 μmol m^{-2} s^{-1} PPF (photosynthetic photon flux), which was measured using an LI-185B quantum meter and LI-190SB quantum sensor (LI-COR, Lincoln, NE). Germination was determined by radicle emergence, recorded daily, and seedlings were identified with a color-coded pin. Length and width measures of the cotyledons were taken after five days of growth. Measures were obtained for both cotyledons and true leaves at 10 and 15 days. Cotyledons and primary leaves are not lobed, do not have serrated edges, and are approximately rectangular; therefore, leaf area was calculated using the algorithm for area of a rectangle (L × W). After 15 days the seedlings were transferred to a greenhouse, where they were initially placed under 50% shade cloth to minimize photodamage and were exposed to higher ambient light levels over a two-week period. Light levels were measured in the greenhouse at 12 noon daily during the study (June and July) and averaged 1500 ± 350 μmol m^{-2} s^{-1} PPF. Pots were watered daily and rotated to minimize environmental variation due to position. Seedling height was measured at 30 days and at 60 days. Because *Boltonia decurrens* is endangered, plants were not harvested for biomass measurements, but were transplanted into the population from which the seeds had been collected.

All analyses were performed using SYSTAT 5.2 (SPSS, Chicago, Illinois). The achene size class and mass relationship was determined using linear regression, and germination and seedling survival data were analyzed using a chi square statistic of a contingency table (Steel and Torrie 1980). For the χ^2 analyses of germination and survival, data from replicates were pooled within each achene class.

The unequally represented size classes, which resulted from differences in the numbers of seeds that germinated within each achene class, produced a non-orthogonal design that would affect the relationship of the other classes in calculating the F-ratio (Steel and Torrie 1980); therefore, we used Multivariable General Linear Hypothesis (MGLH; type III sum of squares) for all analyses of variance (ANOVAs) of leaf area and height. Log transformation was used to normalize leaf area and height data (Steel and Torrie 1980). Linear contrast analyses were used for pairwise comparisons of seedling leaf area and seedling height for each size class and morphology combination in accordance with Steel and Torrie (1980).

RESULTS

Germination of achenes and seedling survival. There was no significant difference in germination among disk and ray achenes of any class ($\chi^2 = 2.751$; $P = 0.432$; df = 3; Figure 1). Of the 1000 seeds used in this experiment, 667 germinated: 339 disk achenes and 328 ray achenes. Although there was no statistical difference in survival among achene classes ($\chi^2 = 2.570$; $P = 0.497$; df = 3), there was a trend for a decrease in survival with a decrease in achene size (Figure 1). Disk and ray achenes of all classes demonstrated the same germination pattern (Figure 2): germination peaked on day 4, with no germination occurring before day 3 or after day 11. There was a positive linear relationship ($r^2 = 0.8165$; $P < 0.05$; df = 3) between achene size (area) and mass (i.e., the larger the achene, the greater the mass).

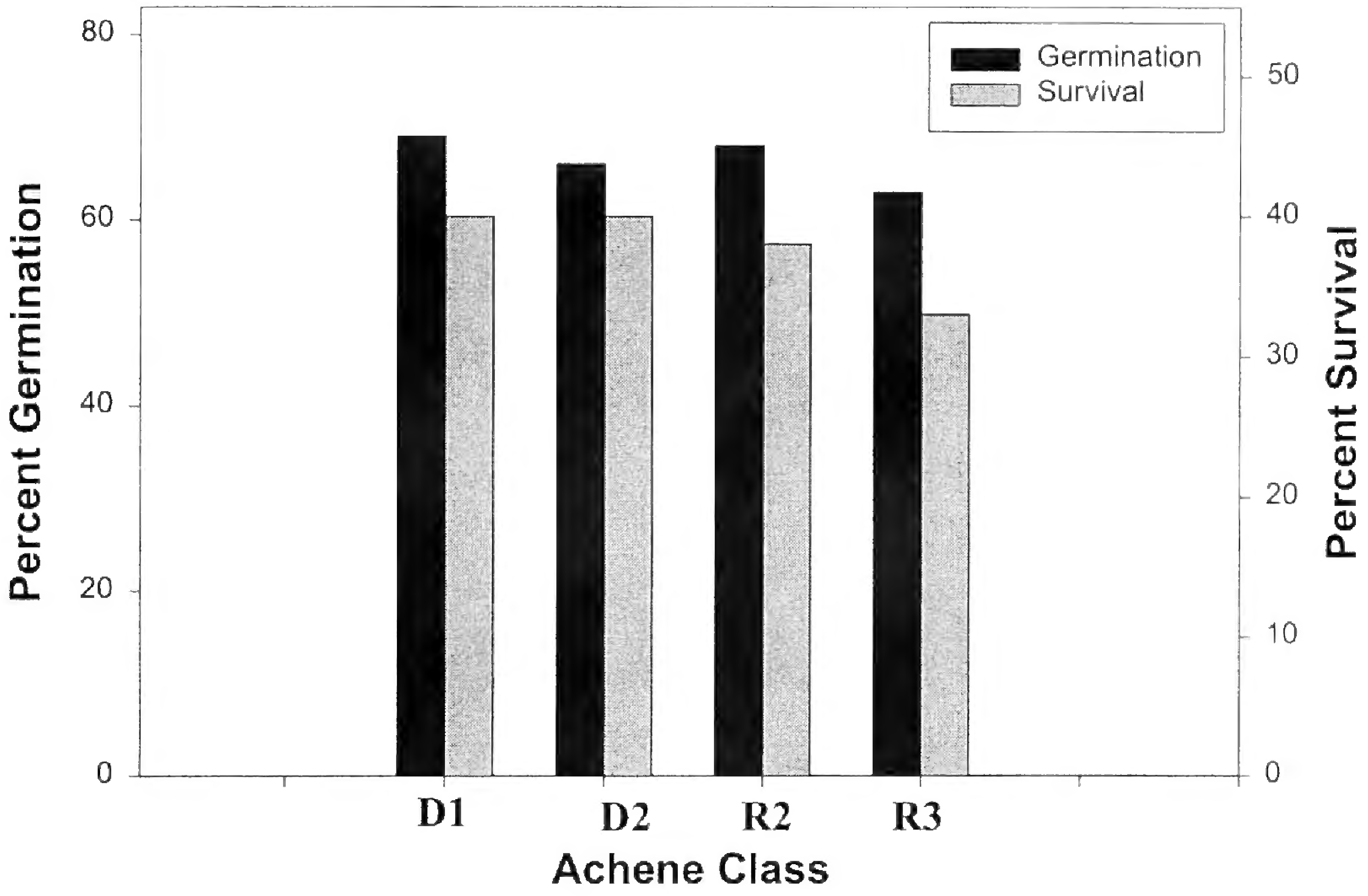

Figure 1. Percent germination and percent seedling survival for achenes from all size classes. D1 = disk achene size class 1 (> 0.841 mm). D2 = disk achene size class 2 (> 0.420 mm, but < 0.841 mm). R2 = ray achene size class 2 (> 0.420 mm, but < 0.841 mm). R3 = ray achene size class 3 (< 0.420 mm).

Seedling growth. One-way analysis of variance (ANOVA) of leaf area measurements taken after 10 days of growth indicated a statistical significance (Table 1). Linear contrast analysis comparing leaf areas of seedlings from both seed types in all size classes indicated statistical significance when contrasting all disk achenes versus all ray achenes (Table 2; Figure 3), the two size classes of ray achenes (R2 and R3), and the largest size class (D1) versus the smallest class (R3; Table 2; Figure 4).

Similarly, ANOVA of 15-day measurements showed statistical difference (Table 1), and linear contrast analysis exhibited statistical significance in comparing all disk achenes versus all ray achenes (Table 2; Figure 3). Additionally, at 15 days, the larger class of disk achenes (D1) proved to have significantly greater leaf area when compared with all other size classes (Table 2; Figure 4). No statistical significance was found by ANOVA of plant height measurements taken after 30 days or after 60 days of growth; furthermore, linear contrast analysis revealed no statistically significant differences in any size class or morphology comparison at 30-day or 60-day measurements. There is, how-

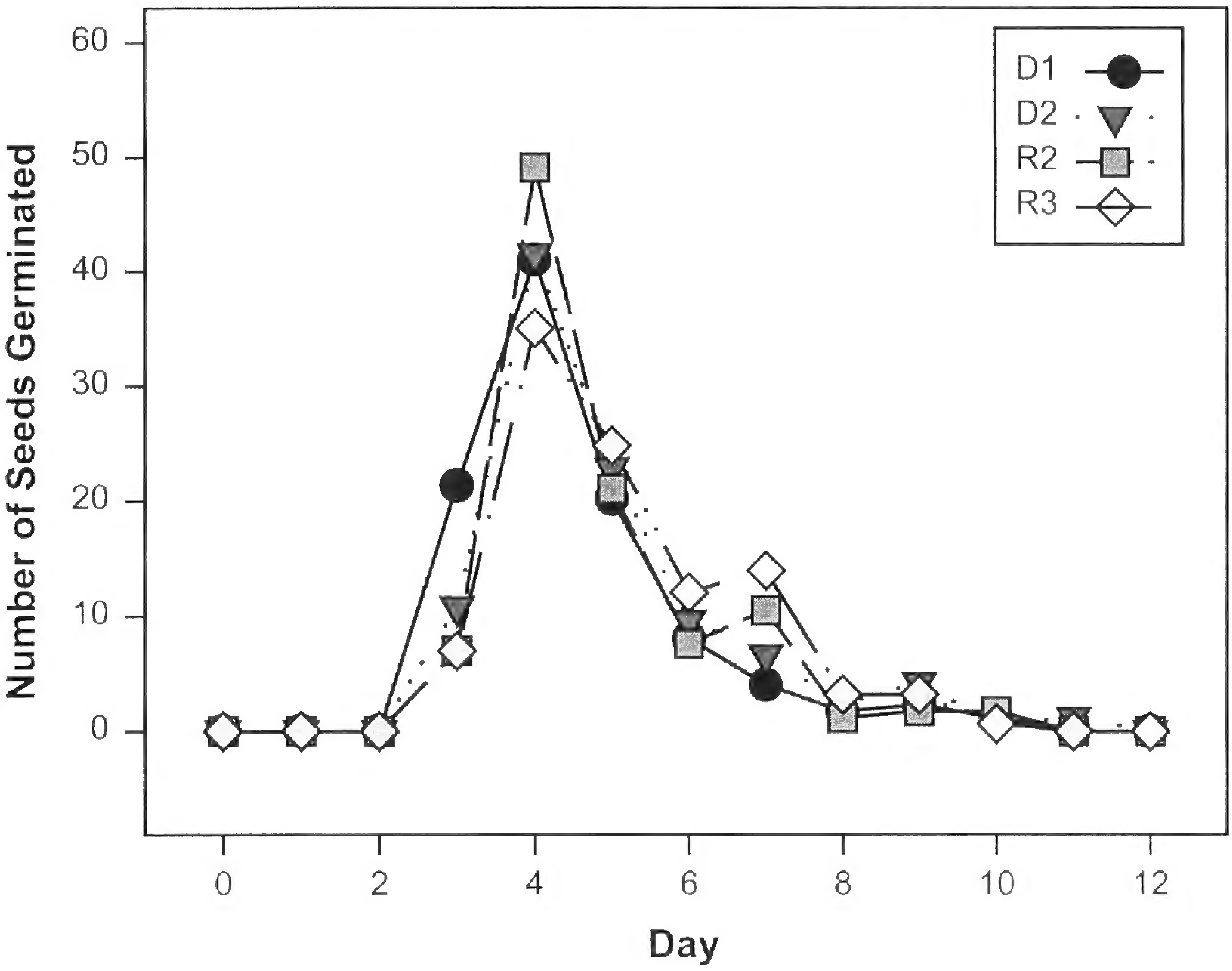

Figure 2. Number of achenes of *Boltonia decurrens* germinating at 22°C and 200 μmol m^{-2} s^{-1} PPF over a 12-day period. D1 = disk achene size class 1 (> 0.841 mm). D2 = disk achene size class 2 (> 0.420 mm, but < 0.841 mm). R2 = ray achene size class 2 (> 0.420 mm, but < 0.841 mm). R3 = ray achene size class 3 (< 0.420 mm).

Table 1. Results of the one-way ANOVAs for seedling leaf area at 10 and 15 days, and seedling height at 30 and 60 days among all four achene classes.

	Source	SSE	df	MSE	F	*P*
10 days	Type	1.923	3	0.641	4.498	0.004
	Error	28.517	200	0.143		
15 days	Type	1.499	3	0.500	4.420	0.005
	Error	16.501	146	0.113		
30 days	Type	0.313	3	0.104	1.358	0.256
	Error	19.273	251	0.077		
60 days	Type	0.196	3	0.128	1.253	0.291
	Error	25.709	251	0.102		

Table 2. Linear contrast analyses for seedling leaf area and seedling height. D1 = disk achene size class 1 (> 0.841 mm). D2 = disk achene size class 2 (> 0.420 mm, < 0.841 mm). R2 = ray achene size class 2 (> 0.420 mm, < 0.841 mm). R3 = ray achene size class 3 (< 0.420 mm).

	Disk vs. Ray		D1 vs. D2		D1 vs. R2		D1 vs. R3		D2 vs. R2		D2 vs. R3		R2 vs. R3	
Contrasts	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
10 days	8.461	0.004	0.067	0.796	1.308	0.254	10.842	0.001	0.768	0.382	9.079	0.003	4.689	0.038
15 days	4.870	0.029	7.684	0.006	6.618	0.011	11.173	0.001	0.039	0.843	0.301	0.584	0.559	0.456
30 days	2.277	0.133	1.770	0.185	3.023	0.083	2.821	0.094	0.174	0.677	0.194	0.660	0.002	0.961
60 days	1.910	0.168	1.816	0.179	2.400	0.123	2.887	0.091	0.045	0.833	0.197	0.658	0.060	0.807

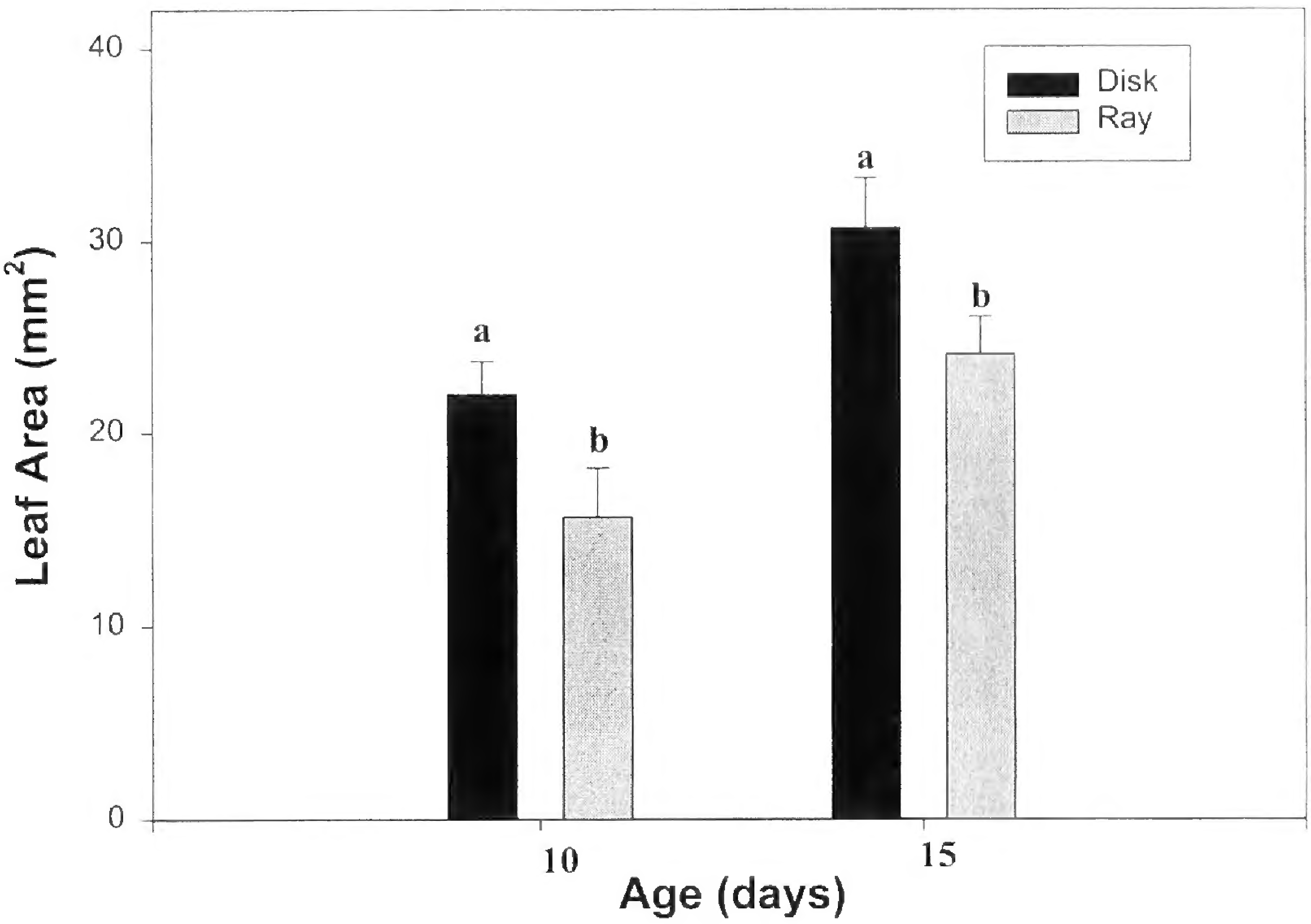

Figure 3. Mean leaf area (± SE) produced by disk and ray achenes, regardless of size class, after 10 and 15 days of growth. Bars with different letters are significantly different between achene types (see Table 2 for *P* values).

ever, an indication that height in the plants produced from the smallest size class, R3, began to lag behind the others in growth at 60 days (Figure 5).

DISCUSSION

Our results suggest that seed morphology influences seedling establishment during the early stages of development; however, any differential competitive advantage due to achene type or mass is less obvious after 10–15 days of growth. Grime (2001) proposed that differences in seed morphology may influence seedling establishment and growth, and our results with *Boltonia decurrens* appear to corroborate his findings. Total leaf area after 10–15 days of growth differed significantly between disk and ray achenes. Additionally, comparison of 10-day growth was significant by size class (i.e., larger achenes produced seedlings with greater leaf area). Since the photosynthetic area of the cotyledon, rather than its mass or stored energy, is the primary consideration in early seedling development (Harper et al. 1970), achenes pro-

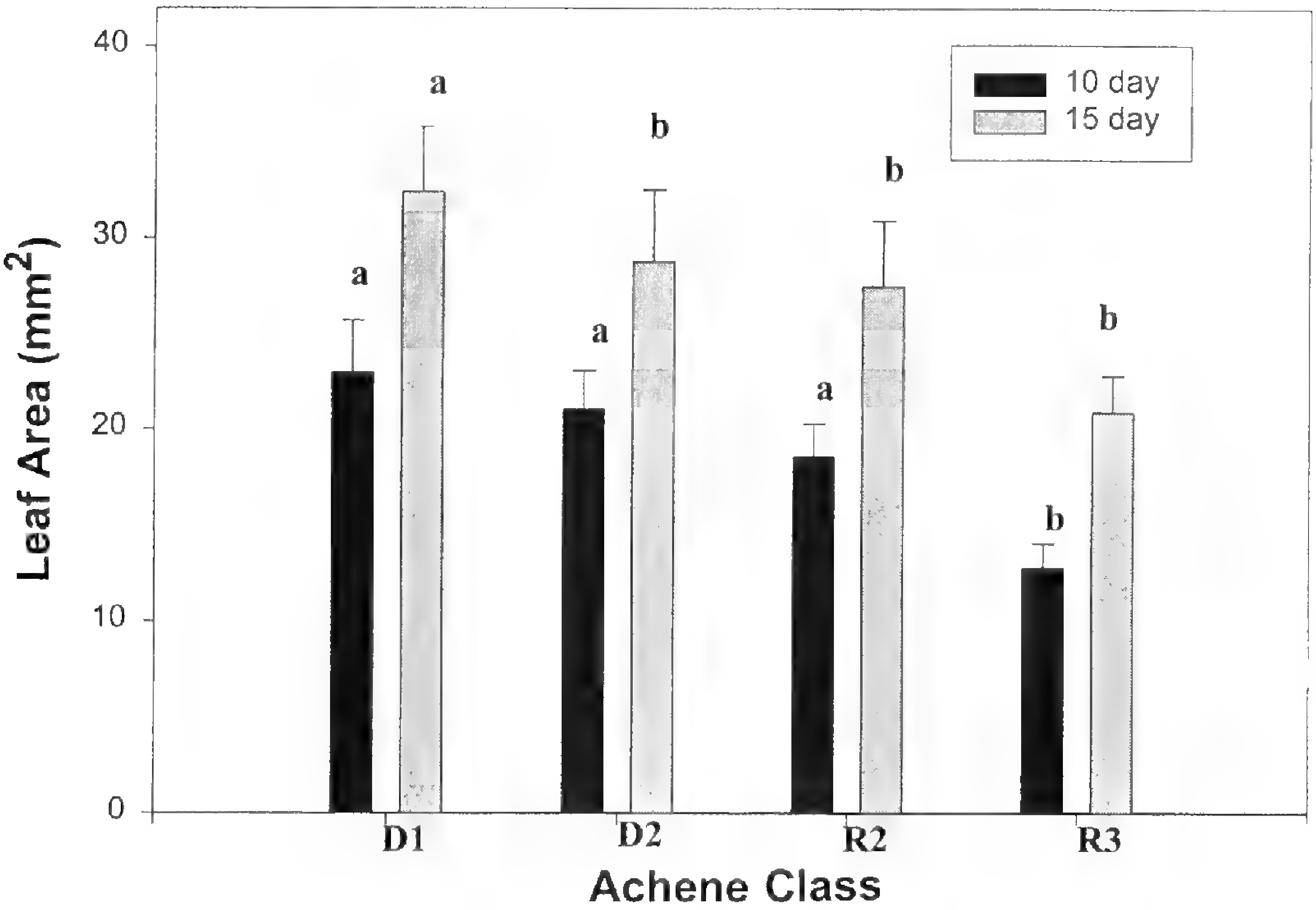

Figure 4. Mean leaf area (± SE) in each achene class after 10 and 15 days of growth. D1 = disk achene size class 1 (> 0.841 mm). D2 = disk achene size class 2 (> 0.420 mm, but < 0.841 mm). R2 = ray achene size class 2 (> 0.420 mm, but < 0.841 mm). R3 = ray achene size class 3 (< 0.420 mm). Bars with different letters are significantly different for each comparison between achene classes (see Table 2 for *P* values).

ducing small cotyledons would have relatively less potential for growth than those possessing large cotyledons. After 15 days of growth, the advantage of greater cotyledon area is reinforced by the greater total leaf area (cotyledons plus true leaves).

Boltonia decurrens requires light for germination (Baskin and Baskin 1988; Smith and Keevin 1998) and high light for growth and seed production (Smith et al. 1993), and seedlings have high mortality when germinated under plant litter (Smith et al. 1995). In natural populations, seedling establishment is extremely low after one year of succession (< 0.01%; Moss 1997; Smith et al. 1998), and *B. decurrens* is often completely replaced by competing vegetation 3–5 years after population establishment (Schwegman and Nyboer 1985; U.S. Fish and Wildlife Service 1990). If achene morphology or mass determines cotyledon and leaf size for the first 10–15 days, greater photosynthetic surface area during this period may enable these seedlings to be more competitive with rapidly growing seedlings of other species. Data

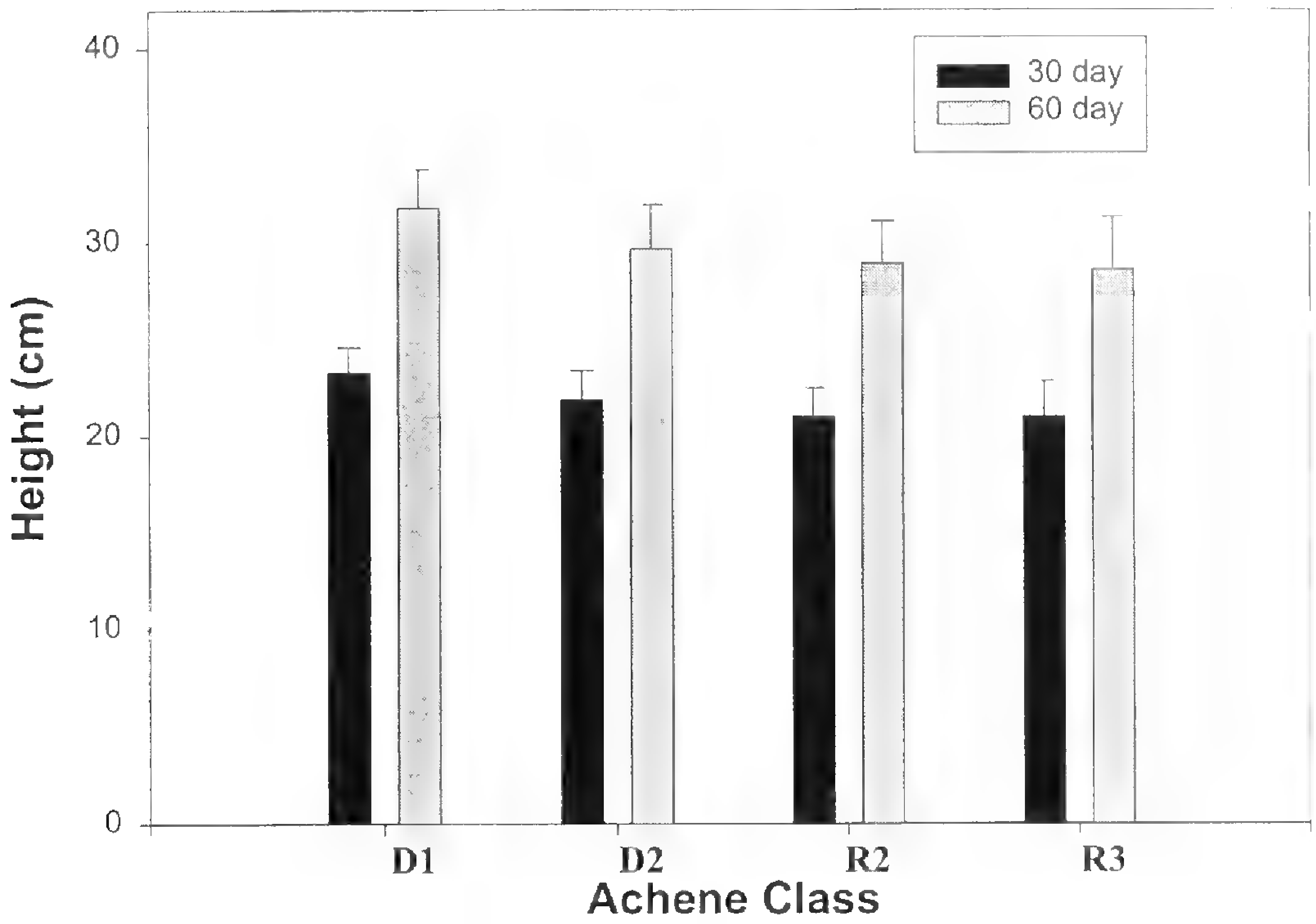

Figure 5. Mean seedling height (± SE) in each achene class after 30 and 60 days of growth. D1 = disk achene size class 1 (> 0.841 mm). D2 = disk achene size class 2 (> 0.420 mm, but < 0.841 mm). R2 = ray achene size class 2 (> 0.420 mm, but < 0.841 mm). R3 = ray achene size class 3 (< 0.420 mm).

from our study indicate that seedlings from disk achenes, regardless of size, would have the highest probability of surviving, and that seedlings from larger ray achenes would fare better than those from smaller ones.

Although there may have been height or mortality differences among seed morphologies and sizes during the earliest stages of growth, at 30 and 60 days there were no statistically significant differences in either. In the present study, the widely spaced distribution of seedlings across the soil surface minimized interactions between individuals. Similar conditions do not exist in the field, however, where thousands of seeds germinate simultaneously. This is particularly so in the case of *Boltonia decurrens,* because its achenes and the seeds of other species are often deposited in densely packed rows by receding floodwaters (Smith and Keevin 1998; Smith et al. 1995). In this environment, where resources are limited and competition increases seedling mortality, a 10–15 day advantage provided by greater photosynthetic surface area may be critical for seedling growth and survival.

In other Asteraceae, Fenner (1983) found that performance of seedlings in the period immediately after germination is critical for establishment. Although Fenner's study was not designed to be a competition experiment, or to represent a field situation, some important inferences can be drawn from his data. Clearly, chronological differences in seedling emergence affect competitive interactions among seedlings: those emerging earlier potentially shade later-germinating seedlings and inhibit their growth. That this effect is largely due to differential seedling size is supported by the results of Gross (1984), who found that within-species differences in seed size had a significant effect on early seedling growth and survival. Although both types of achenes of *Boltonia decurrens* have similar temporal patterns of germination, size differences due to achene morphology or mass produce the same result—larger seedlings that are less likely to be overtopped by other seedlings. In *B. decurrens,* this is particularly important due to its requirement for high light during all stages of growth.

A competitive advantage during early seedling development may be essential to the survival of *Boltonia decurrens* in its current habitat. The construction of a series of levees and navigation dams on the Illinois River over the past 70 years has altered the natural flood regime of the Illinois River Valley (Sparks 1995; Sparks et al. 1998). Areas that once provided the open moist shorelines suitable for the establishment and regeneration of populations of *B. decurrens* are now seldom flooded, resulting in the invasion of the sites by a number of aggressive species that are less flood tolerant than *B. decurrens* (Schwegman and Nyboer 1985; Smith 1991; Smith et al. 1998). In these areas, individuals of *B. decurrens* become smaller and produce fewer and smaller achenes each year following population establishment (Smith 1993). Seedling survival declines rapidly (Moss 1997) as the number and density of aggressive competitors increase. Recent work by Mettler et al. (2001) and Smith (unpubl. data) indicates that the loss of an annual nutrient pulse in years without floods may contribute to the decline of *B. decurrens* by reducing plant size and achene number and mass.

Information provided in the current study indicates that a reduction in achene size would affect seedling growth, and adds to the accumulating evidence that alterations in the natural flood regime in the Illinois River Valley are implicated in the decline of *Boltonia decurrens* (Smith and Mettler 2002; Smith et al.

1998), as has been reported for other native species (Sparks 1995; Sparks et al. 1998). This information may help stimulate efforts to restore connections between the river and the floodplain and to re-establish native plant communities in the Illinois River Valley.

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CROSSING EFFECTS ON SEED VIABILITY AND EXPERIMENTAL GERMINATION OF THE FEDERAL THREATENED *PLATANTHERA LEUCOPHAEA* (ORCHIDACEAE)

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ABSTRACT. We conducted experimental pollination and seed germination trials with *Platanthera leucophaea*, a threatened north temperate grassland orchid species for which propagation and restoration are important conservation needs. Our objectives were to determine how the species' breeding system and modes of pollination interact to affect production of viable seed and seed germination, and how seed germination responds to stratification and to inoculation by mycorrhizal fungi. Outcrossing by hand pollination produced a higher percentage of viable seed than did natural pollination, as did outcrossing between populations in comparison to outcrossing or selfing within populations, indicating a facultative outcrossing breeding system. Outcrossing also enhanced percent germination, which was positively correlated with the percentage, but not number, of viable seeds. A 16 wk. stratification period resulted in significantly higher percent germination than 8 wk. stratification or no stratification. Germination was further enhanced by inoculation with a mycorrhizal fungus (*Ceratorhiza* sp.) isolated from *P. leucophaea*. These results indicate that the breeding system of *P. leucophaea* allows for greater numbers of viable seeds with greater germination rates when plants are outcrossed. Thus, hand pollination and outcrossing can enhance propagation and restoration efforts, especially when coupled with scarification and stratification treatments that maximize germination rates.

Key Words: Orchidaceae, *Platanthera*, seed germination, breeding system, pollination, conservation

Gaining a better understanding of the propagation and restoration requirements of terrestrial orchids has become crucial to their conservation (Johansen and Rasmussen 1992; Zettler 1996a), and is an important conservation objective for the Federal Threatened eastern prairie fringed orchid *Platanthera leucophaea* (Nutt.) Lindl. (Bowles and Bell 1999; U.S. Fish and Wildlife Service 1999). This orchid occurs in tallgrass prairie remnants and wetlands in eastern Iowa, southern Wisconsin, and northern Illinois and Indiana, and in shoreline prairies, sedge meadows, bogs, and fens eastward to Maine (Bowles 1983; Sheviak 1974; Sheviak and Bowles 1986). It has declined by more than 70% from original county records due to habitat conversion to agriculture. Remaining populations are often small and continue to be threatened by succession to woody vegetation, competition from exotic species, illicit collecting, and drainage (Bowles 1983; U.S. Fish and Wildlife Service 1999). In this study, we report on effects of experimental pollination on its seed production, and effects of seed treatment and fungal inoculation on seed germination.

Showy *Platanthera* are thought to have facultative outcrossing breeding systems (Gregg 1990), a well known strategy for avoidance of deleterious effects of inbreeding (e.g., Willson 1983). *Platanthera leucophaea* has the largest flowers and nectar spurs of eastern North American *Platanthera,* and its large floral display and lack of vegetative reproduction indicate a strong investment toward pollination and seed production (Bowles 1983, 1985; Sheviak and Bowles 1986). Pollination is by hawkmoths. The orchid pollinarium, which comprises a pollinium (pollen mass), caudicle, and viscidium, adheres to a hawkmoth's proboscis by the viscidium. Caudicle movement (taxis) positions the pollinium for contact with the stigmatic surface after about 40 seconds, thereby promoting outcrossing (Bowles 1985). Pollen grains are then removed from the pollinium as they adhere to the plant's stigma. Selfing or geitonogamy may occur when moths revisit flowers or inflorescences, especially in small orchid populations, and could potentially influence production of viable seeds if this species is affected by inbreeding depression. As in *P. praeclara* Sheviak & M. L. Bowles (Sieg and King 1995), most plants flower once and the median number of flowering seasons is less than three. Seedling establishment is therefore an important life history stage for this species, and pollination and seed production are critical factors in population viability (Bowles and Bell 1999).

Terrestrial orchids are difficult to propagate due to physiological seed dormancy and the need for mycorrhizal fungi for successful seed germination and seedling development (Rasmussen 1995; Stoutamire 1974; Zettler 1996b; Zettler and McInnis 1992). Experimental propagation with mycorrhizal fungi has been reported for a few species of the widespread north temperate orchid genus *Platanthera,* including *P. integrilabia* (Correll) Luer (Zettler and McInnis 1992), *P. clavellata* (Michx.) Luer (Zettler and Hofer 1998), and *P. leucophaea* (Zettler et al. 2001). Seed germination was highly variable among seed sources in these studies, and was facilitated by, but not dependent upon, the presence of mycorrhizal fungi. Such variation may be influenced by many factors, including sensitivity to inbreeding and levels of genetic diversity within populations of different sizes (e.g., Fenster and Dudash 1994; Weller 1994), and differing germination requirements or different experimental methods used by researchers (Rasmussen 1995; Zettler 1996b).

Seed germination and mycorrhizal fungi of *Platanthera leucophaea* were first investigated by Curtis (1939), who isolated species of the soil fungus *Rhizoctonia* (now *Ceratorhiza*; Andersen and Rasmussen 1996) from *P. leucophaea* roots in different habitats. Curtis was unable to germinate seeds inoculated with these fungi, perhaps due to failure to properly scarify or stratify seeds. Stoutamire (1996) increased asymbiotic seed germination rates by increasing scarification time in diluted NaOCl, and recommended two or more months of cold stratification. Stoutamire (1996) also germinated *P. leucophaea* seeds in 35 mμ Nitex bolt cloth (following Rasmussen and Whigham 1993) buried in prairie sod that contained soil fungi, but neither mycorrhizae nor further seedling development occurred. Zettler et al. (2001) achieved mycotrophic germination of *P. leucophaea* seeds using a *Ceratorhiza* species isolated from roots of this orchid, with development of leaf-bearing seedlings occurring after a second cold treatment.

More information is needed about optimum pollination and germination requirements of *Platanthera leucophaea,* factors that will lead to a better understanding of its reproductive biology, population demographic processes, and restoration requirements. Our study had two related objectives. First, we assessed how different modes of pollination (i.e., natural versus hand pollination, selfing, outcrossing within, and outcrossing between populations) affect the percentage of viable seeds and the germinability of seeds. Because of the breeding system of this species, we expected that outcrossing would enhance seed viability by reducing inbreeding depression. Second, using scarified seed, we tested how stratification periods and symbiotic versus asymbiotic con-

Table 1. Seed sources, sample sizes, and seed collection dates for experimental crossing and germination of *Platanthera leucophaea*; n = number of plants sampled for seed.

Site	Location	Sampling Date and Sample Size by Experiment: Germination Experiment	Crossing Experiment
Abbott Park	Lake Co., Ill.	Aug 1996 (n = 3)	Sep 1997 (n = 5) Sep 1998 (n = 1)
Wadsworth Prairie	Lake Co., Ill.	Aug 1995 (n = 111) Sep 1996 (n= 30)	Sep 1997 (n = 3) Sep 1998 (n = 18)
Lyons Woods	Lake Co., Ill.	Sep 1996 (n = 82)	
Pickerel Creek	Sandusky Co., Ohio	Oct 1995 (n > 10)	

ditions affected germination. We expected that longer stratification and symbiotic conditions would enhance germination.

MATERIALS AND METHODS

Seed and fungus sources. *Platanthera leucophaea* seeds were obtained from one site in Ohio and three sites in Illinois (Table 1). The Pickerel Creek, Ohio, site contains one of the largest known *P. leucophaea* populations, where plants occupy successional wetland habitat of the Lake Erie lake plain (U.S. Fish and Wildlife Service 1999). The Illinois sites are in Lake County, in the Chicago region of northeastern Illinois, and are < 15 km from one other. The Wadsworth Prairie, Lyons Woods, and Abbott Park populations are among the largest in Illinois, with plants occurring in successional prairie and sedge meadow (U.S. Fish and Wildlife Service 1999). All seeds were collected from mature capsules prior to dehiscence in late August or early October, and were stored at 5°C in a desiccator (containing

$CaSO_4$) prior to sowing. The mycorrhizal fungus used in germination treatments has been tentatively identified as a species of *Ceratorhiza* (L. W. Zettler, pers. obs.), and was isolated from the roots of a mature *P. leucophaea* specimen obtained from Abbott Park in 1995, and cultured at the Morton Arboretum.

Crossing effects on seed viability. This study investigated whether manually placing entire pollinia on stigmatic surfaces (= hand pollination) yielded a greater percentage of viable seeds than natural pollination. Hand pollination consisted of crosses between plants within populations, while natural pollination could also have included selfing through geitonogamy. Pollinated plants were not bagged to exclude subsequent natural pollination because placement of the entire pollinium on the stigma excludes additional pollen deposition. Pollinations were conducted in 1998, with one or two mature capsules sampled per plant from ten naturally pollinated plants and from nine hand-pollinated plants (Table 1). Seeds were pooled from capsules within plants, and approximately 200 seeds were sampled per plant. Seeds were briefly surface disinfested in dilute NaOCl, moist stratified for 11 mo. by suspending in sterile deionized water (SDW) at 6°C, and sown on a 1 × 4 cm filter paper strip in a 9 cm diameter petri dish containing 20 ml of modified oats medium (Dixon 1987). The dishes were then examined with a dissecting microscope to count numbers of apparently viable and non-viable seeds based on the presence or absence of distinct, rounded and hyaline embryos (Zettler et al. 2001). Viable seed numbers were expressed as a percent of the total seeds in each sample. These percentages were arcsine-transformed (Zar 1974), and tested against the null hypothesis that hand-pollinated capsules did not contain a greater percentage of viable seeds. We used a one-tailed t-test based on our expectation of more viable seeds with hand pollination because it maximizes pollen availability.

A second study examined crossing effects on production of viable seed using the Wadsworth Prairie and Abbott Park populations. We compared self-pollination (1 Wadsworth plant and 1 Abbott plant), outcrossing within populations (1 Abbott plant and 3 Wadsworth plants), and reciprocal outcrossing between populations (2 plants). These pollinations included $>$ 5 flowers per inflorescence, and were conducted in 1997 (Table 1). Seeds collected from mature capsules were pooled within each plant, disinfested, scarified by shaking in 0.5% NaOCl for one hr., and stratified for 8 wk. at 5°C in SDW. Seed suspension samples were removed from stratification with an eyedropper. Each sample contained about 100 seeds, with $\geq$ 10 samples per cross. As described above, the numbers of seeds containing round distinct embryos were counted with a dissecting microscope and expressed as a percent of the total seeds. One of the selfed plants did not produce mature capsules with seeds, resulting in 0% viable seeds for this cross. Differences between crossing treatments were analyzed by inspection because the non-normal distribution of data and unbalanced design prevented appropriate statistical testing of the hierarchical nesting of seed sources within treatments.

Stratification and symbiotic culture effects on germination. In these experiments, we tested effects of duration of moist stratification, seed age (storage time), and presence or absence of fungal inoculant on seed germination. Seeds were disinfested and scarified in 0.5% NaOCl for 1 hr. We used seedling development stages as defined by Hadley (1983), where Stage 1 germination is achieved by rupturing of the testa (seed coat) by the enlarging embryo, and Stage 2 germination coincides with enlargement of the protocorm beyond the original seed size and development of rhizoids. Our observations suggest that scarification may promote Stage 1 germination by facilitating water imbibition and rupture of the testa by the enlarging embryo. In contrast, other studies (e.g., Zettler and Hofer 1998; Zettler et al. 2001) using unscarified seed describe germination to Stage 1 as production of rhizoids, and Stage 2 as rupture of the testa. In this situation, unscarified seeds may initiate germination by producing rhizoids that help imbibe water and then cause rupture of the testa.

The effect of stratification period on germination to Stage 1 was tested on seeds collected in 1996 (Table 1). After scarification, seeds were plated on sterile filter paper moistened with SDW and given treatments of either no stratification (Abbott population), or moist stratification in darkness at 4°C for 8 wk. (all sites) or 16 wk. (Wadsworth and Lyons populations). Seed numbers ranged from 450 to 1140 per population. Seeds were plated onto modified oats medium in petri dishes, with six to nine replicates per treatment and 30–160 seeds per dish. Petri dishes were wrapped in foil and incubated at 25°C in darkness, and germination was monitored biweekly for 11 mo. with a dissecting microscope. Additional germination that might have occurred with a second cold treatment was not considered in this experiment. As described above, seed viability counts were based on the presence of round distinct embryos. Counts of Stage 1 germinated seeds were pooled among replicate plates within each treatment and tested by Chi-square analysis for differences in numbers of germinated and ungerminated seeds among stratification periods, and between the Wadsworth and Lyons seed sources.

Effects of inoculant, stratification, and seed storage time on germination to Stage 2 were tested between the 1995 seed batch (n – 3621 seeds), which was stored for 18 mo., and the 1996 seed batch (n = 1315 seeds), which was stored for 6 mo. (Table 1). In this study, only scarified seeds were used, and seeds were pooled among seed sources. To test whether a fungal inoculant and stratification resulted in greater germination than either treatment separately, replicate plates for the 1995 and 1996 seed batches were given treatments of 16 wk. stratification, 16 wk. stratification plus inoculant, or inoculant with *Ceratorhiza* sp. As above, seeds were plated onto modified oats medium and seed viability counts were based on presence of distinct embryos. Germination was monitored biweekly for 11 mo. The number of Stage 2 seedlings on each plate was expressed as a percent of the number of viable seeds originally present on the plate.

A two-factorial ANOVA was used to compare germination treatment and seed storage time effects on percent germination. Exclusion of contaminated plates resulted in an unbalanced experimental design (replicates ranged from 4–16 plates), which we tested using a General Linear Model. Prior to analysis, all percentages were arcsine transformed (Zar 1974). We also tested for a correlation between the percentage of viable seeds and the percentage of those seeds reaching Stage 2. To determine whether seedling development (and seed viability) was independent of seed density, we tested for a correlation between the percentage of viable seeds reaching Stage 2 and the total number of seeds (both viable and non-viable) in each plate.

RESULTS

Crossing effects on percent viable seed. Seed viability varied among pollination crossing treatments made in 1997 and in

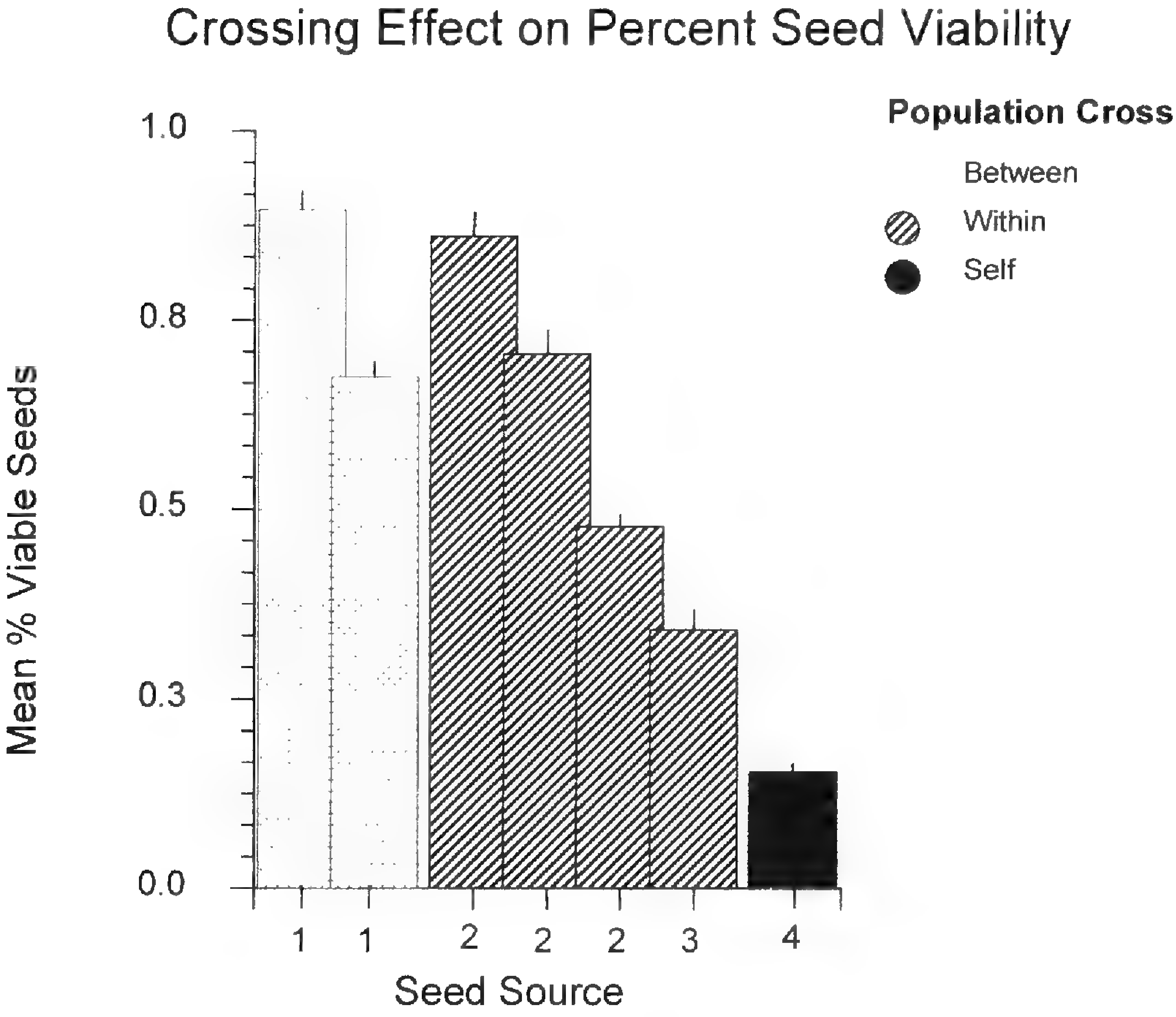

Figure 1. Differences in mean percent viable seed produced by selfing, crossing within, or crossing between populations of *Platanthera leucophaea*. Seed source replicates: 1 = Wadsworth × Abbott, 2 = Wadsworth × Wadsworth, 3 = Abbott × Abbott, 4 = Abbott self. One Wadsworth selfed plant produced no viable seed. Lines represent standard errors.

1998. About 50% of the seeds in capsules obtained from hand cross-pollinations made in 1998 contained viable embryos, almost twice the percentage from naturally pollinated plants ($t = -1.785$, $P = 0.046$). Within-population outcrosses made in 1997 also averaged about 50% viable seed, but between-population crosses averaged almost 70% with wide variation among means (Figure 1). One self-pollinated plant produced no capsules with viable seeds, while the second averaged 15% viable seeds.

Effects of stratification period on Stage 1 germination. Stratification period, but not seed source, significantly affected germination to Stage 1, with percent germination increasing with increasing stratification period across all seed sources (Figure 2). Overall, germination was < 5% for unstratified seeds,

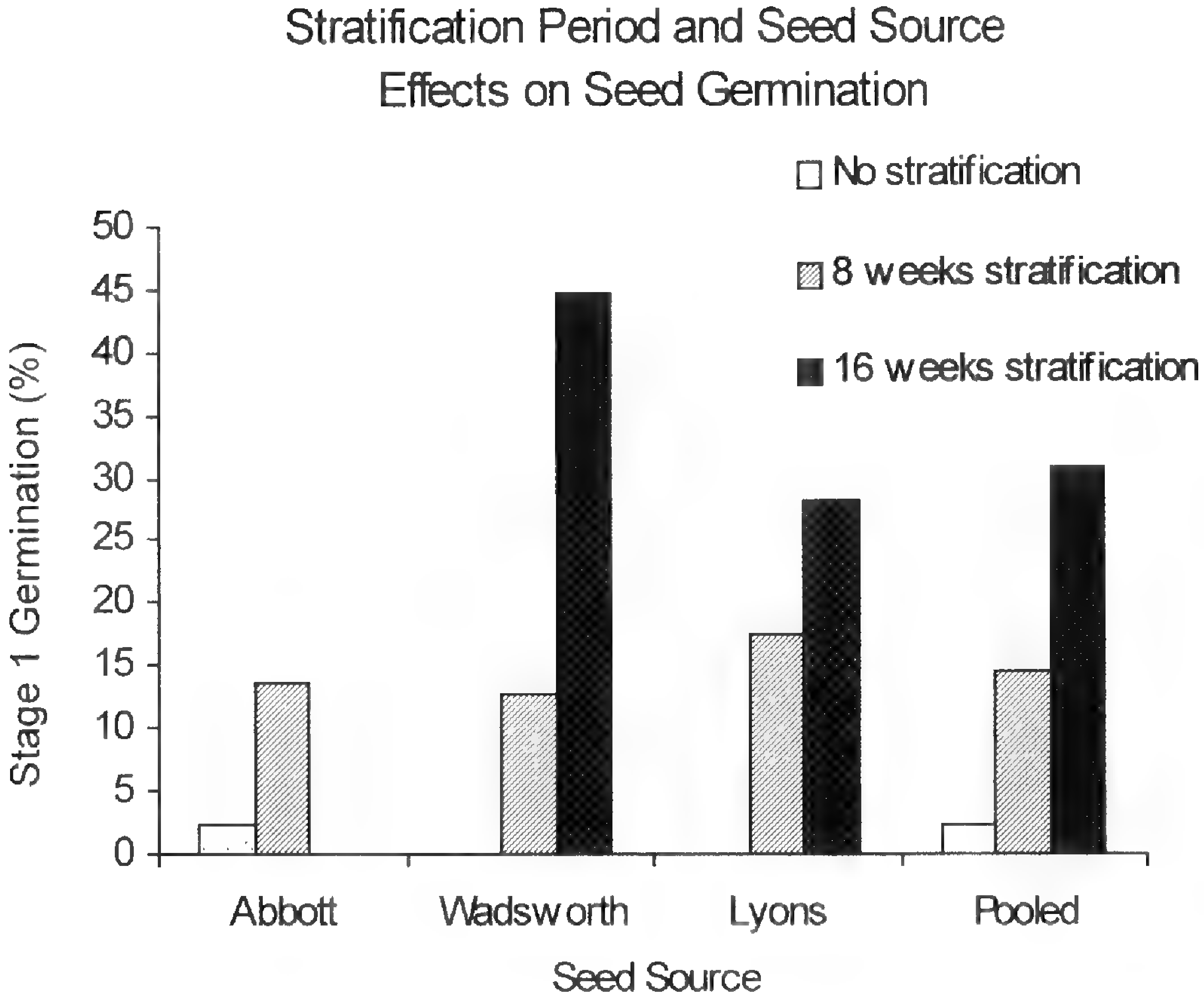

Figure 2. Longer stratification period increases percent seed germination of *Platanthera leucophaea*, with similar effects among seed sources. Chi-square: Stratification period ($\chi^2 = 275.76$, $P < 0.001$), Seed source ($\chi^2 = 0.945$, $P = 0.332$).

10–20% after 8 wk. stratification and > 30% after the 16 wk. stratification.

Effects of seed storage time, germination treatment, and seed viability on germination to Stage 2. No significant effects of seed storage time or germination treatment were found for Stage 1 germination. However, Stage 2 germination (rhizoid production) was significantly higher for seeds from the 1996 seed batch than for seeds collected in 1995 and stored for an additional 12 mo. (Figure 3). Moreover, Stage 2 germination in both seed batches was higher for stratified seeds that were also germinated symbiotically with *Ceratorhiza* than for either treatment alone (Figure 3). Among the 1996 seeds, percent germination to Stage 2 was also significantly correlated with percentage of viable seeds (Figure 4). Percent germination was not, however, significantly correlated with total seed number per plate ($r^2 = 0.003$, $P = 0.85$)

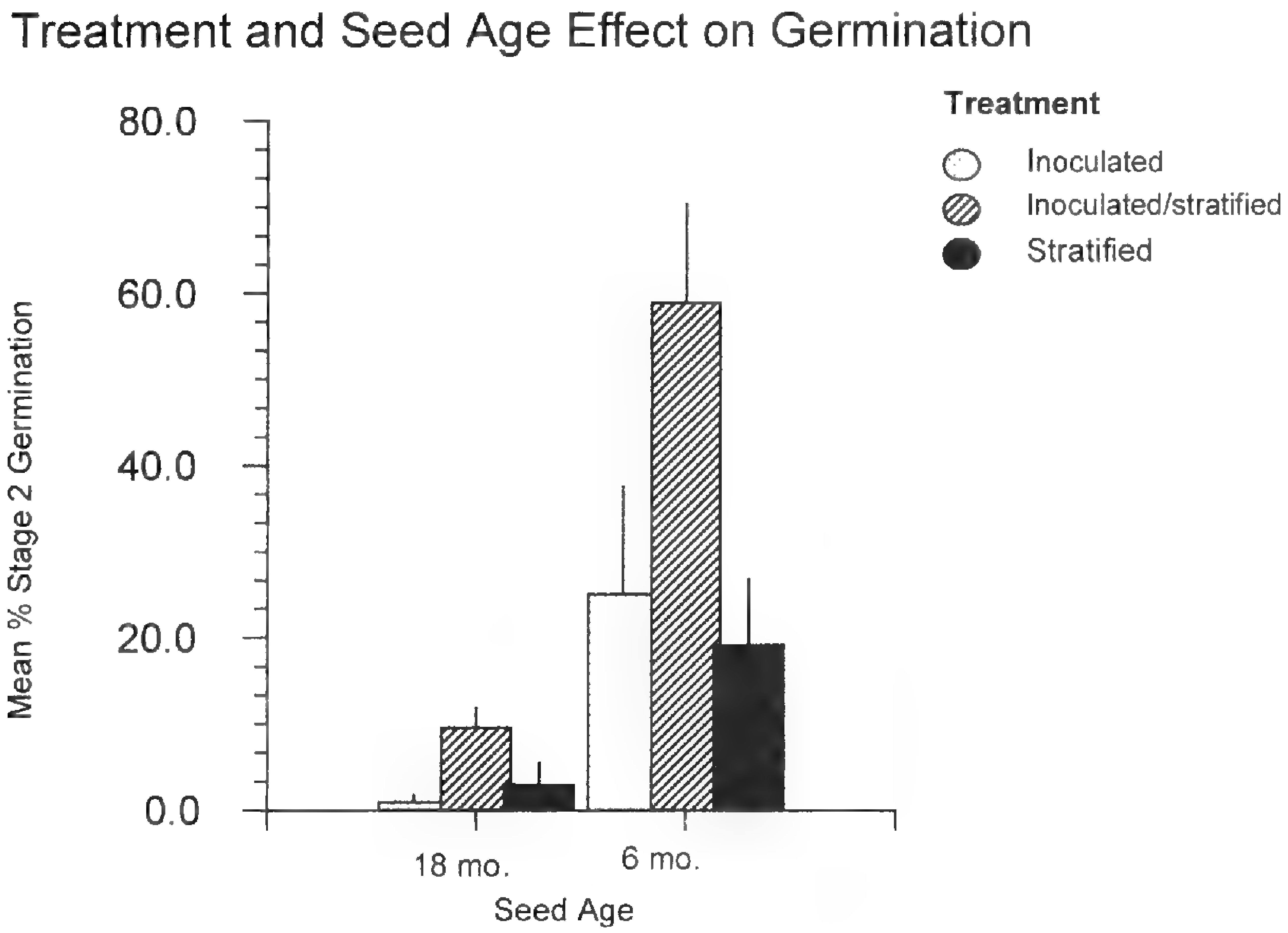

Figure 3. The mean percentage of viable *Platanthera leucophaea* seeds germinating to Stage 2 is lower for older seeds and greater for stratified seeds inoculated with *Ceratorhiza* sp. isolated from *P. leucophaea*. ANOVA: Treatment ($F = 6.97$, $P = 0.003$), Age ($F = 20.74$, $P < 0.0001$), Treatment × Age ($F = 1.78$, $P = 0.1846$). Lines represent standard errors.

nor with total number of viable seeds per plate ($r^2 = 0.008$, $P = 0.755$).

DISCUSSION

Crossing effects on seed viability. As suggested for showy *Platanthera* (Gregg 1990) our pollination experiments indicate that *P. leucophaea* has a facultative outcrossing breeding system. Because this system allows mixed mating, it is apparently vulnerable to inbreeding depression, which can be expressed at different plant life-history stages (e.g., Carr and Dudash 1996; Dudash 1990; Fenster and Dudash 1994). In *P. leucophaea,* inbreeding depression appears to have cascading effects by decreasing the percentage of capsules formed, the percentage of viable seeds within capsules, and the percent germination of those seeds. For outcrossing species, this process may be alleviated in larger populations that maintain high levels of genetic diversity (Schaal et

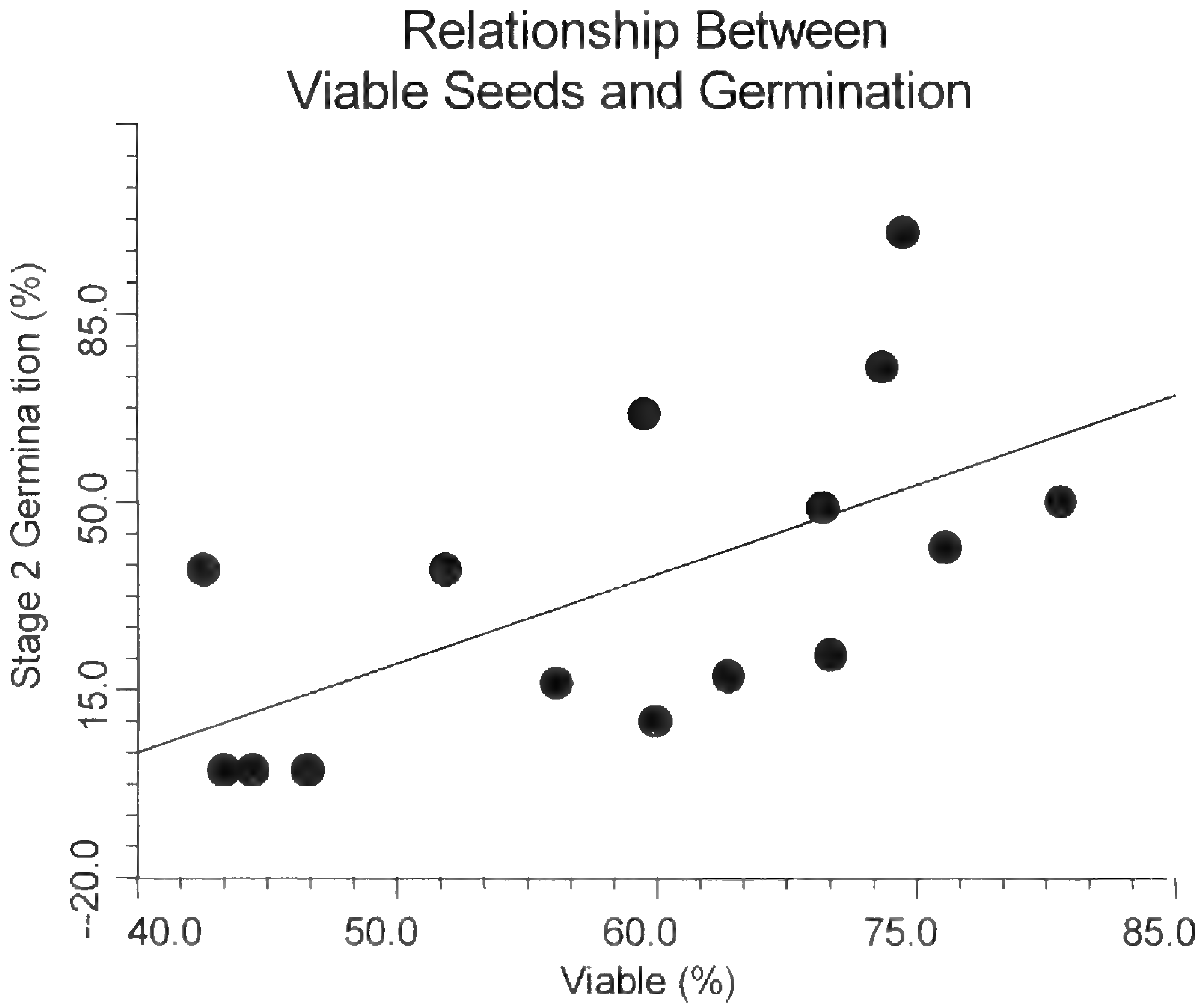

Figure 4. Within plates, the percentage of viable *Platanthera leucophaea* seeds germinating to Stage 2 is positively correlated with the total percentage of viable seeds ($r^2 = 0.374$, $P = 0.015$).

al. 1991; Weller 1994). The amount of inbreeding in small *P. leucophaea* populations could therefore be greater than in large populations because opportunities for outcrossing may be less in small populations. In our study, the lower percentage of viable seeds in naturally pollinated plants than in hand-pollinated plants may have resulted from inbreeding due to geitonogamy and crossing among closely related individuals, as well as from low rates of pollen deposition by hawkmoths. The wide variation we detected in seed viability among outcrosses within populations could reflect different levels of inbreeding based on chance.

Stratification and fungal symbiont effects on germination. *Platanthera leucophaea* seed germination is highly responsive to both stratification time and the presence of a fungal symbiont. As indicated by Stoutamire (1996), optimum germination requires a sequential combination of scarification and moist stratification. Although all of our seeds were scarified, we found extremely low (< 5%) germination without stratification. Further, increasing stratification time from 8 to 16 wk. more than doubled germination from < 15% to > 30%. This suggests that for north temperate orchids, which may have evolved under selective pressure of cold dormant season conditions, both scarification and long-term stratification are necessary to attain high rates of seed germination.

Seed germination experiments that do not include sufficiently long moist stratification periods coupled with scarification and a fungal inoculant could lead to improper conclusions about seed germinability (Rasmussen 1995). For example, although north temperate species seem to depend on mycorrhizal fungi for seedling development (Johansen and Rasmussen 1992), variable results are reported. Zettler and McInnis (1992) found higher germination for *Platanthera integrilabia* with inoculated seeds, but Stoutamire (1996) reported that initial seedling germination for *P. leucophaea* did not require a fungal symbiont if cultured on artificial media containing a carbon source. Our results, along with those of others (e.g., Zettler and Hofer 1998; Zettler and McInnis 1992) underscore the importance of a fungal inoculant for successful germination in *Platanthera* species. The effect was especially apparent for seedling development to Stage 2 germination, which was maximized by the combination of 16 wk. stratification and presence of a fungal inoculant.

Seed age and storage techniques are also important factors in orchid seed germinability (Seaton and Hailes 1989). Stoutamire (1996) reported complete loss of *Platanthera leucophaea* seed viability after 6 mo. of storage at 5°C. Our results were less drastic, but similar, in that about 60% of the seeds reached Stage 2 germination after 6 mo. of storage at 5°C, but only 10% reached Stage 2 after 18 mo. of storage. However, Zettler (1996b) reported viable *P. integrilabia* seeds after 6 yr. of storage at −7°C and 6°C. Loss of viability may be related to failure to adequately dry seeds prior to and during storage (L. W. Zettler, pers. obs.), complex dormancy mechanisms (Johansen and Rasmussen 1992), and different species characteristics.

For north temperate *Platanthera,* including *P. leucophaea,* propagation beyond Stage 2 may be accompanied by high rates of mortality, especially if using an aggressive fungal symbiont (Zettler and Hofer 1998; Zettler and McInnis 1992; Zettler et al.

2001). As a result, symbiotic orchid propagation without host-specific fungi may be problematic. Screening of *P. leucophaea* fungal inoculants from naturally germinating seeds and seedlings could help alleviate this problem. Research is also needed to determine whether the combination of proper scarification, stratification, inoculation, and secondary cold treatments can enhance the transition from Stage 2 germination to further leaf and tuber development (Johansen and Rasmussen 1992), and how pollination outcrossing rates affect this transition.

Conservation applications and concerns. Although *Platanthera leucophaea* is perennial, most individuals flower once, and seedling establishment appears to be a critically important stage in its life cycle (Bowles and Bell 1999). Thus, factors that increase production of viable seeds should enhance population viability. In that regard, hand pollination may be an important tool because it can increase viable seed numbers by maximizing pollen deposition and avoiding inbreeding. Hand crossing among fragmented populations appears most likely to enhance viability, but it is controversial because of concerns that outbreeding depression may result from the disruption of locally adapted gene complexes (Bowles and Whelan 1994). For example, genetic allozyme (Cowden 1993) and random polymorphic DNA (Havens and Buerkle 1999) studies of *P. leucophaea* have found comparatively high levels of genetic differentiation among populations, which indicates potential for outbreeding depression. However, human-caused population fragmentation and reduced gene flow could have contributed to such differences, and it is unknown whether outbreeding depression would actually occur. For example, Fenster and Galloway (2000) found outbreeding depression to be important in *Chamaecrista fasciculata* Michx. only for crosses of ≥ 1000 km, a distance far greater than among our study sites. Hawkmoths are well known for long-distance movement, which may have facilitated landscape-scale gene flow in *P. leucophaea* that would have tended to minimize population differentiation. Human-mediated crosses can alleviate potential inbreeding within fragmented populations of outcrossing species (Richards 2000). For example, heterosis from long-distance crosses has been observed in the orchid *Liparis lilifolia* (L.) A. Rich. *ex* Lindl. (Whigham and O'Neill 1991), and such crosses have been used to obtain viable seed of the orchid *Cypripedium cal-*

ceolus L. var. *pubescens* (Willd.) Correll in Britain (Light and MacConaill 1998). Our results indicate this may be possible for *P. leucophaea,* as the greatest percentage of viable seeds resulted from inter-population crosses.

Another concern is that high levels of seed production from hand pollination could impose a significant cost on terrestrial orchids, as found for *Tipularia discolor* (Pursh) Nutt. (Snow and Whigham 1989) and *Cypripedium acaule* Aiton (Primack and Hall 1990). Calvo (1993) argued that the naturally low rates of orchid seedling recruitment would not select for increased pollination and seed production. Kull (1998) also found that microsite factors, rather than pollinators, limited population growth in the long-lived perennial *C. calceolus.* However, such effects may be less important in short-lived orchid species. The short life span of *Platanthera leucophaea,* its lack of vegetative spread, and its showy, and apparently costly, inflorescence structure suggest that high rates of seed production, and more importantly, high levels of seed viability, are important for population maintenance in this species. Ultimately, successful seedling establishment will depend upon chance coupling of germinating seeds with hyphae of favorable soil fungi, and rates of this demographic process remain essentially unknown for terrestrial orchids.

These concerns, and our crossing experiments, indicate that further work is needed to assess the impacts of translocating genetic material among populations, and whether there are negative demographic consequences of increased rates of pollination. Fully replicated crossing experiments are also needed to test for plant and site effects on seed viability.

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THE IDENTITY AND HISTORY OF *MYRICA CAROLINIENSIS* (MYRICACEAE)

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ABSTRACT. The protologue of *Myrica caroliniensis* is more than adequate to identify it as depicting the bayberry ranging at least from southern New Jersey to Florida and westward into eastern Texas. That species has been mostly known for the past half century as *M. heterophylla*. The alleged differences between the commonly recognized and more northern populations known most recently as *M. pensylvanica* (presumably ranging from Newfoundland at least into northeastern North Carolina) are that the southern elements have more persistent to even evergreen leaves and lack the minute trichomes on both the hardened fruit wall and the young glandular projections or papillae that completely cover the young to just maturing fruit of the northern representatives. The pubescence on the fruit cannot be readily detected on mature fruit due to its heavy deposit of wax. The alleged differences, which seem to be more like tendencies than sharply delineated differences, are not of specific significance any more than those suggested between the northern and southern populations of *Magnolia virginiana*. The name for the bayberry that ranges from Newfoundland south into Florida and westward into eastern Texas should therefore be *Myrica caroliniensis*, the binomial by which it was known throughout most of the nineteenth century. It has been rather conclusively demonstrated that the waxy fruited, papillate species ought to be placed in the genus *Morella*, clearly separate from the genus *Myrica* with the latter's smooth, non-papillate, non-waxy nutlet.

Key Words: *Myrica caroliniensis, M. cerifera, M. heterophylla, M. pensylvanica*, Myricaceae, *Morella caroliniensis, Morella cerifera*

Phillip Miller (1768) published the binomial *Myrica caroliniensis* with the following protologue:

> 3. Myrica (caroliniensis) foliis lanceolatis serratis, caule suffruticosa. *Myrica with spear-shaped sawed* leaves, and a shrubby stalk. Myrtus Brabanticae similis caroliniensis humilior; foliis latioribus & magis serratis. Catesb. Car. vol. 1. p. 13. Lower Carolina Myrtle, or Candleberry-tree resembling that of Brabant, having broader leaves which are more sawed.

The third sort grows naturally in Carolina; this doth not rise

> so high as the former, the branches are not so strong, and they have a grayish bark; the leaves are shorter, broader, and are sawed on their edges, but in other respects is like the second sort [*M. cerifera* L.]; the berries of this are also collected for the same purpose [i.e., for a "sort of green wax from the berries, which they make into candles."]

The above scanty account does not describe unequivocally any one species but it does contrast *Myrica caroliniensis* in a manner adequate to distinguish it from *M. cerifera* for those familiar with the plants in the field. Miller cited Catesby's account (1730, 1: 13, t. 13.), which was accompanied by a convincing illustration. Catesby is quoted in full below:

> "Myrtus Brabanticae similis Caroliniensis humilior; foliis latioribus et magis serratis.
> The broad leaved Candle-berry Myrtle.
> This grows usually not above 3 feet high; in which, and its having a broader leaf than the tall Candleberry Myrtle, it principally differs from it."

Linnaeus (1753, 2: 1024) described *Myrica cerifera* [var.] ß, based solely upon the same Catesby polynomial and illustration (cited as "Catesb. car. 1: p. 13, t. 13") noting its presence in "Carolina, Virginia, Pennsylvania."

Anyone familiar with both *Myrica cerifera* and *M. caroliniensis* in the field in the Carolinas would readily assign the above descriptions of Miller and Catesby to the bayberry (*M. caroliniensis*) with its broader leaves and shorter stature and not to the more commonly encountered wax myrtle, *M. cerifera.*

As is to be expected when a protologue is so lacking in details as is that of *Myrica caroliniensis,* there has been much disagreement for almost two and a half centuries as to the identity of the binomial, especially by those with little or no familiarity with both species in the field. At various times the binomial has been attributed to what has been passing as *M cerifera, M. pensylvanica* Mirb., and *M. heterophylla* Raf. or *M. curtissii* A. Chev. Not surprisingly, our knowledge of the morphological distinctions between these species, as well as their distributional ranges, has greatly increased with the passage of time. Hence we are now better able to determine what the various authors were describing.

Although apparently there is no extant original material of Phillip Miller's *M. caroliniensis,* it seems that the protologue's emphasis on the low stature and the shorter and broader leaves would strongly suggest that a bayberry was being described, and not the wax myrtle (*M. cerifera*). This view is strengthened especially when one considers that *M. cerifera sensu stricto* was already included in a reasonably definitive manner elsewhere in each of the respective publications of Catesby, Linnaeus, and Miller.

Most recent authorities, at least since Fernald (1938), have recognized two bayberries in eastern North America, collectively ranging from southern Newfoundland south into northern Florida and westward into Arkansas and Texas. *Myrica pensylvanica* reportedly is found southward as far as northeastern North Carolina while what has been most recently called *M. heterophylla* reportedly ranges northward from Florida along the coastal plain at least as far as southern New Jersey and perhaps southeastern Pennsylvania as well as westward into Texas. Approximately half the plants are staminate and everyone agrees that staminate plants are exceedingly difficult, if not impossible, for one to distinguish between the two supposed eastern species of bayberry. Bornstein (1997, p. 434) reports that *M. pensylvanica* hybridizes quite readily with both *M. cerifera* and *M. heterophylla* which, if proven to be true, would surely make for an even more bafflingly complex problem in identification. My field experience with these two species in the southeast is considerable and I have not noted evidence of hybridization.

I am unconvinced that there are two species of bayberry in eastern North America. Nothing suggests to me rampant hybridization between the wax myrtles and the bayberries. I cannot recall ever encountering a plant in field or herbarium that could not be identified immediately to species in the southeast. Miller, in publishing *Myrica caroliniensis* failed to distinguish it sharply from even the sympatric *M. cerifera,* not to mention the supposedly largely allopatric *M. pensylvanica.* Only those familiar with the pronounced tendencies exhibited by the plants in the field could expect to recognize the distinction between the species. If there is one bayberry in eastern North America, as my examination of thousands of specimens has convinced me, we can safely conclude that it is *M. caroliniensis* which, besides being the first of the bayberries to be described, is the only bayberry known from South Carolina, the area of Catesby's intensive observations while preparing his *Natural History of the Carolinas, Florida and the Bahama Islands* (1730–1747). In this case, *M. pensylvanica, M. heterophylla,* and *M. curtissii* are all later synonyms of Miller's *M. caroliniensis.* If, contrary to my conclusion, after examining over two thousand specimens from throughout their collective range, there actually are two species of bayberry in eastern North America, the southernmost of them is *M. caroliniensis* (Miller 1768) with *M. heterophylla* (Rafinesque 1838) and *M. curtissii* (Chevalier 1901) as later synonyms, the northern bayberry would then be *M. pensylvanica* (Mirbel 1804).

The principal distinction previously employed to separate *Myrica pensylvanica* from *M. heterophylla* has been the presence of rather abundant but short, stiff trichomes on the densely compacted glandular papillae covering the usually pubescent, hardened wall of the fruit prior to the deposition of the heavy waxy layer. Only a minority of the thousands of specimens examined were of the gender and stage in which this feature could be employed. I have found specimens whose papillae were hirsutulous among collections from the Gulf Coast and the frequency of such puberulently fruited specimens was even much higher in eastern North Carolina than further south. In my experience, species are separable by more and stronger characters than those differentiating these alleged species (i.e., *M. caroliniensis* and *M. pensylvanica*). Leaves of *M. caroliniensis sensu lato* are retained throughout most of the winter in the more southern parts of its extensive range; plants from the more northern portion of the range of *M. caroliniensis sensu stricto* retain their leaves for a shorter period of time. The reverse is true for those plants previously called *M. pensylvanica,* which lose their leaves rather promptly at the approach of winter in the more northern part of the species' collective range. The only other distinctions claimed to differentiate the two generally accepted species is the color of the young twigs, but I have found color to be so highly variable as to be of no help in distinguishing the alleged northern and southern taxa. My understanding is that we are dealing with one not particularly variable species. Those who persist in cleaving the bayberries into two species should at least accept the fact that *M. caroliniensis* has priority over either *M. heterophylla* or *M. curtissii* and that Philip Miller's name applies to the southern representatives of this somewhat variable, widespread species.

Below are keys extracted from two leading treatments (Bornstein 1997; Fernald 1950) purportedly distinguishing the two eastern North American bayberries from one another. In a majority of cases these keys do not separate the taxa, since much fewer than half the specimens bear fruit in a state in which the keys can be applied. Since the vegetative features of the twigs are even less applicable due to the great variability of twig color seemingly dependent upon exposure to light and other environmental variables, I question whether we would be able to distinguish staminate plants, or pistillate plants, in most stages of their annual growth unless we first knew their provenance. An unpublished Master's thesis from the University of Georgia (Houghton 1988) analyzed the morphological characteristics as well as the flavonoid profiles of the eastern North American bayberries and wax myrtles concluding that the two bayberries (i.e., *Myrica caroliniensis* and *M. pensylvanica*) were only varietally differentiated. To date the suggested varietal combinations have not been validly published.

Fernald (1950, p. 524) differentiated the two eastern bayberries in his key as shown below:

Bark of mature branches whitish-gray or drab; leaves dull above, membranaceous, deciduous (subpersistent south); inflorescences all borne below the leafy tips; young fruit densely pubescent, ripe fruit 3.5–4.5 mm in diameter .... *Myrica pensylvanica*
Bark of mature branches blackish; leaves lustrous above; coriaceous, evergreen; inflorescences below or in the axils of the old leaves; young fruit glabrous, ripe fruit 3–3.5 mm in diameter .... *Myrica heterophylla*

Bornstein (1997, 3: 431) distinguished the eastern bayberries in his key as follows:

Fruit wall and warty protuberances densely hirsute when young; branches whitish gray in age; leaves deciduous, membranous; fruits 3.5–5.5 mm .... *Myrica pensylvanica*
Fruit wall glabrous or sparsely glandular, warty protuberances ± glandular; branches black; leaves persistent or tardily deciduous, leathery; fruits 3–4.5 mm ..... *Myrica heterophylla*

Type material or original specimens of Philip Miller vouchering his *Myrica caroliniensis* has not been found although diligently sought by several investigators. Rendle (1903) first reported his failure to find original material of Catesby's two myricas depicted on his Plates 13 and 69. Reveal (in litt.) has also searched without success for original material of Miller vouchering his publication of *M caroliniensis.* Catesby's Plate 69 clearly represents *M. cerifera* and Plate 13 depicts a bayberry. Although specimens of Catesby vouchering his "Myrtus Brabanticae similis Caroliniensis humilior" have not been located, this has not prevented three recent publications from confidently identifying to species, the rather crude drawing and meager description provided by Catesby. Ewan (1974) and Howard and Staples (1983) identified it as the more northern *M. pensylvanica,* while Wilbur (1990) concluded that it was *M. heterophylla,* a determination clearly based more on the largely allopatric distribution of the two alleged species than upon the detail presented in the drawing and description provided by Catesby. Although previously Catesby had lived and observed nature for several years in southeastern Virginia, he was not then focused on the goal of producing a sumptuously illustrated Natural History. A later extended trip by Catesby was mostly spent in South Carolina and the Bahamas as well as allegedly in Florida, a claim questioned by Reveal (in litt.), for the intensive observation and painting that preceeded his long-protracted presentation of *The Natural History of the Carolinas, Florida and the Bahama Islands.*

Fernald (1935, p. 423) made a major effort to straighten out the nomenclature of the eastern wax myrtles and bayberries of eastern North America without complete success. Fernald stated that "the wrong interpretation of *Myrica caroliniensis* is clearly discussed by Chevalier who correctly takes up for the deciduous-leaved and northern species the name of *M. pensilvanica* Loiseleur." [Later, Fernald (1938, p. 410), upon the urgings of Rehder, adopted the spelling *pensylvanica* since Loiseleur (actually the author/editor was Mirbel 1804) employed both spellings and Chevalier (1901) had adopted the more usual form.] Chevalier's clarification of *M. caroliniensis,* which earned Fernald's approval, was that Chevalier refused to take up the earlier *M. caroliniensis* since that binomial had been frequently applied to a more southern species which Chevalier described on the next page as "*M. curtissi,*" another name for the more southern bayberry. If Chevalier ever explained why he felt that those who employed *M. caroliniensis* as the binomial for the southern bayberry were mistaken, I have not found it. It is true that *M. caroliniensis,* as stated on p. 184 of Chevalier's monograph, had been used by many early authors for the entire complex, ranging from Newfoundland south along the coastal plain into Florida and west along the Gulf Coast into Texas and then north into Arkansas, but that sort of confusion was routinely resolved by Fernald and most other authors without abandoning such names. If that were reason enough to routinely drop a name, chaos would reign, as Fernald frequently noted (e.g., 1946, p. 389).

Fernald (1935, p. 423) added to the nomenclatural confusion by unequivocally stating without explanation or stated evidence that *Myrica cerifera* included *M. caroliniensis,* and this was accepted by Rehder (1949, p. 87b), also without discussion. It should not surprise anyone that, after such a thorough muddling, the binomial *M. caroliniensis* dropped from botanical usage. In spite of such flagrant abuse, I do not think the binomial irretrievably lost. Examination of the protologue of *M. caroliniensis,* as presented on the first page of this note, in my opinion confirms that those who employed that binomial for the southern bayberry were correct. *Myrica caroliniensis* (Miller 1768), *M. pensylvanica* (Mirbel 1804), *M. heterophylla* (Rafinesque 1838), and *M. curtissii* (Chevalier 1901) are all, in my opinion, synonyms of the eastern bayberry. Those who recognize two species within the eastern bayberries would agree, I believe, that only *M. pensylvanica* ought not be included in that listing.

Fernald (1935, p. 423), usually so precise in his bibliographic sleuthing, uncharacteristically misled us in equating *Myrica caroliniensis* with *M. cerifera* and also then followed Chevalier in recognizing the southern bayberry as *M. curtissii.* Three years later, Fernald (1938, p. 409–410) took up the earlier *M. heterophylla* for *M. curtissii,* the bayberry with the more southern range ("?Delaware south into Florida and westward into Arkansas and Texas"). Rehder (1949, p. 87), in my opinion mistakenly, followed Fernald (1935) in placing *M. caroliniensis* unquestioningly in the synonymy of *M. cerifera.* Thereafter, Miller's binomial almost completely disappeared from the botanical literature for the next fifty years, except in synonymy.

Fernald (1950, p. 524), in *Gray's Manual of Botany,* summarized his overall unsurpassed knowledge of the flora of northeastern North America by recognizing five taxa of *Myrica* subg. *Morella* in the *Gray's Manual* area: *M. cerifera, M. pusilla* Raf., *M. pensylvanica,* and *M. heterophylla* with its supposed var. *curtissii* (A. Chev.) Fernald.

Gleason (1952, 2: 24) recognized only one species of bayberry, which he called *Myrica pensylvanica,* while placing the earlier *M. caroliniensis* as employed by Robinson and Fernald (1908), Britton and Brown (1913), and Small (1933) in its synonymy. *Myrica heterophylla* was appended to the account of *M. pensylvanica* somewhat uncertainly but perhaps as a hybrid. The treatment of the northeastern bayberry species was unchanged in Gleason and Cronquist (1963, p. 241) but Cronquist in the second edition (Gleason and Cronquist 1991, pp. 80–81) accepted both *M. pensylvanica* and *M. heterophylla* and modified the synonymy of *M. pensylvanica* by including "*Cerothamnus caroliniensis* of authors, perhaps not of Miller." It should be noted that Miller's species was not included in the synonymy of *M. heterophylla* where it most certainly belonged. As a synonym of either *M. pensylvanica* or *M. heterophylla, M. caroliniensis* would take precedence due to priority.

For simplicity's sake the case presented here was not further complicated by earlier discussing the species in the genus *Morella* Lour. to which all waxy-fruited binomials mentioned belong (Baird 1968; Killick et al. 1998; Wilbur 1994). All are agreed that that *Myrica sensu lato* is divisible into three major taxa: *Myrica* L. (fruit water-dispersed), *Morella* (fruit bird-dispersed), and *Comptonia* L'Her. *ex* Aiton (fruit a nut, possibly small mammal-dispersed). That these are meaningful, natural groups seems to be universally accepted even if some still consider them better treated at either sectional or subgeneric ranks. Nearly every investigator in the past eight decades has recognized at least two genera: *Myrica* and *Comptonia,* while in recent decades three genera have been increasingly accepted in North America (e.g., Baird 1968; Chevalier 1901; Kartesz and Meacham 1999; Radford et al. 1968; Wilbur 1994).

The synonymy of the two species accepted here is restricted to the names applied to the eastern North American representatives (i.e., only the eastern United States and Canada). Fortunately the spelling of the binomial "*Myrica curtissii*" below is not of pressing importance since the name is a synonym with little likelihood that it will ever achieve an active role. The specific epithet was originally published by Chevalier as "*curtissi,*" who always employed that form in his published work. It often appears as "*curtissii,*" the correction resting no doubt upon the authority of Article 60.11. Botanists of the earlier part of the previous century, who knew more Latin than most of us, were far more tolerant of the single *i,* actually feeling that in many cases it was superior. In the text I have employed the double *ii* but have used the single *i* when that was the form there published.

Morella caroliniensis (Mill.) Small, Fl. S. E. U.S. 337 & 1329. 1903. [as *Carolinensis*]

Myrica caroliniensis Mill., Gard. Dict., ed. 8. no. 3. 1768. [LECTOTYPE: Catesby's Plate 13 in Volume 1. 1730. First designated here, as suggested by J. L. Reveal (in litt.).]
Myrica cerifera β *latifolia* Aiton, Hortus Kew. 3: 396. 1789. [β = var.]
Myrica cerifera β *frutescens* Castigl., Viagg. Stati Uniti 2: 302. 1790. [Castiglioni cited both Catesby 1: tab. 13 and *Myrica caroliniensis* Mill. but described in most detail plants from Falmouth in eastern Massachusetts.]
Myrica cerifera β *media* Michx., Fl. Bor.-Amer. (Michaux) 2: 228. 1803.
Myrica pensylvanica Mirb. *in* Duhamel, Traité Arbr. Arbust. 2: 190. 1804.
Myrica heterophylla Raf. *in* Raf., Alsogr. Amer. 9. 1838. [as *heterophyla*]
Myrica sessilifolia Raf., Alsogr. Amer. 10. 1838.
Myrica sessilifolia var. *latifolia* Raf., Alsogr. Amer. 10. 1838.
Myrica Curtissii A. Chev., Mém. Soc. Sci. Nat. & Math. Cherbourg 32: 269. (Monogr. Myric. 185.) 1901. [as *Curtissi*]
Myrica Curtissii var. *media* (Michx.) A. Chev., Mém Soc. Sci. Nat. & Math. Cherbourg 32: 270. (Monogr. Myric. 186.) 1901. [as *Curtissi*]
Myrica heterophylla var. *Curtissii* (A. Chev.) Fernald, Rhodora 40: 410. 1938. [as *Curtissi*]
Cerothamnus caroliniensis (Mill.) Tidestr., Elys. Marian., Ferns 3: 41. 1910.
Cerothamnus pensylvanicus (Mirb.) Moldenke, Revista Sudamer. Bot. 4: 16. 1937.
Cerothamnus heterophyllus (Raf.) Moldenke, Phytologia 29: 386. 1975.

Morella cerifera (L.) Small, Fl. S. E. U.S. 337 & 1329. 1903.

Myrica cerifera L., Sp. Pl. 1024. 1753.
Myrica cerifera var. *angustifolia* Aiton, Hortus Kew. 3: 396. 1789.
Myrica cerifera β *arborescens* Castigl., Viagg. Stati Uniti 2: 302. 1790.
Myrica cerifera [var.] *pumila* Michx., Fl. Bor.-Amer. 2: 228. 1803.
Myrica pusilla Raf., Alsogr. Amer. 10. 1838.
Cerophora lanceolata Raf., Alsog. Amer. 11. 1838.
Myrica cerifera β *angustifolia* C. DC., Prodr. (DC.) 16(2.1): 149. 1864.

Nom. illeg. (Art. 53.1), non Aiton. TYPE: Louisiana. prope New Orleans, *Drummond s.n.* (K, not seen).

Myrica pumila (Michx.) Small, Bull. Torrey Bot. Club 23: 126. 1896.

Myrica cerifera var. *dubia* A. Chev., Mém. Soc. Sci. Nat. & Math. Cherbourg 32: 265. (Monogr. Myric. 181.) 1901.

Morella pumila (Michx.) Small, Fl. S. E. U.S. 337 & 1329. 1903.

Cerothamnus arborescens (Castigl.) Tidestr., Elys. Marian., Ferns 3: 41. 1910.

Cerothamnus ceriferus (L.) Small, Fl. Miami 61 & 200. (26 Apr) 1913.

Cerothamnus pumilus (Michx.) Small, Shrubs Florida 8 & 133. (4 Sep) 1913.

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A FLORISTIC INVENTORY OF MANATEE SPRINGS STATE PARK, LEVY COUNTY, FLORIDA

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ABSTRACT. A floristic inventory of the vascular plants of Manatee Springs State Park in Levy County, Florida, was conducted from May 1996 to December 1998. In the 933 ha (2305 acres) park, a total of 360 species was found. The vascular flora comprised 8 ferns, 1 cycad, 6 conifers, and 345 angiosperm species representing 90 families and 241 genera. Twelve natural communities are recognized in the park in addition to ruderal and developed areas: upland mixed forest, xeric hammock, sinkhole, sinkhole lake, swamp lake, basin swamp, bottomland forest, depression marsh, floodplain swamp, floodplain forest, blackwater stream, and spring-run stream.

Key Words: Florida, flora, floristic study, vascular plants

Manatee Springs State Park is located seven miles west of the city of Chiefland in Levy County, Florida, with the Suwannee River forming its western boundary. The park occupies Sections 13, 23-26, 35, and 36 of Township 11 South, Range 13 East. The total area of the park is 933 ha. This includes the Meud-Scot track to the south acquired in 1988 (Department of Natural Resources 1989). The park is managed by the Division of Recreation and Parks for public outdoor recreation. The beautiful artesian spring, named for the manatees that take refuge there, is the major recreational feature of the park. Swimmers and divers enjoy a deep blue spring boil surrounded by bald cypress. Camping facilities and nature trails are also provided for exploring the park. The Suwannee River, as well as all other surface waters in the park, is designated as Outstanding Florida Waters (Department of Natural Resources 1989).

The flora of this area has not received as much attention as that of the panhandle or Southern Florida, and the geographical range of some species is poorly known. Many northern species find their southern limits in the Suwannee River region. This study was conducted in order to provide a detailed checklist of the park's flora, as well as descriptions of its plant communities, which will be valuable in future management of this state park.

Climate. Northern Florida typically has a humid, subtropical climate (Winsberg 1990). Positioned in the northwestern portion of the Florida peninsula, Levy County experiences both the warming effect of being south of the jet stream in the winter and the cooling effect of the nearby Gulf of Mexico during the summer. Average annual maximum daily temperatures are 78°–80°F, while average minimums are only 55°–56°F.

Winter is mild with 20–30% of days between December and February receiving temperatures above 75°F. Cold fronts from the interior United States regularly affect the temperature, however. Around 40% of days between December and February have minimum temperatures below 40°F (Winsberg 1990). Most winter rainfall is the result of these fronts, but on average, winter weather brings less rain than summer (Chen and Gerber 1990; Jordan 1985).

Spring weather usually arrives in March. The polar jet stream passes farther north, and the days are warm and dry. In May average daily maximum temperatures exceed 88°F. Nighttime temperatures rise, and rainfall increases. Afternoon thunderstorms are common by June. These take place an average of 80 days per year, making summer the wettest season. Annually, this region receives an average of 152 cm of rain (Winsberg 1990).

Geology. The park is situated in the Ocala Uplift District as part of the lower basin of the Suwannee River. The Ocala Uplift was formed during post-Oligocene orogeny and has little Miocene sediment. However, there are large outcrops of Eocene and Oligocene carbonates present at or near the surface (Brooks 1982; Vernon and Puri 1964). Oligocene deposits, usually Suwannee Limestone, are not present in Levy County (Department of Natural Resources 1989).

The oldest tertiary sediments in the area are part of the Paleocene Cedar Keys Limestone. This formation is a hard, cream-colored to tan limestone with a thickness of 168 to 183 m and was formed in the open ocean when the coastline was located across what is now Alabama and Georgia (Cooke 1945).

Over this layer, several Eocene limestone deposits common to the Ocala Uplift can be found. These limestones can be divided into three age groups: the Wilcox, Claiborne, and Jackson groups from oldest to youngest (Cooke 1945). The Oldsmar Limestone belongs to the Wilcox group and contains gypsum and chert

(Cooke 1945). This deposit is 122 to 168 m in thickness. Two deposits of the Claiborne group are present in the area. Lake City limestone is the older and consists of both dark-brown and chalky limestones with some gypsum beds. Cooke (1945) reported this layer to be around 152 m thick in Levy County. Above this layer is Avon Park limestone, a cream-colored deposit with some gypsum and chert embedded in it. This limestone may be anywhere from 15 to 91 m thick (Cooke 1945).

The youngest age-group of Eocene limestones, the Jackson group, is represented by the Ocala group, one of three limestone subgroups comprising the layer. These are, from oldest to youngest, the Ocala, Williston, and Inglis members. These form a layer that is around 60 m deep. This limestone is exposed around the main spring and is mined for road construction in Levy County (Department of Natural Resources 1989).

The entire coastal region of Florida lies in the physiographic region called the coastal lowlands, an area that was covered by the sea during the Pleistocene. The ancient shorelines formed several terraces, of which the Pamlico is the most extensive (Cooke 1945). This shoreline was located at 8 m above current sea level. Elevations within the park are from 8 m above to 1.5 m below sea level. The deposits of this age are mostly sand, but may also contain some clay (Cooke 1945).

Sinkholes are common in the park. The abundance of limestone underlying the park is primarily responsible for the karst topography found there. Karst is a landscape formed by the action of dissolving carbonate-rich rocks, which form numerous sinkholes and caves (Myers and Ewel 1990).

Because the limestone in the Ocala Uplift District is only thinly covered, solution sinkholes are the most common type formed within the park. Surface water seeps through the rock through cracks and gradually dissolves the surface limestone, forming depressions over time. This is in contrast to collapse sinkholes, which form after the underlying bedrock has been dissolved and the roof of the cavern formed collapses under the weight of the overlying soil (Beck and Sinclair 1986).

Hydrology. The primary feature of the park is the spring, which empties into the Suwannee River. This area has felt the most impact of human influence. The spring is a popular swimming hole, and crowds of visitors are common in the summer months. In addition to swimming, scuba diving is a frequent activity in the spring boil as well as in Catfish Hotel, a nearby sinkhole, which connects via underground passageways to the main spring (Department of Natural Resources 1989).

Manatee is classified as a first magnitude artesian spring. This means that the average discharge must be at least 2.83 $m^3\ s^{-1}$ (100 $ft.^3\ s^{-1}$). Manatee discharges an average of 5.13 $m^3\ s^{-1}$ of hard fresh water into a pool 30 m in diameter and 14 m deep at the center (Rosenau et al. 1977). This water maintains a stable average temperature of 22.0°C year-round (Myers and Ewel 1990). The warm temperature attracts manatees into the spring during the winter months (Department of Natural Resources 1989).

The spring water travels 381 m westward and empties into the Suwannee River. Classified as a blackwater stream by the Florida Natural Areas Inventory (1988), the Suwannee forms the western boundary of the park. Blackwater streams are characterized by high levels of tannins, particulates, and organic matter from swamp drainage. The pH is 4.0 to 6.0 unless influenced by groundwater (Florida Natural Areas Inventory 1988). Beck (1965) classified the Suwannee as a calcareous stream, mostly of spring origin, and having a pH level of 7.0 to 8.2. Both classifications are probably applicable where the spring run meets the Suwannee. While the river originates from swamp drainage and has a dark tannin color, it also receives heavy influence from Florida springs, such as Manatee, that make it locally more calcareous and clear. This river discharges into the Gulf of Mexico, located only 24 miles southwest of the park (Department of Natural Resources 1989).

The Florida Aquifer is largely uncontained throughout this region, meaning that much of the water is not separated from the atmosphere by impermeable rocks or clay beds (Lane 1986). This contributes to the formation of numerous seeps and flooded sinkholes, which can release water. During floods, however, the aquifer may recharge through these openings (Myers and Ewel 1990).

There are several permanently flooded sinkholes that provide access to an extensive aquatic cave, which is also accessible from the spring. These are Catfish Hotel, Freedman Sink, and Sue Sink. Catfish Hotel is the most commonly used point of entry besides the spring. This sink is 38 m in circumference and 12 m deep. Divers have explored around 3978 m of this system, but further exploration may be dangerous due to the unstable nature of the caves (Department of Natural Resources 1989).

In addition to flooded sinks, the park also contains several sinkhole ponds and a 3 ha sinkhole lake, Graveyard Pond. Close to Graveyard Pond is a 5 ha swamp lake, Shacklefoot Pond. These are located in the northeastern quarter of the park (Department of Natural Resources 1989).

History.

> "About noon we approached the admirable Manate Spring, three or four miles down the river. This charming nymphæum is the product of primitive nature, not to be imitated, much less equalled, by the united effort of human power and ingenuity! As we approach it by water, the mind of the inquiring traveller is previously entertained, and gradually led on to greater discovery. . ." (Bartram 1791).

The naturalist William Bartram was entranced by the beauty of this spring on the Suwannee River. His admiration was undoubtedly shared by the many Indians and Europeans who traveled by or gathered beside this natural fountain. While there is not much information available on the overall history of this land, evidence suggests that the Manatee Spring region has been inhabited by Indians, visited by early explorers, and settled by Florida pioneers (Gulledge 1999).

Manatee Spring was visited by William Bartram in 1774 as he traveled through Florida when it was under British control. He described the flora as being dominated by live oaks, red bay, and magnolias. Manatees, fish, and alligators were abundant in the spring run. Indian activity was noted by the presence of a manatee skeleton on the banks of the spring, indicating that the Seminoles probably valued the area as a source of meat. The flora and fauna does not seem to have changed much in the 200 years since his visit. The flow of water from the spring, however, was quite interesting at that time. Bartram's account is of an intermittent ebullition from the spring, which occurred every 30 seconds (Bartram 1791). The hydrology has changed such that the water now flows continually.

Around the turn of the century, longleaf pine was logged throughout much of the area (Department of Natural Resources

1989). The effects of this destruction are still evident in the plant composition of the park.

In 1949, the majority of Manatee Springs State Park was acquired by the Park Board for use as a state recreational park. Additional land was added up until 1988. While public recreation is the designated use of this park, management has been designed to minimize the impact of humans. The addition of paved walkways around the spring, a wooden boardwalk along the spring run, and camping facilities in the park were inevitable, and accommodate the many people who enjoy this park (Department of Natural Resources 1989). Over time, however, the area's status as a protected natural area will help to ensure its lasting natural beauty.

PLANT COMMUNITIES

Manatee Springs State Park has 13 plant communities, as circumscribed by the Florida Natural Areas Inventory 1988 (Figure 1). Although the overall change in elevation within the park is only a gradual nine meters from the river eastward (Department of Natural Resources 1989), the species composition varies substantially along this gradient. Observations on species dominance within each community were recorded as plant collections were made. Here, each community is described based on personal observations and the ecological literature (Figure 1).

The recently acquired Meud-Scot track, a small strip of land bordering the river south of the major portion of the park and encompassing 93 ha, was not included in the management plan's description of natural areas (Department of Natural Resources 1989). Thus coverage of communities within the rest of the park is given as a percentage of the total land area, excluding the Meud-Scot track. The tract consists predominantly of floodplain swamp with a small strip of floodplain forest and an area of xeric hammock.

Upland mixed forest. Around 13% (117 ha) of the park is upland mixed forest, also known as mesic hammock. Some of the original community has been altered due to the development of camping facilities, but it can also be found scattered in other locations, mostly intergrading with xeric hammock (Department of Natural Resources 1989). This intergradation can be gradual,

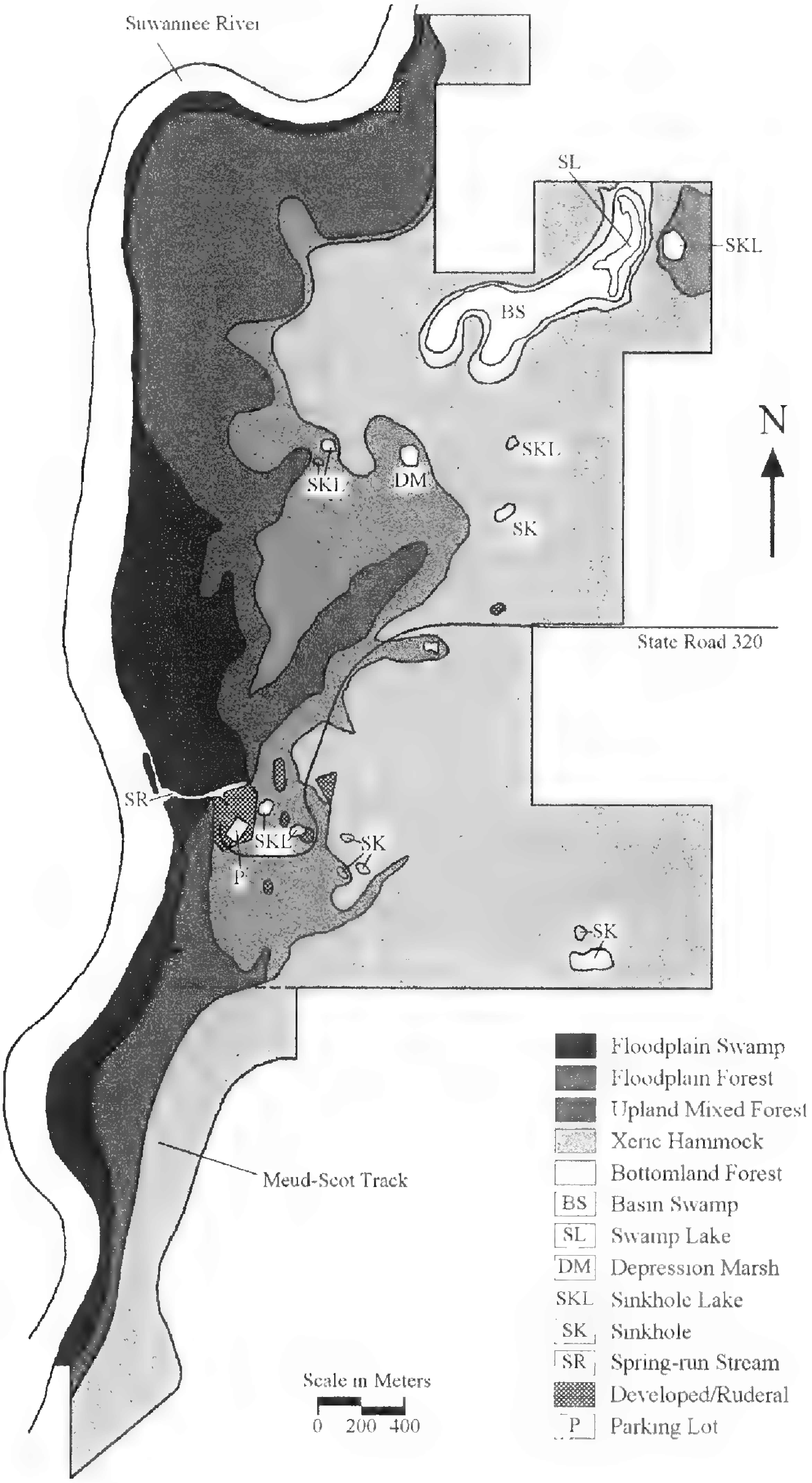

Figure 1. Plant community map of Manatee Springs State Park (adapted from Department of Natural Resources 1989).

and these two plant communities often are arbitrarily delimited (see also Platt and Schwartz 1990). Thus, it is usually impossible to separate this vegetational continuum into distinct, easily demarcated categories. What is called upland mixed forest in this park is simply one of several transition zones from moist to dry woods.

The diversity of tree species is usually high in mesic hammocks. Hardwoods such as *Magnolia grandiflora, Carya glabra, Liquidambar styraciflua, Ostrya virginiana, Ilex opaca, Quercus virginiana, Q. michauxii,* and *Persea borbonia* dominate. *Pinus taeda* and *P. glabra,* however, are also found in this community. Around the camping and picnic areas, *Sideroxylon lanuginosum* and *Tilia americana* are common. Toward the northern fence, *Diospyros virginiana* is frequent. *Symplocos tinctoria* is found more abundantly in the eastern part of the park and near Graveyard Pond, a sinkhole lake found in the northeast corner of the park. In these patches of upland mixed forest, other commonly encountered trees and shrubs are *Celtis laevigata, Juniperus virginiana* var. *silicicola, Osmanthus americana, Prunus caroliniana, P. serotina, Quercus nigra, Sabal palmetto, Vaccinium arboreum,* and *Callicarpa americana.* Various species of *Smilax* are common vines. Typically, the herb layer is not well developed in upland mixed forest, but many grasses and sedges as well as other herbs such as *Galium tinctorium, Amsonia tabernaemontana,* and *Polygala grandiflora* are common.

The mesic conditions prevailing in upland mixed forests are normally attributed to the higher clay and organic content in the soil, deeper leaf mulch, and dense canopy that traps humidity. The higher moisture content in these areas makes them less likely to burn than the surrounding pine dominated communities (Florida Natural Areas Inventory 1988).

Soils in the park that support upland mixed forest are mostly Otela-Tavares complex, but there is also Jonesville-Otela-Seaboard complex underlying this community southeast of the spring (Natural Resources Conservation Service 1996).

Xeric hammock. Xeric hammock replaces upland mixed forest at higher elevations. Typically, it occupies sandy soils of ancient dune origin. The canopy can be low or multi-layered, open or closed. The presence or absence of these characteristics can often be attributed to the stage of succession. Hardwoods such as

Quercus geminata, Q. virginiana, and *Q. hemisphaerica* are the most abundant trees, while the herb layer is sparse (Florida Natural Areas Inventory 1988). Xeric hammock covers 57% of the park, or 533 ha (Department of Natural Resources 1989).

Manatee Springs is situated on the northwest corner of what is called the Gulf Hammock area, one of the larger regions in Florida to contain extensive hardwood forests (Myers and Ewel 1990). The management plan for the park defines the upland portions of the park as consisting of upland mixed forest, upland pine forest, sandhill, scrubby flatwoods, and xeric hammock (Department of Natural Resources 1989). However, with the exception of upland mixed forest, the rest of the upland forests are too uniform and intergrading to be divided into four categories (based upon a subjective assessment by the authors). Probably none of these categories adequately describes the actual pattern of species composition within this community. Xeric hammock is here interpreted to cover all of these upland forest categories.

There are a large number of pines, including *Pinus palustris, P. elliottii,* and *P. taeda.* These could indicate that the area might not always have had dominant hardwoods. Prolonged fire exclusion may have caused a succession from a pine dominated community to xeric hammock. The records of extensive longleaf pine logging early in the century would support this idea. In addition, some ecologists theorize that, historically, dominance in these forests has shifted several times between pines and hardwoods (Myers and Ewel 1990). Controlled burns are performed on this land and may serve to eventually change its characteristics (Department of Natural Resources 1989).

Another aspect that varies in xeric hammock is the presence in the park of both closed- and open-canopied forests. Areas with open canopies may have been interpreted as scrubby flatwoods, but the lack of many characteristic elements, along with the rolling topography, does not support this classification.

Dominant trees and shrubs are *Quercus virginiana, Serenoa repens, Vaccinium arboreum, Quercus geminata, Carya glabra, Quercus incana, Q. falcata, Q. hemisphaerica, Q. myrtifolia, Magnolia grandiflora, Liquidambar styraciflua, Persea borbonia, Lyonia ferruginea, Ilex opaca, Osmanthus americana, Ilex vomitoria,* and *Gaylussacia dumosa. Solidago odora* var. *chapmanii* and *Indigofera caroliniana* are characteristic herbs. Otela-Tavares complex soils underlie this community (Natural Resources Conservation Service 1996).

Sinkhole. The karst terrain of the park is marked by numerous sinkholes of various sizes with a total area of around 6.5 ha (Department of Natural Resources 1989). The majority of these remain dry for most of the year, draining rapidly after periods of rain. However, if the lower reaches of a sinkhole are located below the water level, it remains flooded (Florida Natural Areas Inventory 1988). The majority of dry sinkholes in the park are located southeast of the spring. The surrounding community is primarily upland mixed forest.

Vegetation in sinkholes is affected by the steepness of the sides and whether or not sand and soil cover the limestone walls (Florida Natural Areas Inventory 1988). Ferns are common as well as lichens and mosses. Most of the sinkholes in the park have gradually sloping sides without much exposed limestone.

Sinkhole lake. These are sinkholes that retain water and are therefore constantly flooded (Florida Natural Areas Inventory 1988). There is only one large sinkhole lake in the park, called Graveyard Pond, which occupies about 3 ha in the northeast quadrant of the park. Several small sinkhole ponds can be found as well, which are located near the main spring (Department of Natural Resources 1989). The standing water in these sinkhole lakes and ponds allows for a proliferation of aquatic plants such as *Lemna obscura, Landoltia punctata, Wolffia brasiliensis, Wolffiella gladiata, Pistia stratiotes,* and *Salvinia minima.*

Swamp lake. Shacklefoot Pond, located in the northeast corner of the park, is a 5 ha swamp lake (Department of Natural Resources 1989). Although stumps and trees are found in the lake, it is overall an open, permanent body of water surrounded by a basin swamp.

Hydrophilic trees are found both on the fringe of the lake and occasionally emerging in the middle. These include *Taxodium distichum* and *Gleditsia aquatica.* Throughout the lake itself are many floating and emergent aquatic herbs. The most common of these are *Lemna obscura, Wolffia brasiliensis, Spirodela punctata, Wolffiella gladiata, Limnobium spongia, Ceratophyllum de-*

mersum, Utricularia foliosa, Boehmeria cylindrica, and *Salvinia minima.*

Basin swamp. There is a large basin swamp in the northeast corner of the park. This community takes up about 11 ha and surrounds Shacklefoot Pond, a large swamp lake (Department of Natural Resources 1989). This community is often flooded, so species occurring within it must be adapted to a long hydroperiod. The soils found on this site are Placid and Samsula soils, acidic peat over a dark gray sand (Natural Resources Conservation Service 1996).

The dominant tree in this basin swamp community is *Taxodium distichum.* Other common trees and shrubs are *Myrica cerifera, Cyrilla racemiflora, Cephalanthus occidentalis,* and *Salix caroliniana.* The epiphytes *Tillandsia usneoides* and *T. bartramii* are common, as is the herb *Scutellaria integrifolia.* There is a large feral hog population in the park, and hogs are especially active in this area (Department of Natural Resources 1989). The damage these hogs do to the surface of the peat is evident throughout the swamp. As a result, herbaceous plants are less frequent here than might be expected for a typical basin swamp.

Bottomland forest. A ribbon of bottomland forest covering about 7 ha surrounds the basin swamp around Shacklefoot Pond (Department of Natural Resources 1989). This is basically a simple transition zone from the constantly inundated pond to the surrounding uplands. Along the slope leading down to the pond, there is a gradual increase in the number of flood-adapted species. The appearance is similar to a floodplain forest, but with a more diverse and abundant herb layer (Florida Natural Areas Inventory 1988).

Some of the plants found in this community are *Quercus nigra, Sabal palmetto, Magnolia grandiflora, Pinus taeda, Toxicodendron radicans, Hypericum galioides,* and *Scutellaria integrifolia.*

Depression marsh. One small depression marsh exists within the park; it is located in the middle of the park and occupies 0.5 ha. The center of the marsh is flooded and the surrounding soil remains moist year round. During some parts of the year, the pond itself contains aquatic herbs, including *Brasenia shreberi.* The marsh is dominated entirely by herbaceous species such as

Eupatorium compositifolium, Xyris platylepis, Juncus marginatus, and *Cuscuta compacta,* except for the common shrub, *Cephalanthus occidentalis.*

Floodplain swamp. The entire western edge of the park is a floodplain swamp running along the Suwannee River. The swamp occupies around 158 ha or 17% of the total park area (Department of Natural Resources 1989). Much of the swamp remains inundated throughout the year. The soils found here are Chobee-Bradenton complex, Holopaw-Pineda complex, and Chobee-Gator complex, all frequently flooded soils (Natural Resources Conservation Service 1996).

By far, the dominant tree in the floodplain swamp is *Taxodium distichum,* with *Nyssa biflora* also frequent. Other common plants are *Saururus cernuus, Crinum americanum, Cephalanthus occidentalis, Samolus valerandi* subsp. *parviflorus, Proserpinaca palustris,* and *Senecio glabellus.*

Floodplain forest. Floodplain forests are transitional from floodplain swamps to upland communities and flood less frequently than swamps, typically only during peak water levels. Plants in this community are adapted to only seasonal inundation and cannot survive constant saturation of the soil (Florida Natural Areas Inventory 1988). As would be expected, the floodplain forest occupies a strip of roughly 92 ha between the swamp and the uplands of the rest of the park (Department of Natural Resources 1989). Much of the soil underlying this strip is either of the Ousley-Albany complex, Placid, or Samsula soils (Natural Resources Conservation Service 1996).

Typical trees are *Quercus laurifolia, Q. lyrata, Fraxinus caroliniana, Planera aquatica, Acer rubrum, Carpinus caroliniana, Sabal palmetto,* and *Crataegus* spp. Common shrubs include *Cornus foemina, Serenoa repens,* and *Sabal minor. Toxicodendron radicans* and *Ampelopsis arborea* are characteristic vines. Herbs include *Panicum rigidulum* and *Amsonia tabernaemontana.*

In both the floodplain swamp and floodplain forest communities in Manatee Springs, feral hogs are a constant destructive force. Although trapping is an ongoing effort for park rangers, feral hog populations are large, and evidence of foraging is widespread.

Blackwater stream. The Suwannee River, which forms the western boundary of the park, is classified as a blackwater stream by the Florida Natural Areas Inventory due to the high tannin levels in the water, which give it a characteristic tea color (Florida Natural Areas Inventory 1988). However, a more popular river classification developed by Beck (1965) ranks the Suwannee as a calcareous stream. Both categories are probably generalizations and do not adequately describe the entire river. Blackwater streams are mostly acidic, originate in swamps, and do not usually have either extensive floodplains or large amounts of submerged aquatics (Florida Natural Areas Inventory 1988). Calcareous streams are fed mostly by springs and are generally alkaline with heavy aquatic plant growth. The Suwannee originates in swamps, but in Levy County, it is fed by several large springs such as Manatee, that influence the river locally with calcareous water (Myers and Ewel 1990). With the exception of the entrance to the spring run, emergent plant growth is sparse along the edge of the river. However, both *Senecio glabellus* and the exotic pest *Alternanthera philoxeroides* are common.

Spring-run stream. The 381 m stream that carries water from Manatee Spring to the Suwannee River is described as a spring-run stream (Department of Natural Resources 1989). This alkaline stream is an excellent habitat for many aquatic herbs, both emergent and submerged. The water is clear, allowing light to filter to the bottom of the limestone streambed and promoting the growth of *Vallisneria americana.* Periods of heavy flooding such as during the winter of 1998 can cause tea-colored water from the Suwannee to back up into the spring-run stream (Florida Natural Areas Inventory 1988). The 1998 influx resulted in a partial dieback of submerged aquatics, but a drier than typical spring helped return the stream to its previous state.

In the streambed itself, *Vallisneria americana* is the dominant submerged plant. Along the fringe, however, there are numerous species of both submerged and emergent plants including *Cabomba caroliniana, Sagittaria kurziana, Nuphar advena, Echinodorus berteroi,* and *Pontederia cordata.* Also present is the exotic pest *Hydrilla verticillata.*

Ruderal and developed areas. Due to the popularity of Manatee Springs as a swimming hole and camping area, development has occurred. The most frequented area is the spring itself. A parking lot, bathhouse, and picnic area are present to accommodate visitors, as well as a concrete ramp around part of the spring and a small beach area for swimmers to enter the spring with as little damage to the remaining edge as possible. A boardwalk extends along the spring-run stream to a boat dock on the Suwannee River. There are also two camping areas near the spring and two residences within the park. The development around the spring takes up about 4 ha (Department of Natural Resources 1989). In addition to disturbances such as roads and trails, there is a large borrow pit located southeast of the spring.

Disturbed zones are usually dominated by early successional weeds such as *Eupatorium compositifolium, Paronychia americana, Gnaphalium purpureum, G. obtusifolium,* and *Ambrosia artemisiifolia.* The roadside is especially diverse in the fall, with numerous composites such as *Coreopsis leavenworthii, Liatris elegans, L. graminifolia, Pityopsis graminifolia,* and *Solidago odora* var. *chapmanii.* Other notable roadside plants are *Dicerandra densiflora, Trichostema dichotomum,* and *Arenaria serpyllifolia.* The borrow pit area contains a large population of the exotic *Leonitis nepetefolia,* as well as *Eupatorium compositifolium* and *Rhynchosia michauxii.*

MATERIALS AND METHODS

Plant collections were made from May 1996 to November 1998. Most of the park could be covered by walking the trail system, with occasional transects into the woods. Exceptions to this were the spring-run stream, riverbank, and floodplain swamp/floodplain forest boundary. For the spring-run stream and riverbank, a canoe was used to survey the edge, and a mask and snorkel was necessary to find several aquatics growing in the spring. Foot trips were made that generally followed the floodplain swamp edge and the boundary of the park to assess the species richness in the disturbed vegetation along the fence. Soil maps and previous plant community maps (Department of Natural Resources 1989) were used to identify areas of interest.

The plants were initially identified using Clewell (1985), Wunderlin (1982), and Godfrey and Wooten (1979, 1981). However, after Wunderlin (1998) was published, this guide was used for most of the remaining identifications. Vouchers were deposited in the University of Florida Herbarium (FLAS).

RESULTS

The authors found a total of 360 vascular plant species in the park, representing 253 genera and 100 families. The largest families were Poaceae (41 spp.), Asteraceae (36 spp.), and Fabaceae (27 spp.). The largest genera were *Quercus* (13 spp.), *Dichanthelium* (8 spp.), *Cyperus* (6 spp.), *Rynchospora* (6 spp.), *Smilax* (5 spp.), *Ilex* (5 spp.), and *Vaccinium* (5 spp.). The complete annotated list of the vascular plants of the park is found in the appendix.

DISCUSSION

There were several species of special concern in the park. These were broken down into the following categories: taxonomic problems, species at or near their geographical limits, exotic and endemic species, and rare or endangered species.

There was an interesting *Yucca* population in the park that did not seem to fit completely the description for *Yucca filamentosa.* This entity was a robust plant with stiff leaves up to a meter in length. It bloomed in late July, slightly later than the more common form of this species. This plant may represent a taxonomic entity distinct from the widely distributed form, frequently treated as *Y. flaccida.* Further study is needed to determine the exact pattern of variation within the *Y. filamentosa* complex.

Several species were at the limits of their geographical ranges. An on-line atlas was used to determine species ranges within Florida (Wunderlin et al. 1997). These plants were divided into several categories for this list (i.e., species at their limit and species near their limit for both northern and southern limits). A species at its southern limit does not occur in any counties south of Levy (and the reverse for a species at its northern limit). A species near its southern limit only occurs one or two counties further south (and the reverse for a species near its northern limit).

Ten species were at their southern limit: *Pinus glabra, Sium suave, Betula nigra, Quercus lyrata, Dichanthelium oligosanthes, Saccharum alopecuroides, Crataegus aestivalis, C. michauxii, Galium tinctorium,* and *Planera aquatica.* Nineteen species were

Table 1. State-listed endangered (E), threatened (T), and commercially exploited (CE) vascular plants occurring in Manatee Springs State Park, following Coile (1993).

Species	Status
Asplenium platyneuron	T
Epidendrum conopseum	T
Ilex ambigua	T
Ilex decidua	T
Ilex opaca	CE
Lobelia cardinalis	T
Matelea floridana	E
Osmunda regalis	CE
Sabal minor	T
Tillandsia bartramii	T
Woodwardia areolata	T
Zamia integrifolia	CE

near their southern limit: *Pinus taeda, Justicia ovata, Sagittaria kurziana, Asimina longifolia, Ostrya virginiana, Triadenum walteri, Cuscuta compacta, Cornus asperifolia, Carex dasycarpa, Cyperus plukenetti, Baptisia alba, Desmodium canescens, Lespedeza stuevei, Quercus michauxii, Carya tomentosa, Fraxinus americana, Halesia carolina, Ulmus alata,* and *U. crassifolia.*

Only a few species were at or near their northern limits for Florida. These were *Tillandsia recurvata* and *Senna ligustrina* (at northern limit), as well as *Zamia integrifolia, Pistia stratiotes, Utricularia foliosa, Cenchrus gracillimus, Phlebodium aureum,* and *Ulmus crassifolia* (near northern limit).

Non-native, or exotic, species following Wunderlin (1998) found in the park were *Alternanthera philoxeroides, Chenopodium ambrosioides, Cyclospermum leptophyllum, Pistia stratiotes, Arenaria serpyllifolia, Cyperus lanceolatus, Crotalaria lanceolata, Desmodium canescens, Hydrilla verticillata, Sisyrinchium rosulatum, Hyptis mutabilis, Leonitis nepetefolia, Broussonetia papyrifera, Eremochloa ophiuroides, Lolium perenne, Paspalum notatum, Poa annua, Secale cereale, Sporobolus indicus, Richardia brasiliensis,* and *Xyris jupicai.* There were nine Florida endemics or near endemics (see Muller et al. 1989) growing in the park: *Aristida patula, Coreopsis leavenworthii, Dicerandra densiflora, Matelea floridana, Palafoxia integrifolia, Pycnanthemum floridanum, Rhynchosia michauxii, Solidago odora* var. *chapmanii,* and *Vicia floridana.*

State-listed endangered, threatened, and commercially exploited plants are summarized in Table 1. No federally listed endangered species were found in the park.

The flora of Manatee Springs State Park is a reasonable representation of plants that would be expected in natural communities bordering the Suwannee River in Florida. Exotic plants, while common, are still much less prevalent inside the park than in the surrounding areas, proving the benefits of good land management. It is hoped that continued protection will maintain a diverse and historically representative flora of the region.

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APPENDIX

ANNOTATED LIST OF VASCULAR PLANTS

The species names in this list follow Wunderlin (1998), fern and gymnosperm family circumscriptions follow *Flora of North America North of Mexico* (Flora of North America Editorial Committee 1993), and angiosperm family circumscriptions follow the Angiosperm Phylogeny Group (1998), except when stated otherwise.

The abbreviations for plant communities are as follows: UMF Upland Mixed Forest; XH – Xeric Hammock; SH – Sinkhole; SKL – Sinkhole Lake; SL – Swamp Lake; BS – Basin Swamp; BF Bottomland Forest; DM – Depression Marsh; FS – Floodplain Swamp; FF – Floodplain Forest; BLS – Blackwater Stream; SR – Spring-run Stream; RU – Ruderal/Developed. Some additional notes may also be given regarding specific locations. For abundance, the following abbreviations were used, based on the collectors' observations of the plant in each community: R – rare (1–4 observations); I – infrequent (5–9 observations); O – occasional (10–24 observations); F – frequent (25 or more observations); A – abundant (denotes a plant that is dominant in its habitat and may influence the overall appearance of the community). It should be noted that, in many cases, abundance is seasonal.

A previous unpublished list of plants from the park was made by David Hall (1985), and we have included 31 of these species in the main list that were not found by us. Eight of these are exotic weeds. These entries are denoted with Hall NV (non-vouchered) in place of a collection number. Also, species that were new records for the county (according to Wunderlin et al. 1997) are indicated with the word "new" at the end of the entry, and exotic species are noted with an asterisk. Collection numbers are those of the first author.

FILICOPSIDA

ASPLENIACEAE

Asplenium platyneuron (L.) Britton, Sterns & Poggenb. – BF; R; *230.*

BLECHNACEAE

Woodwardia areolata (L.) Moore – BS; O; *22.*

DENNSTAEDTIACEAE

Pteridium aquilinum (L.) Kuhn var. *pseudocaudatum* (Clute) A. Heller – UMF, XH & RU; F; *377.*

OSMUNDACEAE

Osmunda regalis L. – SH; I; *7.*

POLYPODIACEAE

Phlebodium aureum L. – BF; R; *284.*

Pleopeltis polypodioides (L.) E. G. Andrews & Windham var. *michauxiana* (Weath.) E. G. Andrews & Windham – UMF, XH, SH, BF, FF & RU; F; *409.*

SALVINIACEAE

Salvinia minima Baker – SL & SKL; F; *403.*

THELYPTERIDACEAE

Thelypteris kunthii (Desv.) C. V. Morton – BS; O; *342.*

CYCADOPSIDA

ZAMIACEAE

Zamia integrifolia L. f. *in* Aiton – XH & UMF; O; *229*. [The correct name of this taxon is in doubt. When *Z. integrifolia* was described, "*Z. pumila*. Sp. Pl. 1659. (exclusis synonymis)" was included in its synonomy, causing some authors to believe that *Z. integrifolia* is a superfluous name. However, Dan Nicolson (US), Richard Brummitt (K), and Kanchi Gandhi (GH; pers. comm.) have suggested that by this statement ("exclusis synonymis") Linnaeus f. automatically excluded all the type elements that would otherwise cause superfluity; these authors are of the opinion that this exclusion made the name *Z. integrifolia* legitimate and available for use. They also noted that *Z. pumila* was lectotypified by one of the four elements cited within its protologue, and this LT element was excluded from *Z. integrifolia*. Some authorities, who treat *Z. integrifolia* as superfluous, use the name *Z. floridana* A. DC. for these Florida plants (Daniel Ward, pers. comm.); those considering them conspecific with similar plants occurring in the Greater Antilles use the name *Z. pumila*.]

CONIFEROPSIDA

CUPRESSACEAE

Juniperus virginiana L. var. *silicicola* (Small) Bailey – UMF; O; *443*. (Adams 1986)
Taxodium distichum (L.) Rich. – SL, BS & FS; A; *121*.

PINACEAE

Pinus elliottii Engelm. – UMF & XH; F; *537*.
P. glabra Walter – BF & UMF; O; *608*.
P. palustris Mill. – XH; O; *583*.
P. taeda L. – UMF, BF & XH; F; *529*.

ANGIOSPERMAE

ACANTHACEAE

Justicia ovata (Walter) Lindau – FF; O; *401*.
Ruellia caroliniensis (Walter *ex* J. F. Gmel.) Steud. – UMF & XH; O; *21*.

ACERACEAE (see SAPINDACEAE)

ADOXACEAE

Viburnum obovatum Walter – FF; F & UMF; I; *159*.

AGAVACEAE

Yucca aloifolia L. – UMF; R, only a few plants present at corner of parking lot, possibly planted; *457*.

Y. filamentosa L. – XH; O; *76, 398.*

ALISMATACEAE

Echinodorus berteroi (Spreng.) Fassett – SR; O; *103.*
E. tenellus (Mart.) Buchenau – SL; O; *572,* new.
Sagittaria kurziana Glück – SR; F; *451.*

ALTINGIACEAE

Liquidambar styraciflua L. – UMF & XH; F; *97.*

AMARANTHACEAE (incl. CHENOPODIACEAE)

**Alternanthera philoxeroides* (Mart.) Griseb. – FS; I; *109,* new.
**Chenopodium ambrosioides* L. RU; I; *560.*
Froelichia floridana (Nutt.) Moq. – RU; O; *155, 478.*

AMARYLLIDACEAE

Crinum americanum L. – FS; F; *611.*

ANACARDIACEAE

Rhus copallina L. – XH & UMF; O; *397.*
Toxicodendron radicans (L.) Kuntze – FF, FS & BF; O; *255.*

ANNONACEAE

Asimina longifolia Kral var. *longifolia* – XH; R; *313.* (= *A. angustifolia* Raf.; see Kral 1997)
A. parviflora (Michx.) Dunal – XH; R; *591.*
A. pygmaea (W. Bartram) Dunal – XH; *Hall NV.*

APIACEAE (incl. ARALIACEAE; Judd et al. 1994, 1999; Thorne 1983)

Aralia spinosa L. – XH; I; *290, 399.*
Centella asiatica (L.) Urb. – BS; O; *578.*
**Cyclospermum leptophyllum* (Pers.) Sprague *ex* Britton & P. Wilson – BS; F; *167, 548.*
Hydrocotyle verticillata Thunb. – BS; F; *34.*
Ptilimnium capillaceum (Michx.) Raf. – BS; O; *32, 345.*
Sanicula canadensis L. – XH; O; *61, 77.*
Sium suave Walter – SR; I; *489.*
Spermolepis divaricata (Walter) Raf. – RU; O; *309.*

APOCYNACEAE (incl. ASCLEPIADACEAE)

Amsonia tabernaemontana Walter – FF; F; *3, 173.*
Apocynum cannabinum L. – RU; I; *586.*
Asclepias humistrata Walter – XH; I; *563.*
A. perennis Walter – FS; I; *70, 378.*
A. tuberosa L. – UMF & XH; O; *43, 300.*

Matelea floridana (Vail) Woodson – XH; I; *554.*

AQUIFOLIACEAE

Ilex ambigua (Michx.) Torr. var. *ambigua* – XH & UMF; F; *72, 98, 151, 279, 321, 445, 458, 550.*
I. coriacea (Pursh) Chapm. – XH; O; *533.*
I. decidua Walter – FF & UMF; O; *460, 484.*
I. opaca Aiton var. *opaca* – UMF; F & XH; O; *95.*
I. vomitoria Aiton – XH; O; *296, 389.*

ARACEAE (incl. LEMNACEAE)

Landoltia punctata (G. Mey.) D. H. Les & D. J. Crawford – SKL & SL; A; *404,* new. (Les and Crawford 1999)
Lemna obscura (Austin) Daubs – SKL & SL; A; *405.*
**Pistia stratiotes* L. – SKL; O; *461.* [Considered introduced by Wunderlin (1998) but not by the authors, as the species has been reported by several early botanical explorers (e.g., Bartram 1791).]
Wolffia brasiliensis Wedd. – SKL & SL; F; *616.*
Wolffiella gladiata (Hegelm.) Hegelm. – SKL & SL; F; *617,* new.

ARALIACEAE (see APIACEAE)

ARECACEAE

Sabal minor (Jacq.) Pers. – FF, UMF & BF; I; *584.*
S. palmetto (Walter) Lodd. *ex* Schult. & Schult. f. – FF, UMF & BF; F; *609.*
Serenoa repens (W. Bartram) Small – FF, UMF & XH; F; *388.*

ARISTOLOCHIACEAE

Aristolochia serpentaria L. – FF; R; *487.*

ASCLEPIADACEAE (see APOCYNACEAE)

ASTERACEAE

Acmella oppositifolia (Lam.) R. K. Jansen var. *repens* (Walter) R. K. Jansen – FF; O, on edge of spring; *418.*
Ageratina jucunda (Greene) Clewell & Wooten – UMF & XH; I; *122, 507.*
Ambrosia artemisiifolia L. – RU; F; *152.*
Aster dumosus L. – RU; I; *498.*
Baccharis halimifolia L. – UMF; O, found only in Meud-Scot track; *499.*
Balduina angustifolia (Pursh) B. L. Rob. – RU; O; *129, 437.*
Bidens alba (L.) DC. var. *radiata* (Sch. Bip.) Ballard *ex* Melchert – RU; I; *465.*
Chrysopsis gossypina (Michx.) Elliott subsp. *gossypina* – RU; O; *130.*
Cirsium horridulum Michx. – UMF; I; *168.*
Conoclinium coelestinum (L.) DC. – FF; O, on edge of spring; *117, 406.*

Conyza canadensis (L.) Cronquist var. *pusilla* (Nutt.) Cronquist – RU; O; *87, 133.*
Coreopsis leavenworthii Torr. & A. Gray – RU; F; *68, 142, 374.*
Elaphantopus nudatus A. Gray – UMF; F; *115, 139, 370.*
Erechtites hieracifolia (L.) Raf. *ex* DC. – BS; O; *571.*
Erigeron quercifolius Lam. – RU; O; *10, 308.*
E. strigosus Muhl. *ex* Willd. – RU; F; *41, 131,* new.
Eupatorium album L. – XH; F; *438.*
E. compositifolium Walter – DM & RU; F; *125, 144.*
E. rotundifolium L. – UMF; I; *153.*
Gnaphalium pensylvanicum Willd. – RU; O; *231.*
G. purpureum L. – RU; O; *239, 306.*
Heterotheca subaxillaris (Lam.) Britton & Rusby – RU; I; *581.*
Hieracium gronovii L. – XH & RU; O; *475.*
Krigia virginica (L.) Willd. – XH & RU; O; *242.*
Lactuca graminifolia Michx. – RU; O; *88, 281.*
Liatris elegans (Walter) Michx. – RU; F; *124,* new.
L. graminifolia (Walter) Willd. – RU; F; *123.*
L. tenuifolia Nutt. var. *tenuifolia* – RU; O; *128.*
Melanthera nivea (L.) Small – FF; R; *488.*
Mikania scandens (L.) Willd. – FS; I, on river island opposite spring run entrance; *112, 113.*
Palafoxia integrifolia (Nutt.) Torr. & A. Gray – RU; O; *136.*
Pityopsis graminifolia (Michx.) Nutt. – RU; A; *137.*
Pyrrhopappus carolinianus (Walter) DC. – XH & RU; I; *57, 244, 301.*
Senecio glabellus Poir. – FS; F; *29, 67, 116.*
Solidago odora Aiton var. *chapmanii* (Torr. & A. Gray) Cronquist – XH & RU; F; *145, 473.*
Vernonia angustifolia Michx. – XH; O; *78.*

BETULACEAE

Betula nigra L. – FF; O; *410.*
Carpinus caroliniana Walter subsp. *caroliniana* – FF & UMF; F; *93.* (Furlow 1987)
Ostrya virginiana (Mill.) K. Koch – UMF; F; *11.*

BIGNONIACEAE

Bignonia capreolata L. – UMF & XH; O; *232.*
Campsis radicans (L.) Seem. *ex* Bureau – FF & UMF; F; *612.*

BRASSICACEAE

Lepidium virginicum L. – RU; R; *24.*
**Rorippa nasturtium-aquaticum* (L.) Hayek – SR; *Hall NV.*

BROMELIACEAE

Tillandsia bartramii Elliott – BS & BF; F; *165.*
T. recurvata (L.) L. – UMF, FS, FF, BF, BS & XH; F; *610.*

T. usneoides (L.) L. – XH, UMF, BF, FF & BS; A; *154.*

BURMANNIACEAE

Apteria aphylla (Nutt.) Barnhart *ex* Small – BS; *Hall NV.*
Burmannia biflora L. – FS; I; *45, 495,* new.

CABOMBACEAE (see NYMPHAEACEAE)

CACTACEAE

Opuntia humifusa (Raf.) Raf. var. *humifusa* – RU; I; *5.* (Benson 1982)

CAMPANULACEAE

Lobelia cardinalis L. – FS; O, located along river; *101, 102.*
Triodanis perfoliata (L.) Nieuwl. – RU; I; *542.*

CAPRIFOLIACEAE *pro parte*, (i.e., *Viburnum*—see ADOXACEAE)

CARYOPHYLLACEAE

**Arenaria serpyllifolia* L. – RU; I; *243a, 546.*
Drymaria cordata (L.) Willd. *ex* Schult. – RU; O; *241, 568,* new.
Paronychia americana (Nutt.) Fenzl *ex* Walp. – XH & RU; O; *71.*
P. baldwinii (Torr. & A. Gray) Fenzl *ex* Walp. – XH & RU; I; *576.*
Stipulicida setacea Michx. var. *setacea* – RU; I; *602.*

CELTIDACEAE

Celtis laevigata Willd. – UMF; F; *614.*

CERATOPHYLLACEAE

Ceratophyllum demersum L. – SL; I; *569.*

CHENOPODIACEAE (see AMARANTHACEAE)

CHRYSOBALANACEAE

Licania michauxii Prance – XH; O; *333.*

CISTACEAE

Helianthemum carolinianum (Walter) Michx. – RU; I; *247.*
Lechea minor L. – RU; O; *477,* new.

CLUSIACEAE

Hypericum crux-andreae (L.) Crantz – RU; I; *472,* new.
H. galioides Lam. – BF; F; *30, 44, 307, 575.*
H. hypericoides (L.) Crantz. – UMF & RU; O; *89.*

H. mutilum L. – BF; O; *27, 346.*
Triadenum walteri (J. F. Gmel.) Gleason – BS & BF; I; *574.*

COMMELINACEAE

Commelina erecta L. – XH; O; *51.*

CONVOLVULACEAE

Cuscuta compacta Juss. – DM; O; *497,* new.
Dichondra carolinensis Michx. – XH & RU; O; *250.*
Stylisma patens (Desr.) Myint – UMF; R; *48.*

CORNACEAE (incl. NYSSACEAE)

Cornus asperifolia Michx. – FF; O; *74.*
C. foemina Mill. - FF; O; *253, 452.*
Nyssa biflora Walter – FS; F; *459.* (Burkhalter 1992)
N. sylvatica Marshall var. *sylvatica* - XH; I, but locally frequent at one site on east side of park; *485,* new.

CYPERACEAE

Bulbostylis ciliatifolia (Elliott) Fernald – XH & RU; I; *319.*
Carex dasycarpa Muhl. – XH; O; *264.*
C. granularis Muhl. *ex* Schkuhr *in* Willd. – FF & RU; O, on edge of spring run; *422.*
C. longii Mack. – RU; I; *36, 268, 347.*
Cyperus croceus Vahl – RU; *Hall NV.*
C. distinctus Steud. – FF & RU; O, on edge of spring run; *423.*
C. filiculmis Vahl – XH & RU; O; *320.*
C. flavescens L. – FS, DM & BS; *Hall NV.*
**C. lanceolatus* Poir. *in* Lam. – BS; I; *353,* new.
C. plukenetti Fernald – XH; O; *84,* new.
C. polystachyos Rottb. – FF & DM; *Hall NV.*
C. retrorsus Chapm. – UMF, XH & RU; F; *40, 149, 150.*
**C. rotundus* L. – RU; *Hall NV.*
C. strigosus L. – FF & RU; O, on edge of spring run; *421, 424.*
C. tetragonus Elliott FF & UMF; *Hall NV.*
Eleocharis baldwinii (Torr.) Chapm. – DM; O; *331.*
E. montevidensis Kunth – XH; O; *341.*
Kyllinga odorata Vahl – BS & DM; *Hall NV.*
Rynchospora colorata (L.) H. Pfeiff. – FF & RU; F; *17.*
R. corniculata (Lam.) A. Gray – FS; O; *75, 119.*
R. inundata (Oakes) Fernald FS & RU; I; *466.*
R. megalocarpa A. Gray – XH & RU; F; *92, 316, 334.*
R. microcarpa Baldwin *ex* A. Gray – DM & BS; O; *335.*
R. plumosa Elliott – BS; I; *60.*
Scleria reticularis Michx. – DM; F; *337.*
S. triglomerata Michx. – UMF; O; *265, 395.*

CYRILLACEAE

Cyrilla racemiflora L. – FF; I; *14.*

EBENACEAE

Diospyros virginiana L. – UMF; F; *430, 462.*

ERICACEAE

Gaylussacia dumosa (Andrews) Torr. & A. Gray – XH; O; *613.*
Lyonia ferruginea (Walter) Nutt. – XH; F; *382, 468.*
Vaccinium arboreum Marshall – UMF, F & XH; O; *2, 6, 8.*
V. darrowii Camp – XH; I; *588.*
V. elliottii Chapm. – FF & UMF; F; *1, 164, 592.* (Luteyn et al. 1996)
V. myrsinites Lam. – XH; I; *322, 536.*
V. stamineum L. – UMF; F; *9, 446.*

ERIOCAULACEAE

Lachnocaulon anceps (Walter) Morong – DM; A; *328.*

ESCALLONIACEAE (see ITEACEAE)

EUPHORBIACEAE

Acalypha gracilens A. Gray – UMF; O; *371.*
Chamaesyce maculata (L.) Small – XH & RU; I; *579.*
C. prostrata (Aiton) Small – RU; *Hall NV.*
Cnidoscolus stimulosus (Michx.) Engelm. & A. Gray – XH & RU; F; *236.*
Croton glandulosus L. – RU; I; *135.*
C. michauxii G. L. Webster – XH & RU; O; *80, 373, 435.*
Phyllanthus caroliniensis Walter – FS; I; *553.*
**P. urinaria* L. – RU; *Hall NV.*
Stillingia sylvatica Garden *ex* L. – XH; F; *81, 311.*

FABACEAE

Amorpha fruticosa L. – XH; I; *434.*
A. herbacea Walter var. *herbacea* – XH; O; *246,* new.
Baptisia alba (L.) Vent. – UMF; O; *4, 166.*
B. lecontii Torr. & A. Gray – XH; I; *302.*
Centrosema virginianum (L.) Benth. – XH & RU; O; *49, 305.*
Chamaecrista fasciculata (Michx.) Greene – RU; O; *132.*
Clitoria mariana L. – RU; I; *304.*
**Crotalaria lanceolata* E. Meyer – RU; O; *471.*
C. rotundifolia Walter *ex* J. F. Gmel. – RU; O; *50, 237.*
**Desmodium canescens* (L.) DC. – RU; O; *440,* new.
D. paniculatum (L.) DC. – XH; *Hall NV.*
D. triflorum (L.) DC. – RU; O; *141.*
Erythrina herbacea L. – UMF & RU; I; *16.*
Galactia volubilis (L.) Britton – UMF, XH & RU; O; *69, 90, 372, 429.*

Gleditsia aquatica Marshall – SL; I; *275, 355.*
Indigofera caroliniana Mill. – XH; F; *47.*
Lespedeza hirta (L.) Hornem. – RU; I; *143.*
L. stuevei Nutt. – RU; I; *469*, new.
Medicago lupulina L. - RU; I; *544.*
Mimosa quadrivalvis L. var. *angustata* (Torr. & A. Gray) Barneby – XH; O; *62, 314.*
Rhynchosia difformis (Elliott) DC. – RU; O; *476.*
R. michauxii Vail – RU; O; *436, 607.*
Senna ligustrina (L.) H. S. Irwin & Barneby – UMF; I; *412.*
S. marilandica (L.) Link – FF; F; *431.*
S. obtusifolia (L.) H. S. Irwin & Barneby – RU; O; *433.*
Tephrosia chrysophylla Pursh RU; I; *601.*
T. florida (F. Dietr.) C. E. Wood – RU; I; *303, 376.*
**Trifolium repens* L. – RU; *Hall NV.*
Vicia floridana S. Watson – BS; O; *26, 257.*

FAGACEAE

Quercus austrina Small – UMF; O; *384*, new. (Nixon and Muller 1997)
Q. chapmanii Sarg. – XH; I; *599.*
Q. falcata Michx. – XH; O; *277, 295, 442*, new.
Q. geminata Small – XH; A; *298, 386, 387.*
Q. hemisphaerica W. Bartram UMF & XH; F; *100, 276.* (Muller 1970)
Q. incana W. Bartram – XH; *Hall NV.*
Q. laurifolia Michx. – FF; O; *414.* (Muller 1970)
Q. lyrata Walter – FF; O; *493, 603.*
Q. margaretta Ashe *ex* Small – XH; I; *447.*
Q. michauxii Nutt. – UMF; O; *500.*
Q. myrtifolia Willd. – XH; O; *444, 527, 531.*
Q. nigra L. – UMF & BF; O; *385.*
Q. pumila Walter – XH; O; *526.*
Q. virginiana Mill. – XH & UMF; F; *673.*

GELSEMIACEAE

Gelsemium sempervirens (L.) W. T. Aiton – FF & UMF; O; *251.*

GENTIANACEAE

Bartonia paniculata (Michx.) Muhl. – BS; R; *496*, new.
Sabatia calycina (Lam.) A. Heller – BS & FS; O; *28, 66, 344.*

HALORAGACEAE

Proserpinaca palustris L. – FS; O; *63.*

HAMAMELIDACEAE (see ALTINGIACEAE)

HIPPOCASTANACEAE (see SAPINDACEAE)

HYDROCHARITACEAE

**Hydrilla verticillata* (L. f.) Royle – SR; I; *407.*
Limnobium spongia (Bosc) Steud. – SL; I; *567,* new.
Vallisneria americana Michx. – SR; A; *419.*

HYPOXIDACEAE

Hypoxis curtisii Rose – FS; F; *65, 163.*

IRIDACEAE

Sisyrinchium angustifolium Mill. – RU; I; *235.*
S. nashii E. P. Bicknell – RU; I; *541.*
**S. rosulatum* E. P. Bicknell – RU; I; *310.*

ITEACEAE

Itea virginica L. – FS; *Hall NV.*

JUGLANDACEAE

Carya glabra (Mill.) Sweet – UMF & XH; F; *258, 379.*
C. tomentosa (Poir. *in* Lam.) Nutt. – UMF & XH; O; *332.* (Rehder 1945)

JUNCACEAE

Juncus dichotomus Elliott – FF & RU; O, on edge of spring run; *420.*
J. marginatus Rostk. – DM; O; *39, 336, 564.*

LAMIACEAE

Callicarpa americana L. – UMF; O; *59.*
Dicerandra densiflora Benth. – RU; O; *126.*
**Hyptis mutabilis* (Rich.) Briq. – RU; O; *671.*
**Leonitis nepetefolia* (L.) R. Br. *in* W. T. Aiton – RU; F; *312,* new.
Micromeria brownei (Sw.) Benth. – RU; O, in lawns around spring; *19, 400.*
Monarda punctata L. – RU; I; *566.*
Pycnanthemum floridanum E. Grant & Epling – RU; I; *582.*
Salvia lyrata L. – RU; I; *282.*
Scutellaria integrifolia L. – BS; F; *25,* new.
Teucrium canadense L. – BS & BF; O; *327.*
Trichostema dichotomum L. – RU; O; *127.*

LAURACEAE

Persea borbonia (L.) Spreng. – UMF & XH; F; *413, 449.*
P. palustris (Raf.) Sarg. – BS; O; *585.*

LEMNACEAE (see ARACEAE)

LENTIBULARIACEAE

Utricularia foliosa L. – SL; O; *570.*

LOGANIACEAE (also see GELSEMIACEAE)

Mitreola petiolata (J. F. Gmel.) Torr. & A. Gray – FS; F; *64, 118.*

MAGNOLIACEAE

Magnolia grandiflora L. – UMF, BF & XH; O; *99.*

MALVACEAE (incl. TILIACEAE)

Sida rhombifolia L. – RU & XH; O; *561.*
Tilia americana L. var. *caroliniana* (Mill.) Castigl. – UMF; O; *94.*

MELASTOMATACEAE

Rhexia mariana L. – UMF & XH; O; *46, 325.*

MORACEAE

**Broussonetia papyrifera* (L.) Vent. – XH; I; *598.*

MYRICACEAE

Myrica cerifera L. – BS, FF, BF & UMF; F; *96, 294, 297, 299, 573.*

NYMPHAEACEAE (incl. CABOMBACEAE)

Brasenia shreberi J. F. Gmel. – DM; F; *330.*
Cabomba caroliniana A. Gray – SR; A; *111.*
Nuphar advena (Aiton) W. T. Aiton – BLS; O; *615.* (Wiersema and Hellquist 1994)

NYSSACEAE (see CORNACEAE)

OLEACEAE

Fraxinus americana L. – BS; *447a,* new.
F. caroliniana Mill. – FS & FF; O; *110, 354.*
Osmanthus americanus (L.) Benth. & Hook. f. *ex* A. Gray – UMF & XH; O; *273.*

ONAGRACEAE

Gaura angustifolia Michx. – UMF & RU; I; *86.*
Ludwigia repens J. R. Forst. – FS; R; *467.*
Oenothera laciniata Hill – RU; I; *559.*

ORCHIDACEAE

Epidendrum conopseum R. Br. – XH; I; *508.*

OXALIDACEAE

Oxalis corniculata L. – RU; I; *238.*

PASSIFLORACEAE

Passiflora incarnata L. – RU; R; *315.*
P. lutea L. – XH; I; *558.*

PHYTOLACCACEAE

Phytolacca americana L. var. *rigida* (Small) Caulkins & Wyatt – RU; I; *324.* (Caulkins and Wyatt 1990)

PLANTAGINACEAE

**Plantago major* L. – RU; *Hall NV.*
P. virginica L. – RU; O; *547.*

POACEAE

Andropogon glomeratus (Walter) Britton, Sterns & Poggenb. var. *pumilus* Vasey – XH; O; *535.* (Campbell 1983)
A. ternarius Michx. – XH; O; *502.*
A. virginicus L. var. *decipiens* C. S. Campb. – XH; O; *157,* new. (Campbell 1983)
A. virginicus L. var. *virginicus* – XH; F; *503, 505.* (Campbell 1983)
Aristida patula Chapm. *ex* Nash – RU; I; *482.*
Axonopus affinis Chase – BF; O; *85.*
A. furcatus (Flüeggé) Hitchc. – BF; O; *348.*
Cenchrus gracillimus Nash – RU; O; *147, 480.*
C. incertus M. A. Curtis – RU; F; *494.*
Chasmanthium sessiliflorum (Poir.) Yates – UMF & RU; F; *38, 56, 82, 339, 349, 351.*
**Cynodon dactylon* (L.) Pers. – RU; *Hall NV.*
Dichanthelium aciculare (Desv. *ex* Poir.) Gould & C. A. Clark – XH; O; *391.*
D. acuminatum (Sw.) Gould & C. A. Clark var. *acuminatum* – UMF & FF; O; *37, 263.*
D. commutatum (Schult.) Gould – UMF & FF; F; *35, 283, 287, 352.*
D. dichotomum (L.) Gould – FS; I; *464.*
D. ensifolium (Baldwin *ex* Elliott) Gould – XH & RU; O; *340.*
D. oligosanthes (Schult.) Gould – XH; O; *278.*
D. portoricense (Desv. *ex* Ham.) B. F. Hansen & Wunderlin – XH; O; *285.*
D. strigosum (Muhl.) Freckmann – BF; O; *269.*
Digitaria ciliaris (Retz.) Koeler – RU; O; *426.*
D. serotina (Walter) Michx. – RU; *Hall NV.*
Eleusine indica (L.) Gaertn. – RU; *Hall NV.*
Eragrostis elliottii S. Watson – RU; R; *146.*

E. virginica (Zucc.) Steud. – DM & RU; *Hall NV.*
**Eremochloa ophiuroides* (Munro) Hack. – FF; I; *428.*
Eustachys petraea (Sw.) Desv. – RU; O; *138, 266.*
**Lolium perenne* L. – RU; I; *540.*
Oplismenus hirtellus (L.) P. Beauv. subsp. *setarius* (Lam.) Mez *ex* Ekman – UMF & RU; F; *565.* (Scholz 1981)
Panicum anceps Michx. – DM, BS & BF; F; *83, 148, 338, 350, 393, 481.*
P. rigidulum Bosc *ex* Nees – FF; O; *120, 455, 456, 506.*
**Paspalum notatum* Flüeggé – RU & UMF; O; *54, 317.*
P. plicatulum Michx. – RU; O; *318.*
P. repens Bergius – BLS; I; *108.*
P. setaceum Michx. – RU; O; *55, 425, 439.*
Piptochaetium avenaceum (L.) Parodi – XH; I; *288, 289, 394,* new.
**Poa annua* L. – RU; F; *252.*
Saccharum alopecuroides (L.) Nutt. – XH; O; *501,* new.
S. baldwinii Spreng. – FF; F, on riverbank only; *463.*
Sacciolepis striata (L.) Nash – FS & BS; *Hall NV.*
**Secale cereale* L. – RU; R; *562.*
Setaria geniculata (Poir.) Millsp. & Chase – XH & RU; O; *156, 479.* (Godfrey and Wooten 1979)
Sorghastrum elliottii (C. Mohr) Nash – XH; O; *504.*
Sphenopholis obtusata (Michx.) Scribn. – BS; O; *539.*
**Sporobolus indicus* (L.) R. Br. var. *indicus* – RU; O; *392.*
Stenotaphrum secundatum (Walter) Kuntze – RU; O; *674.*
Vulpia elliotea (Raf.) Fernald – RU; I; *538,* new.

POLYGALACEAE

Polygala grandiflora Walter - UMF & XH; O; *23, 52, 134.*

POLYGONACEAE

Eriogonum tomentosum Michx. – XH; I; *580.*
Polygonum densiflorum Meisn. – FS, DM & BS; *Hall NV.*
P. punctatum Elliott – BS & SR; O; *42, 343, 416.*
Rumex hastatulus Baldwin – RU; I; *245.*

PONTEDERIACEAE

Pontederia cordata L. – SR; O; *104, 105.*

PRIMULACEAE

Samolus valerandi L. subsp. *parviflorus* (Raf.) Hultén – FS; F; *20, 33.*

RHAMNACEAE

Berchemia scandens (Hill) K. Koch – FS; R; *160.*
Rhamnus caroliniana Walter – UMF; *Hall NV.*

ROSACEAE

Crataegus aestivalis (Walter) Torr. & A. Gray – FF; O; *415*, new.
C. crus-galli L. – FS; *Hall NV.*
C. marshallii Eggl. – FF; *Hall NV.*
C. michauxii Pers. – XH; I; *272, 557.*
Prunus caroliniana (Mill.) Aiton – UMF; O; *12.*
P. serotina Ehrh. var. *serotina* – UMF; O; *260, 525.*
P. umbellata Elliott – XH; I; *380*, new.
Rubus argutus Link – BS; *Hall NV.*
R. cuneifolius Pursh XH; O; *329.*
R. trivialis Michx. XH; O; *171.*

RUBIACEAE

Cephalanthus occidentalis L. – BS, FS & DM; O; *326.*
Diodia teres Walter – RU; O; *140, 427.*
D. virginiana L. – FF; O; *114, 408, 450.*
Galium hispidulum Michx. – XH & RU; O; *249, 474.*
G. tinctorium L. – BS; I; *486.*
**Hedyotis corymbosa* (L.) Lam. – RU; *Hall NV.*
H. procumbens (Walter *ex* J. F. Gmel.) Fosberg – XH; O; *532.*
H. uniflora (L.) Lam. – UMF; *Hall NV.*
Mitchella repens L. – UMF; O; *234.*
**Richardia brasiliensis* Gomes – RU; I; *79.*

RUTACEAE

Ptelea trifoliata L. – UMF; I; *15, 73.*
Zanthoxylum clava-herculis L. – UMF; I; *551.*

SALICACEAE

Salix caroliniana Michx. – FS; O; *259, 411.*

SAPINDACEAE (incl. ACERACEAE and HIPPOCASTANACEAE)

Acer rubrum L. – FF & FS; I; *448.*
Aesculus pavia L. – XH; I; *432.*

SAPOTACEAE

Sideroxylon lanuginosum Michx. – UMF; O; *491, 530, 587.*
S. reclinatum Michx. subsp. *reclinatum* FF; I; *490, 492.*

SAURURACEAE

Saururus cernuus L. – FS; A; *18, 106.*

SCROPHULARIACEAE

Bacopa monnieri (L.) Pennell – SR; O; *453.*
Gratiola virginiana L. – BS; I; *670*, new.

Linaria canadensis (L.) Chaz. – RU; O; *543.*
L. floridana Chapm. – RU; O; *243b.*
Mecardonia acuminata (Walter) Small – DM; *Hall NV.*
Micranthemum umbrosum (J. F. Gmel.) S. F. Blake – BS; I; *672,* new.
Veronica peregrina L. – RU; O; *240, 545.*

SMILACACEAE

Smilax auriculata Walter – RU & XH; F; *270, 323, 483, 555.*
S. bona-nox L. – FF, UMF, XH & RU; F; *293.*
S. glauca Walter – XH; I; *291.*
S. pumila Walter – UMF & UMF; O; *169.*
S. smallii Morong – RU & XH; O; *590.*

STYRACACEAE

Halesia carolina L. – XH; I; *31, 383, 528.*

SYMPLOCACEAE

Symplocos tinctoria (L.) L'Hér. – UMF; A; *280, 381.*

TETRACHONDRACEAE

Polypremum procumbens L. – SL & SKL; *Hall NV.*

TILIACEAE (see MALVACEAE)

TURNERACEAE

Piriqueta caroliniana (Walter) Urb. – UMF & RU; O; *13, 53, 91.*

ULMACEAE

Planera aquatica Walter *ex* J. F. Gmel. – FS & FF; O; *161, 604.*
Ulmus alata Michx. – FS; O; *162.*
U. americana L. – FS; O; *254.*
U. crassifolia Nutt. – FS; O; *454.*

URTICACEAE

Boehmeria cylindrica (L.) Sw. – SL; O; *470, 577.*

VERBENACEAE

**Lantana camara* L. – XH & RU; *Hall NV.*
Phyla nodiflora (L.) Greene – RU; F; *402.*

VIOLACEAE

Viola palmata L. – XH; I; *233.*
V. sororia Willd. – UMF; I; *158.*

VISCACEAE

Phoradendron leucarpum (Raf.) Reveal & M. C. Johnst. – UMF; O; *274.*

VITACEAE

Ampelopsis arborea (L.) Koehne – FF & UMF; O; *107.*
Parthenocissus quinquefolia (L.) Planch. – FF, UMF, BF & XH; F; *417.*
Vitis aestivalis Michx. – XH; F; *396.*
V. rotundifolia Michx. – UMF & XH; F; *390.*

XYRIDACEAE

**Xyris jupicai* Rich. – FS; O, but locally A on north edge of Meud-Scot track; *441.*
X. platylepis Chapm. – DM; I; *589.*

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NEW ENGLAND NOTE

ANEURA MAXIMA (HEPATICAE: ANEURACEAE) IN MAINE, U.S.A.

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Aneura maxima (Schiffn.) Steph. Maine: Kennebec Co., Mud Pond, ca. 5 km SW of Litchfield along Highway 126, 44°12′N, 69°58′W, bottom of an animal run over wet peat, minerotrophic edge of fen mat near pond, 19 Sep 1987, *Miller 9497* (NYS).

Two species of *Aneura* are recognized in the North American flora by Schuster (1992), the common and variable *A. pinguis* (L.) Dumort., and *A. maxima,* a species only recently discovered to be widespread in eastern North America but previously known in the flora of tropical and temperate Asia. A third species, *A. sharpii* Inoue & N. G. Mill. (Inoue and Miller 1985) has also been recognized, but in this note I tentatively accept it as a synonym of *A. maxima,* following the circumscriptions and interpretations of Schuster (1992).

Aneura maxima is based on plants first collected in Java and Sumatra (Schiffner 1898). Its known range was subsequently extended to include other parts of Asia, notably Japan, eastern North America (Schuster 1992), and very recently western and northwestern Europe (Finland, Frahm 1997; Belgium, Andriessen et al. 1995; France, Sotiaux and Sotiaux 1996). The pattern of morphological variation in North American populations of *A. maxima sensu lato* is poorly understood, because the species has been collected infrequently so far in our area, and male plants and female ones with mature calyptrae and sporophytes are few or unknown throughout the range of the species.

There is only one previous station for *Aneura maxima* in New England, namely, Rutland County, Vermont, in a fen near the Connecticut River (as *A. sharpii*; Inoue and Miller 1985). Otherwise, the reported North American distribution of *A. maxima* (incl. *A. sharpii*) is eastern New York State, central Pennsylvania, West Virginia, Tennessee, Mountain and Piedmont provinces of

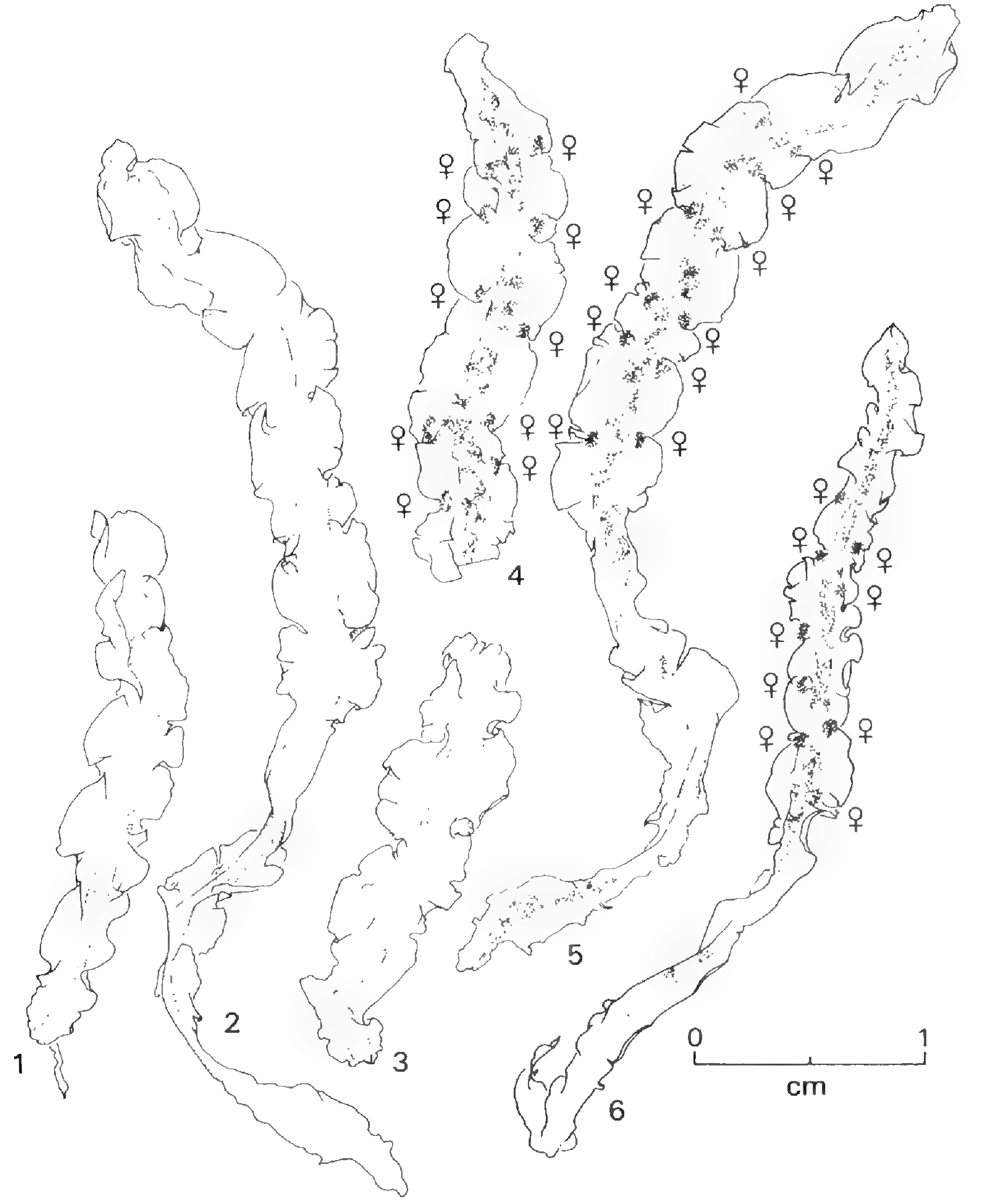
North Carolina, and Louisiana (Inoue and Miller 1985; Reese and Walters 1987; Schuster 1992). *Aneura maxima* appears to be uncommon in all these regions.

Aneura maxima and *A. pinguis* differ vegetatively in the following ways: thallus margins regularly lobate, short, lateral archegonial branches (gynoecia) in most sinuses; unistratose thallus wings 10–20 cells wide, sometimes more; thick, opaque, multistratose mid-thallus region narrow, about one-third of the plant width (*A. maxima*; Figures 1–6), versus thallus margins only sometimes irregularly and unevenly lobate or sinuate, lateral sinuses bearing archegonial branches scattered; unistratose thallus wings when developed (especially in lax plants from moist or wet habitats) to 10 cells wide but usually fewer; thick mid-thallus region wide, sometimes the entire width of the plant, but usually two-thirds (or more) of the plant width (*A. pinguis*; Figures 7, 8).

Thalli of *Aneura maxima* are similar to those of *Pellia* and *Moerckia*. When present, the short, lateral, ciliate archegonial branches of female plants of *A. maxima* (visible only from the underside of plants) easily separate species of *Aneura* from those of the other two genera. In plants of *Pellia* and *Moerckia,* sex organs are variously disposed on the upper thallus surface. Antheridial branches of male plants of *A. maxima* are also short and lateral, but they extend beyond the thallus margins and therefore can be seen from the upper surface of the plant.

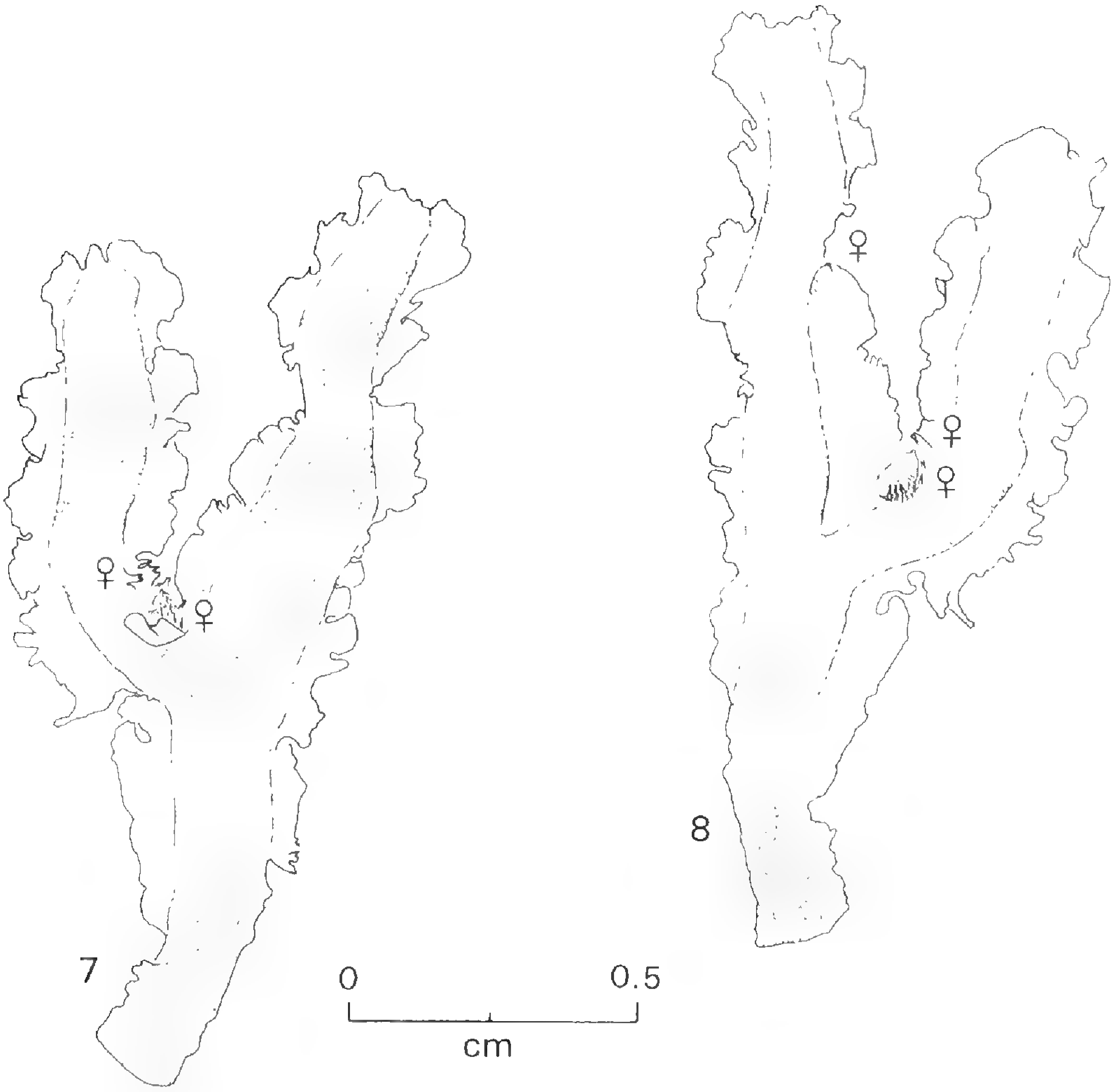
Too few plants of *Aneura maxima* with calyptrae and mature sporophytes are known at present in North America to evaluate potential differentiating character states in these life cycle components. Schiffner (1900), Furuki (1991), and Schuster (1992) stressed that the female inflorescences of *A. maxima* contain long or very long cilia (paraphyses, *sensu* Furuki 1991), whereas in *A. pinguis* they are scalelike (Schuster 1992). However, in young archegonial branches (i.e., those with archegonia cap cells intact) in North American plants I have studied, uniseriate and multiseriate, scalelike paraphyses are present in both *A. maxima* and *A. pinguis* (Figures 9–22). Therefore, at a young stage of development, it does not seem possible to differentiate between the species on the basis of paraphysis morphology. However, this may not hold for plants with mature calyptrae.

Plants of *Aneura pinguis* can be highly variable throughout its nearly cosmopolitan range, but one segment of the variation approaches *A. maxima* in thallus morphology. In a frequently en-



Figures 1–6. *Aneura maxima.* 1–3, thalli, upper surfaces, note lobate wings and narrow mid-thallus rhizoidal region where the thallus is also thickest; 4–6, thalli, lower surfaces, note the regular and repetitious occurrence of archegonial branches, which remain small and cushion-like [Maine, *Miller 9497* (NYS)].

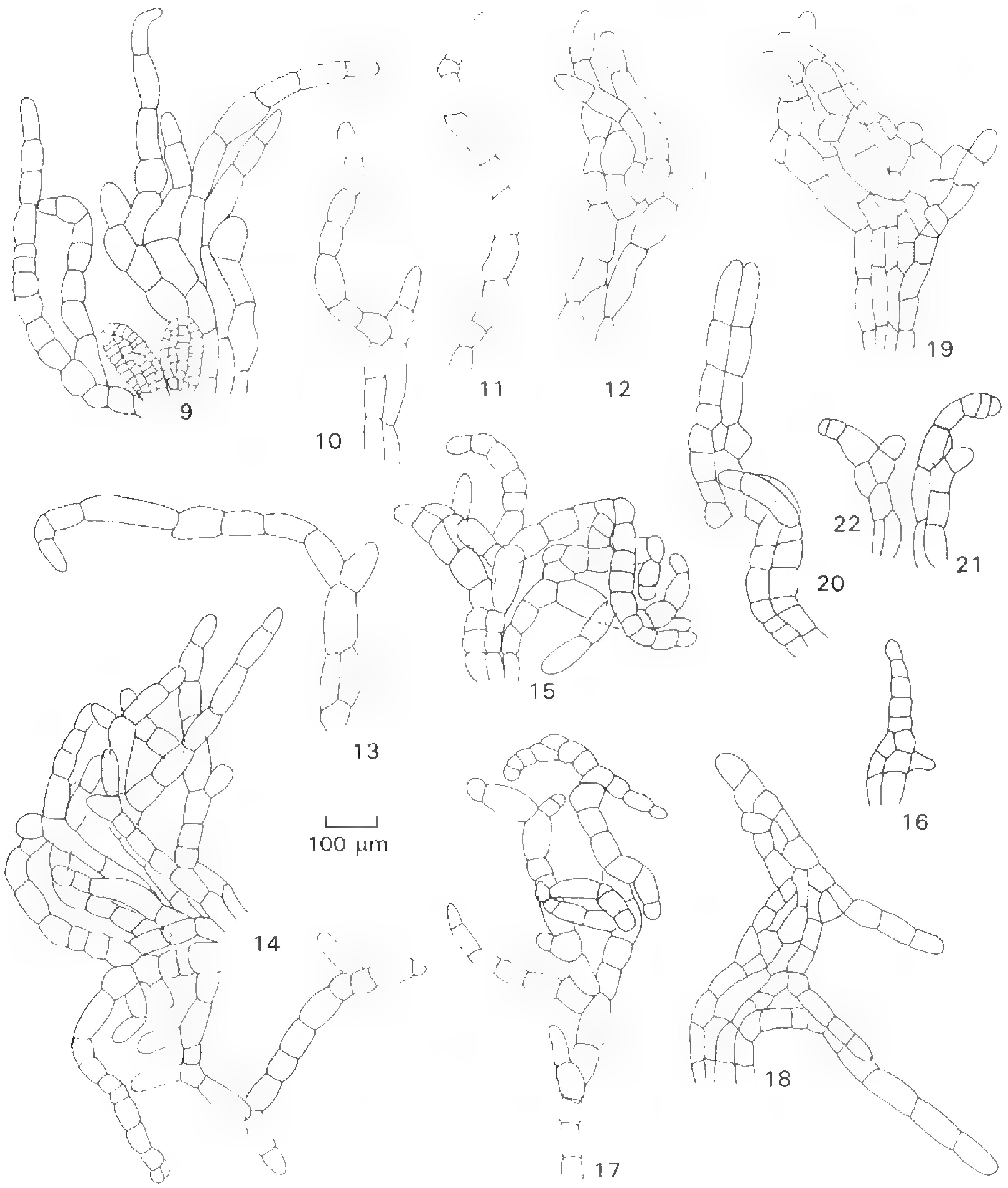
countered expression of *A. pinguis,* the plants are an oily or greasy green, compact, brittle, and multistratose to the margins. However, lax plants in wet habitats can have lateral wings similar to those of *A. maxima* but without the regular lobate configuration of this species. Illustrated in Figures 7 and 8 are the obverse and reverse aspects of the same plant of *A. pinguis* from a wet, shrub-



Figures 7 & 8. *Aneura pinguis,* plant from a wet habitat (circumneutral carr). 7, thallus, upper surface, note irregular, mostly nonlobate wings and broad, thick mid-thallus region; 8, same plant, lower surface of thallus, archegonial branches few and irregular in position [Maine, Aroostook Co., Thousand Acre Bog, Crystal, *Miller 13262* (NYS)].

by fen margin in north-central Maine. The lateral thallus wings in this plant and others in the collection are up to 10 cells wide and the cells are arranged in fan-shaped tiers, suggesting that they grew out from the edge of the massive tissue in the central part of the thallus. Plants of this morphological type retain the wide, thick central thallus region and irregularly placed archegonial branches typical of compact expressions of *A. pinguis* in drier sites.

In the northern portion of its known range in eastern North America (New England and New York), *Aneura maxima* has been found on wet peat in fens beneath a shrub or herb cover and on



Figures 9–22. *Aneura maxima* and *A. pinguis,* filiform and scalelike archegonial paraphyses, all from archegonial branches at the same stage of development. 9–13, *A. maxima,* showing variation from filiform and simple to multiseriate and branched, archegonia in 9 semidiagrammatic [Maine, *Miller 9497* (NYS)]; 14–18, *A. pinguis,* from a lax plant in a hygric habitat [Maine, *Miller 13262* (NYS)]; 19–22, *A. pinguis,* from a compact plant in a mesic habitat [Michigan, Cheboygan Co., shore of Weber Lake, *Miller 9016* (NYS)].

wet organic-rich muck in a *Lythrum salicaria* L. wetland under a dense, tall, herb overstory. To the south in West Virginia, Tennessee, North Carolina, and Louisiana, it grows perhaps exclusively on wet rock in streams and over cliff faces, and on stream banks.

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NOTE

SCIRPUS ANCISTROCHAETUS (CYPERACEAE): FIRST RECORD IN CANADA

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A recent revision of material of *Scirpus atrovirens sensu lato* at the herbarium of the Université de Montréal has turned up an interesting discovery of *Scirpus ancistrochaetus* Schuyler from the Shawinigan region of Québec (valley of the Rivière Saint-Maurice). This discovery is based on a misidentified collection dating from 1934. It represents the first record of this species in Canada.

SPECIMEN CITATION: CANADA. Québec: Sainte-Flore (village), comté de Saint-Maurice, lac Mondor, Rive basse, 15 août 1934, *Gauthier 2231* (MT). The approximate coordinates are 46°37′N, 72°44′W.

Scirpus ancistrochaetus is a relatively unknown bulrush species that was first described by A. E. Schuyler in 1962 (Schuyler 1962). At the time, Schuyler discovered it in several widely isolated localities in the northeastern states of Vermont and Pennsylvania. Presently, it is known from about 60 localities scattered through the Appalachian region from southwest New Hampshire, adjacent Vermont, and New York to western Virginia. Within this fairly restricted area, it is listed by the United States Fish and Wildlife Service as a Federal Endangered species (USFWS 1991), because it is rare or endangered in all states where it is known to occur (Kartesz and Meacham 1999; Mitchell and Tucker 1997; NatureServe 2000; Royte and Lortie 2000; Strong 1994).

This bulrush has sparked considerable interest because of its relatively recent description and its rarity throughout its range. Several studies have been initiated in different states to better evaluate its status and further document sites where it is known to occur (NatureServe 2000). Wherever it occurs, it seems that populations are small and several occurrences are only known historically. The state of Pennsylvania has the highest number of extant populations (Lentz 1998). To explain the isolated occurrences of this bulrush in the northeastern part of the continent, Schuyler (1962) has suggested that it may be a relict species that is persisting only in pockets of its former range.

The Québec specimen was previously identified as *Scirpus atrovirens* Willd. var. *georgianus* (R. M. Harper) Fernald. Plants by this name in our area are now referred to as *S. hattorianus* Makino, as distinct from *S. atrovirens sensu stricto* (Schuyler 1967). However, a closer examination of the specimen revealed that it was neither *S. hattorianus*, nor *S. atrovirens*. In fact, several well-marked characteristics described by Schuyler (1962, 1967) and Strong (1994) permit us to distinguish this species from the other members of the complex. The inflorescence rays of *S. ancistrochaetus* tend to droop more at maturity as opposed to the ascending rays of *S. atrovirens* and *S. hattorianus*. The rays are also antrorsely scabrous their entire length rather than smooth. The bristles of the achenes are more rigid with sharp-pointed, retrorse teeth that extend nearly to the base, while the bristles of *S. atrovirens* and *S. hattorianus* are weaker and have teeth that are finer and concentrated towards the tip of the bristle. To further complicate matters, hybridization has been reported to occur with *S. atrovirens* and/or *S. hattorianus* (Schuyler 1962, 1967).

In August 2000, a brief attempt was made by Hay to re-locate *Scirpus ancistrochaetus* at the Lake Mondor locality. The shoreline and adjacent wetland were explored, but although other closely related species such as *S. hattorianus* (*2000-28, 29,* MT) and *S. microcarpus* C. Presl (*2000-24, 27, 30,* MT) were common, no populations of *S. ancistrochaetus* were found.

The discovery of this species in Québec is a major extension in range from the previous most northern sites known in the Connecticut River Valley, and thus, continues to raise questions about the status and distribution of this unusual species. As our understanding of this species improves, further field exploration and a more exhaustive search of other herbarium specimens will likely uncover other new occurrences. Given what we know presently, and particularly because of its rare status throughout its range in eastern North America, *Scirpus ancistrochaetus* should be added to the list of rare plants in Québec (Bouchard et al. 1983; Lavoie 1992) and Canada (Argus and Pryer 1990).

ACKNOWLEDGMENTS. Mark Strong of the U.S. National Herbarium kindly confirmed the identification of the specimen. Sara Cairns of the State of New Hampshire, Department of Resources and Economic Development made available reports on the status of the species that were done for the New Hampshire Natural Heritage Inventory.

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NOTE

SCHIZAEA PUSILLA IN NORTH CAROLINA

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Schizaea pusilla Pursh, the curly-grass fern, has been found growing at a single location in a white cedar forest in Green Swamp in southeastern North Carolina. A survey of nearby suitable habitat has failed to establish the presence of another population, and an analysis of the extant site suggests that the population is introduced rather than native, raising problematic conservation issues. *Schizaea pusilla* has long been one of the most eagerly sought plants among professional and amateur botanists in North America. Its allure is certainly related to its rarity, its curious disjunct range, and its inconspicuous and unfernlike appearance. The distribution of *S. pusilla* is centered in the pinelands of southern New Jersey, but includes nearby Long Island, New York, and Sussex County, Delaware, disjunct populations in Nova Scotia and Newfoundland, and a remarkably disjunct occurrence in Peru (Montgomery and Fairbrothers 1992; Stolze 1987; Wagner 1993).

The North Carolina Natural Heritage Program (Division of Parks and Recreation) has considered *Schizaea pusilla* among a list of species "not currently known to occur in North Carolina, but which are considered to have some possibility of being found in North Carolina, based on their currently known range and habitat preferences" (Amoroso 1997). *Schizaea pusilla* was considered as potentially occurring in the Coastal Plain and fall line sandhills in "boggy sphagnous sites associated with white cedar" (Amoroso 1997). The suggested possibility of finding *S. pusilla* in North Carolina is based on the presence of potentially suitable habitat, and the close biogeographic and floristic relationship between the Coastal Plain Pine Barrens of southern New Jersey and Coastal Plain pinelands of southeastern North Carolina. This relationship is demonstrated by the many plant species exhibiting a disjunct distribution between the two areas, and often also involving other areas, such as the East Gulf Coastal Plain (Florida panhandle, southern Alabama, southwestern Georgia, southern Mississippi, and southeastern Louisiana), New Brunswick, and Nova Scotia. A few examples are *Rhynchospora pallida* M. A. Curtis, *Gentiana autumnalis* L., *Lophiola aurea* Ker Gawl., and *Leiophyllum buxifolium* (Bergius) Elliott.

Current floristic similarities are based on underlying habitat similarities, both areas having strongly acidic sandy soils, abundant saturated wetlands, and fire as a frequent and vegetation-shaping natural force. Moreover, these areas have had past connections, and during recent glacial periods, plant species now more typical of New Jersey, including *Schizaea pusilla,* occurred in North Carolina:

> "At full-glacial time, a continuous coastal plain from Florida to Cape Cod was exposed. At the latitude of the Outer Banks, this plain was an estimated 90 miles in width; its vegetation can be partially reconstructed from palynological studies of the Dismal Swamp, Virginia, and southeastern North Carolina. . . . The forests of Virginia were apparently more boreal in aspect—spruce was possibly the dominant tree and fir was probably not uncommon. In southern North Carolina at this time, red or jack pine (perhaps both) were apparently the dominant species; spruce was much less abundant and fir was very uncommon. A number of northern species including *Lycopodium lucidulum, L. annotinum, Schizaea pusilla,* and *Sanguisorba canadensis* occurred" (Burk 1968).

Such recent vegetational similarities and the prehistoric occurrence of *S. pusilla* in North Carolina suggest the plausibility of the presence of relict populations.

On June 18, 1997, the first author discovered *Schizaea pusilla* in a moist, peaty opening in a forest community dominated by *Chamaecyparis thyoides* (L.) Britton, Sterns & Poggenb. at Green

Swamp in Brunswick County, North Carolina (portion of one individual collected, 18 Jun 1997, *LeBlond 4757,* NCU). On June 22, 1997, the two authors returned to the site and conducted a careful investigation, and also investigated four other *Chamaecyparis* stands in the vicinity. The *Chamaecyparis* stands themselves were searched, as well as nearby open habitats, such as boggy areas and moist savanna edges. This strategy was suggested by the habitat of the species in New Jersey: "*Schizaea* occurs in the open bogs, not within dense white cedar forests. Plants are found at bases of young or isolated cedar trees, or stumps or logs, or on edges of peat hummocks including edges of old sand roads" (Montgomery and Fairbrothers 1992).

At the discovery site, six individuals of *Schizaea pusilla* grew on a peat hummock about 1 m by 0.5 m, and about 3 dm high. The hummock was in one of many small openings in an otherwise dense *Chamaecyparis* stand, which is classified as a *Chamaecyparis thyoides/Persea palustris/Lyonia lucida – Ilex coriacea* Forest (Weakley et al. 1998) or as Peatland Atlantic White Cedar Forest (Schafale and Weakley 1990). Immediately associated with *S. pusilla* were *Drosera intermedia* Hayne, *D. rotundifolia* L., *D. filiformis* Raf., seedlings of *C. thyoides,* seedlings of *L. lucida* (Lam.) K. Koch, and *Sphagnum* spp. More generally associated in the surrounding community were *C. thyoides, Cyrilla racemiflora* L., *Vaccinium formosum* Andr., *Gaylussacia frondosa* (L.) Torr. & A. Gray *sensu stricto, Eubotrys racemosa* (L.) Nutt., *Persea palustris* (Raf.) Sargent, *Smilax laurifolia* L., *Ilex myrtifolia* Walter, *I. coriacea* (Pursh) Chapm., and *Myrica heterophylla* Raf. Some of these species are frequently associated with *S. pusilla* in its occurrences in southern New Jersey (D. Snyder, pers. comm., New Jersey Natural Heritage Program), and it is notable that Montgomery and Fairbrothers (1992) state that "the best indicator associates are thread-leaf sundew (*Drosera filiformis*) and Carolina clubmoss (*Lycopodium carolinianum*)."

Four additional white cedar stands and associated open habitats were searched carefully, and although microhabitats similar to those at the first site were seen, no plants of *Schizaea pusilla* were found. This raised the question of whether the discovered population of *S. pusilla* is native, or is the result of planting (or the intentional or unintentional scattering of spores by a human). We considered the following lines of evidence:

1. The habitat, location, and associated species are very plausible for a native occurrence of *Schizaea pusilla* in southeastern North Carolina, showing similarities to its natural habitats in southern New Jersey.
2. The site with *Schizaea pusilla* is one of the most accessible and well-known white cedar stands in southeastern North Carolina, and has a small trail into it from a nearby road. The additional four stands investigated (and lacking *S. pusilla*) have less ready access.
3. The small trail into the *Schizaea pusilla* site had been flagged relatively recently, and a flagged wooden stake of unknown purpose was in the opening on the hummock supporting *Schizaea.*
4. The second author had searched the site for *Schizaea pusilla* in late 1980s and did not find any. Of course, *S. pusilla* is an inconspicuous plant, and the opening which has created apparently excellent conditions for *S. pusilla* is recent.
5. Growing within a few centimeters of *Schizaea pusilla* were a few individuals of both *Drosera rotundifolia* and *D. filiformis. Drosera rotundifolia* is not known to occur in southeastern North Carolina (though it does occur in the mountains of North Carolina, with a few disjunct populations in the fall line sandhills). *Drosera filiformis* (*sensu stricto*) is a rare plant in southeastern North Carolina, known from eight extant populations. Notably, its habitat in North Carolina is in open seasonally-flooded depressional wetlands, and it has not been known to occur in, or in proximity to, *Chamaecyparis* stands in North Carolina. This suggests that both *Drosera* species were introduced as seeds or small plants along with *S. pusilla*; it is also possible that *D. filiformis* rather than *Schizaea* was the intentional introduction. An alternative interpretation would be that notably disjunct populations often indicate unusual habitats or relictual conditions, and that disjunct populations of other species often co-occur at such sites.
6. The plants of *Schizaea pusilla* were examined carefully to assess whether they had been transplanted. They appeared to be well established. No apparent discontinuity of soil could be seen; the peaty material at the immediate base of the plants appeared no different than that in the vicinity. If the plants were transplanted, it is likely that they have been

at the site for at least several years, with enough time having passed for the incorporation and intermeshing of soil material.

7. The authors have seen a privately printed document which reports that four occurrences of *Schizaea* have been known from Green Swamp since the early 1990s (Murray 1995). The author of this privately printed document is a naturalist familiar with habitats in both the New Jersey Pine Barrens and southeastern North Carolina, but we are not convinced that these reported populations are naturally occurring. In our opinion they are likely based on deliberate introductions.
8. *Schizaea pusilla* has previously been the subject of a deliberate introduction to a new state, into an artificial cranberry bog in Massachusetts (B.A. Sorrie, pers. comm., formerly of Massachusetts Natural Heritage Program).

The authors conclude that the preponderance of evidence suggests that the single site of *Schizaea pusilla* discovered in North Carolina is the result of transplantation, but that it is also plausible (though less likely) that this represents a native population. Based on current evidence, *S. pusilla* is best considered a nonindigenous and marginally naturalized component of the North Carolina flora. Even if this population is the result of introduction, it remains possible that *S. pusilla* occurs in North Carolina at undiscovered native populations; botanists should continue to seek *S. pusilla* in likely habitats in North Carolina and adjacent eastern South Carolina and southeastern Virginia.

It is unfortunate that the native/introduced status of *Schizaea pusilla* in North Carolina cannot be determined more definitively. If native, the newly discovered population would warrant considerable conservation effort, attention, and resources by conservation organizations and governmental agencies responsible for the conservation of biodiversity in North Carolina; if introduced, it would not. Uncertainty about the native status of populations of plants causes difficulties for scientists, conservation organizations, and government agencies in determining the native distributions of taxa, and the appropriate conservation priorities and actions needed. Plants with high profiles in the amateur botanical world, such as orchids, ferns, and insectivorous species, are particularly likely to be introduced to areas outside their native distributions, and then be found and reported as range extensions. Examples include *Dionaea muscipula* J. Ellis in Alabama, Florida, western North Carolina, Virginia, and southern New Jersey (all introduced); *Drosera filiformis* and *D. intermedia* in West Virginia (considered introduced); *Sarracenia leucophylla* Raf. in eastern North Carolina (probably introduced); and various *Sarracenia* spp. in eastern Virginia and New Jersey (introduced).

The authors urge that the introduction of species to natural areas, such as nature preserves or multiple-use public conservation lands, be avoided. It has been abundantly documented that such introduced species can cause unforeseen management problems (though in this case it is difficult to imagine curly-grass fern as a pest species outcompeting another species!). Even if the deliberate introduction does not become a problem, other species are often introduced unintentionally as well, and these may become aggressive colonizers. If species are introduced, every effort should be made to document their introduced status in the published literature to avoid future confusion regarding native distributions, and conservation and management priorities.

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IN MEMORIAM

ROLLA MILTON TRYON, JR.

1916–2001

SCIENTIST, TEACHER, AND MENTOR

Rolla M. Tryon, Jr., world-renowned pteridologist and long-time member of the New England Botanical Club, died in Tampa, Florida on August 20, 2001 six days short of his 85th birthday. Rolla will be remembered for his scientific contributions to botany, for his role as a teacher and a mentor to his students and colleagues, and for his service to many professional organizations, especially to the New England Botanical Club.

As a scientist, Rolla authored over 100 articles, papers, and books (Gastony et al. 2001). These ranged from his first, at age

18, on ferns of the genus *Osmunda* in the Indiana dunes, to taxonomic revisions of selected fern genera and analyses of fern biogeography, and finally to his comprehensive treatment of the free-sporing vascular plants of the Americas entitled *Ferns and Allied Plants, with Special Reference to Tropical America,* coauthored with his wife and research partner, Alice F. Tryon.

Rolla had a deep interest in the geography of organisms. With the advent of chemical and later, molecular methods for probing the secrets of the evolutionary process, some came to think that the only important information was that carried in the molecular warehouse of the cell. Rolla clearly saw the folly of this. He never lost sight of the forest for the trees. He was able to maintain the broad perspective that the process of divergent evolution involves organisms changing through time and space. He was fascinated by the relationship of organisms to space, that is, to their geography. He understood that organisms may disperse and migrate, but that their geographic range is the direct result of a chain of events leading back in time to the place where divergent evolution occurred. Although that place may never be known, Rolla seemed to have an innate understanding that the evolutionary process is hugely affected by geography, by that interaction of the geology, climate, and biodiversity of a region. Thus, no evolutionary study was complete without a thorough analysis of what could be learned about an organism's geography. This was wonderful for his students. We were encouraged to go to the field as much as possible, to see the plants in their natural habitats, and to learn what we could about the natural history of the place where these organisms occurred.

Rolla was one of those rare individuals who was awed by the natural beauty that is the result of the evolutionary process. For many, it is the human art forms such as sculpture or architecture that bring inspiration. But for Rolla, it was the natural beauty of the free-sporing vascular plants that he found most inspiring. His appreciation of these plants was expressed in many ways. He was a fine artist and won prizes for his watercolor paintings of ferns. He was an avid fern grower and he and Alice always had a backyard filled with ferns they had transplanted from the countryside. He was especially fond of *Botrychium* and often, when he returned from a visit to the farm in Indiana, brought a potted grape fern for his desk in the office at the Gray Herbarium. But mostly, he expressed his appreciation for these plants by devoting his life to their study. Rolla truly loved observing, analyzing, and writing about ferns and this was his ultimate form of human expression.

For those fortunate enough to have known him well, watching Rolla initiate, fully engage, and focus his attention on a project, and then bring the research to publication was perhaps the ultimate academic experience. Rolla had an incredible ability to focus his attention and he had a way of rapidly bringing order to disorder. It seemed that he could see in his mind's eye, not only the scientific conclusions that could be reached from an analysis of the data, but the entire narrative that would unfold, before he ever began to write. The writing was just the final step of putting what had already been assembled in his mind onto paper. For those of us who struggle with the process of getting our thoughts into coherent form, this was awesome to witness.

Students always know when the professor loves his or her subject and those are the courses and experiences that have the greatest impact on students' intellectual development, even if they do not particularly like the subject that is being taught. But when they do like the subject, the professor often becomes an inspiration, propelling students on to ideas, to places, and to careers that were never imagined. Rolla was such an inspiration to many students. This, plus his kindness, his willingness to help even when a student's ideas were in direct conflict with his own, and his example of a life devoted to an incredibly high standard of work have inspired a generation of pteridologists and countless others who have pursued careers in all walks of life.

Rolla received his graduate training at Harvard between 1938 and 1941 where he was mentored by Charles Alfred Weatherby and Merritt Lyndon Fernald, both of whom were influential in Rolla's early years (Barrington et al. 2001). Following graduate school he held positions at Dartmouth, the University of Wisconsin, the University of Minnesota, the Missouri Botanical Garden, and the University of California at Berkeley, finally returning to New England in 1958 where he would spend the rest of his career as Curator and then Professor of Biology at Harvard University until retirement in 1987. While he was at Harvard, Rolla made important contributions to botany in New England. He was a member of the New England Botanical Club for 60 years from 1941 to 2001. During that time he served the Club as Recording Secretary (1964–1968), as an Associate Editor of *Rhodora* (1961–1977), as Editor-in-Chief of *Rhodora* (1977–1981), as

Vice President (1984–1986), and as President of the Club (1986–1988). He also served on the Council for many years. Rolla was also organizer, with Alice Tryon, of the New England Fern Conference, an annual regional meeting for pteridologists held at the Harvard Forest in Petersham, Massachusetts for over twenty years (1970–1994), continuing on after his retirement.

Rolla had a great aversion to leaving anything unfinished. Following his retirement from Harvard University, he and Alice moved to Florida where they became adjunct faculty members at the University of South Florida in Tampa in order to continue their work on ferns. In particular, Rolla wanted to complete the *Ferns of Peru,* a project begun in the early 1960s. Collaborating with Robert Stolze and others, Rolla saw this huge project to completion between 1989 and 1994, publishing a series of six major papers totaling 842 pages.

For many of us, Rolla was and continues to be a role model for balancing careers and lives. We miss his intense academic rigor and his love of picking berries. We miss the attention he gave to training students: the piles of unknown ferns from tropical America we were required to identify, the weekly literature surveys and reports we were required to make, and his love of poker. We miss the days when we could wander into Rolla's office for help with taxonomic or nomenclatorial problems, or to Alice's office for help with cytology and scanning electron microscopy, and finish off the day at their house for one of Alice's incredible dinners and a taste of rum with Rolla. Rolla Tryon was deeply loved by his students and he will always be remembered for the incredible difference he made in our lives.

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BOOK REVIEW

Lichens of North America by Irwin M. Brodo, Sylvia Duran Sharnoff, and Stephen Sharnoff. 2001. xxiii + 795 pp. illus. color photos, line drawings, and dot distribution maps. ISBN 0-300-08249-5 $69.95 (hardcover). Yale University Press, New Haven, CT.

Lichens, lowly, unlovely lichens are the unlikely topic of the volume at hand. *Lichens of North America* is a production of pure visual splendor. It brings lichens to life in a manner that will not soon be matched. It is the result of the prodigious effort, sublime artistry, and singular devotion of Stephen Sharnoff and the late Sylvia Duran Sharnoff, whose photographs of lichens are the best I have ever seen. Their co-author, Irwin Brodo, wrote the accompanying descriptions and commentary for the photographs, nearly every one of which is a small masterpiece. Whether it is a close-up shot or a portrait of lichens in their natural habitat, each image invites the reader to appreciate, to touch, even to smell the lichens. Having attempted on my own over the past two decades to photograph lichens, I am thrilled with and yes, a little jealous of, the success of the images on these pages.

An introduction of over one hundred pages precedes the main (taxonomic) part of the text. Each chapter of the introduction starts with an epigram, sending a potent message that implies the importance of lichens in literature and in natural history. While they are the subject of soliloquies by the likes of Browning and Thoreau, lichens have, in fact, been relatively neglected over the past couple of centuries by the scientific community. The introduction attempts to right this wrong with succinct discussions of lichen morphology, chemistry, classification, biogeography, and reproduction. However, the attempt is less than successful, at least from a scientific perspective. The greatest problem is that the issues raised in the introduction are not treated in sufficient depth. The chapters, which are generally well written, correspond to an abbreviated list of references (not cited in the text) that are found at the back of the book. The bibliography is much too short. Little in the way of new literature is offered, and many of the sources date from the 1970s and '80s, the height of co-author Brodo's lichenological career. For example, the chapter on the geography of North American lichens offers less than ten references. The authors defend this unwarranted brevity with the rationalization that the references are general and that "sixty-five other publications were consulted." The fact that none of these publications was cited for the benefit of interested readers is a hint that *Lichens of North America* is less than a serious scientific contribution. One of the high points of the introduction is a chapter offering useful hints for observing and collecting lichens. Another short chapter on human uses of lichens uses winsome photographs to illustrate the text, but much of the chapter, like most of the diagrams in the book, has been served up in previous works. The too-selective bibliography and the rewarming of a number of old lichen illustrations (some of which were previously redrawn from even earlier sources) provide further hints that this book fails to attain a certain hoped-for standard of scientific relevance. In all fairness, it should be noted that for the libraries of undergraduate students and for an apparently growing audience of amateur lichenologists, the book will provide a good reference, or at least a starting point.

Why do authors still classify the growth forms of lichens as crustose, foliose, and fruticose? Perhaps it fulfills a human need, articulated by Plato, to construct a world of ideals and essences. Unfortunately, the organismic world defies such a construct, and lichens are more frustrating than most organisms when it comes to pigeonholing their morphological characteristics. Yet, co-author Brodo has attempted just this. In view of his wide experience with lichens, one wishes that he would have offered us a more critical perspective on lichen form, but we are disappointed again by a facile account of the gross anatomy of lichens, and by the authors' insistence on redrawing figures from earlier texts that are perfectly accessible in their own right. Perhaps the intent was to attract future scholars to the lichen world. Perhaps the authors hoped to engage an audience of amateurs who may lack access to a good scientific library, but with the sumptuous photographs found throughout the text, we fear that Brodo and his co-authors have gilded the lily. It would have been far better to let the original, beautiful photographs in this text tell their own story of lichen form.

Sadly, abbreviation must suffice in this book, which turns out to be more a digest of the North American lichens than a scientific treatise. For example, to find the author of a name of a species, which might give a serious student a handle on taxonomic concepts and history, one has to dig through the index. That problem is surmountable with enough ambition and patience. Other omissions are more serious. Abbreviation, especially in taxonomic accounts, misleads readers by providing an incomplete picture of the extent and background of the species. The problem is nowhere more palpable than in the taxonomic section of this book, where the authors have simply excluded hundreds of species from the dichotomous keys and their attendant descriptions. I can only speak to the veracity of treatment given the lichen family Cladoniaceae, which has been my focus of study for almost twenty years. As elsewhere in the text, the photographs of *Cladonia* lichens and their allies range from excellent to breathtaking. However, by excluding over a dozen new species in his account, Brodo has taken us back taxonomically to 1978, when *C. verruculosa* was recognized as a distinct entity in the North American lichen flora. The insensitivity of excluding so many species that have been recognized since the late 1970s is inexcusable, notwithstanding the fact that I am the author of many of them! Other authors of *Cladonia* and other genera were also ignored, but Brodo and his collaborators have provided little or no hint as to what else is "out there." They have apparently been selective about their distribution maps as well. At least in the Cladoniacae, it seems that the authors have chosen to ignore several recent accounts of the biogeography of the group.

It will be up to future generations of readers to find the lacunae in this book. They may, however, be distracted by trying to memorize the specious, insulting "common names" that have been appended to taxa described within. The authors have done a real disservice to lichenology by imposing their cloying appellations on readers. Need I refer to the names "pompon shadow lichen," "finger-scale foam lichen," or "changing earthscale" to understand the crust I see on a rock? Does anyone's appreciation of nature benefit from the authors' misleading anthropomorphisms like "rough eyelash lichen" or "split-peg soldiers"? Ultimately, *Lichens of North America* is a scientific disappointment. I hasten to add that not everyone requires scientific accuracy to get a kick out of nature. This handsome volume will be sure to delight the eye of anyone who opens it. It may indeed inspire further nature study, though its large format would tend to take up too much room on a field trip. At just shy of seventy dollars the book is a real bargain, and I suggest you buy it for someone who likes more than just pretty pictures of nature. Larger than a stocking-stuffer and eminently more valuable, *Lichens of North America* will soon take its place as the foremost introductory text to the lichens of this continent. In spite of its shortcomings, it is sure to find its place on the shelves and in the laboratories of lichenologists around the world.

—SAMUEL HAMMER, College of General Studies, 871 Commonwealth Avenue, Boston University, Boston, MA 02215.

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NEW BOOKS

Bioconservation and Systematics: Proceedings of the Canadian Botanical Association Conference Symposium in London, Ontario, June 2000 by J. B. Phipps and P. M. Catling, eds. 2001. iii + 101 pp. US$17.00 (paperback). Published by the Canadian Botanical Association. [send checks to Dr. Mel Fisher, Box 160, 407 Main St., Aberdeen, Saskatchewan S0K 0A0, Canada]

Muenscher's Keys to Woody Plants: An Expanded Guide to Native and Cultivated Species by E. A. Cope. 2001. xi + 337 pp. ISBN 0-8014-8702-1 $50.00 (hardcover), $22.95 (paperback). Cornell University Press, Ithaca, NY.

Seventh Catalog of the Vascular Plants of Ohio by T. S. Cooperrider, A. W. Cusick, and J. T. Kartesz, eds. 2001. x + 195 pp. ISBN 0-8142-5061-0 $29.95 (paperback), 0-8142-0858-4 $65.00 (hardcover). The Ohio State University Press, Columbus, OH.

Vascular Plants of Wyoming, Edition 3 by R. D. Dorn. 2001. iv + 412 pp. illus. $20.00 (paperback). Mountain West Publishing, Cheyenne, WY. [distributed by the Rocky Mountain Herbarium, Department of Botany, University of Wyoming, Laramie, WY 82071-3165; please make checks payable to Rocky Mountain Herbarium]

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NEBC MEETING NEWS

October 2001. President Lisa Standley introduced Dr. Kanchi Gandhi, Gray Herbarium Card Index Bibliographer and Database Manager, and Editor of the International Plant Name Index for Harvard University. Gandhi spoke to us on "The Phytogeography of India." To familiarize the audience with the subcontinent, Gandhi presented a series of slides showing the geographical, geological, and political India. British India at one time included Sri Lanka (Ceylon) and Myanmar (Burma), as well as what is now Pakistan, part of Afghanistan, and Bangladesh. In 1907 J. D. Hooker divided what was then India and Malaysia into nine phytogeographical provinces. Of these, Sri Lanka, Myanmar, and Malaysia represent three provinces, whereas the remaining six provinces encompass what is now recognized as India: (1) the Eastern Himalayan Province (including Nepal) receives 100–600 in. rain/year and the vegetation is lush; (2) the Western Himalayan Province is relatively drier than its eastern counterpart; (3) the Indus Plain is dry, with desert areas and thorny vegetation; (4) the Gangetic Plain receives moderate rainfall and is characterized by dry deciduous forest; (5) the Malabar Province (Western Ghats) along the southwestern coast receives 75–200 in. rain/year with rainfall declining markedly as one moves east, and it supports a variety of forest types; and (6) the Deccan Province on the eastern side of the Indian peninsula is drier, and is characterized by a dry deciduous forest.

Gandhi then showed slides of plants that occur in most parts of India. These included *Ficus religiosa,* commonly called the Bo-tree because Buddha was sitting under this tree when he received enlightenment. It is native in the Himalayas but is planted throughout India, especially in temples. *Ficus benghalensis,* the banyan tree, is a common shade tree; it keeps producing prop roots and can extend over a large area if undisturbed. Others are widely planted because of their economic or medicinal value. Examples included: *Azadirachta indica* (neem); *Mangifera indica* (mango); *Tamarindus indica* (tamarind); *Musa* (banana); *Artocarpus* (Jack fruit); and *Moringa oleifera* (called the miracle plant because of the high vitamin and mineral content of its leaves and fruits). Gandhi also mentioned several other common plants including succulent members of the Euphorbiaceae found in the scrub area of the Deccan phytogeographic province and some common aquatics such as *Trapa, Nymphaea, Nelumbo,* and *Ottelia.*

Next, Gandhi described some of the regional diversity in India, focusing first on the Eastern Himalayan region and its botanical affinities with China. Some genera the region has in common with eastern Asia are *Reevesia, Dillenia, Adina,* and *Alnus.* In contrast, he described a sort of transect of the vegetation in Hassan, which is representative of the diversity in the state of Karnataka on the Arabian Sea. Southwestern Hassan is characterized by moist deciduous forest, rainforest, and semi-evergreen forest typical of the Malabar phytogeographic province. This end of the spectrum receives between 100–200 in. rain/year and one can find species of *Drosera, Garcinia, Costus, Arisaema,* and *Strobilanthus* as well as *Piper nigrum* and several species of palms. In northeastern Hassan the rainfall is only 15–25 in. per year and the vegetation is similar to that of the Deccan phytogeographic province: scrub and dry deciduous forest. Some notable plants of this area are *Gloriosa superba* (a lily with tendril-like leaf tips), *Dodonaea viscosa* (varnish leaf), *Pterocarpus marsupium, Tectona grandis* (teak), and *Santalum album* (the fragrant sandlewood tree).

Once we had some idea of the diversity of the Indian flora, Gandhi went back to the theme of phytogeography. He stated that the broad divisions of Hooker were modified in 1939 by Chatterjee and in 1955 by Razi; the latter identified 21 phytogeographic regions within present-day India. Although India is about one third the size of the United States, it has a relatively diverse angiosperm flora of about 17,000 species compared with 25,000 for the U.S. Hooker commented that India was a "meeting place" for plants from surrounding regions and suggested that it had no recognizable indigenous species. Subsequent work has shown this to be an overstatement; although India has no endemic families, about 140 genera and 5100 species (ca. 30% of the flora) are endemic. Three areas of endemism are identified, with most of the endemics occurring in the Himalayas (3500 spp.) and the Malabar province (1500 spp.). These two regions of high endemism are separated by the largely sedimentary Gangetic Plain, resulting in a second type of unique distribution: disjunct genera. For example, 75 species of *Impatiens* are found only in the Malabar Province and 100 in the Himalayas, while none occur in the Gangetic Plain. Another disjunct genus is *Rhododendron,* with one species in the south and over 100 in the Himalayan region.

Gandhi said there were two hypotheses to explain the disjunct distributions: long distance dispersal and Pleistocene glaciation that once covered southern India. Gandhi concluded his presentation by showing slides representing families and genera with disjunct or endemic distributions within India.

November 2001. The evening's speaker was Jennifer Forman, a graduate student in the Ph.D. program in the Biology Department at the University of Massachusetts—Boston and student representative to the NEBC Council. She presented a talk entitled "Through the Looking Glass: History and Consequences of the Introduction of American Species into Europe."

Jennifer introduced the topic by pointing out that although there was a high level of concern about invasive plants in the United States, many of which were introduced from Europe, few have explored the fate of American introductions into Europe. Jennifer has conducted an extensive literature review and developed a database of 6000 American (North, Central, and South American) plant introductions into Europe to address that issue. Her talk was focused on how the exchange of plant species between Europe and America affected the floras of each region, and on the history and current status of American plants introduced into Europe.

In developing her database, Jennifer grouped introduced plants into four categories. In the first category are benign introductions; this group includes plants that cannot grow on their own in the new area. The second group includes casuals and escapes that are occasionally found outside cultivation, but are not able to maintain their populations. The third group consists of naturalized plants that are able to establish populations and reproduce in the wild. Finally, there are the invasive or weedy species that are established and spreading.

Approximately 26% of the flora of North America consists of naturalized plants, with European introductions having a particularly large impact. Most introductions were intentional and followed colonization, but plants were also introduced accidentally. Currently, about 7% of the North American flora can be considered invasive. Examples of European plants that are now invasive weeds include *Lythrum salicaria*, *Cytisus scoparius*, and *Vincetoxicum nigrum*.

As with European introductions to America, most introductions of American plants into Europe were deliberate. Trees such as *Pinus strobus, Picea sitchensis,* and *Prunus serotina* were introduced so they could be used in shipbuilding and for fuel. Other plants were sent to physic gardens where they were valued for their medicinal properties (e.g., *Sassafras albidum, Podophyllum peltatum*) or because of their horticultural interest (e.g., *Chrysolepis chrysophylla, Cypripedium acaule*). Many of the prominent names in North American botany, such as Mark Catesby, John Bartram, André Michaux, and John Tradescant, were responsible for introductions through the seed and other plant material they sent back to Europe. For example, Tradescant and his son introduced *Robinia pseudoacacia, Rhus typhina,* and *Liriodendron tulipifera* to England. As in America, other introductions were accidental and arrived in Europe along with textiles, in ship's ballast, or with transported animals. Some of the American species introduced into Europe, including the orchid *Bletia purpurea* and the cactus *Echinocereus triglochidiatus* remain in cultivation to this day. Others, such as *Tradescantia pallida,* are occasional escapes. A few, including *Pinus radiata, Lysimachia terrestris,* and *Mimulus guttatus,* have become naturalized. Some of the naturalized plants, such as *Rhus typhina, Rudbeckia hirta,* and *Phytolacca americana* are weedy in the United States. Of the approximately 6000 introductions to Europe from America in her database, about 8% have become either naturalized or weedy in Europe.

Jennifer pointed out that there have been a number of explanations as to why so many European plant species are invasive in America, but not vice versa. One suggestion is that the Old World species are better weeds in that they grow faster and produce more seeds. A second explanation is related to the fact that immigration rates were much greater from the Old World to the New. It may also be that ecosystem damage due to deforestation and post-colonization grazing facilitated the establishment of introduced species.

Using contingency tests, Jennifer was able to test several ideas about the species introduced to Europe from America. She was able to show species from some families (e.g., Poaceae and Amaranthaceae) were more likely than those from other families to become weedy. In addition, the latitude of the origin of the species affected the probability that a species would become naturalized in Europe. For example, more species from North America are naturalized in Europe than those introduced from Central or South America. She also showed a very clear positive relationship between the number of methods of introduction and the likelihood that a particular species would become established. Finally, she pointed out that the weediness of a species in America was a good predictor of whether a species would become established in Europe. She concluded by suggesting that a warning list be made available for the 222 weedy American species introduced into Europe that are not yet invasive there.

—KAREN SEARCY, Recording Secretary *pro tempore.*

ANNOUNCEMENT

INVASIVE PLANT SURVEY OF NEW ENGLAND
A CALL FOR VOLUNTEERS

The New England Wild Flower Society, Silvio O. Conte National Fish and Wildlife Refuge, and the University of Connecticut have recently been awarded a grant from the United States Department of Agriculture to track the distribution and spread of over 100 invasive plant species throughout New England. A corps of volunteers will be trained to identify invasive plants and document their current range. In 2002 we are seeking to train 25 volunteer participants in each New England state to survey their local area. An additional 50 volunteers in each state will be recruited and trained in 2003 and 2004. Trainings will occur in the spring and summer at a series of workshops held in each New England state. Trainings will take two days and include an indoor classroom informational session using slides, herbarium sheets, and other prepared materials, and an outdoor session consisting of field visits to local sites where infestations of invasive species occur.

Information collected by volunteers will be entered into the Invasive Plant Atlas of New England (IPANE) at the University of Connecticut. The data in IPANE will be posted on the Internet and used for early detection of problem species, research, and decision making on how to control invasive species to slow their spread and reduce their impact on our native flora. More information on this project and the survey can be found on the New England Wild Flower Society web site [www.newfs.org] or the web site for the Invasive Plant Atlas of New England [www.eeb.uconn.edu/invasives/ipane].

People interested in volunteering for the Invasive Plant Survey should contact Bryan Connolly, Invasive Plant Survey Coordinator [mailing address: 76 Warrenville Rd., Mansfield Center, Connecticut 06250; phone 860-423-8305 or 508-877-7630 ext. 3209; e-mail bconnolly@newfs.org or connollybryan@hotmail.com].

CHECKLIST FOR CONTRIBUTORS TO *RHODORA*

Please check items and submit with manuscript.

General Instructions

- Type manuscript on one side only of 8½ inch × 11 inch paper. Leave a 1-inch margin on all sides. Use a standard 12-pitch font type throughout the manuscript, including tables and appendices.
- Do not justify the right margin. Avoid hyphens or dashes at the right margin.
- The manuscript should be fully double-spaced throughout, including title, authors' names and addresses, Literature Cited, appendices, tables, and figure legends.
- Each page of the manuscript; excluding page 1 but including Literature Cited, tables, appendices, and figure legends; should be numbered in the upper right-hand corner.
- Correct accents, umlauts, and other diacritical marks should be included. Where appropriate, multiplication symbol must be used rather than the letter x.
- Only names at the rank of genus and below are italicized or underlined. If underlining is used, do not underline spaces or punctuation.
- Special typefaces (italics, bold) should not be used except where indicated in this checklist.
- Do not italicize common Latin words, abbreviations, or phrases (e.g., et al., i.e., etc.).
- Manuscript should be checked for consistency, especially in matters of abbreviation, names of sites or vegetation types, spelling of names, etc.
- *The Chicago Manual of Style*, most recent edition, is used as a reference in most matters of style. Refer to recent issues of *Rhodora*.
- Assemble the manuscript in the following order: (1) Introductory material, (2) Text, (3) Acknowledgments, (4) Literature Cited, (5) Appendices, (6) Tables, (7) Figure legends, (8) Figures.

Introductory Material

- **Running head** should be centered, at top of page, in upper and lower case letters. Include author's surname (if two authors use the word "and"; use "et al." for more than two authors), long dash, and short title. Total characters, including spaces, must not exceed 44.
- **Title** should be centered, in upper and lower case. Only the first word of the title and proper nouns should be capitalized. Do not include authors of scientific names. Include family name in parentheses unless genus studied is type for the family.
- **Author(s) name(s) and professional address(es)** should appear below title, centered, in upper and lower case. Consolidate lines where possible. Two-letter postal abbreviations should be used for states. "Current address:" should appear on a separate line immediately following address if author has moved, not as a footnote. If more than one author at an address, designate current address of author who has moved using a superscript number. Include e-mail address(es) on a separate line following postal address(es). The first author will be considered the corresponding author unless indicated otherwise by a superscript number. The "Author for correspondence" statement follows on a separate line below the address, not as a footnote.
- **Abstract** must be one paragraph. The abstract should be a concise statement of intent, methods used, results, and significance of findings. Do not cite references or taxonomic authors, or use and define abbreviations in the abstract. The word "Abstract" should be indented, in all capital letters, followed

by a period, and should appear on the first line of the abstract.

- **Key Words** are used in indexing and should be chosen with that purpose in mind. The title "Key Words" should appear at the left margin, followed by a colon. Only proper nouns should be capitalized.

Text

- The following are examples of first-level headings, which should appear centered and in all capital letters: MATERIALS AND METHODS, RESULTS, DISCUSSION, TAXONOMIC TREATMENT. The introduction is not titled in *Rhodora*. Do not combine results and discussion without first consulting with the Editor. Do not use a separate section for conclusions or summary; these must be incorporated into the discussion.
- Second-level headings should be indented, bold, upper and lower case, followed by a period, and should appear on the same line as the subsequent text. The text should be written such that additional levels of headings are not used.
- Each figure and table must be cited in the text in numerical order. The word "Figure" must be spelled out. When citing both together, the table should be listed first and a semi-colon used to separate the two (e.g., Table 1; Figure 1).
- Each reference cited in the text must appear in the Literature Cited section and vice versa. Cross-check spelling of author(s) name(s) and dates of publication.
- Literature is cited in the text as follows:
    1. One author: Hill (1982) or (Hill 1982).
    2. Two authors: Angelo and Boufford (1996) or (Angelo and Boufford 1996).
    3. More than two authors: Mathieson et al. (2000) or (Mathieson et al. 2000).
    4. Note that there is no comma separating author and date.
    5. When more than one paper is cited at a time, they should be listed alphabetically by first author rather than chronologically [e.g., Angelo and Boufford (1996), Hill (1982), Mathieson et al. (2000)].
    6. Within parentheses, citations should be separated by a semi-colon (e.g., Angelo and Boufford 1996; Hill 1982).
    7. Manuscripts accepted but not yet published: Tryon (in press) or (Tryon, in press).
    8. Unpublished material: G. Crow (submitted); G. Crow (unpubl. data); G. Crow (pers. obs.); or (G. Crow, pers. comm.); unless otherwise listed or cited in the manuscript or a nationally known authority, professional affiliation should also be given.
- References to companies manufacturing products used in a study should not appear in the Literature Cited. Rather, the company name and location should be given in parentheses within the text [e.g., SYSTAT (SPSS, Chicago, Illinois)].
- Authors of scientific names should be cited for all taxa at the rank of genus and below either at their first usage in the text or in a table or appendix (e.g., in a flora or table of voucher specimens). It should be indicated which taxonomic treatment, revision, or flora nomenclature follows. Use standard abbreviations for author's names found in http://www.rbgkew.org.uk/data/authors.html or *Authors of Plant Names* by R. K. Brummitt and C. E. Powell.

- Names of publications cited in the text should be in italics.
- Avoid abbreviations in the text unless indicating measurement, then use a period unless abbreviating a metric term. Other abbreviations should be defined when first used [e.g., Scanning Electron Microscopy (SEM)]. Herbarium acronyms should follow http://www.nybg.org/bsci/ih/ or *Index Herbariorum*, most recent edition.
- Numbers one through nine should be written out in the text unless a measurement or part of a taxonomic description. No comma is used with 4-digit numbers. A number should always precede a decimal point (e.g., 0.15).
- Back-to-back parentheses should be avoided by using a semi-colon. Parentheses within parentheses should be avoided by using outer brackets.

Taxonomic Treatments

- Use boldface Roman type for new names and new combinations, followed by "*sp. nov.*", "*comb. nov.*", etc.
- For nomenclatural history (i.e., synonymy and typification) use one paragraph per basionym [e.g., *Binomial* author, literature citation. TYPE: collection information from least-to-most-specific, *collector(s) collection number* (Holotype: herbarium acronym; Isotypes: herbarium acronym(s).].
- Exclamation points are used for type specimens examined, and types not seen are indicated as such (e.g., GH!, MO not seen).
- Lectotype designations are included together with an indication of where they were designated, what year, and by whom. This reference is listed in the Literature Cited. If the author of the paper is making the lectotypification, the phrase "here designated" is included.
- References cited only as part of nomenclatural history are not included in the Literature Cited. Books listed here are abbreviated according to *Taxonomic Literature, edition 2*, but with initial letters capitalized.
- Standard abbreviations for author's names should be used according to http://www.rbgkew.org.uk/data/authors.html or *Authors of Plant Names* by R. K. Brummitt and C. E. Powell.
- When dates are given as part of collection information, 3-letter abbreviations with no period are used for months.
- Use http://www.nybg.org/bsci/ih/ or *Index Herbariorum*, most recent edition, for herbarium acronyms.
- Designation of a new taxon should include a brief Latin diagnosis, rather than a full Latin description, which sets forth succinctly how the new taxon differs from its congeners.
- A full description, in English, should follow. This should be parallel with other descriptions at the same rank in the paper, and should not repeat information given in any description of the inclusive taxon (i.e., species descriptions should not repeat information characteristic of the genus, if also described in the paper). All measurements are metric. Hyphens are used for parenthetical extremes. A multiplication symbol is used where appropriate, rather than the letter x.
- Following the description, information should be given on distribution, ecology, uses, and nomenclature and typification, where appropriate. The discussions should be parallel within a given rank. For newly described taxa, this discus-

sion should explain clearly how the new taxon differs in these characteristics from closely related taxa.
- A high-quality line drawing or photograph of the type specimen, illustrating the diagnostic features, should be included for new taxa.
- Specimen citation should be selected critically, especially for common species of broad distribution. A title such as "Specimens examined" or "Representative specimens examined" should be indented, in upper and lower case, followed by a period. Each country begins a new paragraph. The format of information is as follows: COUNTRY. Major political division such as state: smaller political division such as county, detailed location, date (e.g., 26 Sep 1950), *collector(s) last name(s) collection number or s.n.* (herbarium acronym).

Keys
- Keys are dichotomous and indented.
- Leads of each couplet are parallel.
- Information in the key is consistent with that in descriptions, text, tables, and figures.

Data and Voucher Specimens
- Voucher specimens must be cited in a table or appendix to document sources of morphological or molecular data. Format for citation is the same as that for "specimens examined" as part of taxonomic treatments.
- All sequences used as data must be deposited in one of the international nucleotide sequence databases, and sequence database accession numbers included in the paper (GenBank: gsdb@gsdb.ncgr.org).
- All data matrices used in cladistic analyses should be deposited in TreeBASE (http://www.herbaria.harvard.edu/treebase).

Floras
- Long lists of taxa are best treated as an Appendix, so that the readability of the text is not compromised, and so that the list may be used independently by readers.
- A short introductory paragraph explaining terms or abbreviations used in the list of taxa should follow the Appendix title (see Searcy and Hickler 1999, *Rhodora* 101: 356).
- Three levels of headings are possible in lists of taxa: first-level is centered, all capitals, bold (e.g., **ANGIOSPERMAE** or **MAGNOLIOPSIDA**); second-level is centered, all capitals, not bold (e.g., MONOCOTYLEDONEAE or LILIIDAE); third level is flush left, all capitals, bold (e.g., **ACORACEAE**; this level will be converted to small caps by the printer).
- Taxa should be listed alphabetically within each hierarchical category (e.g., species alphabetically within the genus; genera alphabetically within family).
- Standard abbreviations for authors of binomials should be used according to http://www.rbgkew.org.uk/data/authors.html or *Authors of Plant Names* by R. K. Brummitt and C. E. Powell.
- An indication of ecological preference, distribution within the area studied, and abundance should be included, where appropriate.
- Voucher specimens should be listed (collector, collection number, and herbarium acronym; information common to all or most vouchers can be stated in an introductory paragraph).

Acknowledgments
- Acknowledgments should be brief.
- Information on granting agencies, herbaria from which loans were obtained, artists, and colleagues or advisors who have critically re-

viewed the manuscript should be included.
- The word "Acknowledgments" should be indented, in all capital letters, followed by a period, and should appear on the first line of the acknowledgments.

Literature Cited

- The Literature Cited contains all references cited in the text and vice versa.
- The alternative of a general "References" section requires prior approval by the Editor.
- All entries should be cross-checked with the text, checking especially for spelling of authors' names and years of publication.
- All entries should be verified against original sources, checking especially for spelling of authors names and words in languages other than English, exact title, year of publication, and volume and page numbers.
- Cite references in alphabetical order by first author's last name. Entries by a single author should precede multi-authored works with the same first author, regardless of date.
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PHYLOGENETIC RELATIONSHIPS AND BIOGEOGRAPHY OF *STEWARTIA* (CAMELLIOIDEAE, THEACEAE) INFERRED FROM NUCLEAR RIBOSOMAL DNA ITS SEQUENCES

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ABSTRACT. Sequences of the internal transcribed spacers of nuclear ribosomal DNA were used to estimate phylogenetic relationships within *Stewartia.* Eighteen samples were included representing two species of *Hartia,* seven species of *Stewartia,* and *Franklinia alatamaha. Hartia sinensis* and *H. villosa* form a clade that is the sister group of *Stewartia.* Within *Stewartia* the New World and the Old World species form well-supported clades. The subgenera and sections of *Stewartia* proposed by previous authors are not supported by our ITS data. Two clades are recognized within the Old World lineage: *S. serrata* + *S. rostrata* and *S. pseudocamellia* + *S. monadelpha* + *S. sinensis.* Southeastern Asia and China may be a recent center of diversification of *Stewartia* based on the ITS phylogeny and fossil record.

Key Words: biogeography, *Hartia,* nrDNA ITS, phylogeny, *Stewartia,* Theaceae

Stewartia L. comprises 8–21 species (Chang 1998; Li 1996; Spongberg 1974; Yang 1997). Both *S. ovata* (Cav.) Weatherby and *S. malacodendron* L. are native to the eastern United States (Figure 1a; Dove 1981; Kobuski 1951; Wood 1959). Three species are distributed in southern-central Japan, including *S. monadelpha* Siebold & Zucc., *S. serrata* Maxim., and *S. pseudocamellia* Maxim., which is also found in eastern Korea (Hara 1958; Lee 1997), while the rest of the species are distributed in central to southeastern China (Figure 1b). In China the number of species

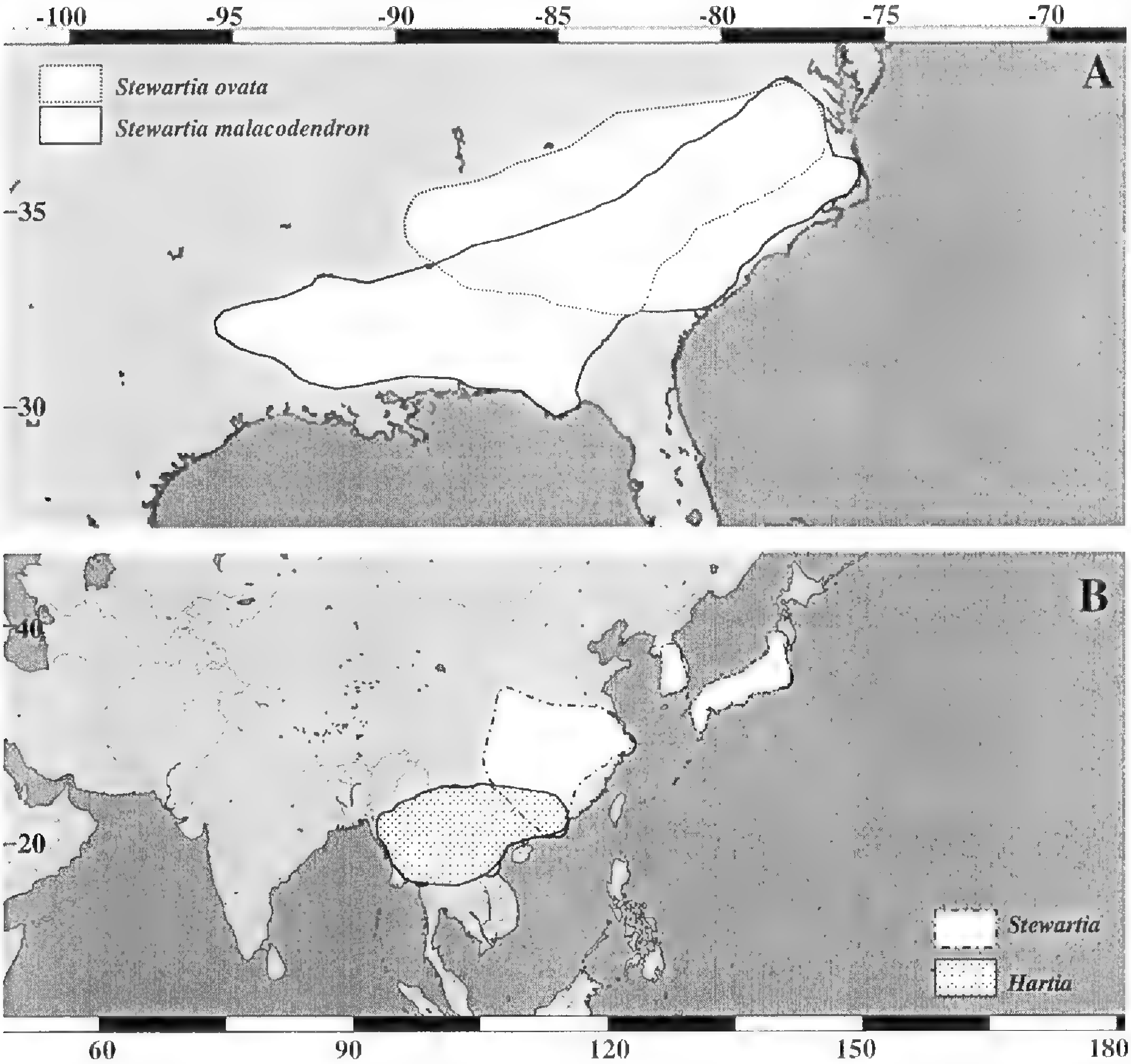

Figure 1. The modern distribution of *Stewartia* and *Hartia* species (Chang 1998; Elias 1980; Hara 1958; Hong 1993; Lee 1997; Li 1996; Spongberg 1974).

of *Stewartia* recognized varies from 3 to 16 (Chang 1998; Chang and Ye 1982; Chien and Cheng 1931; Chiu and Zhong 1988; Li 1996; Spongberg 1974; Yan 1981). *Stewartia rostrata* Spongberg is distributed in Hunan, Jiangxi, and Zhejiang, while *S. rubiginosa* H. T. Chang is endemic to southern Hunan and northern Guangdong. *Stewartia sinensis* Rehder & E. H. Wilson is widespread in central and southern provinces, and its vegetative and floral morphologies are highly variable. Many variants of *S. sinensis* have been described either as species or varieties (Chang 1998; Chang and Ye 1982; Chien and Cheng 1931; Chiu and Zhong 1988; Li 1996; Yan 1981).

Within Theaceae *Stewartia* is generally placed in the taxonomically controversial subfamily Camellioideae. Airy-Shaw (1936), based on morphological and anatomical evidence, revised Melchior's (1925) classification system of the Camellioideae, recognizing two tribes, each with two subtribes. The Gordonieae, to which *Stewartia* belongs, consists of subtribe Gordoniinae (*Gordonia* Ellis, *Franklinia* W. Bartram *ex* H. Marshall, and *Schima* Reinwardt *ex* Blume) and subtribe Stewartinae (*Stewartia,* including *Hartia* Dunn). Ye (1990) proposed a 5-tribe system for Camellioideae, but also recognized the tribe Stewartieae, consisting of two separate genera, *Stewartia* and *Hartia.*

While some authors have supported the inclusion of *Hartia* in *Stewartia* (Airy-Shaw 1936; Li 1996; Spongberg 1974), others have treated them as separate genera (Chang 1998; Chun 1934; Merrill 1938; Wu 1940; Yan 1981; Ye 1982, 1990). In a recent molecular study of the Camellioideae based on chloroplast DNA sequence data, *Hartia* was found not to be monophyletic (Prince and Parks 1997).

The classification of species within *Stewartia* has also been controversial (Table 1). Gray (1849) recognized two subgenera, the first of which, *Stuartia* (= *Stewartia),* included two species (*S. malacodendron* and *S. monadelpha*). The second subgenus, *Malacodendron,* consisted of a single species, *S. pentagyna* L'Her. (= *S. ovata*). Subgenus *Stewartia* is characterized by united styles (vs. free styles in subgenus *Malacodendron*), subglobose capsules (vs. conical capsules), and unwinged seeds (vs. winged seeds). Szyszylowicz (1893) supported Gray's (1849) groupings but treated them as sections and applied different names (*Synstyla* instead of *Stewartia, Dialystyla* instead of *Malacodendron*). Nakai (1950) divided Korean and Japanese *Stewartia* into two sections based on the relative length of sepals and bracts. Section *Pseudocamelliae* has bracts much shorter than the sepals, whereas section *Serratae* possesses bracts subequal to, or longer than, the sepals. Spongberg (1974) did not recognize any of these divisions. In the most recent treatment of *Stewartia* and *Hartia,* Li (1996) recognized *Stewartia s.l.*, including *Hartia* and *Stewartia,* and placed the species of *Stewartia s.s.* into two subgenera and 4 of the 5 sections of *Stewartia s.l.* recognized previously.

The objectives of this study were 1) to estimate interspecific relationships of *Stewartia* based on DNA sequence data, 2) to test the monophyly of the subgenera and sections that have been proposed by previous authors, and 3) to provide possible explanations for modern geographic distribution of *Stewartia.* We chose to use sequence data of the internal transcribed spacers (ITS) of

Table 1. Previous taxonic treatments of *Stewartia* species sampled in this study and their groupings in the ITS trees.

Species	Gray (1849)	Szyszylowicz (1893)	Nakai (1950)	Ye (1982)	Li (1996)	This Study
S. ovata	Subg. *Malacodendron*	Sect. *Dialystyla*	N/A	Sect. *Dialystyla*	Subg. *Dialystyla*	New World clade
S. malacodendron	Subg. *Stewartia*	Sect. *Synstyla*	N/A	Sect. *Stewartia*	Subg. *Stewartia* Sect. *Stewartia*	New World clade
S. monadelpha	Subg. *Stewartia*	Sect. *Synstyla*	Sect. *Serratae*	Sect. *Foliobracteae*	Subg. *Stewartia* Sect. *Racemosae*	Sinensis clade
S. serrata	N/A	N/A	Sect. *Serratae*	Sect. *Foliobracteae*	Subg. *Stewartia* Sect. *Serratae*	Serrata clade
S. sinensis	N/A	N/A	N/A	Sect. *Foliobracteae*	Subg. *Stewartia* Sect. *Serratae*	Sinensis clade
S. rostrata	N/A	N/A	N/A	Sect. *Foliobracteae*	Subg. *Stewartia* Sect. *Serratae*	Serrata clade
S. pseudocamellia	N/A	N/A	Sect. *Pseudocamelliae*	Sect. *Stewartia*	Subg. *Stewartia* Sect. *Pseudocamelliae*	Pseudocamellia clade

nuclear ribosomal DNA. This is because many studies have shown that sequences of this DNA region are informative in resolving phylogenetic relationships of plants among genera and species (Baldwin et al. 1995; Li et al. 1999; Li, Boufford, and Donoghue 2001; Li, Davis, Donoghue, Kelley, and Del Tredici 2001).

MATERIALS AND METHODS

Plant material. Eighteen plants were sampled in this study, representing seven species of *Stewartia,* two species of *Hartia,* and the monotypic *Franklinia* (Table 2). These samples represent all previously recognized subgenera and sections (Gray 1849; Li 1996; Nakai 1950; Szyszylowicz 1893; Ye 1982).

Molecular techniques. DNAs were extracted from silica-gel dried leaves using either a standard CTAB DNA extraction method (Doyle and Doyle 1987) or DNeasy Plant Kit (Qiagen Inc., Santa Clarita, CA) following the manufacturer's protocol with minor modifications.

Procedures and protocols for the polymerase chain reactions (PCR), purification of PCR products, and DNA sequencing are described in detail elsewhere (Li and Donoghue 1999). To examine within-individual variation we cloned the ITS regions for *Franklinia alatamaha* W. Bartram *ex* H. Marshall, *Stewartia ovata, S. pseudocamellia,* and *S. sinensis* using standard T-A tail cloning techniques according to manufacturers' instructions. The pGEM®-T Easy Vector System (cat.# A1360, Promega, Madison, WI) was used to ligate ITS PCR products into pGEM plasmids, which were then transformed into Epicurian Coli® XL1-Blue strain competent cells (cat.# 200249, Stratagene, La Jolla, CA). Three white colonies for each species were picked and cultured for 17 hours at 37°C, and their plasmids were prepared using a Miniprep Kit (Qiagen, Santa Clarita, CA). A small amount of the prepared plasmid (1 μL) was then digested using GibcoBRL EcoRI restriction enzyme (Life Technologies, Rockville, MD) to check the presence of the ITS inserts.

Phylogenetic analysis. Sequences were edited using Sequencher 3.0 (Gene Codes Corp., Inc., Ann Arbor, MI) to verify

Table 2. Species used in this study. Acronyms are as follows: Arnold Arboretum (AA), Jamaica Plain, MA; National Arboretum (NA), Washington DC; Kunming Institute of Botany (KUN), Kunming, China; Smith College (SC), Northhampton, MA; Quarryhill Arboretum (QA), CA; University of British Columbia (UBC), Vancouver, Canada.

Species	Source and Origin	GenBank #
Stewartia sinensis Rehder & Wilson	AA 373-76A; Lushan, Jiangxi, China	AF431932
S. sinensis	AA 431-34B; Lushan, Jaingxi, China	AF431933
S. sinensis	AA 691-94, Wudangshan, Hubei, China	AF431936
S. pseudocamellia Maxim.	QA 89.071; Japan	AF431937
S. pseudocamellia	AA 11440A; Korea	AF339863
S. monadelpha Siebold & Zucc.	AA 653-74A; Japan	AF431934
S. monadelpha	NA 40211; Yakushima, Japan	AF431938
S. rostrata Spongberg	AA 769-36A; Lushan, Jiangxi, China	AF431935
S. rostrata	Yang 991005; Lushan, Jiangxi, China	AF431939
S. rostrata	AA 761-69A; Lushan, Jiangxi, China	AF431941
S. serrata Maxim.	UBC Bot. Gard.	AF431940
S. malacodendron L.	NA 63252; Accomac, VA	AF431943
S. malacodendron	SC 07190; Cape Cod, MA	AF431944
S. ovata (Cav.) Weatherby	AA 18847A, Highlands, NC	AF431942
S. ovata (Cav.) Weatherby f. *grandiflora* (Bean) Kobuski	AA 18244C, Highlands, NC	AF339861
Hartia sinensis Dunn	Yang 98913; KUN	AF431946
H. villosa (Merr.) Merr. var. *serrata* Hu	Yang 98924; Jinxiu, Guangxi, China	AF431945
Franklinia alatamaha Bartram *ex* Marshall	AA 2428-2A; Alatamaha, GA	AF431947

base callings from overlapping sequences and chromatograms generated using different primers. Edited sequences were imported into the computer program PAUP* (version 4.0b3; Swofford 2000) and aligned manually. Characters were weighted equally and their states were unordered. Maximum parsimony (MP) analyses were conducted using both gaps scored as missing data and as a fifth character state. Heuristic tree search options included simple sequence addition, TBR branch swapping, Mulpars on, and steepest decent off. Bootstrap analyses for 300 replicates were conducted to evaluate relative support for individual clades (Felsenstein 1985). All of these analyses were conducted using PAUP*. *Franklinia alatamaha* was included for rooting purposes since several analyses have shown it to be closely related to the clade containing *Stewartia* and *Hartia* (Prince and Parks 1997; Tsou 1998; Ye 1990).

Maximum likelihood ratio test. To test whether ITS sequences in *Stewartia* and *Hartia* evolved in a clockwise fashion, we conducted maximum likelihood (ML) ratio tests using the HKY85+G model, implemented in PAUP* following Baum et al. (1998). ML analyses included the following options: as-is sequence addition, TBR (tree-bisection-reconnection) branch-swapping, and steepest descent option off.

RESULTS

Sequence characteristics. Sequences of the entire ITS region of all samples ranged from 646–657 base pairs (bp) in length, excluding *Franklinia alatamaha,* whose ITS region was 626 bp long. In *Stewartia* the lengths of the ITS-1 and ITS-2 were 246–267 bp and 221–229 bp, respectively. In *Franklinia* the lengths of the ITS-1 and ITS-2 were 242 and 223 bp, respectively. In all samples the sequences of the 5.8S gene were 161 bp in length.

The alignment of all sequences produced a data matrix of 678 characters, 65 of which were parsimony informative. Sequence divergence of the ITS-1 ranged from 0–7.3% (mean, or $\bar{x}$ = 4.4%) among species of *Stewartia,* from 4.9–8.4% ($\bar{x}$ = 6.7%) between species of *Stewartia* and *Hartia,* from 14.6–21.8% ($\bar{x}$ = 16.5%) between species of *Stewartia* and *Franklinia,* and from 17.2–17.7% ($\bar{x}$ = 17.5%) between species of *Hartia* and *Franklinia.*

Sequences of the ITS-2 diverged from 0.0–8.2% ($\bar{x}$ = 4.3%) among *Stewartia* species, from 2.7–8.2% ($\bar{x}$ = 5.1%) between species of *Stewartia* and *Hartia,* from 16.5–19% ($\bar{x}$ = 17.3%) between *Stewartia* species and *Franklinia,* and from 14.8–15.7% ($\bar{x}$ = 15.3%) between *Hartia* species and *Franklinia.* All sequences have been submitted to GenBank (Table 2), and the data matrix and trees are available from the first author upon request and in TreeBASE (http://www.herbaria.harvard.edu/treebase).

Phylogenetic relationships. Parsimony analyses of the ITS data set generated 3 trees of 175 steps when gaps were treated as missing data. The strict consensus (MP-M, maximum parsimony-missing) tree is shown in Figure 2 (solid branches, CI = 0.83, RI = 0.83). Species of *Hartia* form a strongly supported clade (bootstrap, or b = 99%), which is sister to the clade containing all species of *Stewartia* (b = 77%). Within the *Stewartia* clade, the two North American species, *S. ovata* and *S. malacodendron,* form a clade (b = 83%), which is sister to the clade containing all of the eastern Asian species (b = 74%). *Stewartia serrata* and *S. rostrata* form a well-supported clade (b = 85%), which is sister to the clade containing *S. pseudocamellia, S. monadelpha,* and *S. sinensis* (b = 89%). Accessions of *S. pseudocamellia* from Japan and Korea form a clade (b = 100%), which is sister to a clade consisting of *S. monadelpha* and *S. sinensis* (b = 96%). When gaps were treated as the fifth character state, the MP analyses produced a single (MP-F, maximum parsimony-fifth) tree of 254 steps (Figure 2, dashed branches; CI = 0.85, RI = 0.82). The MP-F tree is identical to the MP-M tree except that the three accessions of *S. sinensis* formed a moderately supported clade (b = 70%).

The maximum likelihood ratio test indicated that rates of ITS base substitution in the *Stewartia* and *Hartia* clade are significantly heterogeneous ($P < 0.05$). Thus, we did not attempt to estimate times of divergence for different lineages of *Stewartia.*

DISCUSSION

Monophyly of *Stewartia*. *Hartia* was proposed by Dunn (1902) to accommodate a plant collected from Yunnan province (Spongberg 1974). However, it has been debated whether *Hartia* should simply be included in *Stewartia.* Some authors have main-

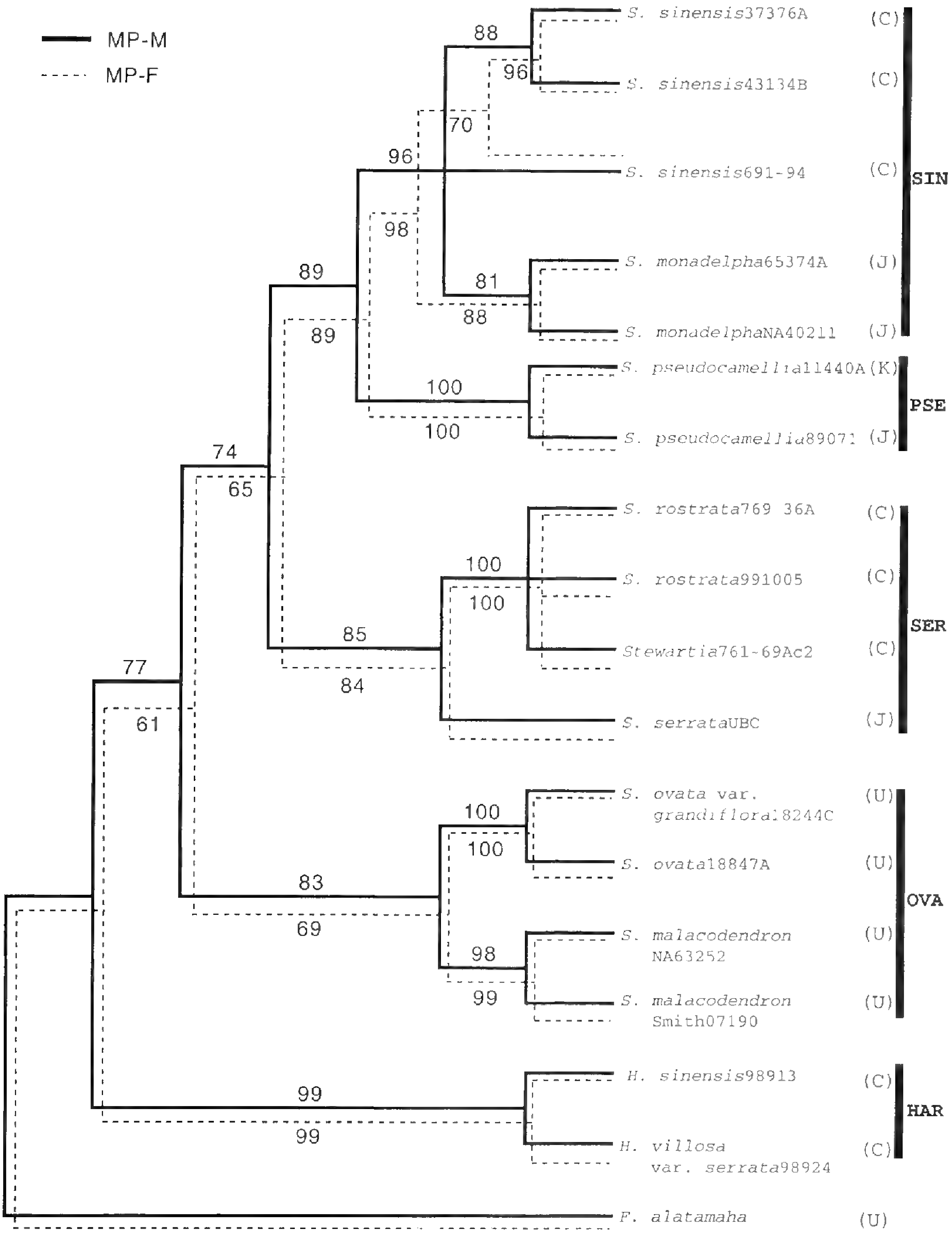

Figure 2. Phylogenetic trees based on maximum parsimony analyses of sequences of nrDNA ITS: strict consensus of 3 trees of 175 steps treating gaps as missing data (MP-M, not dashed), and the single tree of 254 steps treating gaps as the 5th character state (MP-F, dashed). Numbers above and below the branches indicate bootstrap percentages. Clade denotation: SIN, sinensis; PSE, pseudocamellia; SER, serrata; OVA, ovata; and HAR, hartia. Letters in parentheses represent geographic distributions: C for China, J for Japan, K for Korea, and U for the United States.

tained *Hartia* as a separate genus (Chang 1998; Chun 1934; Merrill 1938; Wu 1940; Ye 1982), while others support the inclusion of *Hartia* in *Stewartia* (Cheng 1934; Keng 1962; Li 1996; Sealy 1958; Spongberg 1974). In their phylogenetic study of the Theoideae based on sequences of the chloroplast gene *rbc*L, Prince and Parks (1997) concluded that *Stewartia* might be paraphyletic with *Hartia* nested within it. However, only three species of *Stewartia* and one species of *Hartia* were included in that analysis. In our trees (Figure 2), two species of *Hartia* form a well-supported clade sister to the clade containing species of *Stewartia*. *Hartia* and *Stewartia* have distinct differences in 15 non-molecular characters from morphology, palynology, and wood anatomy (Ye 1982). In addition, *Hartia* and *Stewartia* also differ in chromosome numbers: $n = 15$ in *Stewartia* (Santamour 1963) and $n = 18$ in *Hartia* (Oginuma et al. 1994). Therefore, our results, together with non-molecular data, suggest that both *Hartia* and *Stewartia* are monophyletic genera. Nevertheless, more species of *Hartia* need to be included in the future to further test this hypothesis.

Phylogenetic relationships within *Stewartia*. Although relationships within *Stewartia* have not been explicitly analyzed prior to this study, previous taxonomic treatments are considered as working hypotheses to be tested. Based on fruit, style, and seed characters, *S. ovata* has been separated from the rest of the species as either a monotypic subgenus, *Malacodendron,* or as the section, *Dialystyla* (Gray 1849; Li 1996; Szyszylowicz 1893). This treatment implies that *S. malacodendron,* which is the other North American species and has been placed in the Old World group, is more closely related to the Old World species than it is to *S. ovata.* In our ITS trees (Figure 2) *S. ovata* is linked directly with *S. malacodendron.* That is, the two North American species form a clade that is the sister group to all of the Old World species.

Nakai (1950) recognized two sections mainly based on the relative length of bracts and sepals. *Stewartia pseudocamellia* differs from all the other Asian taxa in having shorter bracts. On this basis it was treated as a monotypic section *Pseudocamelliae,* and the rest of the species were assigned to section *Serratae.* In our ITS trees (Figure 2), *S. pseudocamellia* is not a sister species to a clade containing the remaining *Stewartia* species. In contrast, it forms a strongly supported clade with *S. monadelpha* and *S. sinensis.*

In his review of *Hartia* and *Stewartia,* Ye (1982) recognized three sections within *Stewartia.* The first section, *Stewartia,* characterized by non-foliaceous bracts and orbicular to obovate sepals, included *S. rubiginosa, S. pseudocamellia,* and *S. malacodendron.* Although *S. rubiginosa* was not available for this study, the distant relationship between *S. malacodendron* and *S. pseudocamellia* (Figure 2) indicates that section *Stewartia sensu* Ye (1982) is not supported by the ITS sequences. The second section, *Foliobracteae,* comprising *S. monadelpha, S. sinensis, S. rostrata,* and *S. serrata,* was marked by foliaceous bracts and fused styles. In our ITS trees, species of section *Foliobracteae* form a monophyletic group with *S. pseudocamellia,* which was placed by Ye (1982) in section *Stewartia.* Thus, ITS sequences indicate that section *Foliobracteae sensu* Ye (1982) is not monophyletic. Ye's third section, *Dialystyla,* was unique in having distinct styles and consisted of three species, *S. ovata, S. yunnanensis* H. T. Chang, and *S. oblongifolia* Hu *ex* S. Z. Yan; the latter two species were transferred by Yang (1997) to the distantly related *Pyrenaria* Blume.

Li (1996) included *Hartia* within *Stewartia* and divided *Stewartia s.l.* into two subgenera based on whether the styles are fused (subgenus *Stewartia*) or distinct (subgenus *Dialystyla*). In subgenus *Stewartia,* he recognized five sections. His first section, *Racemosae,* consisted of *S. monadelpha* and six *Hartia* species. In our phylogenetic trees, however, *S. monadelpha* is not directly related to *Hartia.* Li's second section, *Stewartia,* included only one species, *S. malacodendron.* His third section, *Serratae,* contained *S. sinensis, S. serrata,* and *S. rostrata.* In our ITS trees (Figure 2), these three species form a clade that also contains *S. pseudocamellia* of section *Pseudocamelliae* (see below) and *S. monadelpha* of section *Racemosae.* The fourth section, *Pseudocamelliae,* consisted of *S. pseudocamellia,* three *Hartia* species, *S. rubiginosa,* and *S. damingshanica* J. Li & T. Ming. The latter five species were not available for this study, so we are unable to assess the monophyly of this section. Li's fifth section, *Pteropetiolatae,* consisted of four *Hartia* species.

When describing the segregate species, *Stewartia rostrata,* Spongberg (1974) hypothesized that it was most closely related to *S. serrata.* Probable synapomorphies of these two lineages include glabrous ovaries and 2–3 winter bud scales. Recently, Chang (1998) treated *S. rostrata* as a variety of *S. sinensis*. In our ITS trees, *S. rostrata* accessions form a clade with *S. serrata* with strong support (b = 85%). In contrast, *S. sinensis* is distantly related to *S. rostrata*, being most closely related to *S. monadelpha*. A close relationship between *S. sinensis* and *S. monadelpha* also supports Spongberg (1974), who stated that these two species were so closely related that *S. monadelpha* could be considered as a subspecies of *S. sinensis*.

In summary, our results indicate that none of the subgenera and sections of *Stewartia* proposed by previous authors (Gray 1849; Li 1996; Szyszylowicz 1893; Ye 1982) are monophyletic, except possibly for section *Pseudocamelliae sensu* Ye (1982), whose monophyly we were unable to assess due to insufficient sampling.

Evolution of morphological characters. In *Stewartia* all species have fused styles except for *S. ovata*, which has five distinct styles. This condition and a single bract enclosing axillary buds have been used to justify the separation of *S. ovata* from the rest of the *Stewartia* species, including the other North American species, *S. malacodendron* (Gray 1849; Li 1996; Szyszylowicz 1893). In our ITS trees (Figure 2), the two North American species form a well-supported clade, which is sister to the clade containing all of the Old World species of *Stewartia*. All species of *Hartia* have fused styles. Styles are occasionally found to be only half fused in *S. sinensis*; this condition also appears to be derived within *Stewartia*. Therefore, having distinct styles may be a derived condition and therefore an autapomorphy of *S. ovata*.

It is interesting to note that the fruits of *Stewartia* are capsules that split from the top to the bottom loculicidally, releasing seeds. It is possible that the free styles of *S. ovata* facilitate the release of winged seeds by avoiding the hindrance from the fused styles during the top-to-bottom splitting of the capsules. Field studies could be conducted to compare the seed dispersal efficiency of *S. ovata* with its sister species *S. malacodendron*, which has fused styles and unwinged seeds.

The bark of *Stewartia* species is quite variable. Several species develop smooth, mottled bark on the trunks and limbs, resulting in irregularly arranged, buff- or cinnamon-colored patches. These species include *S. malacodendron*, *S. sinensis*, *S. serrata*, *S. pseu-*

docamellia, and *S. monadelpha*. Our ITS phylogenies imply that the mottled bark probably evolved several times independently in *Stewartia*.

Stewartia seeds develop a narrow wing around the perimeter in all species except for the North American *S. malacodendron* and the Japanese/Korean *S. pseudocamellia*. In addition, species of both *Hartia* and *Franklinia* have winged seeds. Therefore, unwinged seeds appear to have been derived twice within *Stewartia*.

Biogeographic implications. Species of *Stewartia* are distributed disjunctly between eastern Asia and the eastern United States (Figure 1). This interesting disjunction has long attracted attentions from both systematists and biogeographers (Boufford and Spongberg 1983; Gray 1849; Hong 1993; Li 1952; Li et al. 2000; Tiffney 1985; Wen 1999). Previous hypotheses concerning interspecific relationships of disjuncts have sometimes proven to be erroneous (Gould and Donoghue 2000; Li, Davis, Donoghue, Kelley, and Del Tredici 2001; Wen 1999; Wen et al. 1998; this study). As more phylogenetic studies are conducted some congruent patterns are emerging. For example, Xiang, Soltis, and Soltis (1998) have shown that phylogenetic relationships in seven plant taxa, including ferns, conifers, and angiosperms, point to a single phylogenetic split between Old World and New World species with western North American species being most closely related to eastern North American species. Our results, together with several other recent phylogenetic investigations (*Aesculus*, Xiang, Crawford, Wolfe, Tang, and DePamphilis 1998; *Pachysandra*, Cuénoud et al. 2000; *Torreya*, Li, Davis, Donoghue, Kelley, and Del Tredici 2001), are consistent with this pattern.

To further understand the formation of this disjunction, the fossil record of both *Hartia* and *Stewartia* should be consulted. In North America, according to Grote and Dilcher (1989), no fossils have been reliably assigned to *Stewartia* or *Hartia*. In the Old World, Mai (1975) described fruits and seeds of *H. quinqueangularis* Mai from the Upper Miocene of western Europe. Knoblock and Mai (1986) reported fossil fruits and seeds assigned to the modern *Stewartia* from the Upper Cretaceous of Europe. Kirchheimer (1957) and van der Burgh (1978) have found fruits and seeds of *S. beckerana* (Ludwig) Kirchheimer from central European deposits of the Pliocene and Miocene. An amber-embedded fossil flower was described from the Oligocene deposit in Germany as *S. kovalewskii* by Raüffle and Helms (1970); however, this assignment is questionable (Mai 1971). Neogene floras of Japan contain two species of *Stewartia* based on fruit and leaf remains (Tanai and Suzuki 1972). As summarized by Grote and Dilcher (1989), the European late Tertiary sediments include both *Hartia* and *Stewartia*, but reliable fossils of *Hartia* or *Stewartia* have not been found in either North America or eastern Asia except for Japan. It is possible that species of *Hartia* and *Stewartia* were absent from China through most of the Tertiary and migrated there relatively recently (Grote and Dilcher 1989). Our analyses suggest that the radiation of *Stewartia* in China might have taken place rather recently.

Neither the Chinese nor Japanese *Stewartia* species form their own clades in ITS trees, indicating that there has been continuing population exchange between these two areas throughout the Tertiary. We did not estimate the time of divergence of *Stewartia* lineages since the maximum likelihood ratio tests have shown significant rate heterogeneity of the ITS sequences in *Stewartia* and *Hartia*. In these ITS trees (Figure 2), the first branching is between the Old and New World clades, implying that the time of divergence of the New World *Stewartia* species from the Old World species is earlier than that of the Japanese and Chinese species. In addition, the Japanese islands were not separated from the Asian continents until late Miocene (Tao 1992). Thus, the Old and New World *Stewartia* species had diverged from each other by the late Miocene.

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THOMAS WALTER'S OAKS FROM THE COASTAL REGION OF SOUTH CAROLINA

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ABSTRACT. Thomas Walter was the first post-Linnaean author of a sizable flora in eastern North America. As such, the *Flora Caroliniana* is an important hallmark in the botanical history of the United States. This paper is intended to be the first of a series of commentaries on the plants included in Walter's *Flora Caroliniana*. The present paper analyzes the thirteen species of oak (*Quercus*) reported by Walter as occurring in the approximately fifty square miles surrounding his plantation on the south bank of the Santee River some 45 miles northwest of Charleston. Walter's thirteen oak binomials with their current equivalents are as follows: (1) *Q. sempervirens* Walter = *Q. virginiana* Mill.; (2) *Q. phellos* L. = *Q. phellos* L.; (3) *Q. humilis* Walter non Mill. = *Q. incana* W. Bartram; (4) *Q. pumila* Walter [There is no type specimen and the brief description is in flagrant conflict with the species that has borne the binomial for the past 213 years. A new species (*Q. elliottii*) is proposed to replace the misapplied name of Walter]; (5) *Q. prinus* L. [a previously suggested "ambiguous name" soon to be formally proposed for rejection; Walter's plant is *Q. michauxii* Nutt.]; (6) *Q. nigra sensu* Walter, non L. = *Q. marilandica* Münchh.; (7) *Q. aquatica* Walter = *Q. nigra* L.; (8) *Q. rubra sensu* Walter, non L. = *Q. falcata* Michx.; (9) *Q. laevis* Walter = *Q. laevis* Walter; (10) *Q. alba* L. = *Q. alba* L.; (11) *Q. lyrata* Walter = *Q. lyrata* Walter; (12) *Q. sinuata* Walter [identity uncertain]; (13) *Q. villosa* Walter = *Q. stellata* Wangenh.

Key Words: *Quercus*, South Carolina

Among the accomplishments of Thomas Walter (c. 1740–1789), emigrant from England, American patriot, South Carolina planter, merchant, community leader, and landowner (4500 acres), to list merely a sample, was the flora describing in Latin the plants found in the vicinity of his plantation (Rembert 1980). Walter sent his manuscript *Flora Caroliniana* for publication in England with his friend, the itinerant plantsman John Fraser (1750–1811). Botanists are probably not exhibiting undue parochialism in concluding that Walter's principal claim to fame rests upon his *Flora Caroliniana* (1788) and that John Fraser's greatest contribution in all likelihood is in encouraging Walter to bring his floristic investigations to completion as well as providing hundreds of species for inclusion in the *Flora* that otherwise were unknown to Walter. Walter's *Flora* was the first descriptive account of a specific area prepared by a resident of eastern North America appearing after what is accepted as the starting point of botanical binomial nomenclature by Linnaeus in his *Species Plantarum* (1753). Fraser (1789) oversaw the publication of this manuscript in London and indicated that he had added 420 species, making the total 1060 species treated in *Flora Caroliniana.* There is no information to my knowledge as to whether (1) Walter and Fraser jointly studied these botanical discoveries from Fraser's wider exploration and together agreed upon their inclusion, or (2) Walter alone drew up the diagnoses, or (3) the inclusions are the result of only Fraser's study and incorporation into the manuscript after he had left South Carolina. The third possibility seems the least likely. In any event, all new binomials and genera published in *Flora Caroliniana* have been attributed only to Thomas Walter.

Unfortunately Fraser's contribution introduced uncertainty as to the area covered by *Flora Caroliniana,* for Fraser traveled widely in search of horticultural subjects while Walter stated, in the preface of the *Flora* (Rembert 1980), that all but a few of the plants came from an area no greater than 50 square miles centered on his plantation on the south bank of the Santee River in northwestern Berkeley County near the village of St. Stephen's, about 45 miles north of Charleston. It is impossible to determine from the contents of the *Flora* if all, or at least most, of the species contributed by Fraser also came from this small area. We certainly know that some species included did not come from the area designated by Walter. Obvious examples would be *Magnolia acuminata* (L.) L. (widespread in eastern North America) and *M. fraseri* Walter, both included in Walter's *Flora* but known only from the mountains of the Carolinas and adjacent montane states. Other examples that must owe their inclusion to Fraser's travels are *Trautvetteria caroliniensis* (Walter) Vail (Ranunculaceae) and *Frasera caroliniensis* Walter (Gentianaceae). Harper (1911) listed twenty-four species included in Walter's *Flora* that probably did not "grow within many miles of his home . . . and a few that probably have not been seen in South Carolina at all . . ." More intensive collecting over the past nine decades has very much reduced Harper's list but there still remain a number of species which are not known from the coastal plain of South Carolina and in all probability never grew there.

Thirteen species of oaks are briefly described in Walter's *Flora Caroliniana,* eight of which were first published in that publication in the belief that they were unknown to science, as indicated by their being printed in italics. (Perhaps it should be noted that in practice, Walter's use of italics was not consistent.) The fate or disposition of all 13 oak binomials included by Walter is discussed in the following paragraphs. Each entry in Walter's *Flora* under the generic name consists of three parts: (1) the specific epithet or what Linnaeus referred to as the trivial name, (2) the species number under each genus, and (3) the Latin diagnosis of the species. Ashe (1916), who had much interest in and experience with the southeastern oaks, concluded that considering the brevity of Walter's descriptions "they are excellent, but each must be considered in connection with the others he describes." The late, astute and careful Howard Rock (1925–1964) noted (1956) that Walter's descriptive phrases, if rearranged, amounted to a brief key to the species in each genus.

***sempervirens* 1. foliis lanceolatis perennantibus integerrimus margine subrevoluto.** All commentators noted for the past two centuries are agreed that *Quercus sempervirens* Walter (1788) is a later synonym of *Q. virginiana* Mill. (1768).

Quercus virginiana Mill., Gard. Dict., ed. 8, *Quercus* no. 16. 1768.

Q. phellos [var.] β L., Sp. Pl. 994. 1753.
Q. sempervirens Walter, Fl. Carol. 234. 1788, non Mill., 1768.
Q. virens Sol. *in* Aiton, Hortus Kew. 3: 356. 1789.
Q. andromeda Riddell, New Orleans Med. Surg. J. 9: 614. 1853.
Q. virginiana var. *virescens* Sarg., Bot. Gaz. 65: 446. 1918.
Q. virginiana var. *eximea* Sarg., Bot. Gaz. 65: 447. 1918.
Q. virginiana var. *macrophylla* Sarg., Bot. Gaz. 65: 447. 1918.
Q. eximea (Sarg.) Trel., Mem. Natl. Acad. Sci. 20: 116. 1924.

Phellos 2. foliis deciduis lanceolatis integerrimis seta terminatis. The willow oak is abundant in Berkeley County, South Carolina, so we can be confident that it was well known to Walter. However, it seems certain that he may well have compounded with it other similar species that are also frequent in the area, such as *Quercus laurifolia* Michx. and perhaps *Q. hemisphaerica* W. Bartram *ex* Willd. The last two mentioned oaks are apparently frequent in Walter's area but he obviously did not differentiate them from one another, which is understandable considering that only in the past half century have botanists made much progress in distinguishing them.

Quercus phellos L., Sp. Pl. 994. 1753.

humilis* 3. foliis lanceolatis integerrimis seta terminatis *subtus tomentosis. *Quercus humilis* Walter (1788) is a later homonym of *Q. humilis* Mill. (1768), a European species. Trelease (1924) included Walter's binomial in the synonymy of the so-called running oak, which has been long referred to as *Q. pumila* Walter for which the diagnosis of *Q. humilis* is a better match than that accompanying *Q. pumila* itself. Walter's epithet "*humilis*" implies that the plant is of humble stature (i.e., a shrub) and its diagnosis stresses the tomentose lower surface of the blade while Walter's diagnosis of *Q. pumila* states that the leaves are glabrous and that the lower surface is glaucous. I cannot disprove Trelease's conviction that *Q. humilis* Walter is the species in Walter's *Flora Caroliniana* that matches the description of the running oak. However, Walter's protologue of *Q. humilis* also agrees with the stated characteristics of the species later known by the binomial *Q. incana* W. Bartram (= *Q. cinerea* Michx.), the bluejack oak, except that a tree growing to 10 meters in height, although often much smaller, would scarcely be expected to receive the epithet *humilis*. Pursh (1814, p. 625) treated the bluejack oak as *Q. phellos* β [= var.] *humilis* citing Catesby's account (1730, 1: 22. t. 22) and noted that the plant was "of low straggling growth." Linnaeus (1753) previously had cited Catesby 1: 22. t. 22 as *Q. phellos* β. Catesby's (1730) comments are included in full in the following quotation:

> Quercus humilior salicis folio breviore.
>
> The Highland Willow Oak
>
> This is usually a small tree, having a dark coloured bark with leaves of a pale green, and shaped like those of a willow. It grows on dry poor land, producing but few acorns, and those small. Most of these oaks are growing at Mr. Fairchild's.

Catesby's description and plate (1: 22. t. 22) were identified by Ewan (1974) as *Quercus laevis* while Howard and Staples (1983) and Wilbur (1990) identified it as *Q. incana* W. Bartram.

Quercus incana W. Bartram, Travels Carolina 378. 1791.

Q. phellos β *brevifolia* Lam., Encycl. Méth. Bot. 1: 722. 1785.
Q. humilis Walter, Fl. Carol. 234. 1788, non Mill., 1768.
Q. cinerea Michx., Hist. Chênes Amér., *Quercus* no. 8. pl. 14. 1801.

pumila* 4. foliis lanceolatis integerrimis glabris *subtus glaucis. As pointed out in the paragraph above, the Latin diagnosis of *Quercus humilis* matches the species originally proposed by Thomas Walter for what has been called for nearly the past two centuries *Q. pumila.* The diagnosis provided for *Q. pumila* by Walter describes a species whose glabrous leaves are glaucous beneath. Walter's protologue for the running oak, *Q. pumila,* strikingly conflicts with the characteristics of the plant which has borne that binomial for over two centuries. Consequently, a name change is necessary for this very distinctive and familiar dwarf oak that ranges along the coastal plain from southeastern North Carolina southward throughout peninsular Florida and westward into Mississippi. To "retypify" *Q. pumila* Walter with a specimen in accord with "current usage" would be in serious conflict with the last three words of the otherwise decidedly uninformative protologue.

Quercus elliottii Wilbur, *sp. nov.*, TYPE: UNITED STATES. South Carolina: Hampton Co., pine savanna along NW margin of Piggys Rd., 1 mi. W of main office at James W. Web Wildlife Center, 4.2 mi. W of Garnett off secondary highway Rt. 20; 32.6216°N, 81.3213°W, 54 ft. elevation, 13 Oct 2000, *Nelson 21668 & Wood* (HOLOTYPE: DUKE; ISOTYPES: BKL, BRIT, CU, DLF, DUKE, F, FLAS, FSU, FTG, GA, GH, IBE, ILL, LSU, MICH, MISS, MISSA, MO, NCSC, NCU, NLU, NY, TEX, UNA, US, USCH, USF, VSC, WIS, WNC).

Differt a *Quercus incana* W. Bartram habitu fruticoso et coloniali sobolibus, caulibus 1(-2) m altis. Fructus hornotini maturescentes, sessiles vel brevipedicelli; cupula 4–5 mm alta, crateriformis, squamis arcte appressis, cinereis, appresso-pilosis; glans (in cupula) inserta.

Shrub, commonly forming extensive clones by subterranean runners; stems 0.5–1 (–2) m tall, profusely sprouting from their bases after burning of pinelands, the leaves of sprouts often larger than those of stems unburned for several years. Woody twigs of the season grayish brown, usually much of their pubescence persisting through the first year. Winter bud or buds at the tips of twigs ovoid-conic, 3–5 mm long, brown, the scales mostly with a fringe of minute trichomes around their apical margins. Leaves all deciduous in autumn or a few of them overwintering and falling just before or as new growth commences in spring. Stems of young shoots moderately to densely stellate-pubescent; edges of unfurling leaf blades downwardly curved and recurved covering perhaps as much as half of the lower surfaces, their upper surfaces with sparse, pale, stellate pubescence but eventually glabrescent; the lower surfaces shortly, densely, and compactly pale-gray, stellate-pubescent. Mature leaves very short-petiolate; petioles stellate-pubescent. Blades mostly 3–10 (–15) × 0.7–2 (–5) cm, oblanceolate or spatulate, narrowly elliptic, elliptic-oblong, or lanceolate, usually with a short bristle tip; bases cuneate to narrowly rounded, apices rounded to acute; upper surfaces glabrous, dark green and lustrous or sublustrous, sometimes dull green, lower surfaces densely and compactly grayish puberulent; flat and with entire margins, sometimes their edges somewhat crisped, only rarely with a few, low, rounded undulations. Fruits maturing in one season, sessile or shortly peduncled, their involucres bowl-like, 4–5 mm deep, embracing about one-third the length of the acorn, scales tightly appressed, grayish brown, broadest basally where many or most of them are humped or bulged, gradually narrowed distally to truncated, flat tips; acorns ovoid, subglobose, or somewhat oblate, 8–12 mm long and broad, basally flat, apically rounded to nearly truncate, outer surfaces light brown, glabrous or faintly and sparsely very short-pubescent near their summits, inner surfaces loosely pale-pubescent near their summits, inner surfaces loosely pale-pubescent, the trichomes blond to tawny.

It might be argued that all that was needed to rehabilitate nomenclaturally a case like that of *Quercus pumila* Walter was that a neotype be designated and published, confirming the identity of the plant in the traditional sense and thereby nullifying the questionable phrases in the original diagnosis. However the original descriptive phrases in Walter's diagnosis are exceedingly brief. If we were to ignore or delete the questionable last three words from the descriptive diagnosis of the running oak, there would remain very little that was distinctly descriptive, and those three descriptive words exclude the species to which the name has been employed.

The preceding entry (i.e., that for *Quercus humilis*; 3. foliis lanceolatis integerrimis seta terminatis *subtus tomentosis*) is clearly a much better fit for what has been passing as *Q. pumila* Walter, than is the descriptive account accompanying *Q. pumila* itself. That account has been attributed to *Q. incana* W. Bartram. In any event, Q. *humilis* Walter (not *Q. humilis* Mill., 1768) is a later homonym and cannot now be applied to any species named after 1768.

Prinus 5. foliis ovatis sinuato-serratis, denticulis uniformibus. The chestnut oak naturally occurring in the coastal plain of South Carolina is *Quercus michauxii* Nutt., the swamp chestnut oak. *Quercus prinus* L. is now most often referred to as *Q. montana* Willd. Hardin (1979) recommended that the binomial *Q. prinus* be treated as an "ambiguous" name since the lectotypic specimen cannot be conclusively identified because the features displayed are not those that distinguish the two species confounded by Linnaeus (i.e., *Q. prinus* and *Q. michauxii*) under the binomial *Q. prinus*. Linnaeus' binomial has been applied to both species (i.e., to either the chestnut oak or to the swamp chestnut oak, for lengthy periods as shown by Hardin's table). Fortunately, for the purposes of this paper, the oak in Walter's area can only be the bottomland swamp chestnut oak, as only that species is known from eastern South Carolina. John Fraser, however, had ample opportunity to observe both species during his extensive travels. It is to be remembered that Sargent (1916) reversed the application of the name *Q. prinus* from the mountain chestnut oak to the swamp chestnut oak nearly nine decades ago based on his belief that the mountain chestnut oak was not to be found in southeastern Virginia, the presumed "type" locality of the Clayton specimen described by Gronovius (1739). Sargent's reversal was generally followed for several decades by American workers and especially by foresters and by E. J. Palmer (1943) whose study convinced him that Sargent was correct in applying *Q. prinus* L. to the swamp chestnut oak. However, additional floristic investigations (e.g., Fernald 1946, p. 391; Harvill et al.1986, pp. 85–86) have demonstrated that both the swamp chestnut oak and the rock chestnut oak are to be found in southeastern Virginia in close proximity to Clayton's home. In my opinion, the name *Q. prinus* L. has not yet been formally disposed of and the binomial needs to be either laid to rest by rejection, or epitypified and adopted. A paper proposing the first alternative will soon be submitted to *Taxon. Quercus michauxii* Nutt. is abundant in the bottomlands of the Santee River upon whose southern bank Walter's plantation was located.

Quercus michauxii Nutt., Gen. N. Amer. Pl. 2: 215. 1818.

Q. prinus L., Sp. Pl. 995. 1753, in part, *nom. rej. prop.*
Q. prinus [var.] *palustris* Michx., Hist. Chênes Amér., *Quercus* no. 5. pl. 6. 1801. ["*Q. Prinus (palustris)* Michx."]
Q. prinus α *palustris* Michx., Fl. Bor.-Amer. 2: 196. 1803.
Q. prinus var. *michauxii* (Nutt.) Chapm., Fl. South. U.S. 424. 1860.
Q. houstoniana C. H. Mull., Amer. Midl. Naturalist 2: 743. fig. 1. 1942.

nigra 6. foliis obcuneiformibus obsolete trilobis *villosis ramis inferioribus declinatis, superioribus adscendentibus.* The advantage that familiarity with plants in the field provides to the investigator is clearly demonstrated by Walter's treatment of this species and the next (Walter's #6 and #7). Walter treated both as species while Linnaeus combined them as varieties of *Quercus nigra* L. Perhaps it would be more accurate to state that Linnaeus treated as a varietal appendage, the β variety of *Q. nigra* as the element that became *Q. marilandica.* Britten (1909) has a detailed explanation of the early travail of the two elements included by Linnaeus within his *Q. nigra.* Britten there informs us that "Walter's herbarium contains a leaf" of both *Q. nigra* and *Q. marilandica* although neither bears an identification by Walter. Walter's solution was to remove the Gronovian and Catesbian (1: 20) references as *Q. aquatica* Walter, leaving the Ray and Catesbian (1: 19) references as *Q. nigra* L. However, Walter's solution to Linnaeus' confusion in placing the water oak and the blackjack oak under the binomial *Q. nigra* was not the first remedy proposed. Münchhausen (1770, 5: 253) had named the blackjack oak, *Q. marilandica,* in effect removing the Linnaean β variety, leaving *Q. nigra* L. as the binomial for the water oak. The result was to segregate the Gronovian and Catesbian references as *Q. nigra* and leaving *Q. nigra* β exemplified by Catesby's 1: 19. t. 19 "Quercus marilandica folio trifida . . ." of Ray and Catesby as *Q. marilandica* Münchh. The species that Walter retained under the Linnaean binomial, *Q. nigra,* is now known as *Q. marilandica.*

Quercus marilandica Münchh., Hausvater 5: 253. 1770.

Q. marilandica . . . Catesby, Nat. Hist. Carol. 1: 19. t. 19. 1730.
Q. nigra [var.] β L., Sp. Pl. 2: 996. 1753.

Q. cuneata Wangenh., Beytr. Teut. Forstwiss. 78. 1787.
Q. ferruginea F. Michx., Hist. Arbr. Forest. 2: 92. pl. 18. 1812.
Q. nigra β *quinqueloba* Alph. de Candolle, Prodr. (DC.) 16(2): 64. 1864.
Q. nigra γ *tridentata* Alph. de Candolle, Prodr. (DC.) 16(2): 64. 1864.
Q. marilandica var. *ashei* Sudw., Jour. For. (Washington) 20: 167. 1922.
Q. marilandica f. *cuneata* (Wangenh.) Trel., Mem. Natl. Acad. Sci. 20: 200. 1924.

***aquatica* 7. foliis obcuneiformibus obsolete trilobis submucronatis *laevibus nitidis*, subperennatibus.** As explained above, Walter divided Linnaeus' *Quercus nigra* into its two component species: *Q. nigra* was the name retained for the blackjack oak, and the water oak, fittingly enough, was named *Q. aquatica* Walter. However, Münchhausen (1770, 5: 253) had corrected Linnaeus' confusion earlier by naming the blackjack oak *Q. marilandica* Münchh., which left the binomial *Q. nigra* L. for the water oak.

Quercus nigra L., Sp. Pl. 995. 1753.

Q. uliginosa Wangenh., Beytr. Teut. Forstwiss. 80. 1787.
Q. aquatica Walter, Fl. Carol. 234. 1788.
Q. nana Willd., Sp. Pl., ed. 4.4(1). 443. 1805.
Q. bumeliaefolia Riddell, New Orleans Med. Surg. J. 9: 614. 1853.
Q. aquatica γ *stipitata* Alph. de Candolle, Prodr. (DC.) 16(2): 68. 1864.
Q. rhombica var. *obovatifolia* Sarg., Bot. Gaz. 65: 431. 1918.
Q. nigra var. *tridentifera* Sarg., Bot. Gaz. 65: 429. 1918.

rubra 8. foliis 3 s. 5 lobis obtusis *subtus villosis, setaceo-mucronatis* glandibus parvis globosis. Totten (Radford et al. 1968) did not map *Quercus rubra* L. as occurring in the coastal plain of South Carolina although it was well-dispersed throughout the piedmont and mountains of that state. The same source shows it to be widely scattered and apparently rare in the coastal plain of North Carolina. Svenson (1939) and Fernald (1946), among others, have pointed out that many Linnaean species include two or more species, based on the included synonymy according to more recent systematists who have had the advantages of greater familiarity with the plants in the field and/or more extensive collections available for comparison. For example, Fernald (1946, p. 391) pointed out that in *Species Plantarum* (Linnaeus 1753), the name *Q. rubra* "covered many (if not most) of the eastern species of subgenus *Erythrobalanus* . . ." including the red oak itself. Svenson (1945) concluded "that the Linnaean species from one point of view was the synthesis of all bibliographic citations under the species, together with the Linnaean herbarium specimens, whether they were associated with the citations."

Du Roi (1772) was apparently the first to restrict the name *Quercus rubra* to a single species. That choice determined that the binomial *Q. rubra* L. thereafter should be reserved for the red oak of northeastern North America as well as covering much of eastern United States and adjacent Canada (see Nixon and Muller 1997, p. 465 for map).

However Sargent's (1915, 1916) own research and sense of propriety convinced him that "the name *Quercus rubra* belonged to the tree which was later called *Q. falcata* by Michaux and not to the tree which has always been called red oak in the northern states." Sargent admitted that "this change of name is one of the most unfortunate which the study of old specimens of American plants has made necessary . . ." Sargent's prestige was such that many, including most foresters and followers of the American Code of Nomenclature, for the next two decades or so applied the Linnaean binomial *Q. rubra* to the southern red oak (= *Q. falcata* Michx.) whose leaves are abaxially densely and permanently tomentose beneath. Sargent seemingly attached great importance to the first synonym appearing in the Linnaean protologue, no doubt influenced by Linnaeus' own statement that the synonym with the best description should be listed first (see footnote in Svenson 1939, p. 522). Sargent was also convinced, based on insufficient field experience, that only *Q. falcata* Michx. of the *rubra*-complex was to be found in southeastern Virginia, the area in which Clayton and Banister lived and from which they sent collections to European botanists such as Gronovius and Ray. The first synonym listed by Linnaeus, as pointed out by Sargent (1915), is that of Gronovius (1739) based on a collection by John Clayton. Sargent found Clayton's specimen to be what has been called *Q. falcata* Michx. and felt that there was no alternative but to apply the name *Q. rubra* to that element of Linnaeus' multiparted concept of *Q. rubra*. Naturally, applying the binomial *Q. rubra* L. to two very different species led to confusion, leading Rehder (1938) to propose unsuccessfully that the name be officially declared a *nomen ambiguum*. Harvill et al. (1986, p. 85–86) maps show that both the red oak and southern red oak are abundant in southeastern Virginia. Others (e.g., Svenson 1939, 1945; Fernald 1946) took strong exception to Sargent's retypification of a species first typified by Du Roi (1772).

Fortunately, for the purposes of this paper there is no problem, as Walter's descriptive polynomial is explicit for the villosity of the leaf's undersurface. He clearly was applying the name to the same element that Sargent mistakenly felt obliged to choose (i.e., the element that Michaux called *Quercus falcata*). The northern red oak has not been found in Walter's area but the southern red oak is abundant there now, as it surely was in Walter's time.

Quercus falcata Michx., Hist. Chênes Amér., *Quercus* no. 16. pl. 28. 1801.

Q. nigra digitata Marshall, Arbust. Amer. 123. 1785.
Q. triloba Michx., Hist. Chênes Amér., *Quercus* no. 14. pl. 26. 1801.
Q. elongata Willd., Ges. Naturf. Freunde Berlin Neue Schriften 3: 400. 1801; Sp. Pl., ed. 4.4(1). 444. 1805.
Q. falcata β *triloba* (Michx.) Nutt., Gen. N. Amer. Pl. (Nuttall) 2: 214. 1818.
Q. carpenterii Riddell, New Orleans Med. Surg. J. 9: 613. 1853.
Q. falcata β *ludoviciana* Alph. de Candolle, Prodr. (DC.) 16(2.1): 59. 1864.
Q. digitata (Marshall) Sudw., Gard. & Forest 5: 99. 1892.
Q. rubra var. *triloba* (Michx.) Ashe, Proc. Soc. Amer. Foresters. 11: 90. 1916. *nom. illegit.*, Art. 34.1(b).
Q. rubra var. *leucophylla* Ashe, Bull. Charleston Mus. 13: 25. 1917.
Q. pagoda var. *leucophylla* (Ashe) Ashe, J. Elisha Mitchell Sci. Soc. 34: 136. 1918.
Q. leucophylla (Ashe) Ashe, Torreya 18: 73. 1918.
Q. rubra sensu Sarg., Bot. Gaz. 65: 426. 1918.
Q. rubra var. *triloba* (Michx.) Sarg., Bot. Gaz. 65: 427. 1918.
Q. joori Trel., Mem. Natl. Acad. Sci. 20: 15. 1924.
Q. rubra f. *triloba* (Michx.) Trel., Mem. Natl. Acad. Sci. 20: 201. pl. 406, fig 3. 1924.
Q. rubra f. *falcata* (Michx.) Trel., Mem. Natl. Acad. Sci. 20: 202. pl. 406, fig. 2. 1924.
Q. rubra var. *triloba* (Michx.) Sudw., Check List For. Trees U.S. 89. 1927.
Q. rubra var. *leucophylla* (Ashe) Sudw., Check List For. Trees U.S. 90. 1927.
Q. rubra var. *digitata* (Marshall) Cory & Parks, Cat. Fl. Tex. 37. 1937.

laevis **9. foliis obtuse sinuatis *laevibus setaceo-mucronatis*, glandibus magnis depresso globosis calyce subtectis.** The synonymy of the turkey oak is as follows:

Quercus laevis Walter, Fl. Carol. 234. 1788.

Q. Catesbaei Michx., Hist. Chênes Amér., *Quercus* no. 17. pl. 29–30. 1801.

Q. flammula W. Bartram, Travels Carolina 228, 344, 359, 403, 470. 1791, *nom. nud.*

alba 10. foliis pinnatifidis laevibus, lobis finus subaequantibus, supra saturate viridibus subtus glaucis, glandibus magnis ovatis. There seems to be no doubt that Walter's concept of the white oak, *Quercus alba* was also that of Linnaeus. This species is abundant about Walter's former plantation.

Quercus alba L., Sp. Pl. 996. 1753.

Q. alba frutescens Münchh., Hausvater 5: 253. 1770.
Q. alba α *pinnatifida* Michx., Hist. Chênes Amér., *Quercus* no. 4. pl. 5, fig. 1. 1801.
Q. alba β *repanda* Michx., Hist. Chênes Amér., *Quercus* no. 4. pl. 5, fig. 3. 1801.
Q. alba var. *latiloba* Sarg., Bot. Gaz. 65: 435. 1918.

lyrata **11. foliis lyratis laevibus sinubus obtusissimis lobis remotis inaequalibus, glandibus magnis globosis subtectis.** Again, no controversy has yet surrounded the identity of the overcup oak first named and described by Walter.

Quercus lyrata Walter, Fl. Carol. 235. 1788.

Scolodrys lyrata (Walter) Raf., Alsogr. Amer. 29. 1838.

sinuata **12. foliis sinuatis laevibus obtusis supra pallidis, subtus subglaucis, glandibus mediocribus globosis *calyce subplano.*** Contrary to the lack of debate concerning the identity of such species as *Quercus alba* and *Q. lyrata,* there has been much uncertainty about the identity of *Q. sinuata* Walter. This uncertainty is not lessened by the lack of original material among Walter's specimens at BM [so reported by Sargent (1918, p. 436) and by Nixon and Muller (1997, p. 497)]. Prior to Camus' (1939, 2: 678), Muller's (1951), and Dorr and Nixon's (1985) acceptances of *Q. durandii* Buckley as a synonym of *Q. sinuata* Walter, there had been a slowly growing consensus that this was the proper disposition of Buckley's binomial (see Elias 1971, p. 183). However, I find that the considerable uncertainty as to the identity of Walter's *Q. sinuata* prevents me from joining that growing consensus.

Original specimens representing Thomas Walter's oak collections are unknown and hence their interpretation must depend upon their original descriptions. Walter's descriptions, in the judgment of W. W. Ashe (1916) are "excellent" in spite of their brevity, but "each . . . must be considered in connection with the others he describes." The description of *Quercus sinuata* has proven to be most problematic. Both Engelmann (1876, p. 400) and Sargent (1895, p. 144) concluded that *Q. sinuata* was the hybrid of *Q. catesbaei* (= *Q. laevis*) × *Q. nigra.* Ashe (1916) challenged this interpretation since the hybrid has a deep acorn cup with a rounded base and not the saucer-shaped cup with a nearly flat base described by Walter, and also foliage that "is dark green and lucid above and not pale [and] is bright green below and not sub-glaucous." Ashe at first unfortunately confused *Q. austrina* Small (1903) with Walter's *Q. sinuata,* overlooking the fact that Small's species was described as having both leaf surfaces bright green and with an acorn cup hemispheric in contrast to the flattened cup described by Walter for *Q. sinuata.* Ashe (1918, p. 11) unobtrusively admitted his error in placing *Q. austrina* in the synonymy of *Q. sinuata* and made thereafter no further pronouncements on the identity of *Q. sinuata.* Trelease (1924, p. 101) however, apparently unaware of Ashe's retraction, followed Ashe's earlier opinion in combining *Q. sinuata* and *Q. austrina.* Unfortunately Trelease paid little or no attention to Walter's description as he separated *Q. sinuata* f. *sinuata* from f. *durandii* (Buckley) Trelease by the former's green lower leaf surface in contrast to the pale lower surface of the latter.

Palmer (1945) thought Engelmann's conclusion (1876–1877) that *Quercus sinuata* Walter was a hybrid between *Q. laevis* and *Q. nigra* was "a more reasonable interpretation" than Ashe's earlier (1916) conclusion that *Q. austrina* Small was a later synonym of *Q. sinuata.* Both Trelease (1924) and Muller (1951) accepted the earlier opinion of Ashe (1916) that *Q. sinuata* was an earlier name for *Q. durandii.* This conclusion was firmly rejected by Ashe (1918). Palmer concluded that *Q. sinuata* had indeed been mistakenly identified as synonymous with *Q. austrina* Small by Ashe, as Ashe (1918) himself had admitted in an obscure retraction. In his detailed study of the *Q. durandii* complex, a group restricted in his opinion to the calciphilic soils of the Gulf coastal plain and east Texas, Palmer (1945) maintained that synonymization with *Q. sinuata* was clearly unwarranted since *Q. durandii* is not known in Walter's region, and in no character except possibly in the shape of the leaves could Walter's description be reconciled with *Q. durandii.* Palmer felt so strongly about the matter that he claimed that "until a specimen named by Walter can be seen the name must remain doubtful." Palmer treated *Q. sinuata* as a *nomen dubium.*

Muller (1951), ignoring or at least making no reference to Palmer's paper, took up *Quercus sinuata* Walter, including in its synonymy both *Q. austrina* Small and *Q. durandii* Buckley, feeling that "arguements against identity of this plant with Walter's name include the inability of contemporary collectors to find the species in Walter's immediate territory, which is distinctly inconclusive." Walter's description of *Q. sinuata* leaves as "subtus subglaucis" and the fruit as "mediocribus globosis calyce subplano" indeed excludes other southeastern oaks and agrees perfectly with the form with silvery lower leaf surfaces that Buckley named *Q. durandii.* [One can't help but point out that Buckley's only mention of surface features in the original description was "when mature, smooth on both sides," which offers little support to Muller's own description (1951) of the species he called *Q. sinuata* (including in synonymy *Q. durandii* and *Q. austrina*): "upper surfaces from sparsely minute-stellate becoming glabrate and glossy dark green, lower surfaces persistently pubescent with minute appressed dense stellate hairs strikingly silver or appearing green if the pubescence is sparse, occasionally tardily glabrate . . ."] Later, Nixon and Muller (1997) recognized *Q. austrina* as a species separate from *Q. sinuata,* but only after Dorr and Nixon (1985) accepted Ashe's (1916) submergence of the two species (i.e., *Q. austrina* within *Q. sinuata*), making no mention of Ashe's retraction (1918). Nixon and Muller (1997, p. 498) stated that "the original description of *Q. sinuata* is consistent with the concept presented . . . by W. W. Ashe (1916) and W. Trelease (1924), and inconsistent with any other oak from the broad area covered by Thomas Walter's *Flora* . . ."

This review of the pertinent literature is not one that gives confidence that enough is known about the identity of the types, the morphological limits of the species involved, or their geographic ranges, etc., to be dogmatic as to the application of the binomials of these little known taxa. The application of the binomial *Quercus sinuata* Walter is too uncertain, in my opinion, to be adopted at the present time; it very much remains a *nomen dubium.* More field work and observation are very much needed for many of the southeastern oaks.

***villosa* 13. foliis obtuse lobatis, supra nitidis subtus villosis glandibus parvis globosis.** Although neither Michaux (1803) nor Pursh (1814) placed Walter's *Quercus villosa* in synonymy of any species in their early floras of North America, later authors have rather unanimously identified *Q. villosa* Walter as a synonym of the earlier *Q. stellata* Wangenh. This post oak is common in Walter's area as well as much of the eastern United States. There is little in Walter's diagnosis that would have convinced me that the plant described was the post oak, but there is nothing that would cause me to question the identity except that the descriptor "villose" would not have occurred to me as describing the very familiar *Q. stellata.* The pubescence on the stem and leaves of the post oak, in my experience scarcely qualifies as being villose.

Quercus stellata Wangenh., Beytr. Teut. Forstwiss. 78. pl. 6, fig. 15. 1787.

Q. alba minor Marshall, Arbust. Am. 120. 1785.
Q. villosa Walter, Fl. Carol. 235. 1788.
Q. lobulata Sol. *in* Smith & Abbot, Insects of Ga. 1: 93. pl. 47. 1797.
Q. obtusiloba Michx., Hist. Chênes Amér. pl. 1. 1801.
Q. stellata β *floridana* Alph. de Candolle, Prodr. (DC.) 16(2): 24. 1864.
Q. minor (Marshall) Sarg., Gard. & Forest 2: 471. 1889.
Q. stellata var. *parviloba* Sarg., Bot. Gaz. 65: 438. 1918.
Q. ashei Sterrett, J. Elisha Mitchell Sci. Soc. 37: 178. 1922.
Q. similis Ashe, J. Elisha Mitchell Sci. Soc. 40: 43. 1924.
Q. stellata var. *similis* (Ashe) Sudw., U.S.D.A. Misc. Circ. 92: 107. 1927.

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RECONSTRUCTING THE BIOLOGICAL INVASION OF EUROPEAN WATER-HOREHOUND, *LYCOPUS EUROPAEUS* (LABIATAE), ALONG THE ST. LAWRENCE RIVER, QUÉBEC

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ABSTRACT. In Québec (Canada), one of the most recently introduced exotic wetland plants is European water-horehound (*Lycopus europaeus*). The first specimens were discovered in 1963 near Montréal. In this study, we used herbarium specimens and conducted field surveys to reconstruct the history of the invasion of European water-horehound in Québec, and to accurately determine its current northeastern distribution. Few European water-horehound specimens were collected before 1970. However, between 1970 and 1974, the range of European water-horehound expanded 380 km northeastward from Sorel to Trois-Pistoles River. In 1999, the northeastern distribution limit of European water-horehound was at Bic Provincial Park, 65 km northeast of Trois-Pistoles River. Between 1963 and 1974, European water-horehound spread rapidly along the St. Lawrence River (45 km/yr.), which was probably related to the fact that seeds remain viable after floating. Between 1974 and 1999, it spread more slowly to the northeast of Trois-Pistoles River (3 km/yr.). The limited range expansion of European water-horehound in eastern Québec between 1974 and 1999 suggests that the salinity of surface waters, and more particularly the scarcity of coastal or riverine marshes east of Rimouski, prevented populations from establishing in the estuarine part of the St. Lawrence River.

Key Words: *Lycopus europaeus*, European water-horehound, Québec, St. Lawrence River, biological invasion, exotic species

In North America, invasion by exotic species is considered to be one of the main threats to preserving the integrity of ecosystems. In the United States alone, approximately 50,000 nonindigenous species cause major environmental damage and financial losses totaling US$137 billion per year (Pimentel et al. 2000). More than 5000 introduced plant species are now naturalized in North American ecosystems. Several of these plant species are problematic. For example, control costs and forage losses associated with purple loosestrife (*Lythrum salicaria* L.) have been estimated at US$45 million in the United States (Pimentel et al.

2000). It is therefore important to understand the mechanisms underlying successful plant invasions, and to develop models to predict the spread of invaders. Such models are useful for improving management plans that have been established to minimize the impacts of invasive species on natural ecosystems (Rejmánek and Richardson 1996).

One of the key components in modelling is the rate at which a species spreads, or the distance its range expands each year, indicated by newly established individuals outside the distribution range of a species (Lonsdale 1993). Rates of spread for plants are highly variable, and mainly depend on autecological characteristics of species and dispersal vectors. For example, between 1970 and 1984, the sedge *Carex praegracilis* W. Boott (a native species in North America) migrated eastward from Illinois, Indiana, and Michigan to New England states at a rate of 73 km/yr. This very rapid expansion rate was probably related to the development of highway networks, since this species is adapted to open and saline habitats commonly found along roads (Reznicek and Catling 1987). On the other hand, the rate of spread for the woody weed species *Mimosa pigra* L. in northern Australia (an exotic species in that country) was only 0.076 km/yr. between 1979 and 1985. Nevertheless, this rate is considered to be rapid for this pest species in Australia (Lonsdale 1993).

Wetland plant species usually spread rapidly because water is an effective dispersal vector (Catling and Porebski 1995; Lonsdale 1993; Pysek and Prach 1995). Wetland exotic plants are also among the most aggressive invaders and have dramatically changed the vegetation of many marshes at temperate latitudes. Several species are known to reduce the biomass of native plants, contribute to filling in small ponds, and form almost monospecific plant communities (Galatowitsch et al. 1999). In Québec (Canada), one of the most recently introduced exotic wetland plants is European water-horehound (*Lycopus europaeus* L., Labiatae). The native distribution range of this species is in Europe and western Asia (Stuckey and Phillips 1970). European water-horehound is a medium-sized plant, 0.4–1 m in height, copiously pubescent, with toothed leaves 4–12 cm long and 1.5–5 cm wide (Henderson 1962). This species is very similar to the widespread native American water-horehound (*L. americanus* Muhl.), but *L. europaeus* can be easily distinguished by its pubescent leaves (Scoggan 1979). Both species colonize marshes and drainage ditches, as well as the shores of ponds, lakes, and rivers (Fleurbec 1987; Stuckey and Phillips 1970). The range of American water-horehound extends from British Columbia to Newfoundland, and from James Bay to Texas (Fleurbec 1987). European water-horehound was introduced into North America about 1860, probably in Virginia. Populations are now widespread along the Atlantic coast, from North Carolina to Nova Scotia. Numerous populations are also located along the shores of Lake Erie, Lake Ontario, and the St. Lawrence River. The introduction of European water-horehound into the Great Lakes–St. Lawrence River system (about 1903) and along the Atlantic coast of the United States were probably distinct events related to the release of ship's ballast (Stuckey and Phillips 1970).

The occurrence of European water-horehound in Québec is recent. The first specimens were discovered in 1964 near Valleyfield (Figure 1; Rousseau 1968). In 1974, Gauthier (1977) established its northeastern distribution limit at the mouth of Trois-Pistoles River (48°06′N, 69°14′W). On the shores of the St. Lawrence River, European water-horehound populations have mainly been found in marshes located in the supralittoral zone, and in the upper part of the intertidal zone (Chrétien 1994; Gauthier and Lavoie 1975). Stuckey and Phillips (1970) suggested that this plant was migrating down the St. Lawrence River, but there has been no historical reconstruction of the spread of European water-horehound in Québec that could be used to substantiate this assertion. In this study, we used herbarium specimens and conducted field surveys to reconstruct the history of the invasion of European water-horehound in Québec, and to accurately determine its northeastern distribution limit. We also calculated the rate at which this species has spread since its introduction into the province. Since water is probably the main dispersal vector for this species (Fleurbec 1987), we hypothesized that European water-horehound has spread along the St. Lawrence River at a rapid and constant rate over the last 35 years.

MATERIALS AND METHODS

To reconstruct past and recent distribution ranges for European water-horehound in Québec, we gathered information on all herbarium specimens of this species collected in the province. Herbarium specimens were requested from a total of eight herbaria:

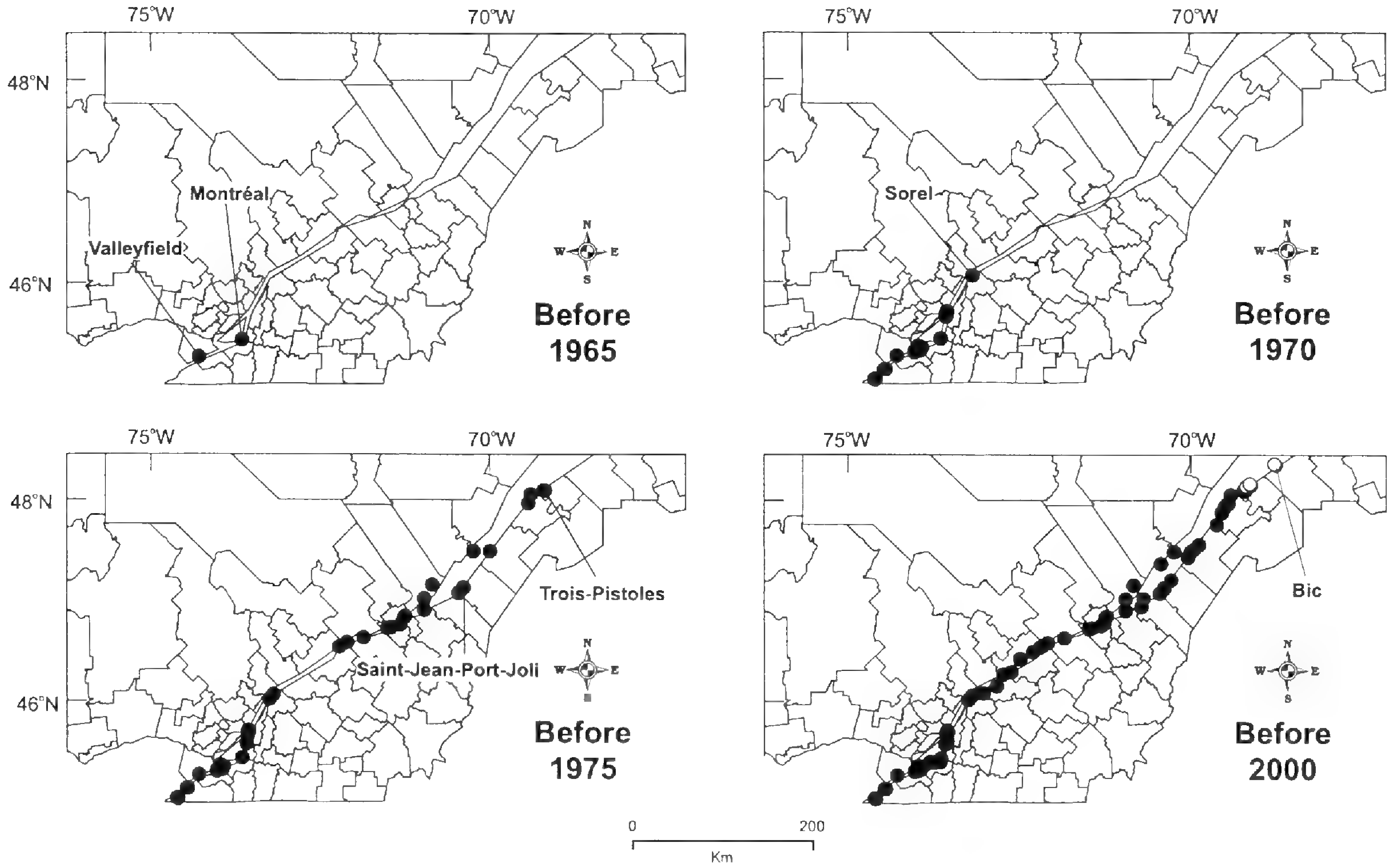

Figure 1. Location of European water-horehound (*Lycopus europaeus*) herbarium specimens collected in Québec before 1965, 1970, 1975, and 2000, respectively. Black dot: specimen found in herbarium; white dot: specimen collected during this study (August 1999). Subdivisions = municipal regional counties.

CAN, DAO, MT, MTMG, QFA, QSA, QUE, and SFS (*Index Herbariorum* website: www.nybg.org/bsci/ih/ih.html). Each herbarium specimen was checked for possible misidentification, and we noted the specimen number, collection location and year, and habitat characteristics. Data on specimens were incorporated into a geographical information system to accurately reconstruct the evolution of European water-horehound's distribution range during the 20th century in Québec. We also examined herbarium specimens of *Lycopus americanus* from QFA (which has the biggest collection of *L. europaeus* and *L. americanus* from different locations in Québec) to find misidentified European water-horehound specimens.

To accurately determine the northeastern distribution limit of the species in Québec in August 1999, we surveyed the south shore of the St. Lawrence River between Trois-Pistoles River (the known distribution limit) and Sainte-Anne-des-Monts (49°08′N, 66°30′W), 300 km to the northeast. This region corresponds to the regional landscape unit of Rimouski (Robitaille and Saucier 1998). The mean annual temperature in the region is 2.5°C, and mean annual precipitation totals 900 mm. The salinity of the St. Lawrence River near Trois-Pistoles River and Sainte-Anne-des-Monts is 24‰ and 27‰, respectively. Approximately 67% of the region is comprised of agricultural land (Bourget 1997; Robitaille and Saucier 1998). We did not survey the steep north shore of the St. Lawrence Estuary because there are very few suitable habitats (coastal marshes) for European water-horehound along this shoreline. Furthermore, surface currents, which are likely to disperse plant seeds, flow upstream near the north shore of the St. Lawrence River (Centre Saint-Laurent 1996). Consequently, an expansion of European water-horehound's distribution range is unlikely to occur along the north shore of the St. Lawrence River Estuary.

Between Trois-Pistoles River and Sainte-Anne-des-Monts, sampling points were chosen systematically every 5 km along the shore of the St. Lawrence River. At each sampling point, where access to the shore was possible, we surveyed the shore of the river (the supralittoral zone and the upper part of the intertidal zone) for a one-hour period to detect the presence of European water-horehound populations. Once a population was discovered, the following information was noted: 1) the exact location of the population on the shore, 2) the number of individuals in the population, and 3) any associated vascular plant species. Furthermore, one or two specimens were collected for further identification in the laboratory. All collected specimens are stored in the Louis-Marie Herbarium (QFA) at Université Laval. All sampling points located within a 100-km distance from the last sampling point with a European water-horehound population were visited. Beyond the 100-km distance, only sampling points with habitats appropriate for the establishment of European water-horehound populations (i.e., marshes located in the supralittoral zone, and/or in the upper part of the intertidal zone, or the mouth of freshwater tributaries) were visited.

RESULTS

One hundred and ninety-nine (199) herbarium specimens (including those collected in this study) from 101 locations were carefully examined. Data from these specimens were used to accurately reconstruct the recent change of European water-horehound's distribution in Québec (Figure 1). We discovered that the oldest specimen was not sampled in 1964, but rather in 1963 on the south shore of Île-des-Sœurs, near Montréal (45°26′N, 73°33′W). This specimen was originally misidentified as *Lycopus americanus.* Few *L. europaeus* specimens were collected before 1970; however, between 1970 and 1974, the range of European water-horehound expanded 380 km northeastward from Sorel to Trois-Pistoles River, which represents a very rapid rate of spread (95 km/yr.).

Before this study, no specimen of European water-horehound had been collected northeast of Trois-Pistoles River. In August 1999, we discovered three populations beyond Trois-Pistoles River (Figure 2):

1. Trois-Pistoles Bay (48°07′N, 69°10′W)
2. Anse-des-Riou (48°09′N, 69°07′W)
3. Anse-à-l'Orignal (48°21′N, 68°46′W), in Bic Provincial Park

These three populations were located 8, 12, and 65 km northeast of Trois-Pistoles River, respectively. These European water-horehound populations (10–15 individuals) were found in the supralittoral zone at the upper edge of *Spartina alterniflora* Loisel. marshes. They were also located very close to small freshwater

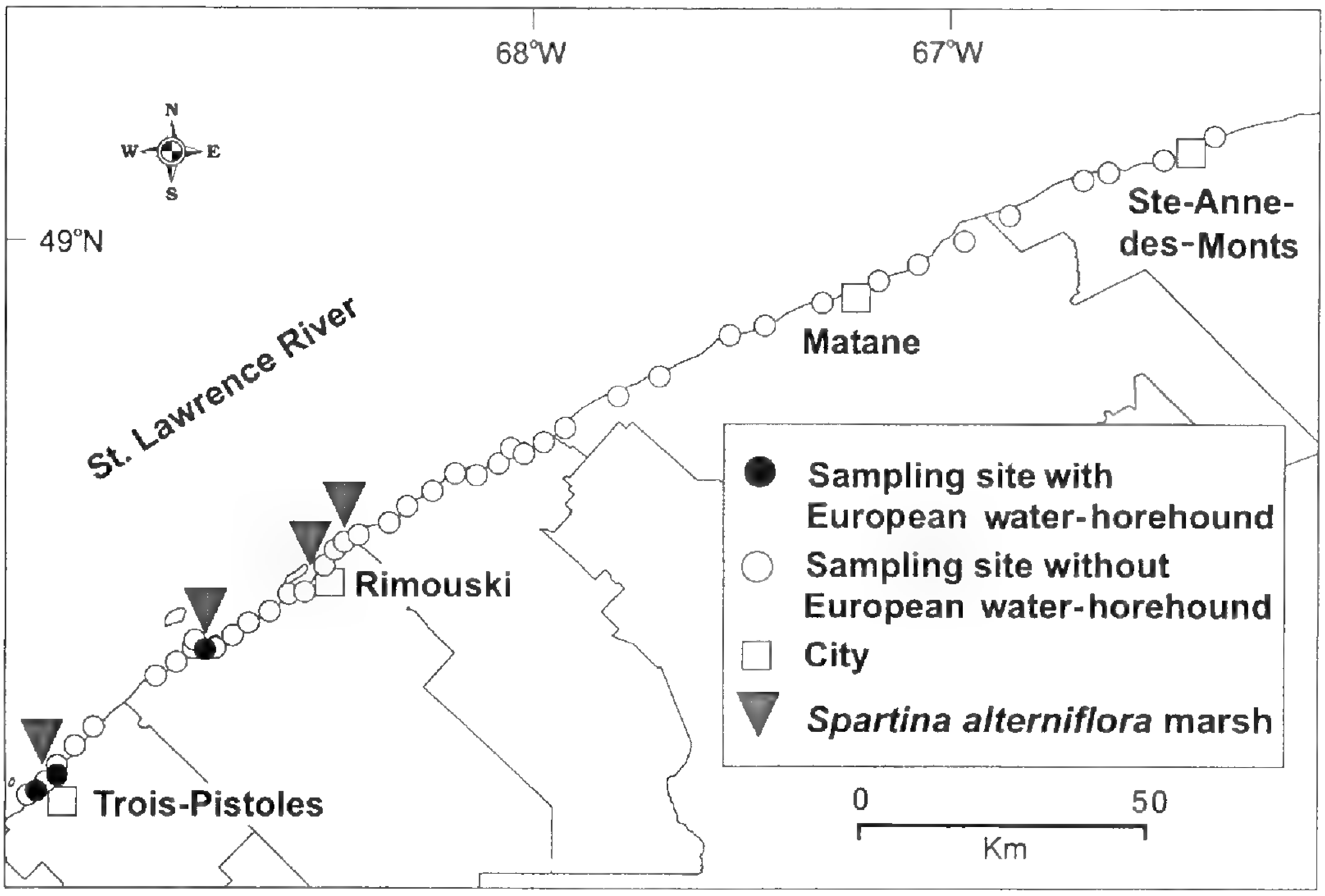

Figure 2. Sampling sites along the shore of the St. Lawrence River that were visited in August 1999 to determine the northeastern distribution limit of European water-horehound (*Lycopus europaeus*) in Québec, and location of *Spartina alterniflora* salt marshes in the area. Subdivisions = municipal regional counties.

brooks, and on silt or clay soils. Populations were surrounded by *Typha angustifolia* L. or *Lythrum salicaria* communities. Between 1974 and 1999, the rate of expansion of European water-horehound northeast of Trois-Pistoles River was only 3 km/yr.

DISCUSSION

Between 1963 and 1974, European water-horehound spread along the St. Lawrence River at a rate of 45 km/yr. During the last 25 years, the species spread from Trois-Pistoles River to Bic Provincial Park at a rate of only 3 km/yr. What could explain this difference? First, it is possible that the expansion of European water-horehound's distribution range northeast of Trois-Pistoles River was limited by the increasing salinity of estuarine waters. For example, upstream from Saint-Jean-Port-Joli (Figure 1; 47°10′N, 70°15′W), where the salinity of the St. Lawrence River surface water is < 1–2‰, European water-horehound populations are located in the supralittoral and intertidal zones (Chrétien 1994; Gauthier 1977; numerous herbarium specimens). Down-stream from Saint-Jean-Port-Joli, the salinity of surface water increases rapidly (from 1–2 to 15‰ over a 60-km distance), and European water-horehound populations are located only in the supralittoral zone (i.e., outside the zone regularly flooded by brackish water tides; Bourget 1997). Second, herbarium specimens and the field survey conducted in 1999 suggest that in the estuarine part of the St. Lawrence River, European water-horehound populations are located only in large *Spartina alterniflora* marshes. These marshes are very small and scarce northeast of Rimouski (Figure 2; Centre Saint-Laurent 1996). Third, the reconstruction of the spread of an invading species using herbarium specimens is highly dependent on the occurrence of field surveys conducted during different periods, and, in this case, on the ability of botanists to distinguish *Lycopus europaeus* in the field from the closely related *L. americanus*. For example, more than 20% of *L. europaeus* herbarium specimens that were examined in this study were originally misidentified as *L. americanus*, and were correctly identified only in 1978–1979 (most of them reviewed by J. Cayouette, DAO). However, no *L. europaeus* specimen was found in the *L. americanus* collection of QFA (206 specimens). Our reconstruction of the spread of European water-horehound in Québec should nevertheless be considered with some degree of caution.

Whatever the exact rate of spread of European water-horehound along the St. Lawrence River, our data clearly indicate that the spread of this exotic species was particularly rapid in Québec. For example, the maximum rate of spread of another exotic wetland plant species, *Hydrocharis morsus-ranae* L., was only 16 km/yr. between 1939 and 1994 within the Great Lakes–St. Lawrence River system. Seeds of *H. morsus-ranae* are dispersed by water, birds, and boats (Catling and Porebski 1995). No animal vector is known for European water-horehound, but the fact that seeds remain viable after floating for 12 to 15 months (Stuckey 1969) certainly facilitated the rapid spread of this species over long distances in Québec.

The limited range expansion of European water-horehound in eastern Québec between 1974 and 1999 suggests that the salinity of surface waters, and more particularly the scarcity of coastal or riverine marshes east of Rimouski prevented populations from establishing in the estuarine part of the St. Lawrence River. However, populations established upstream from Saint-Jean-Port-Joli seem to be expanding, and *Lycopus europaeus* may eventually replace the closely related native species *L. americanus* as one of the main species of the supralittoral and intertidal zones (Chrétien 1994). European water-horehound is still absent from large tributaries of the St. Lawrence River, and its further expansion into these rivers should be attentively surveyed.

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THE SURVIVAL OF *VAUCHERIA* (VAUCHERIACEAE) PROPAGULES IN NEW ENGLAND RIPARIAN SEDIMENTS AFTER REPEATED FREEZE/THAW CYCLES

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ABSTRACT. Previous studies have demonstrated the ability of the alga *Vaucheria* to survive prolonged and stressful periods of desiccation and freezing. However, even during harsh New England winters, the top few centimeters of floodplain alluvium or stream bank mud, where *Vaucheria* is often found, experience repeated thawing and refreezing events. Muds from two Connecticut riparian sites known to contain propagules from as many as eight species of *Vaucheria* were collected in spring and summer, then subjected to a variety of freeze/thaw (F/T) cycles. Six species of *Vaucheria*—*V. aversa*, *V. frigida*, *V. geminata*, *V. prona*, *V. taylorii*, and *V. undulata*—have demonstrated survival tolerance to multiple F/T cycles of intervals from 1–10 days.

Key Words: freeze/thaw cycles, propagules, riparian sediments, seed banks, *Vaucheria*

In New England winters, the natural deep-freezing of subsurface soil for up to four months is common. However, the upper surface of moist stream and riverbank alluvium above the water line rarely remains frozen for extended periods of time. On sunny winter days above 0°C, the top few centimeters of mud will thaw, only to refreeze at night. At times, above-freezing winter temperatures are maintained long enough to thaw the mud for several days before refreezing. Organisms that live in the top few centimeters of mud are subject to these freeze/thaw (F/T) events and therefore must withstand such conditions to survive.

The freshwater members of the cosmopolitan yellow-green alga *Vaucheria* (Vaucheriaceae, Tribophyceae, Chrysophyta) are commonly encountered living in and on riparian muds (Schneider et al. 1999). As the coenocytic siphons of *Vaucheria* grow, they weave in and out of their mud substrate and often between the siphons of sympatric species, forming what is referred to as a "felt-like turf." In order to survive the environmental extremes such as desiccation and freezing that impinge upon it, this alga, like so many others in their specific environments, has developed propagules as resting structures that are deposited in the floodplain soils or riverbank muds. When environmental conditions are optimal, *Vaucheria* grows and reproduces forming zygotes (oospores). But when conditions are limited by abiotic components in the environment, the siphons of *Vaucheria* can form sporangia or "cyst-like" resting fragments (Dunphy et al. 2001). We have recently shown that the propagules of eight species—*V. aversa* Hassall, *V. bursata* (O. F. Müll.) C. Agardh, *V. frigida* (Roth) C. Agardh, *V. geminata* (Vaucher) Alph. de Candolle, *V. prona* T. A. Chr., *V. taylorii* Blum, *V. uncinata* Kütz., and *V. undulata* C. C. Jao—were able to survive desiccation in the laboratory from 63–383 days (Dunphy et al. 2001). The survival of each of these species was likely due to the deposition of a "seed bank" of propagules left in the mud during or after periods of active growth, and the physiological tolerance of these resting cells to prolonged periods without soil moisture. Since the freeze/thaw phenomenon is so prevalent in Connecticut riparian muds and such an important physiological stress for *Vaucheria*, this study examines the survival tolerance of the propagules of these species to repeated freezing and thawing for varying numbers of cycles.

STUDY AREAS

The two Connecticut collection sites where we have observed "felt-like" turfs of *Vaucheria* with high levels of species sympatry (Dunphy et al. 2001; Schneider et al. 1999) were selected for this study:

1. Nipmuck Trail (NK)—Ashford, Windham County, approx. 3 km from an entrance to the Nipmuck Trail, a portion of the Mohawk Trail system, on Conn. Rt. 74 [41°51.301′N, 72°12.821′W (Garmin™ GPS 12, v. 4.57)];
2. Scantic River (SCR)—Enfield, Tolland County, floodplain directly beneath the bridge on Conn. Rt. 190 that crosses over the Scantic River near the intersection with Conn. Rt. 191 (41°58.966′N, 72°30.969′W).

Eight species of *Vaucheria* have been found at SCR—*V. av-*

ersa, *V. bursata*, *V. frigida*, *V. geminata*, *V. prona*, *V. taylorii*, *V. uncinata*, and *V. undulata*—while all of the above except *V. taylorii* are known from NK (Dunphy et al. 2001).

MATERIALS AND METHODS

Bulk samples of mud containing propagules from each site were collected on 24.iv.2000, 5.vii.2000, and 23.viii.2000. The procedures for field collection and preparation of a homogenous mud in the lab are described in Dunphy et al. (2001). After being left uncovered for five days, the moist mud slurry was cut into blocks approximately 36 cm^2, placed in zippered plastic bags and frozen to 0°C. Control mud samples were immediately placed in individual plastic culture dishes (2.3 cm × 8.5 cm) with Bold's basal medium (Bischoff and Bold 1963), and cultured as in Dunphy et al. (2001).

Bags of mud totaling 33 blocks per collection site and date were removed from the freezer for each F/T experiment. The bags were placed in a growth chamber set at 15°C, and the mud was allowed to thaw for the specified length of time for each experiment. Thawing periods of 1–5, 7, and 10 days were used. Three blocks from each collection site were then removed from their bags and placed in individual culture dishes with 4–5 ml of culture medium, labeled, and placed back in the growth chamber. The bags containing the remaining blocks were returned to the freezer for 2 days at which point the cycle was repeated until all of the mud blocks were cultured.

Cultures were monitored for signs of *Vaucheria* siphons using light microscopy. Vouchers of reproductive materials from numerous samples were prepared (20% or 40% Karo™ corn syrup, 1% aqueous aniline blue, and 1 N HCL in a ratio of 20:1:1) and deposited in Herbarium C. W. Schneider at Trinity College, Hartford.

RESULTS

Because the three replicate control dishes of mud collected from each site in April, July, and August produced similar species, survival data for NK and SCR were combined in Table 1. In the control dishes for NK, four species developed: *Vaucheria aversa*, *V. geminata*, *V. prona*, and *V. undulata*. In the controls for SCR, we discovered *V. frigida*, *V. prona*, and *V. undulata*

Table 1. Freeze/thaw cycle survival of six *Vaucheria* species from two Connecticut riparian sites (NK, SCR), and percent survival in total experimental dishes. Numbers represent the maximum number of F/T cycles a species survived at each site for specified number of thaw days per cycle. Species appearing in control dishes are denoted by asterisks (*). Culture dishes that never produced gametangia, hence remaining unidentified, are noted as *V.* spp.

		No. F/T Cycles Survived at Various No. Thaw Days/Cycle							
Species	Collection Site	1	2	3	4	5	7	10	Species Occurrence (% of Total Dishes)
V. aversa	NK*	–	–	8	4	5	7	4	24.4
	SCR	1	–	–	4	4	–	1	0.05
V. frigida	NK	–	–	–	–	–	–	–	0.00
	SCR*	–	7	6	–	8	–	–	0.03
V. geminata	NK*	–	–	–	7	2	–	–	0.01
	SCR	–	7	–	–	–	3	2	0.02
V. prona	NK*	–	5	8	–	–	2	4	0.07
	SCR*	9	8	6	4	7	6	5	26.7
V. taylorii	NK	–	–	–	–	–	–	1	0.01
	SCR	–	–	–	–	–	–	1	0.01
V. undulata	NK*	–	5	–	1	–	–	2	0.04
	SCR*	2	7	6	4	–	5	5	0.07
V. spp.	NK	10	9	–	5	7	6	1	12.2
	SCR	3	9	8	6	9	–	6	15.4

(Table 1). Several species appeared in experimental dishes from the two sites despite not appearing in control cultures; in fact, only *V. prona* and *V. undulata* were found in the control dishes from both sites. *Vaucheria taylorii* was found in neither control, yet appeared in one experimental dish from each site (Table 1). This represents the first report of *V. taylorii* from NK, thus the same eight species are known from both collection sites. Problems associated with assessing muds containing unknown quantities of propagules in the "seed banks" are discussed by Dunphy et al. (2001), but the low frequency of appearances of certain species in experimental dishes and the lack of the same species in the controls suggest small quantities of propagules in our collected muds.

Each of the species found in the control dishes was able to survive multiple cycles of freezing, followed by one or more thaw days in at least some of the experimental dishes (Table 1). In some instances, the survival of a species after experimental treatment may in fact result from a single reproductive population in one of the three replicate dishes for each site. Combined, 45% of the 375 experimental dishes developed *Vaucheria*—42% of those from NK and 49% from SCR. However, in many of the experimental dishes, *Vaucheria* siphons never became reproductive even after months in culture, thus disallowing species identifications in 12% of NK dishes and 15% of those from SCR. Only two species were found in greater than 1% of all of the experimental dishes from a site: *V. aversa* in 24% from NK, and *V. prona* in 27% from SCR. *Vaucheria aversa* appeared more frequently in culture dishes in the late winter to early spring regardless of collection time or experimental regimen, similar to findings for rehydrated desiccated muds containing *V. aversa* propagules from a previous study (Dunphy et al. 2001). The other four species were found at a much reduced frequency (Table 1). As noted above, *V. taylorii* appeared in only two cultures, one from SCR and the other from NK, the latter representing the first report from this site.

Three species survived in most of the experimental treatments of 1–10 days thawing after 2 days of refreezing; *Vaucheria aversa* from NK, and *V. prona* and *V. undulata* from SCR (Table 1). *Vaucheria prona* was found growing in SCR dishes after 9 cycles with 1 day of thaw. For this species at SCR (the site and species that provided the greatest amount of data), as the number of thaw days increased in the trials, we observed that *V. prona* survived the greatest number of F/T cycles with the shortest thaw period (1 day; Table 1). The number of F/T cycles that *V. aversa* and *V. undulata* survived compared with the number of days thawed shows no obvious trend. The remaining species and sites had less complete survival data, no doubt due to their lesser presence in the "seed bank." Nevertheless, all six *Vaucheria* species showed tolerance to F/T stresses more extreme than we suspect they are exposed to at the sites from which they were collected, including the species with a lesser presence. *Vaucheria frigida* survived 8 cycles with 5 days of thaw (SCR), while *V. taylorii* (NK, SCR) and *V. geminata* (SCR) survived 1 and 2 cyles, respectively, with 10 days of thaw.

DISCUSSION

Few studies have been made on the effects of freezing and thawing on algae, although several have looked at the survival of bacteria, often in boreal and arctic soils. Skogland et al. (1988) discovered that a single F/T cycle could kill as many as 50% of a viable soil microbial population, and Schimel and Clein (1996) noted that following these environmental events, the dead cells contributed significant nutrients to the soil for surviving organisms. Other studies have focused on morphological or molecular and biochemical responses of cells disrupted by freezing and thawing, from bacteria and fungi to cereal crop protoplasts (Morris et al. 1988; Steponkus et al. 1983). Although many studies have looked at the effects of prolonged freezing and cryopreservation in unicellular and filamentous algae (Ginsburger-Vogel et al. 1992; Morris 1978), little is known about their survivability after repeated cycles of freezing and thawing, conditions many stream and riparian algae are exposed to in their native environments. In one study, Hawes (1990) observed that the vegetative cells of a filamentous green alga from Antarctic streams—an unidentified species of *Zygnema*—could survive the repeated freezing and thawing cycles typical of austral summers with little effect, but that prolonged exposure to −20°C winter temperatures caused extensive cell mortality. He concluded that the few winter-surviving cells in filaments became the "seed" population for summer growth in *Zygnema* without the involvement of resting spores or other specialized structures typically utilized by freshwater filamentous green algae to survive stressful environmental events (Coleman 1983).

An organism such as *Vaucheria*, whose propagules can survive over a year in desiccated mud, would be expected to survive other environmental stresses normally encountered in its habitat, such as winter freezing in New England. We have observed that *Vaucheria* propagules, including all of the species tested herein for survival in repeated F/T cycles, survive in moist, freezing mud for over a year (unpubl. data). In the present study, the propagules of six species of *Vaucheria* have been shown to survive the stress of multiple F/T cycles (Table 1), conditions these species might normally encounter in a typical Connecticut winter in the upper soil strata of riparian habitats. *Vaucheria aversa*, *V. prona*, and *V. undulata* were the most frequently encountered species in our experimental dishes, showing the greatest survival after repeated F/T cycles. Presumably, these species had left the greatest numbers of propagules in the "seed bank" in our collected muds. Despite being only sporadically found in our culture dishes, the remaining three species, *V. frigida*, *V. geminata*, and *V. taylorii*, nevertheless survived experimental treatments in some of the dishes, showing their ability to survive repeated F/T cycles. Although *V. bursata* and *V. uncinata* were previously reported from both the NK and SCR sites (Dunphy et al. 2001), neither appeared in any of the control or experimental cultures. It is therefore reasonable to assume that their propagules were not present in the mud collections made for this study.

In this and past studies, we have seen *Vaucheria* siphons appear above the substrate surface in as little as ten days after thawing frozen muds. Propagule germination must therefore occur much earlier, within the first few days post thaw. The refreezing of muds that have been thawed for prolonged periods of time tests not only the ability of propagules to survive refreezing, but the ability of germinated siphons to survive as well. With ten-day thaw intervals, a large percentage of propagules will likely germinate and thus become susceptible to freezing injury with each F/T cycle. Without the cellular partitioning found in filamentous freshwater algae such as the chlorophyte *Zygnema* (Hawes 1990), the siphons of *Vaucheria* would appear to have fewer options for cellular protection and therefore be more susceptible to mortality. If some percentage of the "seed bank" survives after each F/T cycle, the species with the most numerous propagules should show the greatest success even if its ability to withstand the stress is no greater than any other species. Therefore, it would appear to be important for species to deposit a large number of propagules in the environment to have a greater chance of surviving F/T stress, as it appears that individual mortality must take its toll. Because *V. aversa*, *V. prona*, and *V. undulata* were commonly collected species in a great sampling of riparian Connecticut habitats (Schneider et al. 1999), and therefore could have deposited the most numerous propagules in our NK and SCR samples, it is not surprising that they showed greater success with longer thawing times than the other species (5 cycles with 10-day thaw intervals). Thus, they continue to appear to be ecologically opportunistic, having already demonstrated survivability after long periods of desiccation—145, 359, and 383 days, respectively (Dunphy et al. 2001).

Vaucheria prona and *V. undulata* survived the greatest number of F/T cycles (5) with thaw periods of 10 days. In Connecticut, the surfaces of floodplain alluvium or river banks would rarely, if ever, thaw once for ten continuous days and then refreeze during the winter freezing period of December to March. These two species, along with *V. aversa* and *V. geminata*, have shown great success in surviving multiple F/T cycles with longer thaw intervals. If they can survive such an extreme and repeated stress, unlikely to occur in their natural habitats, it seems probable they can survive any series of F/T cycles that would naturally occur in New England, assuming the propagules have not all germinated and died in the young siphonous form. The survival of all six *Vaucheria* species exposed to the stress of repeated freezing and thawing cycles further demonstrates the ability of this alga to survive severe environmental stress. Survival appears to depend not only on the species' ability to physiologically handle the stress of repeated F/T cycles and the length of thaw intervals, but also upon the abundance of their propagules in a given habitat. Long thaw intervals more than likely allow the germination of *Vaucheria* propagules, and it would appear young siphons would be more vulnerable to repetitive refreezing than resting propagules left ungerminated.

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STUDIES IN NEOTROPICAL APOCYNACEAE I: A REVISION OF THE GENUS *LAUBERTIA*

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ABSTRACT. A synopsis of the three species of the genus *Laubertia* (Apocynaceae, Apocynoideae, Echiteae) is presented here. Keys, descriptions, distributional data, and taxonomic index are provided.

Key Words: Gentianales, Apocynaceae, Apocynoideae, *Laubertia*, Neotropics

The small genus *Laubertia* was described by Alph. de Candolle in 1844, with a single species, *L. boissieri.* It was characterized by a corolla tube having a conspicuous annular corona, but without free corona lobes within, and by eglandular sepals without basal colleters. Following the classification of Endress and Bruyns (2000), within the tribe Echiteae, *Laubertia* is closely related to *Hylaea* J. F. Morales and *Prestonia* R. Br. The three genera are characterized as having in common features such as corolla tubes with conspicuous annular coronas or with five free corona lobes within. However, *Laubertia* is easily distiguished by its eglandular sepals, without basal colleters within, and corolla tubes without free corona lobes within. Because of the confusion concerning generic limits in the family, the species of this genus were described or placed in other genera (e.g., *Echites, Haemadictyon*). Other workers, such as Miers (1878) or Hemsley (1881), reduced the genus to the synonymy of *Exothostemon* G. Don and *Prestonia,* respectively. In 1897, unaware of the main features of *Laubertia,* Greenman described the monotypic genus *Streptotrachelus.* The next and most recent treatment of the genus was that of Woodson (1936). He considered *Laubertia* to comprise four species, reduced *Streptotrachelus* to synonymy, made two new combinations, and described one new species. Since then, there has been no comprehensive treatment of the genus. The description of several taxa in the last 60 years, new synonymy, and the necessity of taxonomic changes after the examination of types in European herbaria convinced me to update the genus.

Specimens of *Laubertia* are usually rare in herbaria: of the three species here recognized, only two are known from more than one collection, while the third one is known from just the type collection. For this review, about 136 collections from 26 herbaria were examined. As a reference for infrageneric classification within the Apocynaceae, I used the work of Endress and Bruyns (2000).

NOTEWORTHY MORPHOLOGICAL FEATURES

The main morphological characters are described in the taxonomic treatment. However, several features that deserve more detailed commentary are described below.

Leaves. The leaves of *Laubertia* are distinctive because of the presence of very diminutive cavities at the junction between the midvein and the secondary veins (Figure 1). These structures are very similar to domatia, but are formed by the disconnection of the side vein from the lamiar tissue, thus they do not represent that feature exactly. These inconspicuous structures are not present in every vein axil and may be lacking in some leaves, but are totally absent in the related genera *Hylaea* and *Prestonia.*

Domatia are foliar structures not very common in the family. In the neotropics they are present in several species of the genera *Forsteronia* G. May, *Malouetia* Alph. de Candolle, and *Tintinnabularia* Woodson.

Sepals. The sepals in *Laubertia* are eglandular (Figure 2), that is without basal colleters, while *Hylaea* and *Prestonia* always have calycine colleters that are entire to variously lacerate. Despite the fact that there are genera in other tribes of different subfamilies (e.g., Rauvolfioideae, Plumeriae) in which the sepals are variously glandular or eglandular (e.g., *Allamanda*), in the subfamily Apocynoideae the presence or absence of calycine colleters in the sepals is a very helpful feature for generic delimitation.

Corolla and corona. The corolla tube in *Laubertia* lacks free corona lobes within (Figure 3c). In *Prestonia,* these lobes [called epistaminal appendages by Woodson (1936)] are present and obvious in most of the species, reduced to callus ridges in some

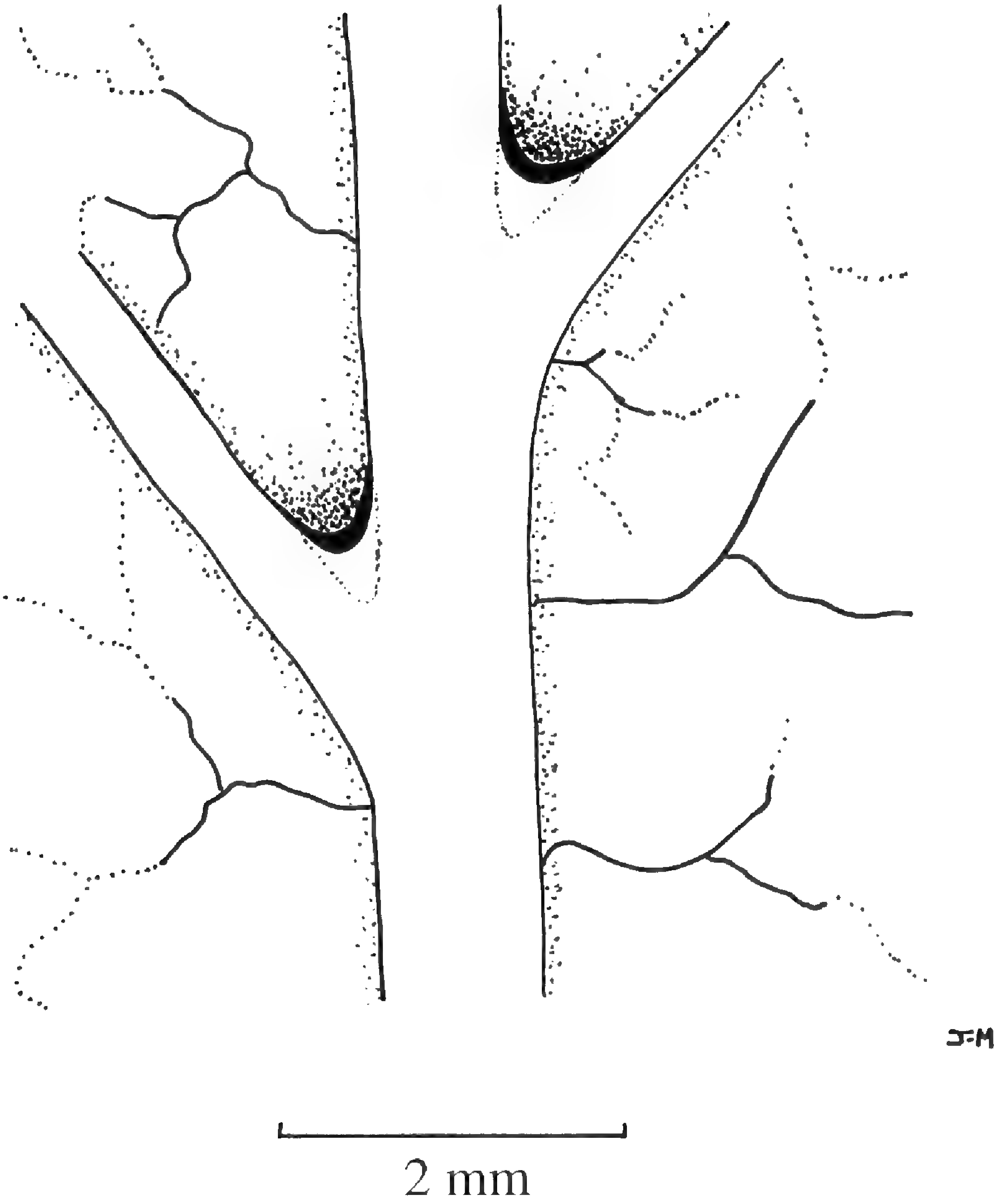

Figure 1. *Laubertia boissieri* (*Neill 10081*, INB). Midvein, showing cavities in their junction with secondary veins.

others, or are totally absent in just a few species. In *Hylaea*, the corona lobes are always present and totally exserted, but that genus lacks an annular corona, a character always present in *Prestonia* and *Laubertia*.

TAXONOMIC TREATMENT

Laubertia Alph. de Candolle, Prodr. 8: 486. 1844. TYPE: *L. boissieri* Alph. de Candolle.

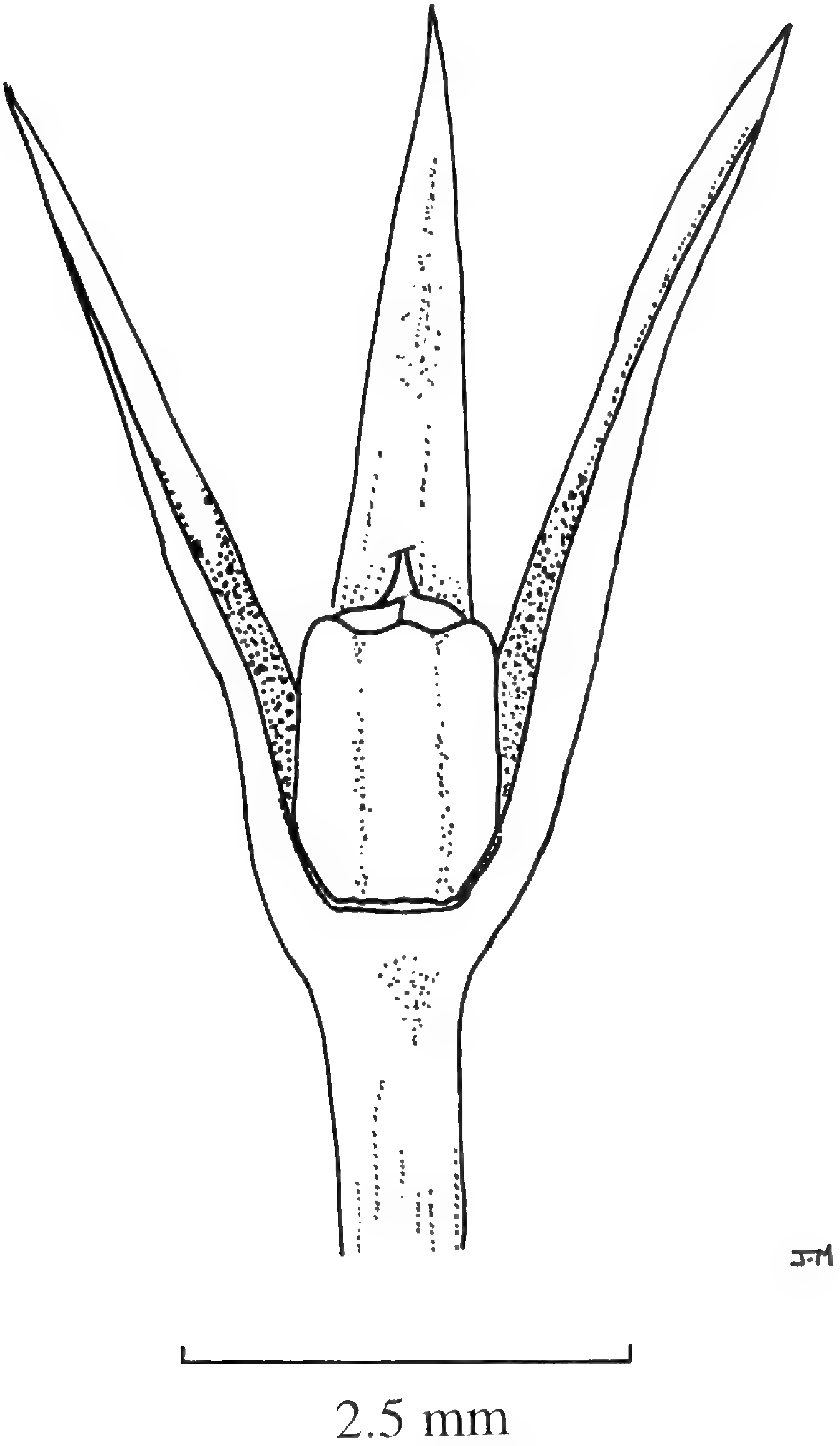

Figure 2. *Laubertia boissieri* (*Neill 10081*, INB). Calyx with eglandular sepals.

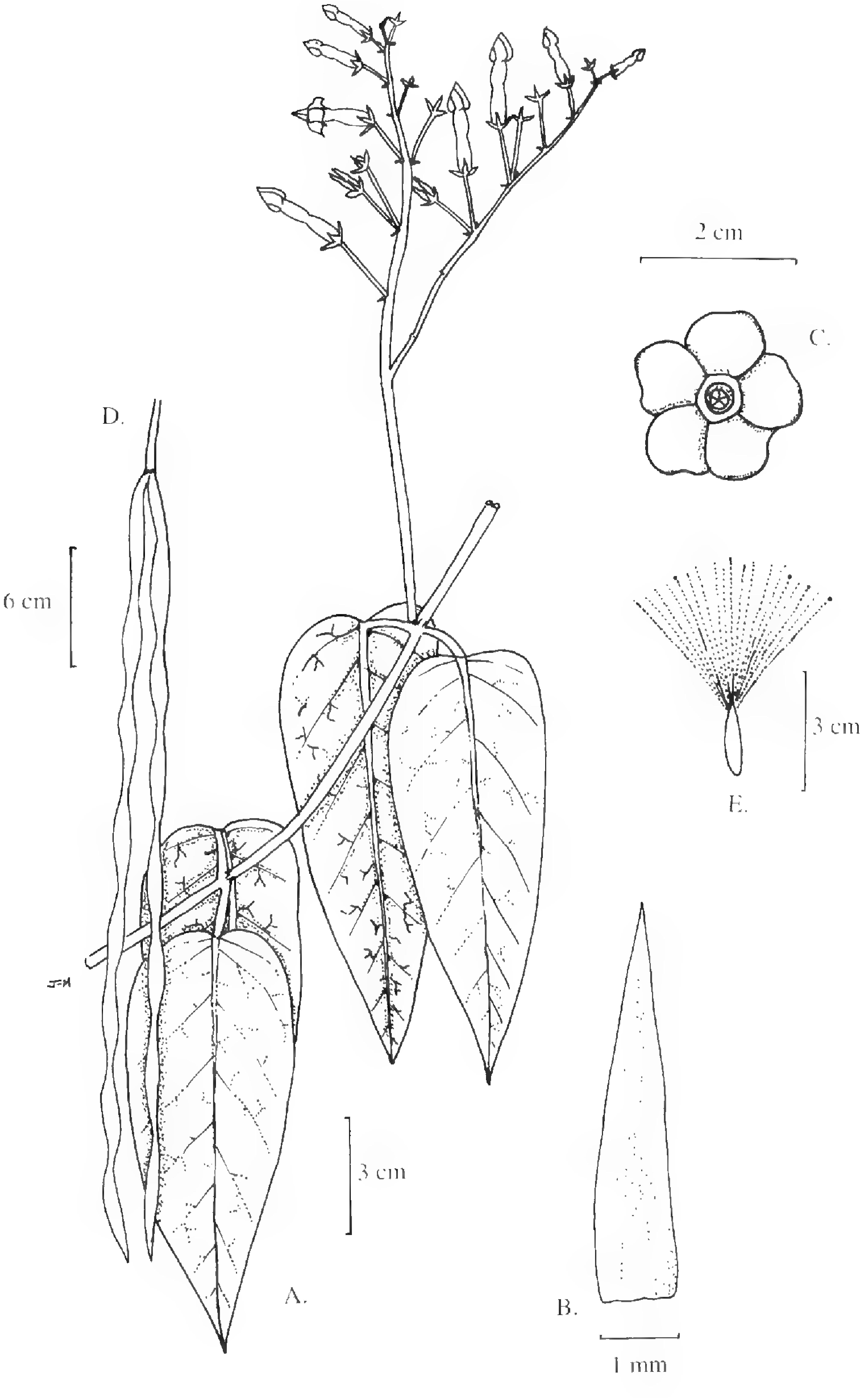

Figure 3. *Laubertia boissieri* (*Neill 10081*, INB). A. Habit; B. Sepal; C. Corolla; D. Fruits; E. Seed.

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Haemadictyon Lindl., Trans. Hort. Soc. London 6: 70. 1825 (1826), in part.
Exothostemon G. Don, Gen. Hist. 4: 70, 82. 1837, in part.
Streptotrachelus Greenm., Proc. Amer. Acad. Arts 32: 298. 1897. TYPE: *S. pringlei* Greenm. [= *Laubertia contorta* (M. Martens & Galeotti) Woodson].

Fruticose or suffruticose lianas. Stems terete to subterete, variously puberulent when young, usually glabrous to glabrate at maturity. Leaves opposite (very rarely ternate), petiolate, petioles slightly fused at the base, mostly glandular in the axils, with several inconspicuous and diminutive fusiform or conic colleters; blade glabrous, glabrate to very minutely puberulent, eglandular, without basal colleters adaxially. Inflorescence a scorpioid cyme, sometimes reduced and appearing simple or umbelliform, axillary, few- to many-flowered, glabrous or glabrate to minutely puberulent, pedunculate, bracts scarious, inconspicuous. Sepals 5, essentially equal, barely imbricate basally, without basal adaxial colleters within; corolla salverform, very minutely puberulent abaxially; tube straight to conspicuously twisted around the stamens, with an annular corona, without free corona lobes within, the limb 5-parted, actinomorphic, dextrorsely convolute; stamens 5, usually somewhat exserted, inserted in the upper part of the corolla tube; anthers connivent and adnate to the pistil head, consisting of 2 parallel, uniformly fertile thecae borne adaxially near the apex of an enlarged, peltate connective; auricles short, acute; carpels 2, united at the apex; pistil head fusiform or subcapitate; ovules numerous, multi-seriate, borne on an axile, biseriate placenta; disk glands 5, separate to very inconspicuously concrescent at the base, entire, distinct. Follicles 2, apocarpous, moniliform to more rarely continuous, glabrous, glabrate to very minutely puberulent, dehiscing along the ventral suture; seeds numerous, dry, truncate, comose apically, usually minutely rugose.

The genus comprises three species: one found in México; the second in Guatemala and Belize; and the third in South America in Colombia, Ecuador, Peru, and Bolivia.

KEY TO THE SPECIES OF *LAUBERTIA*

1. Corolla tube straight, not twisted around the stamens; plants

from Colombia, Ecuador, Peru, and Bolivia . . . . 1. *L. boissieri*

1. Corolla tube twisted around the stamens; plants from México, Guatemala, and Belize . . . . (2)
   2. Corolla purple to lilac, the tube 18–23 mm; anthers 6.5–7.5 mm long; México . . . . 2. *L. contorta*
   2. Corolla white, the tube 10–14 mm long; anthers 5 mm long; Guatemala and Belize . . . . 3. *L. peninsularis*

1. Laubertia boissieri Alph. de Candolle, Prodr. (DC.) 8: 487. 1844. TYPE: ECUADOR. Locality lacking, 1778–1788 (fl), *Pavón s.n.* (LECTOTYPE selected here: G-BOIS!; ISOLECTOTYPES: F!, G-BOIS!, G-DC!, photograph Field negative 34137 at F!, INB!, MO!, NY *ex* G-DC!). Figure 3.

Echites dichotoma Kunth *in* Humboldt et al., *syn. nov.*, Nov. Gen. Sp. 3: 217 (ed. qui), 9 Jul 1819 [1818], non Thunberg, 21 Apr 1819. *Mesechites dichotoma* (Kunth) Miers, Apocyn. S. Am. 233. 1878. TYPE: COLOMBIA. Vaupés: between Jaen and Amazon River, Aug (year lacking; fl), *Humboldt & Bonpland 3627* (HOLOTYPE: P-HB!, photograph at INB!).

Echites sanctae-martae Rusby, Descr. S. Amer. Pl. 85. 1920.

Laubertia sanctae-martae (Rusby) Woodson, *syn. nov.*, Ann. Missouri Bot. Gard. 18: 555. 1931. TYPE: COLOMBIA. Magdalena: Above Jiracasaca, 3000 ft., 25 Aug 1898–1899, (fl, fr), *Smith 2525* (HOLOTYPE: NY!; ISOTYPES: BR!, CM!, F!, G! [2 sheets], GH!, K! [2 sheets], MICH!, MO!, P! [2 sheets], photocopy at INB *ex* BR!; photograph Field negative 56466 at INB *ex* F!).

Echites eggersii Markgr., Notizbl. Bot. Gart. Berlin-Dahlem 9: 78. 1924. TYPE: ECUADOR. Manabí: near El Recreo, 30 Apr 1897 (fl), *Eggers 15684* (HOLOTYPE: B destroyed; LECTOTYPE selected here: O!; ISOLECTOTYPES: C!, F!, K! [2 sheets], M!, MO!, NY!, O!, P!, S!, photocopy at INB *ex* O!, photograph Field negative 56465 at INB *ex* F!).

Liana; branchlets terete to subterete, very minutely and inconspicuously brownish puberulent to ferrugineous-puberulent, glabrous to glabrate at maturity; nodal colleters inconspicuous, ca. 1 mm long. Leaves usually opposite, very rarely ternate; petioles 5–17 mm long; blade 5.2–14 (16) × (1.5) 2–5.6 cm, membranaceous to firmly membranaceous, elliptic to ovate-elliptic, very sparsely or minutely and inconspicuously puberulent when young, usually glabrous to glabrate on both surfaces at maturity, acuminate or short-acuminate to narrowly acute apically, obscurely cordate to more or less obtuse basally. Inflorescence conspicuously longer than the subtending leaves, axillary, very minutely and inconspicuously ferrugineous puberulent to glabrate, few- to many-flowered; peduncle 22–80 mm long; pedicels 8–18 mm long; bracts 1–3 × 0.5–1 mm, scarious. Sepals 2–6 × 1–1.5 mm, narrowly ovate to narrowly linear-ovate, long-acuminate, very minutely and sparsely ferrugineous puberulent to glabrate; corolla reddish-pink, or reddish-purple to purplish, very minutely brownish puberulent without, tube 12–27 × 3–5 mm, conspicuously inflated basally, straight, not twisted; lobes 10–18 × 6–11 mm, narrowly obovate to narrowly elliptic, spreading; anthers 5–6 mm long, glabrous to very minutely puberulent dorsally; ovary 1.5–2 mm long, glabrous to glabrate; style head 2–2.5 mm long; disk glands about as long as the ovary. Follicles 25–75 × 2–4 mm, glabrous or glabrate to very inconspicuously, minutely, and sparsely puberulent, obscurely moniliform; seeds 15–19 mm long, glabrous, glabrate, to minutely papillate, coma 2.5–4.8 cm long, creamish to tannish.

DISTRIBUTION AND PHENOLOGY. The species is found in northern Colombia, southern Ecuador, Peru, and Bolivia at 200–1600 m elevation. It flowers and fruits all year, but mostly July to February.

Laubertia boissieri is easily recognized by its straight corolla tube and distribution disjunct from the other two species of the genus.

Echites dichotoma was included in the synonymy of *Mesechites trifida* (Jacq.) Müll. Arg. by Woodson (1936). However, it is obvious that he never saw the type, because it is obviously conspecific with the type of *Laubertia boissieri.*

Laubertia sanctae-martae is here relegated to the synonymy of *L. boissieri.* Woodson (1936) separated these taxa based on the inflorescence structure and sepal shape. At the time of his revision, only five collections were available from these two species. Since then, many further collections reveal that sepal shape can vary from ovate and acute apically to very narrowly ovate and long acuminate. Corolla length is also very variable in the specimens examined and does not warrant the distinction of these taxa. Regarding inflorescence structure, Woodson cited "Inflorescence rather obscurely compound to essentially simple" for *L. sanctae-martae*; however, the Brussels (BR) isotype, which was not examined by Woodson, shows a conspicuously compound inflorescence. Therefore, all supposed differential characters are ineffective, so *L. sanctae-martae* is relegated to the synonymy of *L. boissieri.*

SPECIMENS EXAMINED: BOLIVIA. La Paz: Inquisivi, Lakachaka, mouth of the Río Aguilani, 21 Sep 1991 (fl), *Lewis 40417* (LPB, MO); NorYungas, Río Unduavi valley, 6 Sep 1987 (fl, fr), *Seidel & Vargas 1103* (LPB, MO); Sud Yungas, E of Puente Villa, road to Chulumani, 28 Sep 1985 (fl, fr), *Solomon & Nee 14272* (INB, MO).

COLOMBIA. Magdalena: flanco N de la Sierra Nevada de Santa Marta, 3 Mar 1948 (fl), *Romero-Castañeda 762* (COL, MO); Sierra Nevada de Santa Marta, 1898–1899 (fl), *Smith 1643* (G).

ECUADOR. Esmeraldas: Fila de Bilsa, E of San José de Bilsa, 20 Jan 1991 (fl), *Gentry et al. 72942* (MO). Los Ríos: Río Palenque Science Center, between Santo Domingo and Quevedo, 16 Jul 1986 (fl, fr), *Gentry & Dodson 54859* (MO [2 sheets], WAG). Napo: Jatun Sacha Biological Reserve, near Puerto Misahualli, 8 Nov 1987 (fl, fr), *Cerón 2628* (MO, USF); Jatun Sacha Biological Station, Río Napo, E of Misuahuallí, 17 Feb 1988 (fl), *Cerón 3687* (MO, USF); Orellana, Pompeya, 5 Aug 1992 (fr), *Neill 10081* (INB, MO, QCNE). Orellana: Yasuní National Park, 3 Nov 1998 (fl, fr), *Burnham 1794* (INB, MICH, MO). Province unknown: San José, Chimborazo, Jul 1876 (fl), *André 4051* (K [2 sheets]).

PERU. Cajamarca: San Ignacio, Chirinos, Mandinga, 5 Feb 1996 (fl, fr), *Campos & Díaz 2412* (INB, MO); San Ignacio, Huarango – San Martín, 15 May 1996 (fr), *Vásquez & Vásquez 20860* (INB, MO); Pucará, 14 Apr 1960 (fl), *Woytkowski 5680* (G, MO). Junín: Chanchamayo, La Merced – Villa Rica Road, between Puente Paucartambo and Río Colorado, 6 Jan 1984 (fl, fr), *Smith et al. 5625* (MO, USF); Yaupi, 23 Jun 1961 (fr), *Woytkowski 6326a* (MO), 30 Jun 1961 (fl, fr), *Woytkowski 6353* (MO [2 sheets]). San Martín: Muña, 23 May–4 Jun 1923 (fl), *Macbride 3902* (F, US); La Merced, Aug 1923 (fl, fr), *Macbride 5473* (F, K, US).

2. Laubertia contorta (M. Martens & Galeotti) Woodson *in* Britton, N. Amer. Fl. 29: 187. 1938. Figure 4.

Haemadictyon contortum M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11: 360. 1844. *Exothostemon contortum* (M. Martens & Galeotti) Miers, Apocyn. S. Am. 241. 1878. *Prestonia contorta* (M. Martens & Galeotti) Hemsl., Biol. Cent.-Amer., Bot. 2: 311. 1881. TYPE: MEXICO. Oaxaca: Zacatepec, date lacking (fl), *Galeotti 1588* (HOLOTYPE: BR!).

Streptotrachelus pringlei Greenm., Proc. Amer. Acad. Arts 32: 298. 1897. *Laubertia pringlei* (Greenm.) Woodson, Ann. Missouri Bot. Gard. 18: 555. 1931. TYPE: MEXICO. Morelos: lava beds near Cuernavaca, 23 Sep 1896 (fl), *Pringle 6554* (HOLOTYPE: GH!; ISOTYPES: F!, G!, GH!, K! [2 sheets], MO! [2 sheets], NY!, P!, S!).

Prestonia langlassei Standl., Contr. U.S. Natl. Herb. 23: 1159. 1924. TYPE: MEXICO. Michoacán: La Correa, 50 m, 8 Oct 1898 (fl), *Langlassé 435* (HOLOTYPE: US!; ISOTYPES: G! [2 sheets], GH!, K!, P!).

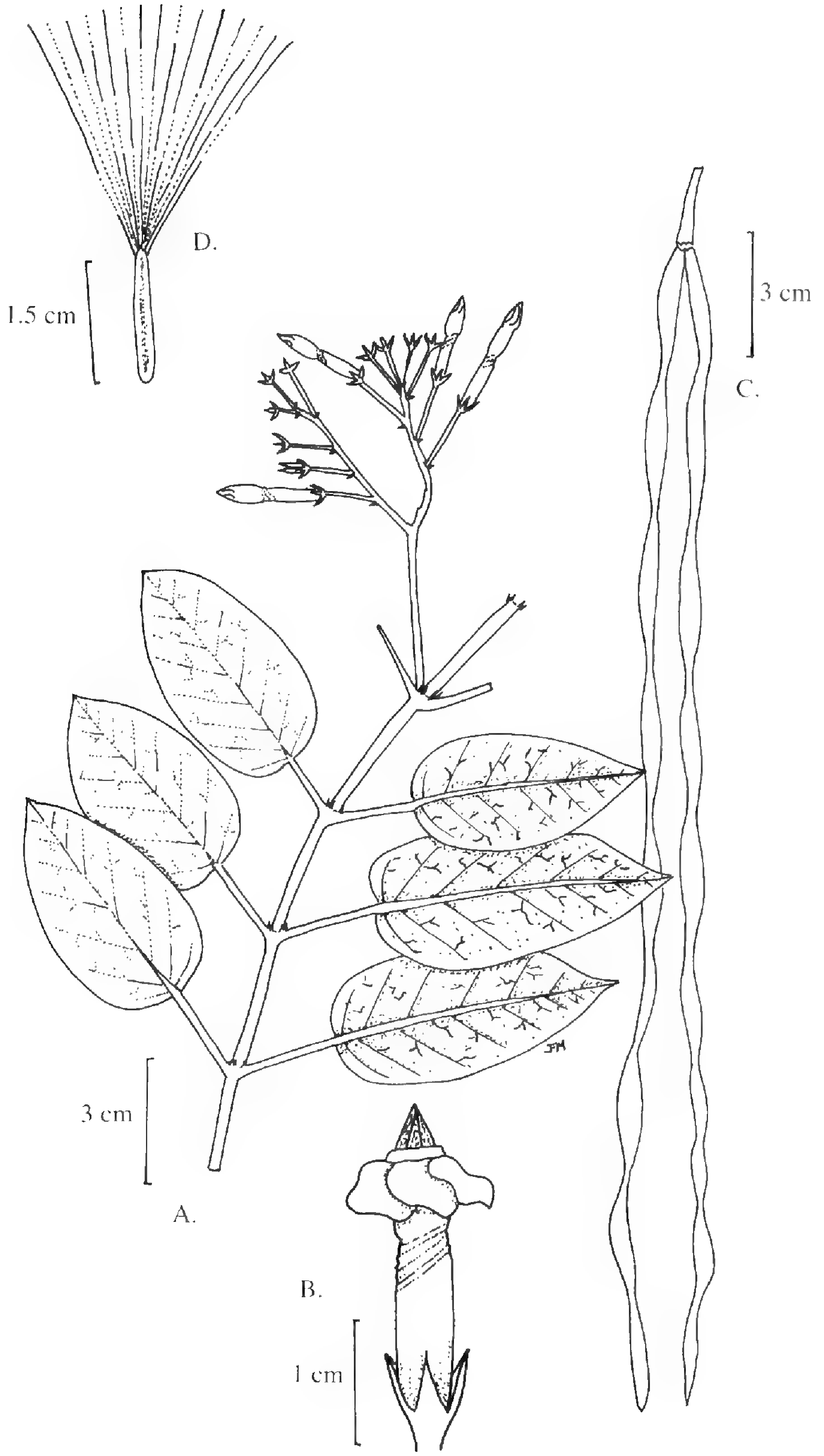

Figure 4. *Laubertia contorta* (*Martínez & Stevens 23849,* INB). A. Habit; B. Corolla; C. Fruits; D. Seed.

Liana; branchlets terete to subterete, very inconspicuously to sparsely and minutely puberulent when young, glabrate at maturity; nodal colleters 1–2 mm long. Leaves opposite; petioles 10–32 mm long; blade 4–9 × 2.5–5.7 cm, membranaceous, elliptic or ovate-elliptic to narrowly ovate, very sparsely and inconspicuously puberulent to more commonly glabrous or glabrate on both surfaces, acute to shortly and abruptly cuspidate to acuminate apically, obtuse to inconspicuously or conspicuously cordate basally. Inflorescence variously shorter or longer than the subtending leaves, axillary, densely and minutely puberulent, many-flowered; peduncle 25–65 mm long; pedicels 7–27 mm long; bracts 1–1.5 × 0.5 mm, scarious. Sepals 3–5 × 1–1.5 mm, narrowly ovate, acuminate to long-acuminate, densely and minutely puberulent, corolla purple to lilac, moderately to sparsely puberulent without, tube 18–23 × 3–5 mm, conspicuously inflated basally, twisted around the stamens; lobes 7–10 × 3.5–5 mm, narrowly obovate, spreading; anthers 6.5–7.5 mm long, minutely puberulent dorsally, rarely glabrate, the tips exserted; ovary ca. 1.5 mm long, densely hirtellous; style head 2.5–3 mm long; disk glands about as long as the ovary. Follicles 27–31 × 0.2–0.4 cm long, very minutely and densely puberulent, moniliform; seeds 14–16 mm long, very minutely papillate puberulent, coma 2.7–3.5 cm long, tannish.

DISTRIBUTION AND PHENOLOGY. *Laubertia contorta* is endemic to central and southern Mexico, at 50–1550 m elevation. It flowers from June to October. Fruiting collections are from September to December.

This species is somewhat related to the South American *Laubertia boissieri*, from which it can be distinguished chiefly by the twisted corolla tube and its disjunct geographical distribution.

SPECIMENS EXAMINED: MEXICO. Chiapas: along road from Tuxtla Gutiérrez to the Chicoasen, San Fernando, 9 Sep 1976 (fl), *Breedlove 39960* (MO); E of Motozintla, road to Frontera Comalapa, Amatenango, 18 Sep 1988 (fl, fr), *Martínez & Stevens 23849* (INB, MEXU); Tuxtla Gutiérrez, 5 Jul 1990 (fl), *Reyes et al. 1755* (BM, INB, MEXU). Guerrero: Temascaltepec, Ixtapan, 23 Jul 1932 (fl), *Hinton 1156* (G, K, MO); Chorrera, Temascaltepec, 24 Jun 1933 (fl), *Hinton 4581* (K); Naranjo, Temascaltepec, 17 Oct 1933 (fl, fr), *Hinton 5009* (K [2 sheets], MO); Ixtapan, 24 Jun 1935 (fl), *Hinton 7919* (K, MO); Placeres, Mina, 31 Jul 1936 (fl), *Hinton 9183* (K, MO); Montes de Oca, 1 Jul 1937 (fl), *Hinton 10544* (K, MO [2 sheets], TEX); Atoyac, Galeana, 12 Aug 1937 (fl), *Hinton 11005* (K); Petatlán, Acapulco – Zihuatanejo Road, 22 Oct 1983 (fl), *Martínez*

& Silva 5898 (INB, MEXU). Jalisco: Estación Chamela, Arroyo Colorado, 12 Aug 1985 (fl), *Ayala 115* (MEXU, MO); Estación Biológica Chamela, 13 Oct 1983 (fl), *Lott & Hernández 1484* (MEXU, MO). México: near Mexicaltepec, NW of Iguala, 6 Jul 1982 (fl), *Soto & Martínez 3969* (MEXU, MO). Nayarit: SW of Jesús María, road to La Mesa del Nayar, 28 Jul 1990 (fl), *Flores et al. 2127* (MEXU, MO). Oaxaca: Chinantla, 1840 (fl), *Galeotti 1596* (G), *Galeotti 1600* (G, P); La Gritona, SW of Putla to Pinotepa Nacional, 5 Apr 1982 (fl), *Torres & Tenorio 230* (MEXU, MO). San Luis Potosí: San Luis Potosí, Huasteca Potosina, date lacking (fr), *Villa s.n.* (CIIDIR, INB). Sinaloa: Concordia, Mazatlán – Durango Road, 6 Dec 1982 (fr), *Aguilar et al. 102* (INB, MEXU); Rosario, NE of Chilillos, 26 Jul 1983 (fl), *Martínez et al. 4067* (MEXU, MO); Sierra Madre, near Colomás, Jul 1897 (fl), *Rose 1716* (MO, US). Data lacking: *Sessé y Lacasta & Moçiño 5175* (MA, photograph Field negative 41244 at INB).

3. Laubertia peninsularis Woodson, Ann. Missouri Bot. Gard. 23: 374. 1936. TYPE: BELIZE. Undesignated locality near Belize–Guatemala boundary, date lacking (fl), *Schipp s.n.* (HOLOTYPE: MO!). Figure 5.

Laubertia gentlei Lundell, Wrightia 5: 256. 1976. TYPE: BELIZE. Toledo: Manga Camp, Edwards Road beyond Columbia, 12 Apr 1948 (fl), *Gentle 6505* (HOLOTYPE: TEX!; ISOTYPES: F!, MO!, S!, photograph Field negative 61421 at INB *ex* F!).

Liana; branchlets terete to subterete, densely ferrugineous-tomentulose, sparsely puberulent at maturity; nodal colleters less than 1 mm long, inconspicuous. Leaves opposite, petioles 9–36 mm long; blade 4.2–11.5 (–13.2) × 1.5–4.7 (–6.8) cm, membranaceous, elliptic or narrowly elliptic to narrowly ovate-elliptic, very sparsely puberulent above, densely ferrugineous-puberulent beneath, turning glabrate at maturity, acuminate to caudate-acuminate apically, obtuse or rounded to very obscurely cordate basally. Inflorescence variously shorter or longer than the subtending leaves, axillary, densely and minutely ferrugineous-puberulent, many-flowered, the flowers agglomerate at ends of the branches; peduncle 41–60 (–155) mm long; pedicels 7–11 mm long; bracts 2–4 mm × 0.5–1 mm, scarious. Sepals 5–10 × 1.5–2 mm, narrowly elliptic to linear, acuminate, ferrugineous-puberulent within and without. Corolla white, tube 10–14 × 2 mm, conspicuously inflated basally, twisted around the stamens; lobes 7–11 × 2 mm, narrowly obovate, spreading; anthers ca. 5 mm long, the tips exserted; ovary 1.5–2 mm long, glabrous; style head ca. 2.5 mm long; disk glands somewhat shorter than the ovary. Follicles unknown.

DISTRIBUTION AND PHENOLOGY. Known only from type collection,

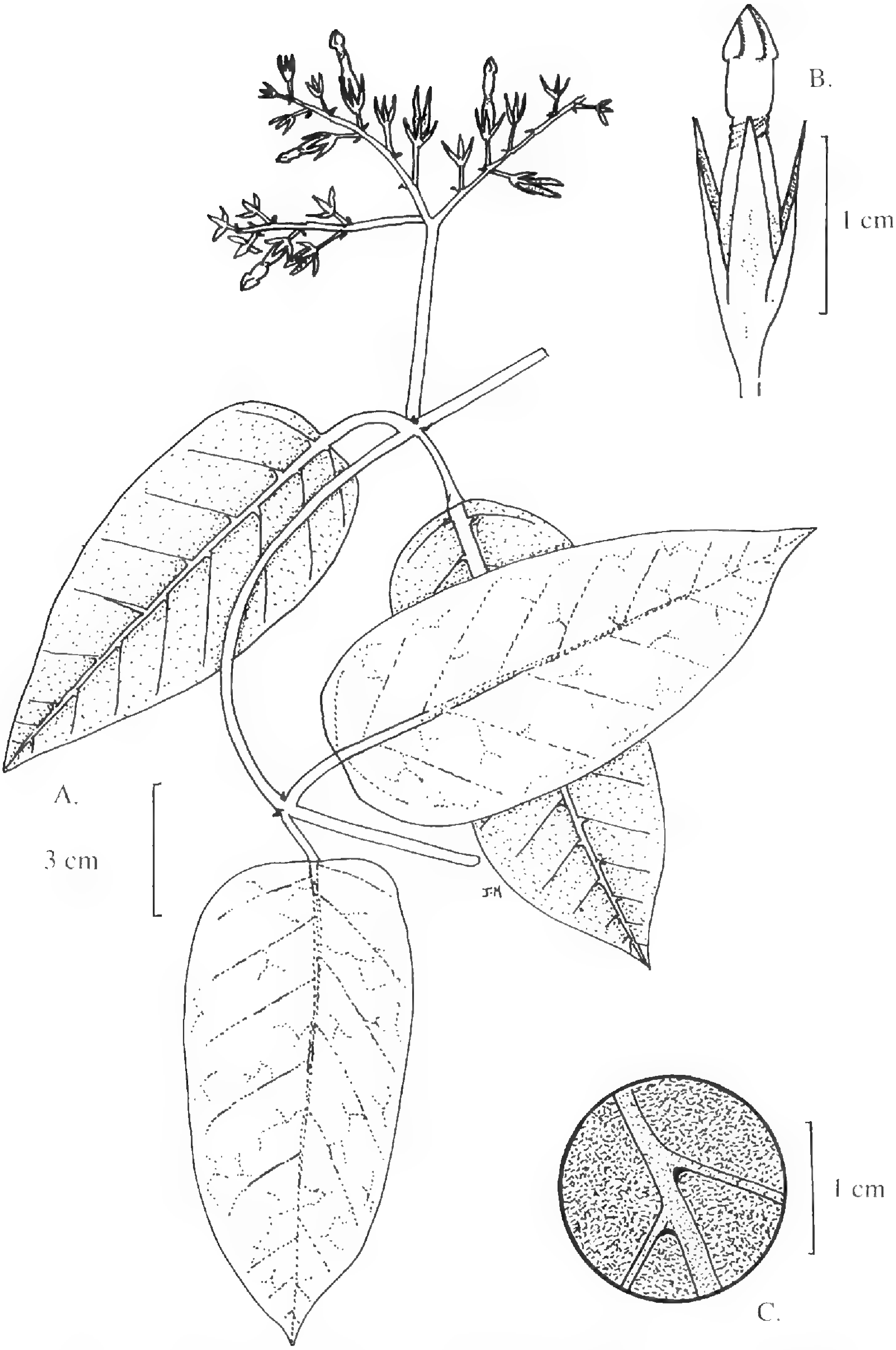

Figure 5. *Laubertia peninsularis* (*Gentle 6505*, MO). A. Habit; B. Corolla and calyx; C. Leaf pubescence (abaxial).

this species is restricted to eastern Guatemala and Western Belize, below 200 m. It flowers in April.

This very distinctive species is poorly known and it has not been collected since the type collection. The main distinguishing character is the small corolla tube, which is twisted around the stamen attachment. The characters used to distinguish *Laubertia gentlei* Lundell from *L. peninsularis* are spurious, as was shown by Morales (1999).

EXCLUDED SPECIES

Laubertia laxiflora Rusby, Bull. New York Bot. Gard. 4: 408. 1907. TYPE: BOLIVIA. Data lacking, *Bang 2056* (HOLOTYPE: NY; ISOTYPES, NY, US, photocopy at INB *ex* NY) = *Odontadenia laxiflora* (Rusby) Woodson.

ACKNOWLEDGMENTS. I thank the curators and directors of BM, BR, C, CIIDIR, CM, COL, F, G, G-BOIS, G-DC, GH, K, LPB, MEXU, MICH, MO, NY, O, P, P-HB, QCNE, S, US, and USF for providing specimens on loan.

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APPENDIX I

INDEX TO NAMES IN SYSTEMATIC TREATMENT

Accepted names in italics.

  E. sanctae-martae Rusby (= *L. boissieri*)

Exothostemon G. Don
  E. contortum (M. Martens & Galeotti) Miers (= *L. contorta*)

Haemadictyon Alph. de Candolle
  H. contortum M. Martens & Galeotti (= *L. contorta*)

Laubertia Alph. de Candolle
  L. boissieri Alph. de Candolle
  L. contorta (M. Martens & Galeotti) Woodson
    gentlei Lundell (= *L. peninsularis*)
  L. peninsularis Woodson
    pringlei (Greenm.) Woodson (= *L. contorta*)
    sanctae-martae (Rusby) Woodson (= *L. boissieri*)

Prestonia R. Br.
  P. contorta (M. Martens & Galeotti) Hemsl. (= *L. contorta*)
  P. langlassei Standl. (= *L. contorta*)

Streptotrachelus Greenm.
  S. pringlei Greenm. (= *L. contorta*)

APPENDIX 2

INDEX TO EXSICCATAE

Aguilar, R. et al. 102 (2)
André, E. 4051 (1)
Ayala, M. et al. 115 (2)
Breedlove, D. 39960 (2)
Burham, C. 1794 (1)
Campos, J. & O. Díaz 2412 (1)
Cerón, C. 2628 (1); 3687 (1)
Eggers, B. 15684 (1)
Flores, G. et al. 2127 (2)
Galeotti, H. G. 1588 (2); 1596 (2); 1600 (2)
Gentle, P. 6505 (3)
Gentry, A. & C. Dodson 54859 (1)
Gentry, A. et al. 72942 (1)
Hinton, G. 1156 (2); 4581 (2); 5009 (2); 7919 (2); 9183 (2); 10544 (2); 11005 (2)
Humboldt, F. W. H. A. & A. J. A. Bonpland, 3627 (1)
Langlassé, E. 435 (2)
Lewis, M. 40417 (1)
Lott, E. & R. Hernández 1484 (2)
Macbride, J. 3902 (1); 5473 (1)
Martínez, E. & N. Silva 5898 (2)
Martínez, E. & W. Stevens 23849 (2)
Martínez, E. et al. 4067 (2)
Neill, D. 10081 (1)
Pavón, J. A. *s.n.* (1)

Pringle, C. 6554 (2)
Reyes, A. et al. 1755 (2)
Romero-Castañeda, R. 762 (1)
Rose, J. 1716 (2)
Schipp, W. *s.n.* (3)
Seidel, R. & E. Vargas 1103 (1)
Sessé y Lacasta, M. & J. Moçiño 5175 (2)
Smith, D. N. et al. 5625 (1)
Smith, H. 1643 (1); 2525 (1)
Solomon, J. & M. Nee 14272 (1)
Soto, J. & E. Martínez 3969 (2)
Torres, E. & P. Tenorio 230 (2)
Vásquez, R. & R. Vásquez 20860 (1)
Villa, J. *s.n.* (2)
Woytkowski, F. 5680 (1); 6326a (1); 6353 (1)

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STUDIES IN NEOTROPICAL APOCYNACEAE II: A REVIEW OF THE GENUS *FERNALDIA*

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ABSTRACT. A synopsis of the three species of *Fernaldia,* a genus of Neotropical Apocynaceae restricted to Central America, is presented here. A summary of descriptive morphology, specific relationships, and synonymy is provided.

Key Words: Gentianales, Apocynaceae, Apocynoideae, *Fernaldia,* Neotropics

Fernaldia Woodson is a genus of vines characterized by eglandular leaves that lack colleters along the midrib adaxially, sepals with a single colleter within, racemose inflorescence, corolla tube without annular corona or free corona lobes within, and corolla lobes usually villose adaxially. The genus was first proposed by Woodson in 1932 in honor of Merrit Lyndon Fernald (1873–1950), of the Gray Herbarium (GH), Harvard University. It occurs from Mexico to northern Panama. Despite their ornamental and edible features, these plants are rarely collected and very few herbarium specimens exist. *Fernaldia* was last treated by Woodson (1936), when two species were known. Several new names for species or varieties have been published since then, but no recent revision exists. Therefore, a revision of the genus is presented here. A key to the species, along with descriptions, illustrations, and citations of selected specimens are given below. Specimens from St. Petersburg (formerly Leningrad), Russia (LE), cited here were examined at the Missouri Botanical Garden (MO), where some material is on loan.

NOTEWORTHY MORPHOLOGICAL FEATURES

Sepals. In *Fernaldia,* the sepals are further solitary, truncate, and sometimes very deeply lacerate apically (Figure 1). The sepals are characterized by having a single colleter within adaxially. Within the subfamily Apocynoideae, the sepal colleters can be a very helpful character to distinguish genera.

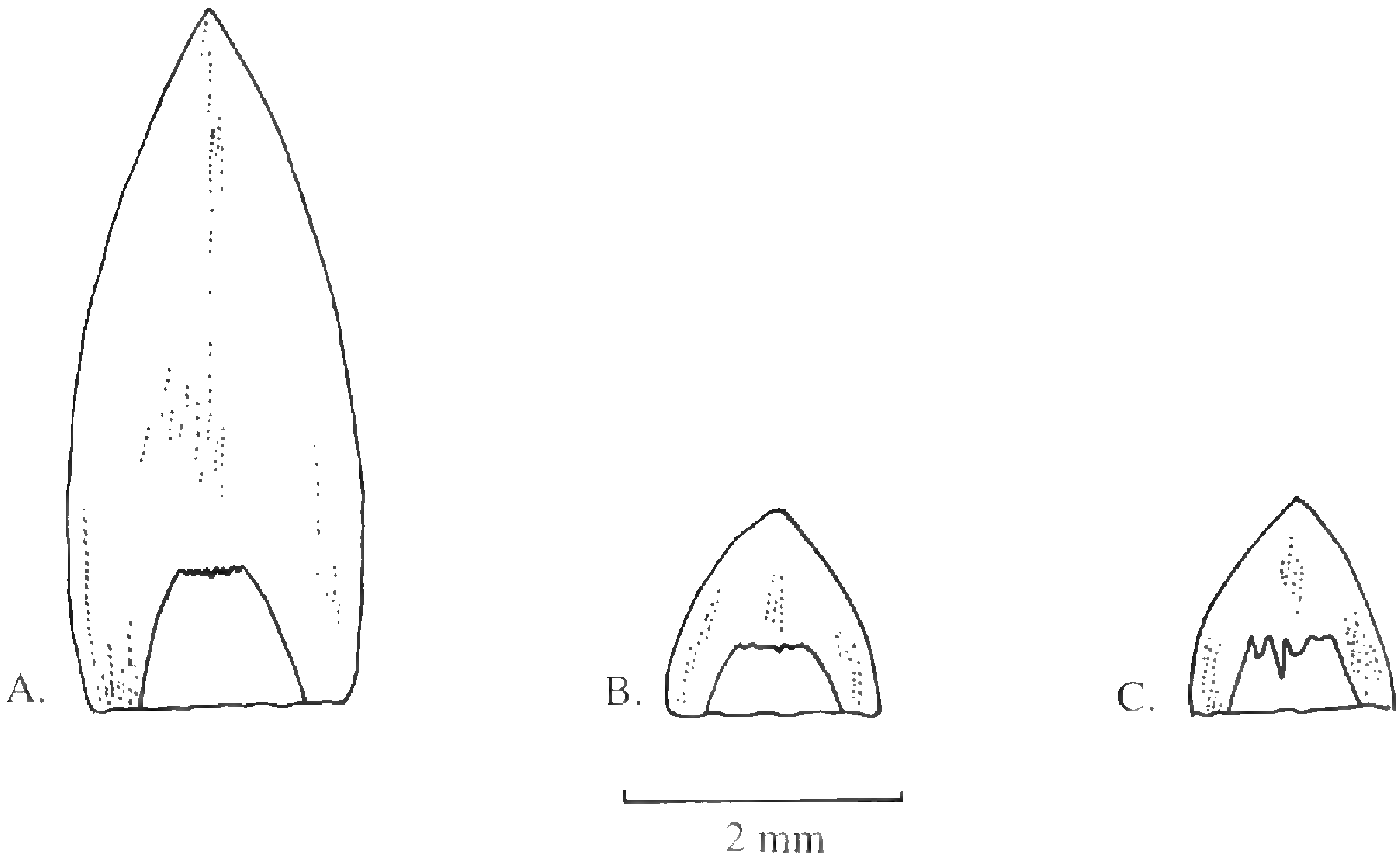

Figure 1. *Fernaldia* sepals. A. *F. speciosissima* (*Morales 7131,* INB); B. *F. pandurata* (*Morales 3074,* INB); C. *F. asperoglottis* (*Mexia 8751,* INB).

Corolla pubescence. When Woodson described *Fernaldia* (1932), one of the features mentioned by him to distinguish the genus was the conspicuously arachnoid-villous corolla lobes. After careful field study of the three species of the genus, it is suitable to note that the pubescence is restricted mostly to the corolla throat and just at the base of the lobes. The hairs are long (2–3 mm), always conspicuous in fresh material, and invariably white to greenish-white. In related genera (e.g., *Echites, Temnadenia*), the upper part of the corolla tube and the mouth are glabrous to glabrate, and never with long hairs.

Following Morales (1999), in the key and species descriptions in this paper, the lower part of the corolla tube is measured from the base of the corolla up to the position where it is expanded abruptly (stamens attachment). The length of the upper part is measured from this point to the base of the lobes.

Anthers. The anther shape in *Fernaldia* is a very important feature to recognize this genus from other closely related genera such as *Echites* and *Temnadenia.* In *Fernaldia,* the anther auricles are usually obtuse to almost rounded basally, while in the other genera the auricles are conspicuously acute to acuminate; only *F. pandurata* (Alph. de Candolle) Woodson has auricles very shortly and broadly acute. However, the most striking difference is the

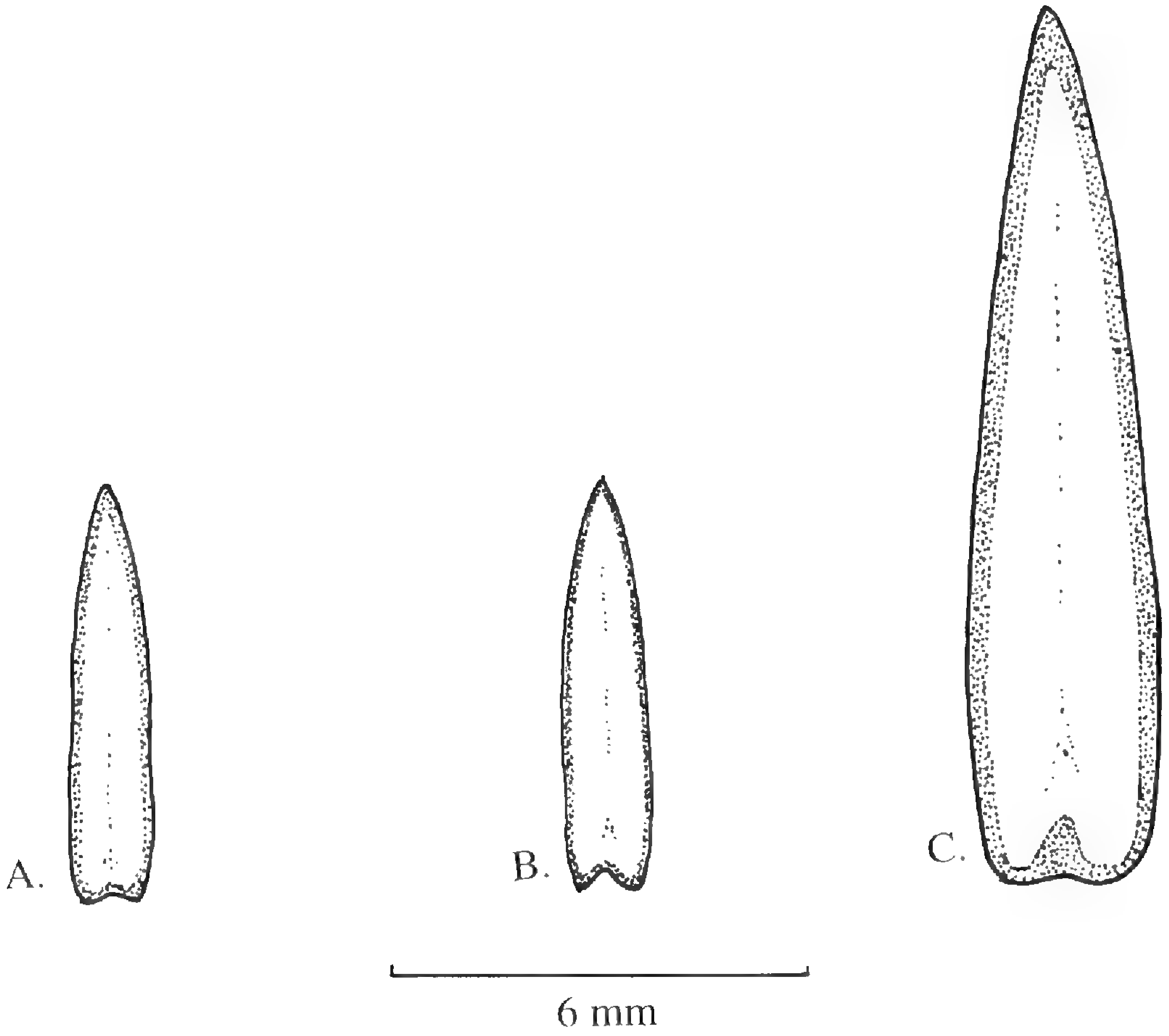

Figure 2. *Fernaldia* anthers. A. *F. asperoglottis* (*Mexia 8751,* INB); B. *F. pandurata* (*Morales 3074,* INB); C. *F. speciosissima* (*Morales 7131,* INB).

presence of a hyaline border in the anthers of *Fernaldia* (Figure 2), a character never present in the three other related genera.

TAXONOMIC TREATMENT

Fernaldia Woodson, Ann. Missouri Bot. Gard. 19: 48. 1932.TYPE: *F. pandurata* (Alph. de Candolle) Woodson.

Echites P. Browne, Civ. Nat. Hist. Jamaica. 182. 1756, in part.
Mandevilla Lindl., Edward's Bot. Reg. 26: t. 7. 1840, in part, *nom. cons.*
Amblyanthera Müll. Arg., Fl. Bras. (Martius) 6(1): 141. 1860, in part.
Urechites Müll. Arg., Bot. Zeitung (Berlin) 18: 22. 1860, in part.
Angadenia Miers, Apocyn. S. Am. 173. 1878, in part.

Suffruticose lianas. Stems terete to subterete, glabrous or glabrate to very minutely and variously puberulent; nodes with few intrapetiolar conical to conical-fusiform inconspicuous colleters.

Leaves opposite, petiolate, petiole slightly fused at the base; blade glabrous or glabrate to variously puberulent beneath, eglandular, without basal colleters adaxially. Inflorescence racemose, axillary, usually many-flowered, very minutely puberulent to glabrous or glabrate, pedunculate, bracts scarious, inconspicuous. Sepals 5, essentially equal, very slightly imbricate basally, with a single colleter within, truncate, entire to variously and very minutely erose or fimbriate; corolla infundibuliform, glabrous or glabrate to very minutely and variously puberulent without, the lobes variously pubescent adaxially (very rarely almost glabrous in *Fernaldia pandurata*) with long white hairs, sometimes these restricted mostly to base of the lobe or around the corolla mouth; tube straight, without annular corona or free corona lobes within, the limb 5-parted, actinomorphic, dextrorsely convolute; stamens 5, included, inserted in the upper part of the corolla tube; anthers connivent and adnate to the pistil head, conformed by 2 parallel, uniformly fertile thecae borne adaxially near the apex of an enlarged, peltate connective; auricles almost inconspicuous, broadly rounded basally; carpels 2, united at the apex; pistil head fusiform or subcapitate; ovules numerous, several-seriate, borne on an axile, biseriate placenta; disk annular, usually 5-lobed. Follicles 2, apocarpous, continuous, glabrous to glabrate, dehiscing along the ventral suture; seeds numerous, dry, truncate, comose apically, usually minutely rugose.

The genus comprises three species, ranging from Mexico to northern Panama.

KEY TO THE SPECIES OF *FERNALDIA*

1. Lower part of the corolla tube 2–5 mm long; corolla lobes 8–12 × 7–9 mm .... 1. *F. asperoglottis*
1. Lower part of the corolla tube 18–30 mm long; corolla lobes 9–24 × 9–15 mm .... (2)
    2. Peduncles 2–4.5 cm; upper part of the corolla tube 10–15 mm long; anthers 5–6 mm long; dry forest .... 2. *F. pandurata*
    2. Peduncles 15–23 cm; upper part of the corolla tube 19–24 mm long; anthers 11.5–12.5 mm long; wet forest .... 3. *F. speciosissima*

1. Fernaldia asperoglottis Woodson, Ann. Missouri Bot. Gard. 26: 96. 1939. Type: MEXICO. Guerrero: Sierra Madre del Sur, N

of Río Balsas, 5 Nov 1937 (fl), *Mexia 8751* (HOLOTYPE: MO!; ISOTYPES: ARIZ not seen, CAS!, F!, G!, GH!, NY!, photograph Field negative 56468 at INB *ex* F!). Figure 3.

Liana; branchlets sparsely puberulent to glabrate; nodal colleters inconspicuous or absent, only intrapetiolar colleters present. Leaves: petiole (0.3–) 0.6–2.1 cm; blade 1.8–8 (–11) × 0.8–6.8 cm, membranaceous, ovate, narrowly ovate to elliptic, caudate-acuminate at the apex, obtuse, attenuate to obscurely cordate basally, glabrate above; densely puberulent to glabrate beneath, more rarely glabrous. Inflorescence lax, longer than the subtending leaves, many-flowered, puberulent; peduncle 2–16 (–20) cm; pedicels 4–9 mm; bracts 1.5–2 × 1 mm, scarious; sepals 1–1.5 × 1–1.5 mm, ovate to narrowly ovate, acute, sparsely puberulent, colleters ca. 0.5 mm long, variously erose apically to conspicuously lacerate; corolla white to white-yellow, sparsely puberulent to glabrate without; lower part 2–5 × 2–3 mm; upper part broadly conical to conical-campanulate, 9–19 × 7–12 mm in diameter at the orifice; lobes 8–12 × 7–9 mm, obovate to narrowly-obovate, spreading; anthers 4.5–6 mm, glabrous; ovary 1.5–2 mm, glabrous; style head ca. 1.5 mm; disk ca. 1.5 mm long, annular, irregularly lobed. Follicles 20–23 × 0.5–0.6 cm, smooth and glabrate; seeds 1–1.2 × 0.2 cm, rugose, very minutely and inconspicuously puberulent, coma 3–3.5 cm, creamish.

DISTRIBUTION AND PHENOLOGY. This species is restricted to Mexico, in Guerrero, Michoacán, and Mexico states, at 200–1350 m. *Fernaldia asperoglottis* flowers September to March. Fruits are borne from October to April.

Fernaldia asperoglottis is distinguished from other species in the genus by having a conspicuously short corolla tube. Furthermore, the corolla lobes are shorter than in any of the other species, only 8–12 mm long. This species may also resemble some species of the genus *Mandevilla,* more specifically the complex around *M. convolvulacea* (Alph. de Candolle) Hemsl. and *M. andrieuxii* (Müll. Arg.) Hemsl., with which it shares a similar leaf shape and inflorescence structure. However, *F. asperoglottis* is easily recognized by its eglandular leaves, without colleters along the midrib adaxially.

SPECIMENS EXAMINED: MEXICO. Guerrero: Temascaltepec, Guayabal, 11 Feb

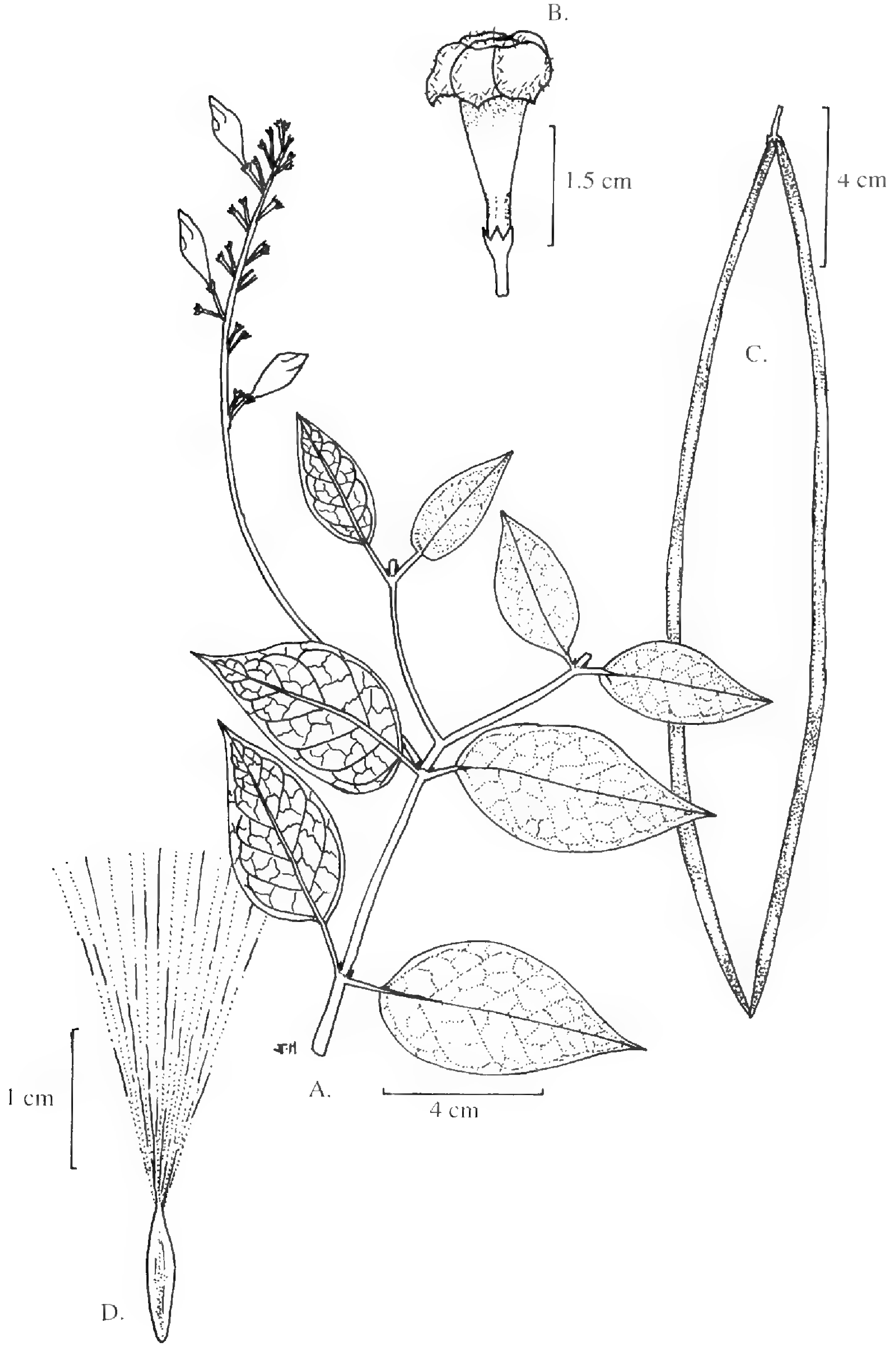

Figure 3. *Fernaldia asperoglottis* (*Mexia 8751*, MO). A. Habit. B. Calyx and corolla. C. Fruits. D. Seed.

1933 (fl, fr), *Hinton 3372* (K [2 sheets]); Pungarabato, Coyuca, 23 Feb 1934 (fr), *Hinton 5683* (K [2 sheets]); Temascaltepec, Guayabal, 16 Jan 1935 (fl, fr), *Hinton 7239* (K [2 sheets]); Coyuca, Quebradas, 22 Jan 1935 (fr), *Hinton 7261* (K [2 sheets]); Placeres, Cigarillo, 11 Mar 1936 (fl, fr), *Hinton 9786* (K); N of La Unión, road to Coahuayatla, 24 Oct 1983 (fl), *Soto & Nuñez 6067* (MEXU, MO). Mexico: San Antonio Tlatlaya, 25 Jan 1953 (fl), *Matuda et al. 28003* (MEXU, MO); between Sultepec and Amatepec, 31 Dec 1953 (fl), *Matuda 30097* (MEXU, MO); Los Bejucos, Tejupilco, 27 Aug 1954 (fl), *Matuda et al. 31389* (MEXU, MO); Otzoloapan, Valle del Bravo, 5 Sep 1954 (fl), *Matuda et al. 31416* (MEXU, MO); La Junta, Valle del Bravo, 11 Sep 1954 (fl), *Matuda et al. 31649* (MEXU, MO). Michoacán: Tuzantla-Paso Tierra Caliente, 10 Mar 1938 (fl, fr), *Hinton 13308* (K, MO, NY); Ajuage, Apatzingán, 13 Oct 1939 (fl), *Hinton 15329* (G, K, NY, P); Puente Las Pilas, road Zitácuaro-Huetamo, 3 Dec 1983 (fl), *Lott 2157* (INB, MEXU, MO); SW of La Huacana, 31 Dec 1977 (fr), *Soto 592* (MEXU, MO); NW of La Eréndina, road to Casácuaro, 6 Sep 1981 (fl), *Soto 3016* (MEXU, MO); San Jerónimo, road Huetamo–San Jerónimo, 8 Oct 1981 (fl), *Soto 3227* (MEXU, MO); Tumbiscatio, road Nueva Italia–Playa Azul, 28 Oct 1981 (fl, fr), *Soto 3586* (MEXU, MO).

2. Fernaldia pandurata (Alph. de Candolle) Woodson, Ann. Missouri Bot. Gard. 19: 48. 1932. Figure 4.

Echites pandurata Alph. de Candolle, Prodr. (DC.) 8: 458. 1844. *Amblyanthera pandurata* (Alph. de Candolle) Müll. Arg., Linnaea 30: 448. 1860. *Angadenia pandurata* (Alph. de Candolle) Miers, Apocyn. S. Am. 182. 1878. TYPE: MEXICO. Oaxaca: San Dionicio, Aug 1832 (fl), *Andrieux 245* (LECTOTYPE selected here: G-DC!; ISOLECTOTYPES: K!, photograph Field negative 7559 at F!, INB!, MO!, NY!, US *ex* G-DC!).

Urechites karwinskii Müll. Arg., Linnaea 30: 440. 1860. TYPE: MEXICO. Tamaulipas?: "Huefulta," 1841–1842 (fl), *Karwinsky 474* (LECTOTYPE selected here: LE!).

Echites barbata Sessé & Moc., Naturaleza (Mexico City), Ser. 2, 2 (App.): 45. 1893, non Desvaux *ex* Hamitten 1825, nec. D. Dietrich 1839. TYPE: MEXICO: Data lacking (fl in August), *Sessé y Lacasta & Moçiño 5671* (HOLOTYPE: MA not seen; ISOTYPE: F!).

Mandevilla velutina K. Schum. *in* Engl. & Prantl, Nat. Pflanzenfam. 4(2): 171. 1895. TYPE: COSTA RICA. Data lacking (fl), *Hoffmann 710* (HOLOTYPE: B-destroyed, photograph Field negative 4533 at F!, INB!, MO!, US!); COSTA RICA. Guanacaste: Nandayure, Pacífico Norte, Bejuco, Cerro La Picuda, 24 Aug 1994 (fl), *Estrada & Rodríguez 193* (NEOTYPE selected here: INB!; ISONEOTYPES: CR!, MO!).

Mandevilla potosina Brandegee, Univ. Calif. Publ. Bot. 4: 276. 1912. TYPE: MEXICO. San Luis Potosí: Rascón, Aug 1911 (fl, fr), *Purpus 5408* (HOLOTYPE: UC!; ISOTYPES: F!, BM!, MO!, NY!, photograph Field negative 56477 at INB *ex* F!).

Echites pinguifolia Standl., Publ. Field Columbian Mus., Bot. Ser. 8(1): 35. 1930. TYPE: MEXICO. Yucatán: Izamal, 1895 (fl, fr), *Gaumer 815* (HOLOTYPE: F!; ISOTYPE: MO!; photograph Field negative 56462 at INB *ex* F!).

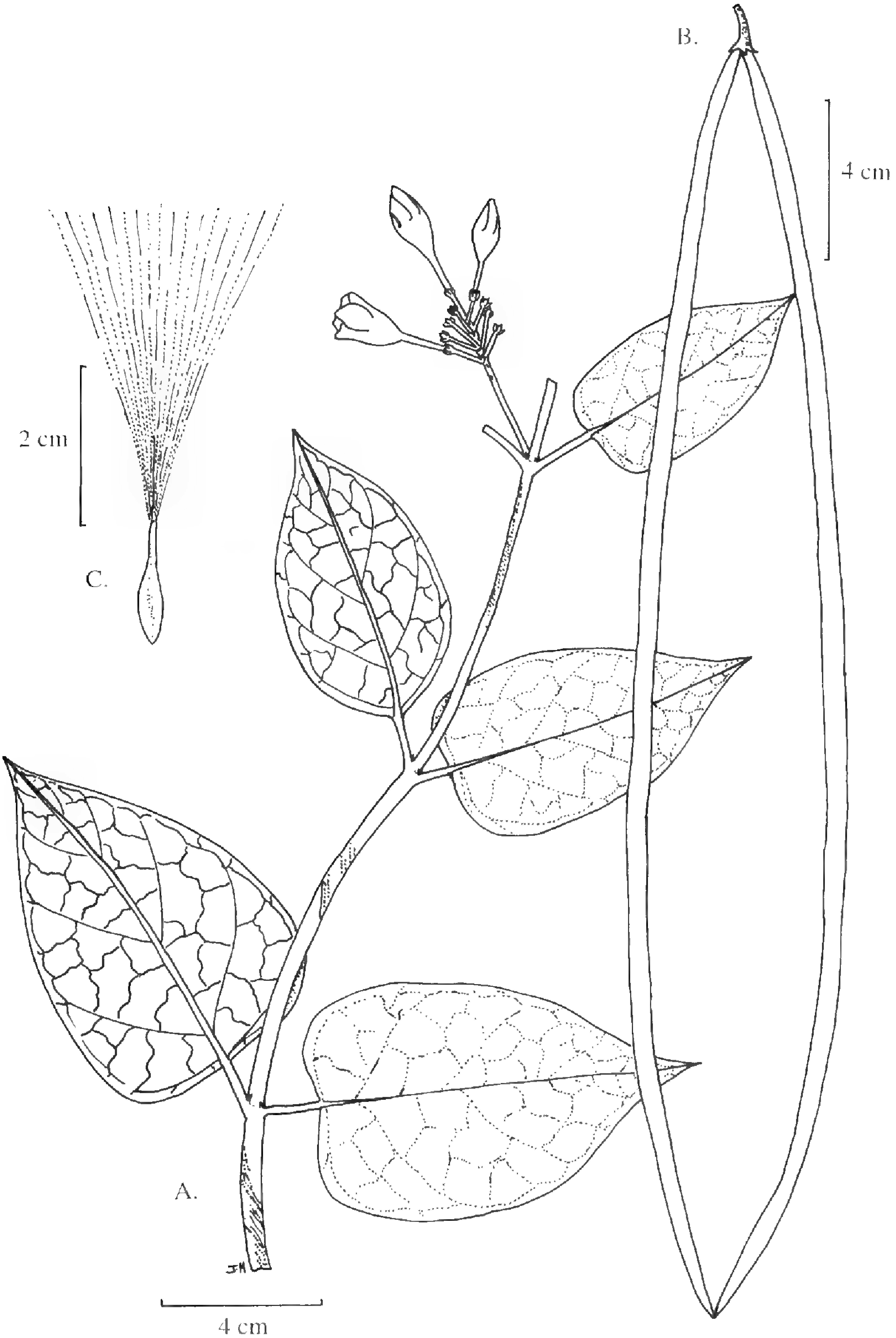

Figure 4. *Fernaldia pandurata* (*Morales 3074*, INB). A. Habit; B. Fruits; C. Seed.

Fernaldia brachypharynx Woodson, *syn. nov.*, Ann. Missouri Bot. Gard. 19: 380. 1932. TYPE: GUATEMALA. Along the road from Escuintla to the port of San José de Guatemala, 23 Aug 1860 (fl), *Hayes s.n.* (HOLOTYPE: GH!).

Fernaldia pandurata var. *glabra* Ant. Molina, Ceiba 3: 95. 1952. *Fernaldia glabra* (Ant. Molina) Lundell, Wrightia 5: 256. 1976. TYPE: HONDURAS. Cortés: faldas de la Montaña Santa Ana, Río Santa Ana, 6 Dec 1950 (fl), *Molina 3640* (HOLOTYPE: EAP!; ISOTYPES: F!, photograph Field negative 56469 at INB *ex* F!).

Liana; branchlets sparsely puberulent to glabrate; nodal colleters inconspicuous or absent, only intrapetiolar colleters present. Leaves: petiole 0.9–4 cm; blade 5–14 (17) × 4–11 cm, membranaceous, ovate, ovate-elliptic, narrowly elliptic to variously pandurate, acuminate to caudate-acuminate at the apex, rounded, obtuse to obscurely cordate basally, glabrous to glabrate above, densely puberulent to glabrate or more rarely glabrous beneath. Inflorescence agglomerate, usually shorter than the subtending leaves, rarely longer, few- to many-flowered, glabrate to very minutely and densely puberulent; peduncle 2–4.5 cm; pedicels 4–12 mm; bracts 1.5–3 × 1–1.5 mm, scarious; sepals 1.5–3 × 1.5 mm, ovate to narrowly ovate, acute, very minutely and sparsely puberulent, colleters ca. 0.5 mm long, apex variously lacerate; corolla white to greenish-white or creamish, glabrous to glabrate or very sparsely and minutely puberulent to glabrate without; lower part 18–22 × 2–3 mm; upper part conical, more rarely broadly conical, 10–15 × 8–11 mm in diameter at the orifice; lobes 9–14 × 9–11 mm, obovate to narrowly-obovate, spreading and distally reflexed; anthers 5–6 mm, glabrous to glabrate, rarely minutely puberulent; ovary 1.5–2 mm, glabrous; style head ca. 2.5 mm; disk 1–1.5 mm long, 5-lobed to variously lobed. Follicles 21–36 × 0.5–0.6 cm, rugose, glabrous to glabrate; seeds 1.4–1.6 × 0.2 cm, minutely rugose, coma 4–4.5 cm, creamish.

DISTRIBUTION, PHENOLOGY, AND LOCAL NAMES. México to northwestern Costa Rica, mostly in dry forest or in open and second-growth forest, 0–1200 m. Flowering June to December. Fruiting March to January. Known locally as Loroco (Jutiapa, Guatemala; Cortez, Honduras; Ahuachapán, El Salvador).

The available specimens of *Fernaldia pandurata,* the most common and widespread species, show that leaf shape and pubescence are morphological features that are highly variable within this taxon. Although there are slight differences scattered throughout the plant's geographic range, they are mostly sporadic in ocurrence and do not merit taxonomic recognition. Within the Apocynaceae subfamily Apocynoideae, the acceptance of species defined only by pubescence is unwarranted (Morales 1997, 1999). Therefore, *F. pandurata* var. *glabra* and the subsequent combination based on this name are not recognized here.

Fernaldia brachypharynx is here considered a synonym of *F. pandurata,* showing only slight differences in corolla length. Additional specimens examined since Woodson's monograph reveal that this feature is variable within the geographical range.

In northern Mesoamerica, the flowers of this species have been used as a flavoring for rice (Woodson 1936). For further references, see the work of Morton et al. (1990).

Mandevilla velutina K. Schum. is neotyfied here. No other duplicates were found in BM, C, or K, where Hoffmann specimens are located.

SPECIMENS EXAMINED: COSTA RICA. Guanacaste: Cañas, La Pacífica, 10 Nov 1969 (fl, fr), *Daubenmire 256* (F, USJ), 2 Mar 1970 (fl, fr), *Daubenmire 592* (F, USJ); Finca La Pacífica, 3 Sep 1972 (fl), *Heithaus 350* (MO); Parque Nacional Palo Verde, 30 July 1994 (fl, fr), *Morales 3074* (INB); La Pacifica, NW of Cañas, 20 Nov 1972 (fl), *Opler 1568* (CR, F, MO [2 sheets]); Palo Verde National Park, 11 Dec 1996 (fl, fr), *Rodríguez et al. 1829* (INB, MO); Palo Verde, 7 Sep 1973 (fl, fr), *Solomon 611* (CR, F, USJ).

EL SALVADOR. Ahuachapán: San Benito, E of San Alfonso, El Imposible, 12 Jun 1993 (fl), *Sandoval & Sandoval 1309* (B, LAGU, MO); El Imposible National Park, San Alfonso, 10 Jul 1990 (fl), *Sermeño 232* (B, LAGU, MO).

GUATEMALA. Chiquimula: between Ramírez and Cumbre de Chiquimula, 15 Oct 1940 (fl), *Standley 74496* (F, MO). Jutiapa: vicinity of Jutiapa, 1940 (fl), *Standley 75297* (F, MO). Petén: exact locality lacking, 12 Aug 1967 (fl), *Contreras 7008* (K, LL). Santa Rosa: vicinity of Chiquimula, 1940 (fr), *Standley 79683* (F, MO).

HONDURAS. Cortés: Santa Ana mountain, Río Santa Ana, 6 Dec 1950 (fl), *Molina 3640* (BM, EAP, MO). Morazán: Villa San Roque, Sep 1948 (fl), *Standley 26257* (BM, F).

MEXICO. Chiapas: near Chiapilla, 14 Nov 1980 (fl), *Breedlove 47493* (MO); along the road from Acala to Venustiano Carranza, 25 Oct 1966 (fl), *Laughlin 2669* (MO); Ocozocoautla, 19 Sep 1988 (fl), *Reyes & Urquijo 1015* (BM, MEXU). Guerrero: Sierra Madre, 8 Nov 1898 (fl, fr), *Langlassé 597* (G [3 sheets], K, P); Acapulco, Oct 1894 – Mar 1895 (fl), *Palmer 259* (K). Jalisco: Tonalá, La Cruz, Barranca de la Cruz, 9 Jan 1975 (fr), *Díaz 5484* (ENCB, INB). Nayarit: SE of Ahuacatlán, 2 Jan 1986 (fr), *Téllez 9371* (INB, MEXU). Oaxaca: exact locality lacking, 1834 (fl), *Andrieux 246* (G-DC, K); W of Tuxtepec, along road to Ixcatlán, 7 Aug 1971 (fl), *Stevens 1391* (MO). San Luis Potosí: Tamazunchale, 7 Oct 1937 (fl), *Taylor 479* (MO, TEX). Tamaulipas: Sierra de Tamaulipas, region of Rancho Las Yucas, NNW of Aldama, 27 Jul 1957 (fl), *Dressler 2037* (MO). Veracruz: Laguna Encantada, NE of San Andrés Tuxtla, 2 Nov 1971 (fr), *Beaman 5225* (MEXU, MO); El Salto de Eyiplanta, near Sihuapan, 9 Oct 1974 (fl), *Calzada 1567* (MO); Baños del Carrizal, Aug 1912 (fl), *Purpus 6020* (BM, MO); Baños del Carrizal, Aug 1912 (fl), *Purpus 6232* (MO). State unknown: Boca del Monte, date lacking (fl), *Andrieux s.n* (G); 1833 (fl), *Andrieux 399* (G, K). Data lacking: (fl), *Coulter 958* (K [2 sheets]); *Sessé y Lacasta & Moçiño 5080,* (MA; photograph Field negative 41240 at INB).

NICARAGUA. Boaco: San José de los Remates, N of Teustepe, Cerro Alegre, 10 Oct 1982 (fl), *Sandino 3680* (MO). Chinandega: along road Somotillo – Cinco Piños, 11 Oct 1993 (fr), *Rueda & Dolmus 1170* (MO); Volcán San Cristobal, N of Chinandega, 23 Aug 1984 (fl), *Soza & Grijalva 166* (MO). Estelí: San Juan de Limay, Valle La Cascada, 1 Sep 1980 (fl), *Moreno 1893* (MO); Paso León a Estelí, 23 Oct 1983 (fl), *Moreno 22321* (MO). León: La Paz Centro, road to Momotombo, 13 Jul 1981 (fl), *Moreno 9834* (MO); along Río Sinecapa, 15 Sep 1977 (fl), *Stevens 3865* (MO); S of Estelí, road to Estanzuela, 11 Aug 1978 (fl), *Stevens 9960* (MO). Matagalpa: Ranchería, NE of Muy Muy, 20 Aug 1984 (fl), *Moreno 24434* (MO). Nueva Segovia: N of edge of Ocotal, Quebrada El Nancital, 7 Aug 1977 (fl), *Stevens 3057* (BM, MO). Rivas: Isla Ometepe, Volcán Concepción, San José del Sur, 12 Dec 1984 (fl), *Robleto 1566* (MO); SE of San Juan del Sur, NW of Río La Flor, Playa El Coco, 11 Sep 1977 (fl), *Stevens 3865* (BM, MO).

3. Fernaldia speciosissima Woodson, Ann. Missouri Bot. Gard. 26: 300. 1939. TYPE: PANAMA. Chiriquí: Río Chiriquí to Remedios, 11 Jul 1938 (fl), *Woodson et al. 1179* (HOLOTYPE: MO!, photograph at INB!). Figure 5.

Liana; branchlets glabrous; nodal colleters inconspicuous, ca. 1 mm long. Leaves: petiole 2.5–6 cm; blade 9.5–14 × 4–10 cm, membranaceous, elliptic to broadly elliptic, glabrous, shortly acuminate to caudate-acuminate at the apex, obtuse to rounded basally. Inflorescence lax, longer than the subtending leaves, many-flowered, glabrous; peduncle 15–23 cm; pedicels 10–18 mm; bracts 1.5–2.5 × 1 mm, scarious; sepals 3–5 × 1.5–2 mm, ovate, acute to obtuse, glabrous; colleters ca. 1 mm long, apex scarcely and very minutely fimbriate; corolla creamish to creamish-white, glabrous; lower part 20–30 × 1.5–2 mm; upper part 20–30 × 6–8 mm in diameter at the orifice; lobes 19–24 × 10–15 mm, obovate to narrowly-obovate, spreading and somewhat reflexed; anthers 11.5–12.5 mm, glabrous; ovary 3 mm long, glabrous; style head ca. 3 mm; disk ca. 1 mm long, inconpicuously 5-lobed. Follicles 33–34 × 0.6–0.7 cm, smooth, glabrous to glabrate; seeds unknown.

DISTRIBUTION, HABITAT, AND PHENOLOGY. This species is restricted

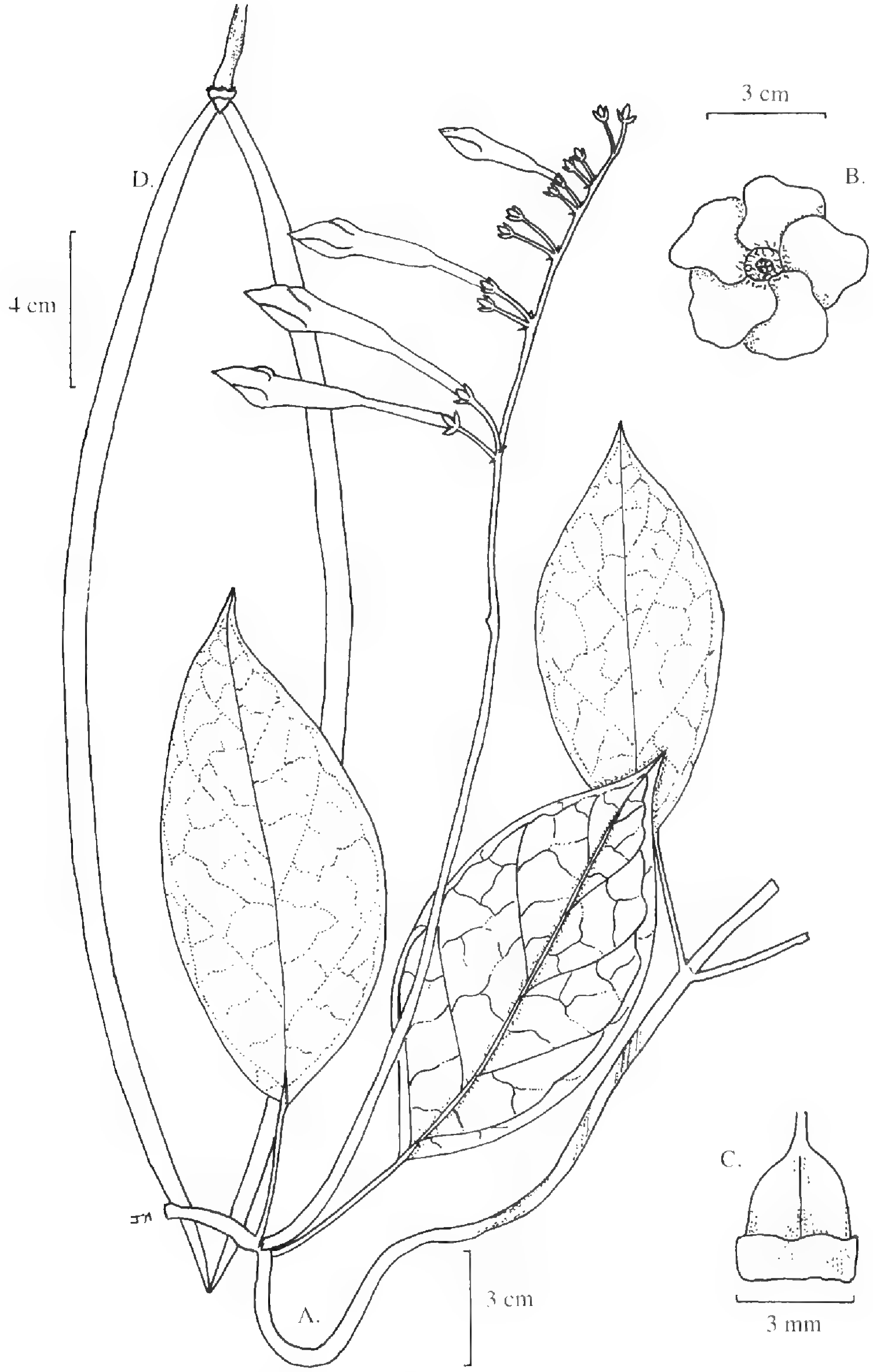

Figure 5. *Fernaldia speciosissima* (*Morales 7131*, INB). A. Habit; B. Corolla lobes; C. Ovary and disk; D. Fruits.

to wet forest or seasonal wet forest in southwestern Costa Rica and northwestern Panama, at 90–600 m. Until recent flowering collections from Costa Rica were made, the species was known only from the type collection. *Fernaldia speciosissima* flowers in July and fruits from December to January.

Fernaldia speciosissima was described by Woodson based on just three fallen corollas found in Chiriquí, Panama in 1938. Although he was exasperated to base a new species on such limited material, Woodson (1939) said that "The anthers, stigma and arachnoid internal villosity of the corolla are all unmistakable characters," which was nicely confirmed with the Costa Rican flowering material.

The flowers are very fragant, with a smell similar to crushed fig leaves (*Ficus carica* L., Moraceae), and upon tasting they produce a very sweet flavor. However, none of the local people from the collection locality know of any use for the plant.

SPECIMENS EXAMINED: COSTA RICA. San José: Acosta, Fila Aguabuena, Río Tiquires, on road to Zoncuano, 11 Jul 1999 (fl), *Morales 7131* (CR, INB, MO, K).

PANAMA. Panamá: SE side of Madden Lake, near Puente Natural, 1 Jan 1975 (fr), *Nee & Hansen 14056* (MO)

ACKNOWLEDGMENTS. I thank the curators and directors of ARIZ, BM, BR, C, CIIDIR, CM, CR, ENCB, F, G, G-BOIS, G-DC, GH, K, MEXU, MICH, MO, NY, O, P, P-HB, S, US, USF, USJ, and UVAL for providing specimens on loan.

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APPENDIX 1

INDEX TO NAMES IN SYSTEMATIC TREATMENT

Accepted names in italics.

Amblyanthera
  A. pandurata (Alph. de Candolle) Müll. Arg. (= *F. pandurata*)

Angadenia
  A. pandurata (Alph. de Candolle) Miers (= *F. pandurata*)

Echites
  E. barbata Sessé & Moç. (= *F. pandurata*)
  E. pandurata Alph. de Candolle (= *F. pandurata*)
  E. pinguifolia Kunth Standl. (= *F. pandurata*)

Fernaldia
  F. asperoglottis Woodson
  F brachypharynx Woodson (= *F. pandurata*)
  F. pandurata (Alph. de Candolle) Woodson
  F. speciosissima Woodson

Mandevilla
  M. potosina Brandegee (= *F. pandurata*)
  M. velutina K. Schum. (= *F. pandurata*)

Urechites
  U. karwinskii Müll. Arg. (= *F. pandurata*)

APPENDIX 2

INDEX TO EXSICCATAE

Andrieux, G. *s.n.* (2); 245 (2); 246 (2); 399 (2)
Beaman, J. 5225 (2)
Breedlove, D. 47493 (2)
Calzada, J. 1567 (2)
Contreras, E. 7008 (2)
Coulter, E. 958 (2)
Daubenmire, F 256 (2); 592 (2)
Díaz, C. 5484 (2)
Dressler, R. 2037 (2)
Estrada, A. & A. Rodríguez 193 (2)
Gaumer, G. 815 (2)
Hayes, S. *s.n.* (2)
Heithaus, E. 350 (2)
Hinton, G. 3372 (1); 5683 (1); 7239 (1); 7261 (1); 9786 (1); 13308 (1); 15329 (1)
Hoffman, C. 710 (2)
Karwinsky, W. F 474 (2)

Langlassé, E. 597 (2)
Laughin, R. 2669 (2)
Lott, E. 2157 (1)
Matuda, E. 30097 (1)
Matuda, E. et al. 28003 (1); 31389 (1); 31416 (1); 31649 (1)
Mexia, Y. 8751 (1)
Molina, A. 3640 (2)
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Palmer, E. 259 (2)
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Robleto, W. 1566 (2)
Rodríguez, A. et al. 1829 (2)
Rueda, R. & R. Dolmus 1170 (2)
Sandino, J. 3680 (2)
Sandoval, E. & M. Sandoval 1309 (2)
Sermeño, A. (2)
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Solomon, J. 611 (2)
Soto, J. 592 (1); 3016 (1); 3227 (1); 3586 (1)
Soto, J. & A. Núñez 6067 (1)
Soza, D. & A. Grijalva 166 (2)
Standley, P. 26257 (2); 74496 (2); 75297 (2); 79683 (2)
Stevens, D. 1391 (2); 3057 (2); 3865 (2); 9960 (2)
Taylor, M. 749 (2)
Téllez, O. 9371 (2)
Woodson, R. et al. 1179 (3)

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NEW ENGLAND NOTE

A NEW NATIVE PLANT FOR MASSACHUSETTS, *CAREX BACKII* (CYPERACEAE)

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Carex backii Boott is one of two members of the section *Phyllostachyae* of the genus *Carex* found in New England. It is distinguished from the other species, *C. willdenowii* Schkuhr *ex* Willd., by having a lower pistillate scale that is wider than the perigynia and concealing them (Catling et al. 1993). It occurs from the Gaspé Penninsula, Québec south through New England, and west to British Columbia, Wyoming, and Colorado (Saarela and Ford 2001). It formerly occurred but has not been found recently in New Jersey and Pennsylvania (Kartesz and Meacham 1999), and appears to have a patchy distribution in its current range. It is uncommon in New England, previously having been reported from Maine, New Hampshire, Vermont, and Connecticut. It is most common in Vermont, with a ranking of S3, corresponding to 21–100 occurrences. Its rank is undetermined in New Hampshire (where it is being reviewed for state listing), and S1 and Endangered in both Connecticut and Maine, with one and several occurrences, respectively (Connecticut Department of Environmental Protection 1998; Maine Department of Conservation 1999; A. Haines, New England Wildflower Society, pers. comm.). The species is a new addition to the native flora of Massachusetts, where it is listed as Endangered. This note reports on the two known Massachusetts occurrences.

One population was discovered in 1997 in open woods on an east-facing slope of Wachusett Mountain in Worcester County

(*Bertin 1587,* 24 Jun 1997, MASS). The population consisted of about 42 clumps, each containing multiple shoots of this "tufted" (Gleason and Cronquist 1991) species. The shallow rocky soil overlies bedrock mapped as biotite granodiorite to tonalite gneiss (Zen 1983). The tree canopy consisted of *Fraxinus americana* L. and *Quercus rubra* L., with a few *Carya ovata* (Mill.) K. Koch. The shrub layer included *Acer pensylvanicum* L., *Crataegus* sp., *Q. rubra*, *Prunus serotina* Ehrh., *P. virginiana* L., and *Betula lenta* L. The herb layer was relatively dense, and was dominated by *Polygonum cilinode* Michx. Other herbaceous species included *Carex communis* Bailey, *C. pensylvanica* Lam., *Deschampsia flexuosa* (L.) Trin., *Parthenocissus quinquefolia* (L.) Planch., *Festuca subverticillata* (Pers.) E. B. Alexeev, *Elymus hystrix* L., *Circaea lutetiana* L., *Maianthemum racemosum* (L.) Link, *Poa* sp., and *Viola* sp.

The second population was discovered during 2001 in the Holyoke Range in Hampshire County (*Searcy 403,* 19 Jun 2001, MASS). Approximately 18 widely separated clumps, each supporting 4–38 culms, were found near the summit of Long Mountain in shallow soil on a steep north-northeast-facing slope of the basalt ridge that makes up the crest of the range. Based on tests conducted by the Soil Testing Lab at the University of Massachusetts, the pH of the A horizon in these soils was 4.7–5.0. Calcium concentrations were high (ca. 2200 ppm), at least an order of magnitude higher than in soils overlying nearby sedimentary rock. As with the first population, the forest canopy was relatively open. Woody species included *Betula lenta, B. papyrifera* Marshall, *Acer rubrum* L., *Ostrya virginiana* (Mill.) K. Koch, *Carya glabra* (Mill.) Sweet, *Tsuga canadensis* (L.) Carrière, *Hamamelis virginiana* L., and *Viburnum acerifolium* L. Conspicuous herbs included *Dryopteris marginalis* (L.) A. Gray, *Parthenocissus quinquefolia, Carex pensylvanica,* and one or more *Carex* in the section *Laxiflorae.*

Carex backii is sometimes considered a calciphile (Scoggan 1950; M. Lapin, consulting ecologist, pers. comm.). The one Connecticut site is a marble ridge in Canaan, Litchfield County (Mehrhoff 1995; T. Rawinski, Massachusetts Audubon Society, pers. comm.). Many of the Vermont records are from soils derived from limestone, dolomite, or other calcareous rocks (M. Lapin, pers. comm.; T. Rawinski, pers. comm.). Maine occurrences seem to span a wider range of soil types. Dibble (1993) reported the species from a rocky bluff with oak-hornbeam forest along with *Hepatica nobilis* Mill. A second Maine location also supports associates that suggest non-acid conditions [e.g., *Carex platyphylla* Carey, *Woodsia obtusa* (Spreng.) Torr., *Aquilegia canadensis* L., *Ranunculus fascicularis* Muhl. *ex* Bigelow, *Arabis missouriensis* Greene; Rawinski, pers. comm.]. However, other Maine sites are in red oak-northern hardwoods forests on apparently acid soils (Haines, pers. comm.). Neither Massachusetts site is basic, though they may be less acid than most Massachusetts soils. We have no information on the Princeton soil type, though areas within several hundred meters downslope support *Adiantum pedatum* L., *Sanguinaria canadensis* L., *Actaea rubra* (Aiton) Willd., *Geranium robertianum* L., and *Caulophyllum thalictroides* (L.) Michx. The New Hampshire site supports a soil with pH of 6–7 on calcite-rich diorite/granodiorite. Associated species include *Cypripedium calceolus* L., *Carex platyphylla, Cynoglossum virginianum* L., and *Dryopteris goldiana* (Hook. *ex* Goldie) A. Gray (E. B. Engstrom, consulting ecologist, pers. comm.).

Carex backii is a relatively inconspicuous plant and rarely seems to occur in extensive populations. This is reflected in the fact that although both Massachusetts and Connecticut are well botanized, the first records from these states are from the last 15 years. Several of the Maine and Vermont records were also added during this period. It seems likely that additional populations of the species occur in New England, and further botanizing on neutral and alkaline soils during the late June to early July fruiting period will reveal some of these.

ACKNOWLEDGMENTS. We thank Lois Somers and Ann E. Silveri for help with field observations and the following individuals for sharing information on occurrences of *Carex backii* in other states: E. Brett Engstrom, Marc Lapin, Les Mehrhoff, Bill Nichols, Tom Rawinski, and Dan Sperduto. Two anonymous reviewers made helpful suggestions on the manuscript.

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NEW ENGLAND NOTE

OCCURRENCE OF *SCIRPUS GEORGIANUS* (CYPERACEAE) IN MAINE

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Scirpus georgianus R. M. Harper is a perennial, grass-like herb of wetland communities. It is closely related to *S. atrovirens* Willd., and the two are part of a group of five morphologically similar species in North America [e.g., *S. atrovirens, S. flaccidifolius* (Fernald) Schuyler, *S. georgianus, S. hattorianus* Makino, and *S. pallidus* (Britton) Fernald]. The *S. atrovirens* complex is recognized by: trifid styles; mucronate scale apices; relatively straight perianth bristles with thin-walled, round-tipped retrorse barbules confined to the distal ½ of the bristle; and a haploid chromosome number of $n = 25–28$ (Schuyler 1967; Schuyler and Whittemore, in press).

Identification of *Scirpus georgianus* relies primarily on perianth bristle morphology. This species frequently lacks bristles altogether. When bristles are present, they number 1–3 per flower, are typically very short (rarely up to 0.75 times the length of the achene), and are smooth or have a few retrorsely oriented barbules near the very tip of the bristle. All other species of the *S. atrovirens* complex have 5 or 6 perianth bristles that are usually more than 0.75 times as long as the achene and are retrorsely barbellate in the distal ½ or more of the bristle. Further, the haploid chromosome numbers of *S. georgianus* ($n = 25$, 26, and 27) are relatively unique in this complex (Schuyler and Whittemore, in press). Only the $n = 27$ cytotype is shared with another species—*S. flaccidifolius* of the mid-Atlantic and southeastern United States.

The taxonomic boundaries of *Scirpus georgianus* have been interpreted differently by different authors over the years. Fernald (1921) reduced this species to a variety as *S. atrovirens* var. *georgianus* (R. M. Harper) Fernald. He recognized this taxon by its shorter perianth bristles and lower leaves with fewer cross-septae. The illustration that accompanies the description in *Gray's Man-*

ual of Botany, (page 274; Fernald 1950) clearly shows four perianth bristles (only one side of the fruit is visible) that are nearly as long as the achene. This indicates that Fernald included within *S. atrovirens* var. *georgianus* a plant considered to be a different species by Schuyler (1967)—*S. hattorianus.* Cronquist (in Gleason and Cronquist 1991) went a step further and included all the species in the complex into a large, variable *S. atrovirens.*

While reviewing specimens of *Scirpus georgianus* at the Harvard University Herbaria, I discovered a specimen annotated by A. E. Schuyler as *S. georgianus* from Maine. This was the first voucher known to me of this species from Maine. Unfortunately, the label did not contain detailed locality information.

SPECIMEN CITATION: UNITED STATES. Maine: York Co., North Berwick, springy, grassy bank, local, 22 Jul 1899, *Parlin 1194* (NEBC).

On 5 August 2001, Lisa Kuronya and I performed a vehicle survey of rural roads in North Berwick for *Scirpus georgianus.* Species of this complex routinely occur in human-disturbed habitats such as low areas in fields, ditches, and on farm pond shores (Schuyler and Whittemore, in press). A small colony of *S. georgianus* was discovered in a wet ditch on a narrow, gravel road in the eastern half of the township. Seventeen stems were counted in a 3 × 1 m area. Associated species included *Viburnum dentatum* L. var. *lucidum* Aiton, *Glyceria striata* (Lam.) A. S. Hitchc., *Carex projecta* Mack., *C. scoparia* Schkuhr *ex* Willd., *Juncus effusus* L., *Euthamia graminifolia* (L.) Nutt., and *Symphyotrichum lanceolatum* (Willd.) G. L. Nesom. The site occurred at 62 m above mean sea level. A few stems had been cut or knocked over by mowing for road maintenance.

SPECIMEN CITATION: UNITED STATES. Maine: York Co., North Berwick, roadside ditch, E side of Billy Lane, at 62 m elevation, with *Viburnum dentatum* var. *lucidum, Glyceria striata, Carex scoparia, Juncus effusus,* and *Euthamia graminifolia,* 5 Aug 2001, *Haines & Kuronya s.n.* (MAINE)

The occurrence of *Scirpus georgianus* in Maine is not surprising given that it occurs on Prince Edward Island and in Strafford County, New Hampshire (Schuyler and Whittemore, in press). Though this species is widely distributed over much of the eastern half of the United States, it is rare and disjunct in the northern part of its range, including New England (Schuyler 1967). *Scirpus* *georgianus* is a target species of the Herbarium Recovery Project. This two-year project, directed by the New England Wild Flower Society, is collecting information on some of New England's rarest and/or poorly known native taxa through herbarium survey. Information gathered from this research will be used to direct conservation efforts in New England.

ACKNOWLEDGMENTS. A portion of the information presented herein was collected during review of specimens for the Herbarium Recovery Project. The New England Wild Flower Society is thanked for permission to use this information. Alfred Schuyler is also thanked for permission to use the draft *Scirpus* contribution for the *Flora of North America North of Mexico*.

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BOOK REVIEW

Seventh Catalog of the Vascular Plants of Ohio by Tom S. Cooperrider, Allison W. Cusick, and John T. Kartesz, eds. 2001. x + 195 pp. illus. map. ISBN 0-8142-5061-0 $29.95 (softcover); ISBN 0-8142-0858-4 $65.00 (hardcover). Ohio State University Press, Columbus, OH.

The *Seventh Catalog of the Vascular Plants of Ohio* augments major works published since 1961 that focus on Ohio vascular plants (Andreas 1989; Braun 1961, 1967; Cooperrider 1995; Cusick and Silberhorn 1977; Fisher 1988; Weishaupt 1971). Tom Cooperrider first conceived of the new catalog in 1960; in the 1970s and 1980s he drafted a preliminary checklist and began planning the *Seventh Catalog*. John Kartesz independently prepared a preliminary checklist for Ohio, and in 1994 suggested that he and Cooperrider combine their efforts. Five additional contributors were enlisted to help compile the *Seventh Catalog*. Included among the seven authors are some of Ohio's foremost floristic botanists of today.

There has been profound need for the *Seventh Catalog*. A period of seventy years has elapsed since publication of Schaffner's (1932) catalog of Ohio vascular plants. Since then, many taxa have been discovered to occur in Ohio, and marked changes have been made in taxonomy and nomenclature. The *Seventh Catalog* reflects these developments.

According to the Statistical Summary of the *Seventh Catalog*, Ohio has 2716 species of vascular plants and 139 interspecific hybrids: 108 pteridophytes, 17 gymnosperms, 1994 dicotyledons, and 736 monocotyledons. An additional 143 infraspecific taxa are also listed. Approximately 34% of species, 17% of interspecific hybrids, and 17% of infraspecific taxa are alien to Ohio.

The *Seventh Catalog* has nine main parts, numbered here for convenience: (1) Introduction, (2) Natural History of the Ohio Flora, (3) Catalog of Vascular Plants, (4) Appendix 1: Statistical Summary, (5) Appendix 2: Deletions, (6) Literature Cited, (7) Index to Scientific Names, (8) Index to Common Names, and (9) Contributors. Authors include Tom Cooperrider (Part 1) and Guy L. Denny and Cooperrider (Part 2). Part 3 has four main sections: Pteridophytes (Allison Cusick), Gymnosperms

(Cusick), Dicotyledons (Cooperrider, John J. Furlow, and Cusick), and Monocotyledons (Barbara K. Andreas, Cooperrider, Cusick [Cyperaceae], and John V. Freudenstein [Orchidaceae]). Authors are unspecified for Parts 4–9, which represent joint contributions.

The actual Catalog of Vascular Plants (Part 3; 79 pages) is the major part of the book. The nomenclature, circumscription, and sequence of suprageneric taxa are based on Cronquist (1981), Gleason and Cronquist (1991), and/or Flora of North America Editorial Committee (1993, 1997). Nomenclature and circumscription of taxa below the rank of family follow unspecified sources. Genera, species, and interspecific hybrids are listed alphabetically within families. The following information is given for each species or hybrid: Latin name and author(s); status as native, naturalized, or adventive (or otherwise not established in the flora); and common name. Provided for selected taxa are synonym(s) and sometimes additional information crucial for understanding circumscription. Varieties are given for some species. Interspecific hybrids are listed by the hybrid name, if available [e.g., *Asplenium* ×*inexpectatum* (E. L. Braun *ex* Friesner) C. V. Morton], followed by parentage (e.g., *Asplenium rhizophyllum* × *A. ruta-muraria*). No illustrations or keys are provided, although they are nonessential for this work.

Clearly, great effort was required to compile this *Seventh Catalog*. In addition to the numerous taxonomic and nomenclatural decisions involved, I know personally that Tom Cooperrider was determined that listed taxa be correctly identified. Comparison of Cusick's treatment of Ohio pteridophytes (Part 3 of the *Seventh Catalog*) with that of Weishaupt's (1971) *Vascular Plants of Ohio, Third Edition* exemplifies the extent of contribution of the *Seventh Catalog* in updating available resources. First, Cusick's study resulted in the listing of 87 species and 21 hybrids, compared with Weishaupt's 70 species and 2 hybrids; this includes the deletion of four species and one hybrid. Second, Cusick's list reflects the considerable changes in pteridophyte nomenclature since 1971 (following Kartesz 1994). Among the many examples that could be given here: he listed eight families in place of the more broadly circumscribed Polypodiaceae; the four currently recognized genera (*Diphasiastrum, Huperzia, Lycopodiella,* and *Lycopodium sensu stricto*) in place of *Lycopodium*; and the three currently recognized genera (*Athyrium sensu stricto, Diplazium,* and *Deparia*) instead of the more broadly circumscribed *Athyrium*. Assembly of the *Seventh Catalog* must have demanded extensive research, meticulous organization, and, ultimately, intensive and prolonged proofreading.

The *Seventh Catalog*, however, has two unfortunate deficiencies. There are no indications of which taxa and how many taxa are newly added to the known flora of Ohio. Thus, considerable burden is placed upon users to extrapolate this information from additional sources. In contrast, Cusick and Silberhorn (1977) provided a list of such taxa. Neither voucher specimens nor herbaria are cited for any of the listed taxa; this would have been especially desirable for new Ohio records. Thus, any misidentifications, however improbable their existence, are likely to go uncorrected for years to come. In contrast, for rare Ohio species Andreas (1989) and Cusick and Silberhorn (1977) cited voucher specimens and herbaria.

It is also surprising that some taxa listed for Ohio by Kartesz and Meacham (1999) are neither included in, nor listed as deletions from, the *Seventh Catalog*. Examples include *Alopecurus geniculatus, Cardamine ×maxima, Phellodendron amurense,* and *Tagetes patula.* One wonders if authors of these two works, respectively, employed different standards of proof for the occurrence of taxa within Ohio.

A minor complaint relates to the nonalphabetical organization within the *Seventh Catalog* of taxa of higher rank, particularly of orders and families. Readers unfamiliar with Cronquist's (1981) system may have difficulty locating taxa. More efficient would have been a strictly alphabetical listing of families, as was provided by Andreas (1989). One recalls favorably the strictly alphabetical arrangement of taxa within Swink and Wilhelm's (1994) *Plants of the Chicago Region,* a feature contributing substantially to that volume's ease of use.

Overall, however, the *Seventh Catalog of the Vascular Plants of Ohio* represents a most welcome and necessary contribution for persons seriously interested in the Ohio flora. As indicated earlier, reference to the *Seventh Catalog* reveals that the most recent manual of Ohio vascular plants (Weishaupt 1971) is very out-of-date. One hopes that among Ohio's floristic botanists there are or will be one or more individuals who will properly revise Weishaupt's standard work.

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BOOK REVIEW

Bioconservation and Systematics: Proceedings of the Canadian Botanical Association Conference Symposium in London, Ontario, June 2000 by James B. Phipps and Paul M. Catling, eds. 2001. 101 pp. ISBN 0-9689565-0-5 US$17.00, CAN$23.00 (softcover). Canadian Botanical Association. [for copies contact Paul M. Catling, catlingp@em.agr.ca]

This report comprises seven papers that provide a useful picture of how current trends in systematics and taxonomy affect plant conservation in the Canadian setting. Since Canada, despite its geographical size, has a relatively small flora and a relatively high number of taxonomists and herbaria (Parnell 1993), one might assume that sufficient systematic resources exist to support plant diversity studies and conservation biology. This volume provides interesting examples of systematic research for conservation, but also suggests that here, as elsewhere, there are not enough skilled taxonomists, and there is an inadequate infrastructure for collection, management, and use of systematic data.

In the first paper, "A never-ending role for biosystematics in the protection of vascular plant diversity in Canada," Catling discusses the several contributions that taxonomy and systematics make to conservation biology, with plentiful Canadian examples. In addition to re-analyses of nomenclature and the study of specific taxa of known concern, new taxa are being added to the flora, such as *Platanthera praeclara,* an orchid newly described in 1986. Canada's 147 endemics remain understudied as well, as do the successive waves of invasives. These and other tasks require more sophisticated information tools, including the development of national and local taxonomic databases, and their interfacing with global and regional data systems like the Integrated Taxonomic Information System for North America.

At the other end of the volume, Anton Reznicek ("Can systematists help conserve rare plants in the twenty-first century?") argues that there is a growing dearth of systematists acquainted with plants in their ecological settings, and that this reflects both the increased emphasis on molecular techniques and on landscape-level ecological study. This means a lack of information needed for good conservation decisions, and it is related to the impoverishment of systematic collections, which has been noted for other groups as well (e.g., Winker 1996).

Oldham and Sorrill ("The role of conservation data centres in the conservation of Canada's flora") describe the relatively recent establishment of Conservation Data Centres, or Natural Heritage Programs—the first being set up in Québec in 1988. The authors point out that the Centres' work is hampered and perhaps threatened by the paucity of biologists trained in field identification and in the use of (and contribution to) reference collections.

Another aspect of the biodiversity infrastructure in Canada, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) is described by Catling in "Protecting vascular plant biodiversity in Canada: Progress and problems with the taxon approach." Once again, the basic challenge of up-to-date, comprehensive, and reliable catalogs of taxa and their status is urgent, at a time when government policy on biodiversity is evolving.

Roberts ("Planning with plants in Illinois") contributes a description of the interconnected efforts that have contributed to the evaluation and protection of centers of biodiversity in that intensively settled and studied state. Brouillet ("Floristics and conservation: An example from Newfoundland") points out that while a basic inventory of the boreal flora may be nearly achieved, much remains to be known about the distribution of the taxa across the huge expanse of the biome. He describes three complementary surveys undertaken in Newfoundland, at three different scales, and demonstrates that such studies provide much new information about species distribution and abundance. He also shows that the electronic cataloguing and management of floristic data are essential elements of basic floristic studies of this sort, as well as being essential to management policy.

Finally, Husband and Burgess discuss "Evaluating hybridization as a cause of species endangerment: A role for systematics in plant conservation." Specifically, they discuss studies that evaluate the impact of hybridization of the rare red mulberry (*Morus rubra*) with the introduced white mulberry (*M. alba*). Here is an interesting case in which some hybrids are morphologically identifiable, but molecular studies reveal much more hybridization than hitherto suspected.

There are no breakthrough papers in this collection, but botanical libraries should have it on hand. This will be a useful volume for those with an interest in the current state of plant conservation in Canada. For those with a more general interest in the role of systematics in the protection of biodiversity, the articles provide an interesting patchwork of issues and examples very practically grounded in the current science and policy climate of Canada. Almost every page reemphasizes the urgent need for taxonomists skilled in the field and the herbarium, and the papers provide concrete examples of how this need affects the progress of plant conservation.

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NEBC MEETING NEWS

February 2002. Vice President Paul Somers introduced the evening's speaker, Dr. Scott Bailey, U.S.D.A. Forest Service. Bailey began his talk, "Case studies in Geobotany: Refining our understanding of the influence of substrate on plants," by mentioning that though his degree was in geology, he has always had a strong interest in botany. After winning over the crowd with this confession, he launched into a discussion of water and nutrient movement in forests. Watershed studies in the eastern U.S. examined how nutrients accumulate and predicted future changes in storage. While nitrogen had a net accumulation, mostly due to acid deposition, phosphorus and potassium storage have changed very little. Calcium (Ca) and magnesium (Mg) supplies have decreased substantially, a cause for great concern. Soil exchange sites store nutrients as cations, but there is a question as to whether mineral weathering can keep up with nutrient losses. Weathering occurs at widely varying rates (e.g., a small amount of calcite can have a much larger impact than the very common plagioclase feldspar, because calcite weathers 100,000 times faster). The potential for air pollution and land management to change the balance between mineral weathering and cation storage has renewed interest in the roles of Ca and Mg in plant distribution and health.

The first of three case studies presented was conducted on the Allegheny Plateau (NY, PA), a region that has experienced extensive mortality of sugar maple (*Acer saccharum*) since 1980. Maple death was attributed to Multiple Stress Syndrome (MSS). As its name indicates, MSS can have many causes, and in this case was due to low soil Mg levels (below 0.03 cmol+/kg) and multiple insect defoliation events during the 1970s. In the absence of defoliation, stands tolerated lower Mg levels, and with high soil Mg, stands could withstand several defoliation events. Experimental liming application in 1985 produced a positive response in sugar maple, though other species such as beech (*Fagus grandifolia*) and black cherry (*Prunus serotina*) showed no response.

The second study was an investigation of landscape patterns found in nutrient availability. Two adjacent unglaciated stands, one on a summit with low pH and Ca, the other on a mid-backslope with 100 times more Ca, illustrated the effect of physical geography on herb diversity and MSS. Bailey and his colleagues discovered that the soil at the mid-backslope site was influenced by groundwater seepage from the underlying bedrock. Although dominated by quartz, the sandstone bedrock contained 10% calcite. Bailey suggested that acid rain played a role in MSS by increasing the portion of the landscape with nutrient levels under the threshold necessary to support healthy maple. An expansion of the study suggested that poor base cation supply is just as common in New England.

After noting the wide difference in plant diversity, Bailey and colleagues surveyed the flora with the idea of creating an indicator system for site nutrient status. Canonical correlation analysis, used to evaluate relationships between floral composition and environmental conditions, identified four species groups:

(1) Strong Indicators—confined to sites with the highest pH, Ca, and Mg;
(2) Medium Indicators—prefer higher pH and base cations but also influenced by organic matter and moisture;
(3) Weak Indicators—prefer better sites but occasionally found at nutrient-poor sites;
(4) Cosmopolitan Species—no site preference. No species reliably indicated acidic or nutrient-poor conditions.

Current efforts to explain spatial patterns in site quality involve analyzing and predicting bedrock and soil composition. While attempting to deal with these issues in northern hardwood ecosystems, Bailey simplified things by studying species that grow directly on rocks. Epipetric (rock-loving) ferns turned out to be the perfect candidates for the third case study, based on several cliffs in New Hampshire. His study showed that fern species categorized as "calcicoles" are often found on rock types considered to be Ca-poor. Three hypotheses could explain this:

(1) Plants may be rooted in Ca-rich organic matter that accumulates on rocks;
(2) The rocks have atypical mineral content, such as sandstone containing small amounts of calcite;
(3) Lengthy hydrologic flowpaths carry Ca-rich water to the ferns.

Bailey concluded his talk with suggestions for the better understanding of the influence of substrate on plants. Researchers should focus on mineral content rather than the general lithology and should look at horizontal movement of water, rather than focusing on vertical movement. Also, GIS data should be used with discretion, because they are generally compiled on a large scale. As his research has shown, many site-specific "quirks" in soil development and hydrologic flowpaths may turn up only in a close examination.

—JENNIFER FORMAN, Recording Secretary *pro tempore.*

ANNOUNCEMENT

MERRITT LYNDON FERNALD AWARD

Merritt Lyndon Fernald was born in 1873 in Orono, Maine. In 1891 he enrolled in Harvard University and started working at the Gray Herbarium, both of which he remained associated with until his death in 1950. During those 60 years he intensively studied the flora of eastern North America, made numerous field expeditions throughout the northeastern United States and southeastern Canada, and authored over 800 papers on floristically related subjects. Two of his most important contributions were: *Persistence of Plants in Unglaciated Areas of Boreal North America* (1925) and *Gray's Manual of Botany, 8th Edition* (1950). Fernald served as an Associate Editor of *Rhodora, Journal of The New England Botanical Club* from its inception in 1899 to 1928, and as Editor-in-Chief from 1928 until his death in 1950. He was an active member and promoter of the Club.

The Council of the New England Botanical Club has decided to honor Fernald's exemplary contributions to the botany of northeastern North America through a new award, the Merritt Lyndon Fernald Award. The award will be given annually, if deemed appropriate, to the author(s) of the best paper published in each volume of *Rhodora* that has made use of herbarium specimens and/or involved fieldwork. Topics to be considered include, but are not limited to, biogeography, floristics, life-history studies, monographs, and revisions. Papers on vascular or nonvascular plants, lichens, fungi, and algae will be considered. The competition is not limited to a particular geographic area, but is open to studies in any part of the world.

Recipients of the Fernald Award will receive $1000.00 and a certificate acknowledging their achievement. The award will be presented when the New England Botanical Club hosts its annual Distinguished Speaker.

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THE FLORA OF PENIKESE ISLAND, MASSACHUSETTS: THE FIFTH SURVEY(1998–1999), WITH EMPHASIS ON THE WOODY VEGETATION

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ABSTRACT. Five vascular plant surveys have been made between 1873 and 1999 on Penikese, one of the Elizabeth Islands (Massachusetts). The five surveys have noted a total of 326 species, the most recent survey, 218 species. Almost half of the species noted are alien on all five survey lists. Four rare (state-listed) native species were found in 1998–1999. The most significant change in the island's vegetation over 125 years is the great increase in woody vines and shrubs following cessation of the farming that stripped the island of its presettlement forest. Fifteen woody species, some of them recent introductions, are thought to be increasing. Two of the island's ponds—Tubs and South—are brackish, supratidal pools without vascular plants. Four ponds—North, Leper, Tern, and Typha—are fresh, shallow, and usually dry up annually, at which time their bottoms support a dense, diverse flora. Salt marsh species and numbers are fewer than formerly. There is evidence that the island as plant habitat is drier than in the past, perhaps as a result of the increase in woody vegetation. For instance, ferns, once common on Penikese, are now almost wholly absent. Certain species common on nearby islands are missing; for instance, no blueberries or other ericads are found on Penikese. In the absence of further disturbance, it is possible that Penikese will again become forested with red cedar *(Juniperus virginiana)* as a presettlement account of

1602 describes it, but island-wide burns are suggested for destroying invasive woody plants and encouraging native grasses. Such burns might also restore former tern-nesting sites to usefulness.

Key Words: alien species, *Juniperus virginiana,* Penikese Island, prescribed burns, rare species, red cedar, woody vegetation

The first botanical survey of Penikese was made in 1873 by David Starr Jordan, who spent the summer on the island as a student of Louis Agassiz at the latter's Anderson School of Natural History (Jordan 1874). Jordan preserved no specimens of vascular plants, but listed 114 species using the fifth (1867) edition of Gray's Manual (Fogg 1930). Six species were restricted to the little satellite, Gull Island, which now, at high tide, shows only as a heap of rocks. Bartholomew Gosnold had visited Penikese in 1602 when it was "full of cedars" (Archer 1625 as quoted in Quinn and Quinn 1983), but after many decades of cultivation and grazing, it was, in 1873, "absolutely treeless and nearly shrubless . . . about as barren looking a pile of rock and stone as one could well imagine" (Jordan 1874). Settlers had cut trees and grazed sheep there as early as 1675 (Buckley 1997). Early history of the island is also given by Howland (1964).

The second botanical survey was made from Woods Hole in 1923 by the Marine Biological Laboratory (MBL) and the Fisheries Biological Station of the U.S. Bureau of Fisheries on the 50th anniversary of the founding of the Anderson School (Lewis 1924). The island had served the Commonwealth of Massachusetts as a leper colony from 1905 to 1921, during which period gardening was encouraged (Buckley 1997). The leper colony kept sheep for some of its years, but grazing was likely reduced or intermittent from about 1865 or 1870 to about 1915, when it ceased altogether. Lewis (1924) said of the second survey that "one day was devoted to collection, July 24, and casual visits in August added a few observations." Four people observed the vegetation, eight others collected vascular plants. The final list of the latter was provided by John M. Fogg, Jr., then at work on his Ph.D. dissertation on the flora of the Elizabeth Islands under M. L. Fernald. One hundred fifty-nine species of vascular plants were listed. Specimens were deposited in the herbarium at the MBL (SPWH). When Fogg published his thesis (Fogg 1930), 19 additional species were noted for Penikese. Altogether, 90 species not seen in 1873 were recorded. while 40 species seen in that year went unreported.

The third survey was conducted from the MBL in 1947. The list of vascular plants was prepared by Edwin T. Moul (1948). He and five colleagues collected on July 6, July 31, and August 3. Specimens were deposited in SPWH. Moul noted that the asters recorded in earlier surveys were missing or "were overlooked because of their late summer flowering." Moul listed 156 plant species, 24 of which had not been reported earlier, while about 90 seen previously were not found. Moul (1961) records a return visit to the island.

During much of the interval between the second and third surveys (1923–1947), the Commonwealth had used the island as a game farm and wildlife refuge. Annual reports (Massachusetts Division of Fisheries and Game 1925–1939) mention much that is relevant to the natural history of the island. The following were noted (by common names, as given here) as having been planted for wildlife food or cover: arbor vitae, bayberry, beach plum, blueberry, buckthorn, Carolina poplar, inkberry, Japanese barberry, laurel, mulberry, Norway spruce, privet, rose (native), sago pondweed, Scotch pine, sumac, viburnum, and widgeon grass.

The fourth survey was made in 1973 by botanists from Smith College as a part of the M.A. thesis research of Scott D. Lauermann under C. J. Burk (Lauermann 1974; Lauermann and Burk 1976). Some or all of five people collected on June 12, July 14 and 15, August 8, 9 and 13, and September 20. By 1973, the island had been uninhabited for about 40 years and ungrazed for at least 50. Twenty-nine species not reported earlier were noted, while 109 species listed earlier were not found. Specimens were placed in the Smith College Herbarium (SCHN). Also in 1973, the Penikese Island School was established on the island, bringing new gardeners with new plants. Altogether, it is clear from Penikese's history that there have been waves of plant introduction and extirpation as land use has changed.

SITE DESCRIPTION

Penikese Island (41°27′N, 70°55′W) lies 19 km from Woods Hole, Massachusetts at the southern extremity of Buzzards Bay in the Town of Gosnold, Dukes County. The island consists of a fragment of the now partly submerged Buzzards Bay Moraine of

Wisconsinan glaciation (Zinn and Kahn 1972). Save for Penikese, the Elizabeth Islands lie in a straight northeast-southwest string from Woods Hole, with Cuttyhunk at the southwest end. Penikese is out of line with this string, being one mile north of Cuttyhunk, the land nearest to it.

Penikese, totalling about 185 hectares (75 acres), consists of two hilly parts connected by a narrow, flat strip of land called "the Isthmus" or, in the past, the "Neck" or "Causeway" (Figure 1). The maximum elevation, 25 m, is found on the greater part; the smaller portion, known as Tubs Point, is a few meters lower. The Isthmus is formed from the coalescing upper parts of two back-to-back beaches that head embayments indenting the eastern part of the island—a shallow indentation from the north, a deep one from the south. The beach on the south side of the Isthmus is wide and sandy, and there are sandy stretches of shore south along the east side of the island almost to its southern extremity, South Point; otherwise the perimeter of the island is a jumble of cobbles and boulders. The New England hurricane of 1938 is estimated to have reduced the island by about 25 hectares (10 acres; Massachusetts Division of Fisheries and Game, Annual Report for 1938).

The "Soil Survey of Dukes County, Massachusetts" (Fletcher and Roffinoli 1986) describes the Elizabeth Islands as having "very deep . . . well drained, sandy and loamy soils formed in reworked glacial outwash or in glacial till." Most Penikese soil is of the Eastchop-Montauk complex (EnC) or the Plymouth-Montauk complex (PtC and PtD). These soil-map units are described as rolling or hilly, very or extremely bouldery, and consist of loamy sands or sandy loams. Soil permeability is mostly moderate to rapid, and available water capacity is moderate to very low. Nothing appears to have been published regarding the island's soil chemistry.

Edgartown, Martha's Vineyard, about 32 km to the east-southeast of Penikese, is thought to have a climate similar to the latter's. Climatic averages for Edgartown for the period 1961–1990 are as follows: annual rainfall, 45.25 inches; wettest month, November, 4.45 inches; driest month, July, 2.92 inches; annual temperature, 49.7°F; coldest month, January, 29.2°F; warmest month, July, 69.8°F (Northeast Regional Climate Center, 1123 Bradfield Hall, Cornell University, Ithaca, NY).

The island is the nesting site for gulls and terns. In 1999, there

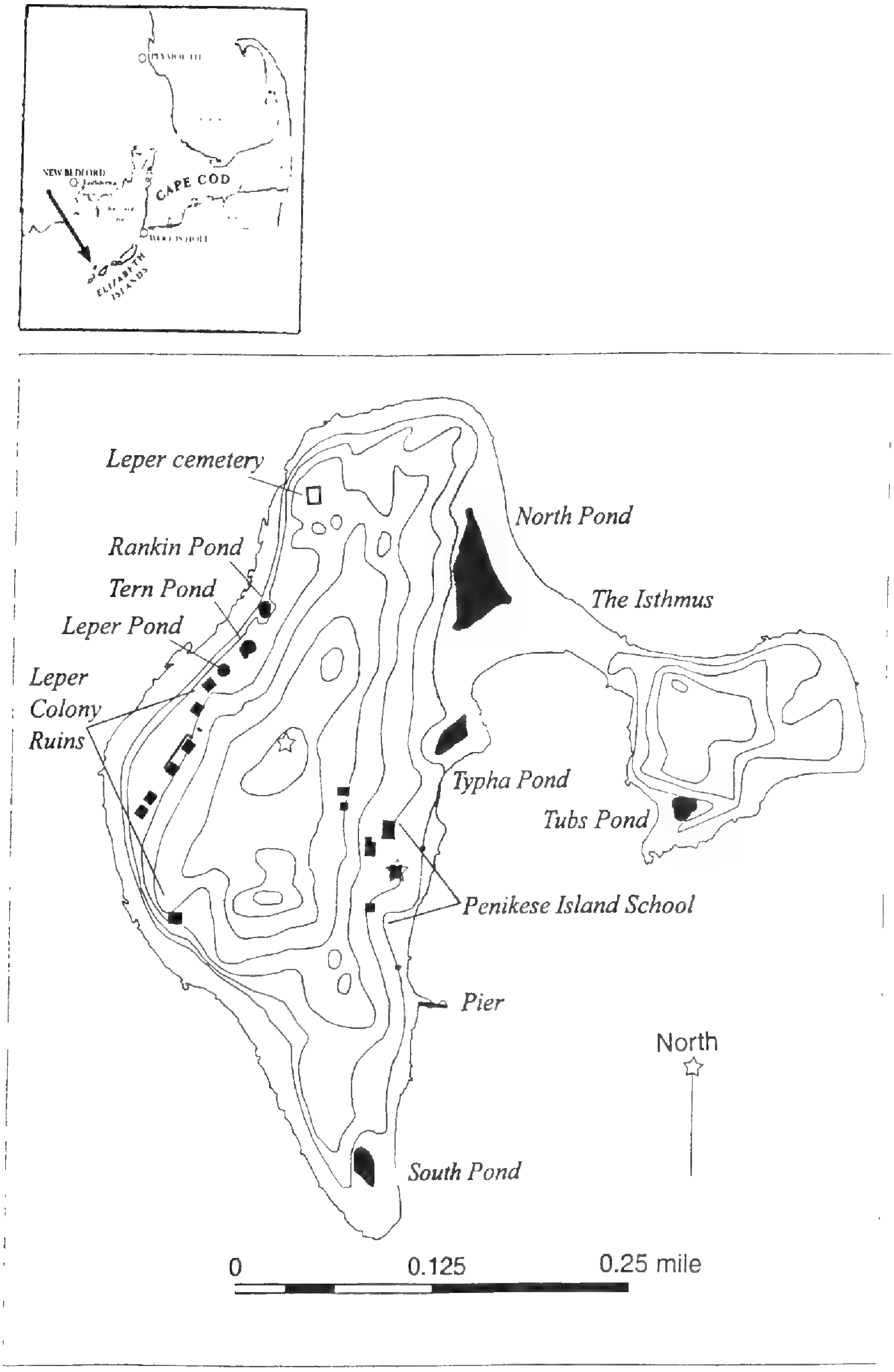

Figure 1. Penikese Island; insert showing its location off the Massachusetts coast; from Buckley (1997).

were about 1000 gull nests on the main part of the island (about 87% herring gull, *Larus argentatus,* and 13% great black-backed gull, *L. marinus)* and a tenth that number of tern nests (almost wholly common tern, *Sterna hirundo,* with a few arctic terns, *S. paradisaea*) divided among three spots—on the Isthmus, on the south shore of Tubs Point, and at South Point (Blodget 1999). Most of the food of these birds comes from the surrounding sea or from places remote from Penikese, with much excretion and egestion occurring on the island. Thus, since there is little export of organic material, Penikese would seem to be accruing an ever-larger supply of plant nutrients.

Penikese is streamless, but has several shallow ponds. Except for a few planted trees and gardens near existing buildings and the vegetation at the shore and around the ponds, the rolling island is best thought of as long-abandoned pasture and cropland covered with grasses or grasses mixed with low shrubs or vines. Here and there are individual tall shrubs or patches of the same, some of the patches being of many square meters (Figure 2).

MATERIALS AND METHODS

Plants were collected on Penikese in 1999 by R. H. Backus, T. O. Hendrickson, P. T. Polloni, B. L. Reid, and Jessica Schultz. One to three of this group worked on April 28, May 14–17, June 11–13, July 9–12, August 20–23, September 18–21, and October 15–17. The whole island was walked over repeatedly. Estimates of plant cover are visual ones based on these explorations, and statements of abundance are subjective. About 430 specimens were pressed, then studied in the herbarium at the MBL (SPWH), where R.H.B. and P.T.P. prepared and deposited about 230 sheets. Much of the 1999 material was identified by the last two, although B.L.R. identified most of the grasses, graminoids, and goldenrods. Paul Somers made some identifications and verified others. Paul and Lois Somers and Jeanne Livingston collected on the northern two-thirds of the island on June 24–26, 1998. Among the 95 specimens collected by the Somers party were three species not found in 1999—*Amaranthus blitoides, Scleranthus annuus,* and *Agrostis hyemalis*; these are included on the list for 1999. A few observations were made by R.H.B. on July 8–11, 2000 and P.T.P. made a few on February 7, 2001. Plant names have been brought into conformance with Sorrie and Somers (1999).

Figure 2. Looking east-southeast to Tubs Point from the northeast slope of the main part of Penikese Island.

RESULTS

The vascular plant species found at Penikese in 1998 and 1999 are listed in the Appendix together with the results of the earlier surveys. Certain groups of garden plants observed in 1998–1999 are not listed. One group, just north of the Schoolhouse, contained three apple trees of cultivated varieties, three trees of a *Prunus* sp., probably a plum, and one white spruce, *Picea glauca*. These plants were overgrown to varying degrees with Asian bittersweet, sumac, and Japanese honeysuckle. A catalpa stood nearby at the southeast corner of the Schoolhouse. Another group, called the Lower Garden, was about 300 yards north of the House (the residence and principal building of the Penikese Island School). It was planted with nursery stock and contained the following in July 2000: two apples, one pear, four blueberries, four grapevines, one nectarine, one peach or nectarine, one cherry, one plum or cherry, one Rose-of-Sharon, and eight of a horticultural variety of *Juniperus virginiana*. No annual flowers or vegetables in gardens near the House have been listed, although the weeds of these gardens have been included.

DISCUSSION

Alien species. The five surveys together report 326 species, one of which is represented by two varieties, for a total of 327 taxa. Of the species on the composite list for the five surveys, 48% are alien (155), the same ratio as in the most recent survey (105 of 218 species). The percentage of alien species for each of the earlier four surveys between 1873 and 1973 are 44, 48, 43, and 48, respectively. Although the percentage of aliens on Penikese is close to that reported by Sorrie and Somers (1999) for the entire Commonwealth of Massachusetts (45% of 2814 species), Massachusetts itself is high in aliens in comparison with New England as a whole and with the other New England states for which numbers are available. A recent summary (Mehrhoff 2000) shows that 31% of New England's 2882 species are alien, for Connecticut 35% of 2625 species, for Maine 30% of 2103 species, and for Rhode Island 24% of 1618 species. The following smaller New England areas for which floral lists have recently been prepared can be compared with Penikese with respect to percentage of alien species (arranged in order of diminishing size of flora):

Berkshire County, Mass.	27% alien of 1675 taxa (up from 17% of 1586 taxa in 1922; Weatherbee 1996)
Southeastern Connecticut	25% of 1550 species (Tucker 1995 as cited in Hill 1996)
Nantucket, Mass.	39% of 1265 taxa (Dunwiddie and Sorrie 1996)
Caledonia County, Vt.	24% of 1180 species (Gilman 1999)
Worcester, Mass.	32% of 1154 species (Bertin 2000)
Dukes County, Mass.	28% of 1082 taxa (calculated from Sorrie and Somers 1999)
A part of Stonington, Conn. ...	36% of 385 species (Hill 1996)
Cuttyhunk Island, Mass.	31% of 263 species (O'Neill 1981)

Monomoy Islands, Mass.	ca. 16% of ca. 263 species (calculated from Lortie et al. 1991)
Flood plain forest communities in Massachusetts	17% of 214 species (Kearsley 1999)

In reporting the Penikese survey for 1973, Lauermann and Burk (1976) noted that the percentage of aliens on Penikese is "strikingly higher than [for] adjacent coastal areas." This large proportion must result from the fact that for much of its recent (say, 250-year) history most or all of the island has been used for farming and gardening.

Rare species. The following rare (state-listed) native species (Massachusetts Division of Fisheries and Wildlife 1998, 2001) were found during the 1998–1999 survey: Threatened: *Diplachne maritima*; Watch list: *Angelica lucida, Cuscuta polygonorum,* and *Polygonum glaucum.* A few other rare species have been found on Penikese in the past. They are: Endangered: *Juncus debilis* and *Myriophyllum verticillatum;* Watch list: *Cirsium horridulum* and *Myriophyllum pinnatum.*

The increase in woody vegetation. The principal change in Penikese's vegetation over the 125-year record has been the increase in the number of woody species and the space occupied by them judging from the published accounts of the several surveys. Forty-five woody species have been recorded by at least one of the five surveys, 31 by the survey in 1998–1999. Of the 31 woody species currently present, 15 are abundant or conspicuous as individual plants and are known or thought to be spreading. Of these 15, of which nine are native, only one was recorded in 1873, nine were first found in 1923, two first found in 1947, and three first found in 1999. Collectively, we estimate the 15 to be present on 80–90% of the island's surface, although they are often mingled with grasses and other herbs. A brief history of these spreading species shows their increase.

Rubus flagellaris is the sole woody species noticed by all five surveys (1873 to present), and annotations suggest that it was always common: "Common locally, in patches" (Lewis 1924); "Large areas covered in upland grassland" (Moul 1948); "covering large areas in the upland grasslands of the larger section"

(Lauermann 1974). At present, this blackberry is widely distributed on both the main island and on Tubs Point and is probably Penikese's most abundant woody plant. It fruits but sparingly.

The nine spreading woody species noticed by all surveys except the first are *Lonicera japonica, Myrica pensylvanica, Populus alba, Prunus serotina, Rhus hirta, Rosa rugosa, Rubus laciniatus, R. pensilvanicus,* and *Sambucus canadensis. Rosa rugosa* exemplifies the spread of these species between 1923 and the present. Lewis (1924) said, "(Escaped.) Occasional." Moul (1948) said, "Large patches in grassland, eastern shore." Lauermann and Burk (1976) said, ". . . reported previously only on the east side of the main portion of the island near the dock, [it] is now well established over the main portion and borders South, Typha, and Leper Ponds and the marsh." In 1999, beach rose was found as described by Lauermann and Burk (1976), but also on the near side of Tubs Point. An along-shore patch just south of the pier measured about 35 × 45 m.

The two spreading woody species first noted on Penikese proper in 1947 were *Toxicodendron radicans* and *Rhus copallinum,* although Jordan (1874) had found poison ivy on Gull Island. Of poison ivy, Moul (1948) said, "Occasionally on grasslands. Not common."; Lauermann and Burk (1976) said, ". . . occurs in dense patches in the upper grasslands on the main portion of the island." In 1999, we found poison ivy to be generally distributed over the main part of the island with a lesser amount on Tubs Point. One patch northwest of the House on the path to Plow Rock was about 30 × 30 m. Moul (1961) called attention to the spread of *R. copallinum* between 1947 and 1960.

The three woody species first noted in 1999 and thought to be spreading are: *Celastrus orbiculatus, Rosa multiflora,* and *Juniperus virginiana.* Asian bittersweet is growing vigorously and fruiting both on the main part of the island and on Tubs. About 100 m northwest of South Pond, for example, are two conspicuous patches—one approximately 5 × 15 m, the other approximately 5 m in diameter. There are scattered clumps of multiflora rose along the path between the pier and the buildings of the Penikese Island School and at a few other places. These are growing vigorously and fruiting, and the spread of this species seems assured.

About 10 *Juniperus virginiana* are conspicuous because they stand as isolated specimens a little taller than most of the island's shrubby growth. According to David Masch (Associate Director, Penikese Island School, pers. comm.) at least some of these scattered small trees (1–2 m high) antedate the Lower Garden, which was planted about a decade ago and where there are fruiting specimens of this species. Two of the largest of the naturally planted trees bore immature cones early in 2001. Since this species grows well on abandoned southern New England farmland, and since the Penikese trees seem little, if at all, disfigured by the wind, the continued increase of red cedar on the island seems certain.

Tree growth. The annual report of the Massachusetts Division of Fisheries and Game for 1935 said, ". . . it is almost impossible to get any trees to grow on the island," and the adverse conditions for tree growth there are well illustrated by a row of five specimens of *Acer pseudoplatanus* just south of the Schoolhouse. These are the tallest trees (up to about 8 m) of which the island can boast. This maple, a vigorous weed on the nearby mainland, probably was planted in leper-colony days. The trees are partly protected from the southwest wind, summer's prevailing one, by a hill immediately to windward and more or less conform to the contour of that hill. Though multi-stemmed and gnarled, the most protected trees are taller and thicker than the less protected, which have been severely wind-pruned. Some inferior-looking fruit is produced by the stronger trees, but no seedlings have been observed.

The growth and occurrence of *Prunus serotina* is also illustrative. Lewis (1924) said, "South end of island," and Moul (1948) said "Grassland n. of Typha Pond. Suckers only, 4 feet tall. Dead twigs also only that high. (Not reported from south end of island as formerly.)" In 1999, there were a dozen or so small specimens of black cherry scattered about the island. Like many of the island's shrubs these trees grow vigorously, but suffer much winterkill and disfigurement by the wind. Most of them have recumbent trunks and wider-than-high silhouettes. One tree about 2 m tall was about 15 cm in diameter at the ground and had divided into five stems about 30 cm above the ground. The length of the previous summer's twigs averaged about 43 cm, of which about 10 cm at the top of the tree had been winterkilled, somewhat less at the sides. There is a tall tree (DBH 33.1 cm), probably planted and with flavorsome fruit, in a protected spot near the Schoolhouse that may have been the seed source for these small trees. The latter have not been observed to flower.

Penikese ponds in 1999. Penikese ponds (Figure 1) are South, Tubs, North, Typha, Leper, Tern, Rankin, and (formerly) Dry. Considerable confusion exists in the island's biological literature with respect to their names. We follow the designations on Lewis's (1924) map, except that what he called "swamp area" (and was later called "Marsh Pond") is now called North Pond and his two "Tub Ponds" are now but one, called by us "Tubs Pond." Rankin Pond has been recognized since Lewis wrote. It is likely that the loss of the second pond at Tubs Point and of salt marsh here and at South Point was due to the erosion by the 1938 hurricane noted earlier.

South and Tubs Ponds are only a few inches above sea level and close to the southern extremities of the greater and lesser parts of the island, respectively. They are turbid pools a few feet deep, holding water the year round. According to Zinn and Rankin (1952), salinity in South Pond was 23‰ in August 1923 and 13.2‰ in August 1947; in Tubs Pond salinity was 9‰ in August 1923 and 34.4‰ in August 1947, the last being close to the salinity of the adjacent bay. When we measured salinity on July 10, 2000, it was 10‰ in South Pond and 28‰ in Tubs Pond. These ponds, which supported no submersed or emergent vascular plants in 1999, probably should be thought of as supratidal pools with fluctuating salinity. Both seem to have had shallow connections to salt water at one time, but in 1999 were narrowly separated from the adjacent bay by low piles of cobbles such as those moved by storm surges. Tubs Pond still supported some vegetation characteristic of brackish habitats around its edges, being completely encircled by a narrow band of *Bassia hirsuta,* mixed in a few spots with *Suaeda* sp. Along the north edge of the pond were narrow patches of *Spartina patens* and *Distichlis spicata.* Just south of the ridge of cobbles that separated the pond from the bay lay a flat beach of cobbles that was submerged by high tides. Here there was a 2 × 3 m patch of *Salicornia maritima* surrounded by a few outlying plants, the only occurrence of this species on the island.

No plants characteristic of brackish habitats were found at South Pond in 1999, although such plants have been found there in the past. For instance, Fogg (1930) listed for South Pond the characteristic salt marsh plants *Juncus gerardii* (*Fogg 1094*) and *Distichlis spicata* (*Fogg 1092*). Also, the label of a specimen of *Scirpus pungens* from the 1947 survey (*Erskine & Hulbert s.n.*, SPWH 90), reads "Salt marsh pocket by South Pond," and a specimen of *Bassia hirsuta* from the 1947 survey (*Erskine & Hulbert s.n.*, SPWH 1454) reads, "Mud around South Pond." *Juncus gerardii* was not found on Penikese in 1999, but past collections have come not only from around South Pond, but from North Pond as well. Two other characteristic salt marsh species not found on the island in 1999 were *Iva frutescens* and *Spartina alterniflora*.

Leper Pond lay on the west side of the island only 20 m or so north of the ruins of the leper colony laundry. It was about 8 × 16 m with a single specimen of *Salix atrocinerea* growing at its western margin. The pond had a maximum depth of about 15 cm on May 15, but had been 30 cm higher. The pond is said to dry every year and was so at the time of our visit on June 13. Later, the pond bottom and edges were rife with *Bidens connata*, *Cyperus erythrorhizos*, *Gnaphalium uliginosum*, *Hypericum mutilum*, *Lycopus americanus*, *L. uniflorus*, *Mentha arvensis*, *Polygonum lapathifolium*, and *P. pensylvanicum*. A few flowering individuals of *Viola lanceolata* were found there in May.

Tern Pond, about 12 × 15 m, lay a little north-northeast of Leper Pond. It is said to dry every year and had only a small puddle left in its middle by May 15, 1999. This was gone two days later. In May, the drying pond was much frequented by Canada geese, which had grazed almost to the ground a sizeable patch of *Phalaris arundinacea* at the pond's southern edge. In June, the pond was half-surrounded by blooming *Iris versicolor*. Later, there were rich growths of *Chenopodium ambrosioides*, *Cuscuta polygonorum*, *Cyperus erythrorhizos*, *Gnaphalium uliginosum*, *Juncus effusus* var. *pylaei*, *Lycopus* spp., *Polygonum* spp., *Rorippa palustris*, and other herbs.

Rankin Pond, just north-northeast of Tern Pond, was larger than the latter, though its boundaries were ill-defined. The first botanical survey to mention this pond was the one by Lauermann and Burk (1976), who said that it held water in June 1973, which had "fallen markedly" by July 14, and that it was completely dry by August 8. In 1999, the pond showed no sign of having held water in the recent past, perhaps not for years, and in 1999 could scarcely be called a pond. In May, it was wholly covered with tall plants, including *Calystegia sepium, Galium tinctorium, Juncus effusus* var. *pylaei,* and *Panicum virgatum.*

Dry Pond, shown by Lewis (1924) as being near the leper cemetery, was described in 1923 as having held water in the spring as "its surface was cracked mud" when visited in July (Lewis 1924). Moul (1948) made little mention of Dry Pond, noting only that *Cuscuta polygonorum* was growing there on *Polygonum punctatum* and that *Rubus pensilvanicus* was growing around it. Lauermann and Burk (1976) said for 1973 that "Dry Pond supports large stands of various grasses, *Polygonum persicaria, Rubus [pensilvanicus], Sambucus canadensis* and *Solidago rugosa.*" In 1999 we were unable to decide where Dry Pond once had been.

Typha Pond, 20 × 50 m, lay near the west edge of the southern embayment at the east side of the island. Although low and narrowly separated from the bay, it was somewhat protected from the east by Tubs Point and seemed to maintain its freshwater integrity. There was a large stand of *Typha latifolia* at its eastern edge. Found at Typha Pond by the 1923 and 1947 surveys, cattail was not found there when particularly sought by the 1973 survey (Lauermann and Burk 1976; C. J. Burk, pers. comm.). In May 1999, the pond held a little water, but was dry at our June 12 visit. On July 9, a considerable piece of the pond bottom was covered with young plants of *Portulaca oleracea.* Some other plants of the pond bottom and edges were *Gnaphalium uliginosum, Hibiscus moscheutos, Hypericum mutilum, Impatiens capensis, Iris versicolor, Juncus effusus* var. *pylaei, Ludwigia palustris, Mentha arvensis, Myrica pensylvanica, Panicum virgatum, Polygonum* spp. (including *P. persicaria*), *Rosa rugosa, Scirpus pungens, Solanum dulcamara,* and *Xanthium strumarium.*

North Pond lay near the western extremity of the Isthmus. It was the largest pond on Penikese, about 90 × 150 m. The pond held a little water in May and June, 1999, but by our visit on July 10 it "was dry, save for a tiny puddle" at its western edge "although kneeling on its plant-covered bottom dampened the knees" (field notes). According to David Masch (pers. comm.), North Pond dries completely about once every five years. Portions of the most recently dried pond bottom were covered by a "garden of miniatures" whose plants were well on their way to making seed. The smallest species were *Eleocharis parvula* and *Limosella subulata.* Described as "a giant" among them was

Chenopodium glaucum, only 8–10 cm high. Another diminutive species was *Rumex maritimus* var. *fueginus.* The parts of pond bottom that had been dry longer held taller species dominated by *Pluchea odorata.* By our visit on August 20, much of the pond was pink-purple with the last, and it and other tall species had succeeded the tiny flora noted in July. By our September 18 visit, the pond again held a few centimeters of water in its center. Conspicuous among the pond-bottom flora then were *Cyperus diandrus, C. erythrorhizos,* and *C. filicinus.*

Other conspicuous species in or at the edges of North Pond were *Angelica lucida, Aster novi-belgii, A. subulatus, Bidens connata, Carex lurida* and other *Carex* spp., *Cuscuta polygonorum, Gnaphalium uliginosum, Hibiscus moscheutos, Hypericum mutilum, Impatiens capensis, Iris versicolor, Juncus effusus* var. *pylaei, Lycopus americanus, L. uniflorus, Mentha arvensis, Polygonum pensylvanicum, P. lapathifolium, P. punctatum, Scutellaria galericulata, Scirpus pungens, S. tabernaemontani, Sparganium eurycarpum, Spartina patens,* and *Xanthium strumarium.*

Beach plants. In 1999, common species of the rocky shore were *Achillea millefolium, Anagallis arvensis, Bromus tectorum, Lathyrus japonicus, Leucanthemum vulgare, Oenothera biennis, Raphanus raphanistrum, Rumex crispus, Solanum dulcamara, Solidago sempervirens,* and *Verbascum thapsus.* Common species of the sandy shore, where they grow particularly strongly in piles of decaying *Zostera,* were *Ambrosia artemisiifolia, Atriplex* spp., *Chenopodium macrocalycium, Datura stramonium,* and *Erechtites hieraciifolia. Glaucium flavum* was very conspicuous in the wrack on the Isthmus and at South Point when it was in flower in June.

The loss of ferns. Ferns, once common on Penikese, were very rare in 1999. *Dennstaedtia punctilobula,* the only fern reported by Jordan (1874), was included by Lewis (1924) in a list of "the more common plants of the grassland area." Lewis also listed *Athyrium filix-femina,* the only Penikese survey to do so, ("South end of island") and *Thelypteris palustris* ("Low wet places, Typha and Tub Ponds"). Moul (1948) said for *Dennstaedtia,* "Grassy hillside, n.w. of the reservoir," then said that in 1960 both this species and *T. palustris* "are no longer growing at their former sites" (Moul 1961). With the 1973 survey by Lauermann and Burk (1976) *T. palustris* dropped from the list of Penikese plants, and they noted but "a single specimen" of hay-scented fern. In 1999, we noted only a single poorly growing plant of the latter species, curiously, at the mouth of a petrel burrow in the rock retaining wall near the House. The only other fern reported from Penikese is *Onoclea sensibilis,* found in 1999 in a tangle of other plants at the north end of North Pond. It may have been a recent arrival on Penikese or, judging by the difficulty we had in re-locating the few fronds we had found earlier, simply overlooked by the other surveys.

Why have ferns been lost to Penikese? Is it simple competition with species that are spreading such as the woody species noted earlier, or is the island drying a little superficially, perhaps also attributable to the spread of (deeper-rooted) woody species and a consequent increase in evapotranspiration? The label of a sheet of *Thelypteris palustris* collected in 1923 (*Fogg 460,* SPWH) says, "Low wet places. All parts of is." With the exception of the ponds, there were, in 1999, no places on the island that could be called low and wet. The total disappearance of Dry Pond and the dryness of Rankin Pond lend additional support to the notion that Penikese as plant habitat was somewhat drier in 1999 than formerly.

Plants not found. Conspicuous among woody shrubs and vines common on the Elizabeth Islands as a whole (Cherau 1998; Fogg 1930), but missing on Penikese in all surveys, were members of the family Ericaceae. Aside from the planted blueberries in the Lower Garden (growing very poorly), we know of but a single ericaceous plant on the island in 1999—an old and overgrown specimen of *Vaccinium corymbosum* on the west bank of Typha Pond, perhaps a survivor of blueberries planted by the Commonwealth about 1930. Moul (1948) listed *V. fuscatum* saying, "Rare" and *Kalmia angustifolia,* "One colony in grassland." These, too, were probably survivors of plantings made around 1930. These are the only records of ericads for Penikese. We suppose that edaphic factors explain the lack of these plants.

Penikese and Cuttyhunk compared. O'Neill (1981) described the vascular flora of Cuttyhunk for 1974 and compared it to the one described by Lauermann and Burk (1976) for nearby Penikese for 1973. O'Neill calculated the Simpson Index of Resemblance, $100c/n_1$ (where c is the number of species common to the two floras and n_1 is the number of species in the smaller flora), to be 67.6, Penikese (163 species) and Cuttyhunk (264 species) having 110 species in common. The more diverse Cuttyhunk flora was attributed to the island's greater size and consequent greater diversity of its plant communities. O'Neill reported an increase in the number of species of shrubs from the eight given for Cuttyhunk by Fogg (1930) to 40 for 1974 and also found a recent general increase in the island's shrubby vegetation.

The floral future on Penikese. Earlier writers on the Penikese flora have usually speculated as to whether the island will regain the forest that once covered it, but often with ill-founded assumptions about what that presettlement forest was like. Jordan (1874), without citing any authority, said, "When Penikese was first known it was covered with a growth of trees said to be similar to those now found on Martha's Vineyard and Naushon. Among these may be mentioned the red cedar, pitch pine, red maple, shag bark etc." Lewis (1924) said, "The original vegetation, like that of neighboring islands, is said by Jordan to have been of a forest type, with pitch pine, red cedar, red maple, shagbark etc." and "As the early records of the island mention trees belonging to forests of an advanced type, it is possible that such a forest may again develop." Moul (1948) said, "the original climax of forest mentioned by Dr. Jordan may return," but the same author (1961) said, "In 1948, I expressed the belief that the original tree cover, mentioned by Gosnold's naturalists in 1602, might return, but today the evidence indicates that a grass 'subclimax' may persist into the future."

Fogg's (1930) consideration of the question is more thoughtful. He argued that the post-glacial forest of the Elizabeth Islands (including Penikese) developed when sea level was much lower than at present so that the shoreline was then many miles south of what are now the islands. Thus, the current regrowth of the islands' forests must occur under a much harsher set of conditions than those prevailing during their original growth and "it would seem futile to hope that the devastated areas can ever regain their former wooded luxuriance" (Fogg 1930).

Gabriel Archer's and John Brereton's (1625 and 1602, respectively, as cited in Quinn and Quinn 1983) descriptions of a diverse oak-hickory forest (including cedars) for Cuttyhunk, where the Gosnold party camped, must ultimately be the source of Jordan's remarks about nearby Penikese's presettlement forest. But the forest on Penikese was different from the one on Cuttyhunk as indicated by the facts that the Gosnold party, which visited Penikese several times, described the latter as "full of Cedars" and came there especially to cut a cargo of that tree for taking back to England ("Captain Gosnoll fell downe with the ship to the little Ilet of Cedars etc."; Archer 1625 as quoted in Quinn and Quinn 1983). This seems to indicate that the pre-settlement forest on Penikese was dominated by red cedar. (We take "cedar" to be *Juniperus virginiana.* Both "cedar" and "cypresse" are mentioned in accounts of the voyage, although only "cedar" is attributed to Penikese. We take "cypresse" to be *Chamaecyparis thyoides.*)

By 1930 *Juniperus virginiana* was rare in the Elizabeth Islands. Fogg (1930) recorded it only for Naushon, where it was "Plentiful in the woods near the East Gutter." But seven decades later, Cherau (1998) found many "in all parts of Naushon." Probably the species is generally increasing in the Elizabeth Islands.

Thus, while two arborescent species, *Prunus serotina,* black cherry, and *Juniperus virginiana,* red cedar, seemed to be slowly increasing on Penikese in 1999 as noted above, we subscribe to Fogg's (1930) argument as to the difficulty of reforestation of the island and believe that a hardwood forest such as has been described for presettlement Cuttyhunk and assumed for presettlement Penikese will not come about. A regrowth of the red cedar that the Gosnold party found in 1602 is quite possible, as this species' increase on Penikese suggests. Why red cedar, an early successional species, might have dominated on Penikese when Gosnold visited remains an interesting question. We can only suggest that this dominance may have resulted from deliberate or accidental burns by the aboriginal Pokanokets who, according to the Gosnold reporters, were seen on Penikese, but did not have a settlement there.

Management. A beautiful place, Penikese is disfigured, when viewed at close hand, by the winterkilled sticks of elderberry, white poplar, and sumac; by the dead canes of blackberries; and by weedy species such as poison ivy, Japanese honeysuckle, and Asian bittersweet. These woody plants together with herbaceous weeds such as *Cynanchum louiseae,* black swallowort, first noticed for Penikese in 1999, will increasingly affect the island adversely. The handsomest parts of Penikese's uplands (becoming more and more restricted) are the grasslands that are free of woody plants. Since fire probably can encourage these grasslands at the expense of aggressive woody plants, we suggest repeated prescribed burns for Penikese on an island-wide scale. The island, wholly under the control of the Commonwealth, is isolated, and burning there does not endanger other places. Restricted parts of the island (including its buildings) not wanted to be burned are or can be protected readily. The destruction of woody weeds and the increase of grasses by burning might at the same time restore certain parts of the island to their former utility as nesting grounds for terns, although the birds at present are not limited by a lack of the brush-free nesting grounds that they prefer. In the past, these birds have used different and more extensive parts of the island than they do at present as is shown, for instance, by the map in Lewis (1924).

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APPENDIX

PENIKESE VASCULAR PLANTS, 1873–1999

Species indicated by Sorrie and Somers (1999) as introduced to the northeastern United States are marked with an asterisk (*). Species noted in the works recording them for Penikese as "escaped," or are known or thought to have been deliberately planted on Penikese, are marked +. The 1999 status of all woody species ever reported from Penikese is noted. The dates showing the occurrence of species refer to Jordan (1874), Lewis (1924), Fogg (1930), Moul (1948), Lauermann and Burk (1976), and the current survey (1999). Voucher specimens from the 1999 survey are followed by the senior author's collection numbers. Three exceptions are specimens, collected by P.S. in

1998, of species not found in 1999; these are listed with SPWH accession numbers. All 1998/1999 vouchers have been deposited in SPWH.

POLYPODIOPHYTA

DENNSTAEDTIACEAE

Dennstaedtia punctilobula (Michx.) T. Moore – 1874, 1924, 1948, 1976, 1999 (*RHBP 2279*)

DRYOPTERIDACEAE

Athyrium filix-femina (L.) Roth – 1924
Onoclea sensibilis L. – 1999 (*RHBP 2355*)

THELYPTERIDACEAE

Thelypteris palustris Schott var. *pubescens* (G. Lawson) Fernald – 1924, 1948

CONIFEROPHYTA

CUPRESSACEAE

Juniperus virginiana L. – 1999 (*RHBP 2600*); scattered trees and presumed increasing

PINACEAE

*+*Pinus sylvestris* L. – 1924, 1948; extirpated

MAGNOLIOPHYTA

MAGNOLIOPSIDA

ACERACEAE

*+*Acer platanoides* L. – 1924; extirpated
*+*Acer pseudoplatanus* L. – 1930, 1948, 1976, 1999 (*RHBP 2275*); a few old trees

AMARANTHACEAE

**Amaranthus blitoides* S. Watson – 1999 (*Somers s.n.*, SPWH 8545)
**Amaranthus blitum* L. – 1999 (*RHBP 2443*)
**Amaranthus retroflexus* L. – 1874, 1930, 1976, 1999 (*RHBP 2400*)

ANACARDIACEAE

Rhus copallinum L. – 1948, 1976, 1999 (*RHBP 2405*); abundant and widespread on both parts of the island
Rhus hirta (L.) Sudw. – 1924, 1948, 1976, 1999 (*RHBP 2282*); mostly shrub-like and widely distributed, though relatively little on Tubs Point
Toxicodendron radicans (L.) Kuntze – 1874 (Gull Island only), 1948, 1976, 1999 (*RHBP 2434*); in large patches

APIACEAE

Angelica lucida L. – 1874, 1976, 1999 (*RHBP 2378*)
**Daucus carota* L. – 1924, 1948, 1976, 1999 (*RHBP 2285*)
Ligusticum scothicum L. – 1924, 1948, 1976

AQUIFOLIACEAE

Ilex verticillata (L.) A. Gray – 1999 (*RHBP 2456*); a single old plant

ARALIACEAE

*+*Hedera helix* L. – 1976; extirpated

ASCLEPIADACEAE

Asclepias incarnata L. subsp. *pulchra* (Ehrh. *ex* Willd.) Woodson – 1874, 1976
Asclepias syriaca L. – 1924, 1999 (*RHBP 2322*)
**Cynanchum louiseae* Kartesz & Gandhi – 1999 (*RHBP 2189*)

ASTERACEAE

Achillea millefolium L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2221*)
Ambrosia artemisiifolia L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2383*)
**Anthemis cotula* L. 1874, 1924, 1976
**Artemisia stelleriana* Besser – 1999 (*RHBP 2261*)
Aster ericoides L. – 1930
Aster novi-belgii L. – 1976, 1999 (*RHBP 2453*)
Aster pilosus Willd. var. *pringlei* (A. Gray) S. F. Blake – 1924
Aster subulatus Michx. – 1976, 1999 (*RHBP 2492*)
Aster undulatus L. – 1924
Bidens connata Muhl. *ex* Willd. – 1924, 1948, 1976, 1999 (*RHBP 2504*)
**Cirsium arvense* (L.) Scop. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2291*)
Cirsium horridulum Michx. – 1976
**Cirsium vulgare* (Savi) Ten. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2292*)
Conyza canadensis (L.) Cronquist – 1874, 1924, 1948, 1976, 1999 (*RHBP 2403*)
*+*Coreopsis lanceolata* L. – 1924, 1948
Erechtites hieraciifolia (L.) Raf. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2416*)
Erigeron strigosus Muhl. *ex* Willd. – 1948, 1976
Euthamia graminifolia (L.) Nutt. – 1948, 1976, 1999 (*RHBP 2467*)
Euthamia tenuifolia (Pursh) Nutt. – 1924, 1948, 1976, 1999 (*RHBP 2412*)
**Galinsoga quadriradiata* Ruiz & Pavón – 1999 (*RHBP 2537*)
Gnaphalium obtusifolium L. – 1924, 1948, 1976, 1999 (*RHBP 2437*)
Gnaphalium uliginosum L. – 1874, 1976, 1999 (*RHBP 2349*)
*+*Helianthus annuus* L. – 1924, 1976
**Hieracium piloselloides* Vill. – 1999 (*RHBP 2226*)
**Hypochaeris radicata* L. – 1999 (*RHBP 2250*)
Iva frutescens L. subsp. *oraria* (Bartlett) R. C. Jackson – 1874; extirpated

Lactuca biennis (Moench) Fernald – 1999 (_RHBP 2468_)
Lactuca canadensis L. – 1976, 1999 (_RHBP 2417_)
*_Lactuca serriola_ L. – 1999 (_RHBP 2458_)
*_Leontodon autumnalis_ L. – 1924
*_Leucanthemum vulgare_ L. – 1874, 1924, 1948, 1976, 1999 (_RHBP 2204_)
*_Matricaria discoidea_ Alph. de Candolle – 1976, 1999 (_RHBP 2198_)
Pluchea odorata (L.) Cass. var. _succulenta_ (Fernald) Cronquist – 1976, 1999 (_RHBP 2392_)
*_Rudbeckia hirta_ L. var. _pulcherrima_ Farw. – 1924
Solidago canadensis L. – 1924, 1999 (_RHBP 2490_)
Solidago juncea Aiton – 1924, 1976
Solidago nemoralis Aiton – 1924
Solidago rugosa Mill. – 1924, 1948, 1976, 1999 (_RHBP 2436_)
Solidago sempervirens L. – 1874 (Gull Island only), 1924, 1948, 1976, 1999 (_RHBP 2469_)
*_Sonchus arvensis_ L. – 1924
*_Sonchus asper_ (L.) Hill – 1924, 1948, 1976, 1999 (_RHBP 2498_)
*_Sonchus oleraceus_ L. – 1924, 1948, 1999 (_RHBP 2462_)
*_Tanacetum vulgare_ L. – 1930
*_Taraxacum officinale_ Weber _ex_ F. H. Wigg. – 1874, 1924, 1976, 1999 (_RHBP 2155_)
Xanthium strumarium L. – 1874, 1930, 1999 (_RHBP 2382_)

BALSAMINACEAE

Impatiens capensis Meerb. – 1999 (_RHBP 2332_)

BERBERIDACEAE

*+_Berberis thunbergii_ Alph. de Candolle – 1999 (_RHBP 2428_); a single old plant

BETULACEAE

Betula populifolia Marshall – 1874; extirpated

BORAGINACEAE

*+_Symphytum officinale_ L. – 1999 (_RHBP 2257_)

BRASSICACEAE

*+_Armoracia rusticana_ G. Gaertn., B. Mey. & Scherb. – 1948, 1976
*_Barbarea vulgaris_ R. Br. – 1948, 1999 (_RHBP 2200_)
*_Brassica juncea_ (L.) Czernj. – 1924, 1948
*_Brassica nigra_ (L.) W. J. D. Koch – 1874
Cakile edentula (Bigelow) Hook. – 1874, 1924, 1948, 1976, 1999 (_RHBP 2320_)
*_Capsella bursa-pastoris_ (L.) Medik. – 1874, 1924, 1976, 1999 (_RHBP 2191_)
*_Coronopus didymus_ (L.) J. E. Smith – 1999 (_RHBP 2328_)
*_Lepidium campestre_ (L.) Aiton f. – 1999 (_RHBP 2371_)

Lepidium virginicum L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2241*)

**Raphanus raphanistrum* L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2188*)

*+*Raphanus sativus* L. – 1924

Rorippa palustris (L.) Besser – 1976, 1999 (*RHBP 2345*)

**Sinapis arvensis* L. – 1874, 1948

**Sisymbrium altissimum* L. – 1924, 1948, 1976

**Sisymbrium officinale* (L.) Scop. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2424*)

CALLITRICHACEAE

Callitriche heterophylla Pursh – 1924, 1948, 1976

CAMPANULACEAE

Triodanis perfoliata (L.) Nieuwl. – 1948

CAPRIFOLIACEAE

**Lonicera japonica* Thunb. – 1924, 1948, 1976, 1999 (*RHBP 2206*); found almost everywhere and after *Rubus flagellaris,* the island's most abundant woody plant

**Lonicera morrowii* A. Gray 1999 (*RHBP 2455*); a single old plant

Sambucus canadensis L. 1924, 1948, 1976, 1999 (*RHBP 2277*); patches are scattered on both Tubs Point and the main part of the island with large thickets at the north end of the latter.

Viburnum dentatum L. – 1976, 1999 (*RHBP 2259*); a few scattered plants

+*Viburnum nudum* L. var. *cassinoides* (L.) Torr. & A. Gray – 1999 (*RHBP 2395*); a single old plant

CARYOPHYLLACEAE

**Cerastium fontanum* Baumg. subsp. *vulgare* (Hartm.) Greuter & Burdet – 1924, 1948, 1976, 1999 (*RHBP 2158*)

**Cerastium glomeratum* Thuill. 1874

*+*Dianthus barbatus* L. – 1924

*+*Gypsophila paniculata* L. – 1924

Honckenya peploides (L.) Ehrh. – 1874, 1924, 1976

**Sagina procumbens* L. – 1874, 1924, 1948, 1976

**Scleranthus annuus* L. – 1999 (*Somers s.n.,* SPWH 8544)

**Silene latifolia* Poir. subsp. *alba* (Mill.) Greuter & Burdet – 1924, 1948, 1976, 1999 (*RHBP 2167*)

**Spergula arvensis* L. – 1874

Spergularia rubra (L.) J. & C. Presl – 1924, 1948, 1976, 1999 (*RHBP 2156*)

Spergularia salina J. & C. Presl – 1874, 1924, 1976

**Stellaria graminea* L. – 1924, 1948, 1976, 1999 (*RHBP 2185*)

**Stellaria media* (L.) Vill. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2177*)

CELASTRACEAE

**Celastrus orbiculatus* Thunb. 1999 (*RHBP 2429*); well established

CHENOPODIACEAE

Atriplex littoralis L. – 1999 (*RHBP 2566*)
Atriplex pentandra (Jacq.) Standl. – 1874
Atriplex prostrata Boucher *ex* Alph. de Candolle – 1874, 1924, 1948, 1976, 1999 (*RHBP 2569*)
**Bassia hirsuta* (L.) Asch. – 1948, 1999 (*RHBP 2474*)
**Chenopodium album* L. – 1874, 1976, 1999 (*RHBP 2540*)
**Chenopodium ambrosioides* L. – 1976, 1999 (*RHBP 2404*)
**Chenopodium glaucum* L. – 1999 (*RHBP 2365*)
Chenopodium macrocalycium Aellen – 1924, 1948, 1999 (*RHBP 2459*); *Fogg 1401*, *Moul 3070*, and *Moul 3091* are treated as *C. macrocalycium*, not *C. album* as labeled, although none hold mature fruit, making identification uncertain.
**Chenopodium pumilio* R. Br. – 1976, 1999 (*RHBP 2353*)
Chenopodium rubrum L. – 1999 (*RHBP 2358*)
Salicornia maritima S. L. Wolff & Jefferies – 1874, 1999 (*RHBP 2473*)
Salsola kali L. – 1874, 1948, 1976, 1999 (*RHBP 2318*)
Suaeda sp. – 1874, 1999 (*RHBP 2418*); we defer identifying the Penikese plants to species until material with mature seeds can be collected. Jordan's *S. maritima* may or may not have been that species as the edition of Gray's Manual that he used offered no alternatives.

CLUSIACEAE

Hypericum mutilum L. – 1874, 1948, 1999 (*RHBP 2389*)
**Hypericum perforatum* L. – 1924, 1948, 1976, 1999 (*RHBP 2283*)

CONVOLVULACEAE

Calystegia sepium (L.) R. Br. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2217*)
**Convolvulus arvensis* L. – 1924

CUCURBITACEAE

*+*Cucucumis melo* L. – 1976
*+*Cucurbita maxima* Duchesne – 1924

CUSCUTACEAE

**Cuscuta polygonorum* Engelm. – 1948, 1976, 1999 (*RHBP 2406*); possibly native; in 1999 on *Aster subulatus*, *Bidens connata*, *Lactuca sp.*, *Lycopus americanus*, and *Polygonum punctatum*

ELAEAGNACEAE

**Elaeagnus umbellata* Thunb. – 1999 (*RHBP 2315*); a single plant found in 1999 was not present in 2000

ERICACEAE

+*Kalmia angustifolia* L. – 1948; extirpated
+*Vaccinium corymbosum* L. – 1999 (*RHBP 2234*); a single old plant found

+*Vaccinium fuscatum* Aiton – 1948; extirpated

EUPHORBIACEAE

Chamaesyce maculata L. – 1874, 1948, 1976, 1999 (*RHBP 2295*)
Chamaesyce polygonifolia L. – 1874, 1948, 1999 (*RHBP 2380*)

FABACEAE

Lathyrus japonicus Willd. – 1874 (Gull Island only), 1924, 1948, 1976, 1999 (*RHBP 2216*)
Trifolium arvense L. – 1874, 1924
Trifolium aureum Pollich – 1924, 1999 (*RHBP 2260*)
Trifolium dubium Sibth. – 1874, 1999 (*RHBP 2236*)
Trifolium hybridum L. – 1930, 1948, 1999 (*RHBP 2190*)
Trifolium pratense L. – 1924, 1948, 1999 (*RHBP 2193*)
Trifolium repens L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2196*)
Vicia cracca L. – 1924, 1976, 1999 (*RHBP 2244*)
Vicia sativa L. – 1948, 1999 (*RHBP 2587*)
Vicia tetrasperma (L.) Schreb. – 1924, 1948, 1999 (*RHBP 2230*)

FAGACEAE

+*Quercus rubra* L. – 1924, 1948; extirpated

GERANIACEAE

Erodium cicutarium (L.) L'Her. *ex* Aiton – 1976, 1999 (*RHBP 2157*)
Geranium carolinianum L. – 1924
Geranium robertianum L. – 1976

HALORAGACEAE

Myriophyllum pinnatum (Walter) Britton, Sterns & Poggenb. – 1874, 1924, 1948, 1976
Myriophyllum verticillatum L. – 1976

LAMIACEAE

Glechoma hederacea L. – 1948, 1976, 1999 (*RHBP 2154*)
Leonurus cardiaca L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2293*)
Lycopus americanus Muhl. *ex* W. Bartram – 1924, 1948, 1976, 1999 (*RHBP 2350*); *Moul 3403*, called *L. uniflorus* by him, has been re-identified as *L. americanus*, as has Lauermann and Burk's *L. rubellus* in SCHN.
Lycopus europaeus L. – 1874; the edition of Gray's Manual that Jordan used lists only *L. virginicus* and *L. europaeus*. Since the latter is uncommon in North America, the best thing to be said of this record, perhaps, is "not *virginicus*."
Lycopus uniflorus Michx. – 1924, 1976, 1999 (*RHBP 2514*)
Mentha arvensis L. – 1948, 1976, 1999 (*RHBP 2323*)
Nepeta cataria L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2325*)

*+*Origanum vulgare* L. – 1999 (*RHBP 2199*)
Scutellaria galericulata L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2359*)
Teucrium canadense L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2317*)

MALVACEAE

Hibiscus moscheutos L. – 1999 (*RHBP 2386*)
**Malva neglecta* Wallr. – 1874, 1924, 1999 (*RHBP 2239*); the 5th edition of Gray's Manual does not offer *M. neglecta* as an alternative to *M. rotundifolia,* the name that Jordan gave to the plant that he observed. *Fogg 1442,* called by him *M. rotundifolia,* has been re-identified as *M. neglecta.*

MOLLUGINACEAE

**Mollugo verticillata* L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2299*)

MORACEAE

*+*Morus alba* L. – 1948, 1976, 1999 (*RHBP 2233*); a few trees in three widely separated places

MYRICACEAE

Myrica pensylvanica Loisel. – 1924, 1948, 1976, 1999 (*RHBP 2237*); found in numerous small to medium-sized patches, mostly near the shore

OLEACEAE

*+*Ligustrum ovalifolium* Hassk. – 1924, 1948, 1976, 1999 (*RHBP 2286*); a few old plants; all of the privets on the island, about two dozen, were examined while in flower and are *L. ovalifolium* save for a single *L. vulgare,* the smallest and poorest-growing plant in the middle of a row of privets planted by the Penikese Island School about 1975. Fogg's *L. vulgare* (*1451*) has been re-identified as *L. ovalifolium,* as have Lauermann and Burk's specimens in SCHN. Moul's *L. vulgare* (*3100*), with immature flowers, has glabrous twigs and is assumed to be *L. ovalifolium.*
*+*Ligustrum vulgare* L. – 1999 (*RHBP 2601*); one plant as noted above

ONAGRACEAE

Epilobium coloratum Biehler – 1999 (*RHBP 2407*)
Ludwigia palustris (L.) Elliott – 1874, 1924, 1948, 1976, 1999 (*RHBP 2333*)
Oenothera biennis L. – 1924, 1948, 1976, 1999 (*RHBP 2477*)
*+*Oenothera glazioviana* Micheli – 1924

OXALIDACEAE

**Oxalis corniculata* L. – 1976
Oxalis dillenii Jacq. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2298*); *Fogg*

1439 and *Moul 3147*, labeled *O. stricta*, have been re-identified as *O. dillenii*, and we suppose that Jordan's observations pertain to this species also.

PAPAVERACEAE

**Glaucium flavum* Crantz – 1976, 1999 (*RHBP 2215*)

PHYTOLACCACEAE

Phytolacca americana L. – 1948, 1976, 1999 (*RHBP 2213*)

PLANTAGINACEAE

**Plantago lanceolata* L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2161*)
**Plantago major* L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2280*)

PLUMBAGINACEAE

Limonium carolinianum (Walter) Britton – 1874 (Gull Island only)

POLYGONACEAE

**Polygonum aviculare* L. – 1874, 1924, 1999 (*RHBP 2484*)
**Polygonum convolvulus* L. – 1924
Polygonum glaucum Nutt. – 1874, 1999 (*RHBP 2290*)
Polygonum hydropiper L. – 1874
Polygonum lapathifolium L. – 1999 (*RHBP 2390*)
Polygonum pensylvanicum L. – 1976, 1999 (*RHBP 2388*)
**Polygonum persicaria* L. – 1874, 1924, 1976, 1999 (*RHBP 2327*)
Polygonum punctatum Elliott – 1924, 1948, 1976, 1999 (*RHBP 2326*)
*+*Rheum rhaponticum* L. – 1948
**Rumex acetosella* L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2163*)
**Rumex crispus* L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2278*)
Rumex maritimus (L.) var. *fueginus* (Phil.) Dusen – 1924, 1948, 1976, 1999 (*RHBP 2398*)
**Rumex obtusifolius* L. – 1874, 1976, 1999 (*RHBP 2421*)

PORTULACACEAE

**Portulaca oleracea* L. – 1874, 1976, 1999 (*RHBP 2324*)

PRIMULACEAE

**Anagallis arvensis* L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2192*)

RANUNCULACEAE

**Ranunculus acris* L. – 1924, 1948, 1976, 1999 (*RHBP 2232*)
**Ranunculus bulbosus* L. – 1976, 1999 (*RHBP 2160*)
Ranunculus cymbalaria Pursh – 1874, 1924, 1948
Ranunculus flabellaris Raf. – 1924

ROSACEAE

Amelanchier arborea (Michx. f.) Fernald – 1924; extirpated
Argentina egedii subsp. *egedii* (Wormsk.) Rydb. – 1948
*+*Fragaria vesca* L. – 1874
Fragaria virginiana Duchesne – 1874, 1924, 1948
**Malus pumila* Mill. – 1999 (*RHBP 2483*); a single old plant
**Potentilla argentea* L. – 1874, 1924, 1948
Potentilla canadensis L. – 1924
Potentilla norvegica L. – 1924
Prunus serotina Ehrh. – 1924, 1948, 1976, 1999 (*RHBP 2509*); scattered small trees and slowly increasing
**Rosa multiflora* Thunb. *ex* Murray – 1999 (*RHBP 2228*); well established
Rosa palustris Marshall – 1930; extirpated
*+*Rosa rugosa* Thunb. – 1924, 1948, 1976, 1999 (*RHBP 2169*); abundant and spreading
Rubus flagellaris Willd. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2201*); abundant and spreading
*+*Rubus laciniatus* Willd. – 1924, 1948, 1976, 1999 (*RHBP 2202A & B*); heavily fruiting in three patches tens of meters in diameter west of the reservoir hill
Rubus pensilvanicus Poir. – 1924, 1948, 1976, 1999 (*RHBP 2203*); this sparsely fruiting, least abundant blackberry grows on both the main part (especially the north end) and on Tubs Point. We may be putting more than one species under this name as individuals with irregular, arching canes and ones with vertical, straight canes were both observed.

RUBIACEAE

Galium tinctorium (L.) Scop. – 1930, 1948, 1976, 1999 (*RHBP 2344*)

SALICACEAE

*+*Populus alba* L. – 1924, 1948, 1976, 1999 (*RHBP 2431*); several patches tens of meters in diameter of plants 1–2 m tall grow on the east side of the island, but have not been seen to flower. Fernald (1950) said, ". . . spreading by suckers (especially after destruction of parent trunk)," and so we suppose it to be increasing on Penikese.
*+*Populus deltoides* Bartram *ex* Marshall – 1924, 1948; extirpated
**Salix atrocinerea* Brot. – 1999 (*RHBP 2445*); two small trees; this species was called *S. cinerea* by Sorrie and Somers (1999).
Salix discolor Muhl. – 1874; extirpated
*+*Salix pentandra* L. – 1924, 1948; extirpated
*+*Salix* ×*rubens* Schrank – 1924, 1948, 1976, 1999 (*RHBP 2584*); one old, small tree

SCROPHULARIACEAE

*+*Digitalis purpurea* L. – 1924
Limosella australis R. Br. – 1948, 1999 (*RHBP 2362*)
**Linaria vulgaris* Mill. – 1924

Lindernia dubia (L.) Pennell – 1924, 1948, 1976, 1999 (*RHBP 2335*)
Nuttallanthus canadensis (L.) D. A. Sutton – 1874, 1924, 1948, 1976, 1999 (*RHBP 2247*)
**Verbascum thapsus* L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2220*)
**Veronica arvensis* L. – 1976, 1999 (*RHBP 2182*)

SOLANACEAE

**Datura stramonium* L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2316*)
**Lycopersicon esculentum* Mill. – 1976
**Solanum dulcamara* L. – 1976, 1999 (*RHBP 2218*)
**Solanum nigrum* L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2336*)
**Solanum physalifolium* Rusby – 1976

VIOLACEAE

Viola lanceolata L. – 1976, 1999 (*RHBP 2178*)
Viola sagittata Aiton – 1874, 1924

VITACEAE

Parthenocissus quinquefolia (L.) Planch. – 1924, 1948, 1999 (*RHBP 2180*); a few plants
*+*Parthenocissus tricuspidata* (Siebold & Zucc.) Planch. – 1930, 1948; extirpated

LILIOPSIDA

COMMELINACEAE

**Commelina communis* L. – 1999 (*RHBP 2425*)

CYPERACEAE

Carex annectens E. P. Bicknell – 1999 (*RHBP 2243*)
**Carex contigua* Hoppe – 1924, 1948, 1976, 1999 (*RHBP 2166*)
Carex longii Mack. – 1924, 1948, 1976, 1999 (*RHBP 2305*)
Carex lurida Wahlenb. – 1999 (*RHBP 2225*)
Carex muhlenbergii Schkuhr *ex* Willd. – 1948
Carex scoparia Schkuhr *ex* Willd. – 1874
Carex silicea Olney – 1930, 1948
Carex stipata Muhl. *ex* Willd. – 1999 (*RHBP 2263*)
Carex straminea Willd. *ex* Schkuhr – 1874, 1930, 1999 (*RHBP 2356*)
Cyperus diandrus Torr. – 1999 (*RHBP 2507*)
Cyperus erythrorhizos Muhl. – 1976, 1999 (*RHBP 2444*)
Cyperus filicinus Vahl – 1999 (*RHBP 2526*)
Cyperus lupulinus (Spreng.) Marcks subsp. *macilentus* (Fernald) Marcks – 1874, 1948, 1999 (*RHBP 2544*)
Eleocharis acicularis (L.) Roem. & Schult. – 1874
Eleocharis palustris (L.) Roem. & Schult. – 1874, 1924, 1948
Eleocharis parvula (Roem. & Schult.) Link *ex* Bluff, Nees & Schauer – 1948, 1999 (*RHBP 2361*)

Scirpus maritimus L. – 1874, 1924, 1948
Scirpus pungens Vahl – 1874, 1924, 1948, 1999 (*RHBP 2341*); *Fogg 486* and *Moul 3339* are this species, although reported as *S. americanus* Pers. in keeping with the nomenclature of their days. Jordan listed *S. pungens* Vahl, the accepted name for this species then as it is now.
Scirpus tabernaemontani K. C. Gmelin – 1924, 1948, 1999 (*RHBP 2369*)

IRIDACEAE

*+*Iris ×germanica* L. – 1948, 1976
Iris versicolor L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2205*)
Sisyrinchium angustifolium Mill. – 1874, 1924, 1948, 1999 (*RHBP 2329*)
Sisyrinchium atlanticum E. P. Bicknell – 1976

JUNCACEAE

Juncus acuminatus Michx. – 1924, 1948, 1976, 1999 (*RHBP 2457*)
Juncus articulatus L. – 1930
Juncus bufonius L. – 1948
Juncus debilis A. Gray – 1924
Juncus dichotomus Elliott – 1930, 1948
Juncus effusus L. var. *pylaei* (Laharpe) Fernald & Wiegand – 1924, 1948, 1976, 1999 (*RHBP 2338*)
Juncus gerardii Loisel. – 1874, 1930, 1948, 1976
Juncus greenei Oakes & Tuck. – 1924, 1976, 1999 (*RHBP 2287*)
Juncus pelocarpus E. Mey. – 1874, 1999 (*RHBP 2334*)
Juncus tenuis Willd. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2337*)

LILIACEAE

**Allium vineale* L. – 1999 (*RHBP 2186*)
*+*Asparagus officinalis* L. – 1924, 1948, 1976, 1999 (*RHBP 2211*)
*+*Lilium lancifolium* Thunb. – 1924
*+*Narcissus pseudonarcissus* L. – 1999 (*RHBP 2153*)

POACEAE

**Agrostis capillaris* L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2312*)
Agrostis hyemalis (Walter) Britton, Sterns & Poggenb. – 1999 (*Somers s.n.*, SPWH 8543)
Agrostis perennans (Walter) Tuck. – 1999 (*RHBP 2301*)
Agrostis stolonifera L. var. *palustris* (Huds.) Farw. – 1874, 1930, 1948, 1976, 1999 (*RHBP 2308*)
Ammophila breviligulata Fernald – 1874, 1930, 1948, 1976, 1999 (*RHBP 2377*)
Andropogon virginicus L. – 1999 (*RHBP 2543*)
**Anthoxanthum odoratum* L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2164*)
**Arrhenatherum elatius* (L.) J. & C. Presl – 1999 (*RHBP 2231*)
**Avena sativa* L. – 1924, 1948
**Bromus commutatus* Schrad. – 1948
**Bromus hordeaceus* L. – 1930

**Bromus secalinus* L. – 1924

**Bromus tectorum* L. – 1999 (*RHBP 2159*)

**Dactylis glomerata* L. – 1924, 1948, 1976, 1999 (*RHBP 2197*)

Danthonia spicata (L.) P. Beauv. *ex* Roem. & Schult. – 1924, 1948, 1976, 1999 (*RHBP 2246*)

Dichanthelium acuminatum (Sw.) Gould & C. A. Clark var. *fasciculatum* (Torr.) Freckmann – 1924, 1948, 1976, 1999 (*RHBP 2466*)

Dichanthelium acuminatum (Sw.) Gould & C. A. Clark var. *lindheimeri* (Nash) Gould & C. A. Clark – 1999 (*RHBP 2548*)

Dichanthelium clandestinum L. – 1976

Dichanthelium columbianum (Scribn.) Freckman – 1924, 1948

Dichanthelium dichotomum (L.) Gould – 1874

Dichanthelium meridionale (Nash) Freckmann – 1930

**Digitaria ischaemum* (Schreber) Muhl. – 1999 (*RHBP 2541*)

**Digitaria sanguinalis* (L.) Scop. – 1874, 1976, 1999 (*RHBP 2538*)

Diplachne maritima E. Bicknell – 1999 (*RHBP 2410*)

Distichlis spicata (L.) Greene – 1930, 1976, 1999 (*RHBP 2464*)

**Echinochloa crusgalli* (L.) P. Beauv. – 1874, 1930

Elymus virginicus L. – 1874 (Gull Island only), 1924, 1948, 1976, 1999 (*RHBP 2381*)

**Elytrigia pungens* (Pers.) Tutin – 1999 (*RHBP 2207*)

Elytrigia repens (L.) Desv. *ex* B. D. Jackson – 1874, 1924, 1948, 1976, 1999 (*RHBP 2254*)

**Festuca filiformis* Pourr. – 1976

**Festuca ovina* L. – 1874, 1948, 1976, 1999 (*RHBP 2174*)

**Festuca pratensis* Huds. – 1874, 1924

Festuca rubra L. – 1924, 1948, 1976, 1999 (*RHBP 2214*)

**Holcus lanatus* L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2235*)

**Lolium perenne* L. – 1999 (*RHBP 2340*)

Panicum dichotomiflorum Michx. – 1976, 1999 (*RHBP 2449*)

Panicum virgatum L. var. *spissum* Linder – 1930, 1948, 1976, 1999 (*RHBP 2294*)

Paspalum setaceum Michx. – 1948

Phalaris arundinacea L. – 1999 (*RHBP 2270*)

**Phleum pratense* L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2256*)

**Poa annua* L. – 1874, 1976, 1999 (*RHBP 2314*)

Poa palustris L. – 1874, 1999 (*RHBP 2357*)

**Poa pratensis* L. – 1874, 1924, 1948, 1976, 1999 (*RHBP 2173*)

**Poa trivialis* L. – 1999 (*RHBP 2209*)

Puccinellia maritima (Huds.) Parl. – 1874

Schizachyrium scoparium (Michx.) Nash – 1948, 1999 (*RHBP 2555*)

**Setaria glauca* (L.) P. Beauv. – 1874, 1976

**Setaria viridis* (L.) P. Beauv. – 1874

Spartina alterniflora Loisel. – 1874, 1924, 1948, 1976

Spartina patens (Aiton) Muhl. – 1874, 1924, 1948, 1999 (*RHBP 2373*)

RUPPIACEAE

Ruppia maritima L. – 1874, 1948

SMILACACEAE

Smilax rotundifolia L. – 1924, 1999 (*RHBP 2394*); one patch 2–3 m in diameter, perhaps a single plant; not seen to flower

SPARGANIACEAE

Sparganium eurycarpum Engelm. *ex* A. Gray – 1999 (*RHBP 2482*)

TYPHACEAE

Typha latifolia L. – 1924, 1948, 1976, 1999 (*RHBP 2330*)

ZOSTERACEAE

Zostera marina L. - 1874, 1924, 1948, 1976, 1999 (*RHBP 2274*)

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ALLOZYME EVIDENCE FOR THE HYBRID ORIGIN OF *DESMODIUM HUMIFUSUM* (FABACEAE)

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ABSTRACT. *Desmodium humifusum,* one of the rarest members of the New England flora, always occurs with two conspecifics, *D. paniculatum* and *D. rotundifolium,* and a hybrid origin for *D. humifusum* has been proposed. Protein (allozyme) electrophoresis was used to test this hypothesis. Allozyme data demonstrated that the extant *D. humifusum* populations totaled eight genetic individuals rather than the 100+ previously estimated. The Rogers genetic similarity between the putative parental species was 0.797 and they were fixed for different alleles at a single locus, *Tpi-1.* All but one individual of *D. humifusum* were heterozygous at this locus, combining alleles unique to both of the putative parental species. *Desmodium humifusum* exhibited excess heterozygosity (relative to Hardy-Weinberg expectations), in sharp contrast to the consistent heterozygote deficiency in the parental species. *Desmodium humifusum* consists of both F_1 interspecific hybrids, as well as later-generation hybrids; introgression between the parental species was not obvious.

Key Words: *Desmodium humifusum, D. paniculatum, D. rotundifolium,* hybridization, allozymes, rare species, New England flora

Ground-spreading Tick-trefoil, *Desmodium humifusum* (Muhl.) L. C. Beck (Fabaceae) is a rare and enigmatic member of the New England flora. Its obscurity owes not only to its rarity, but also to the general difficulty of species delimitation in this genus. Additional confusion has resulted because the name of a related species, *D. glabellum* (Michx.) Alph. de Candolle [= *Meibomia glabella* (Michx.) Kuntze], was misapplied to this species (Gleason and Cronquist 1963; Robinson and Fernald 1908; Vail 1892). The nomenclatural error was subsequently corrected (Gleason and Cronquist 1991; Schubert 1950a) and a detailed description of *D. humifusum* was provided by Schubert (1950b).

Prior to 1996, *Desmodium humifusum* was listed as a "Category 2" species by the U.S.D.A. Fish and Wildlife Service [Federal Register 58(188): 51144]. The Category 2 list comprises species under consideration for protected status but for which avail-

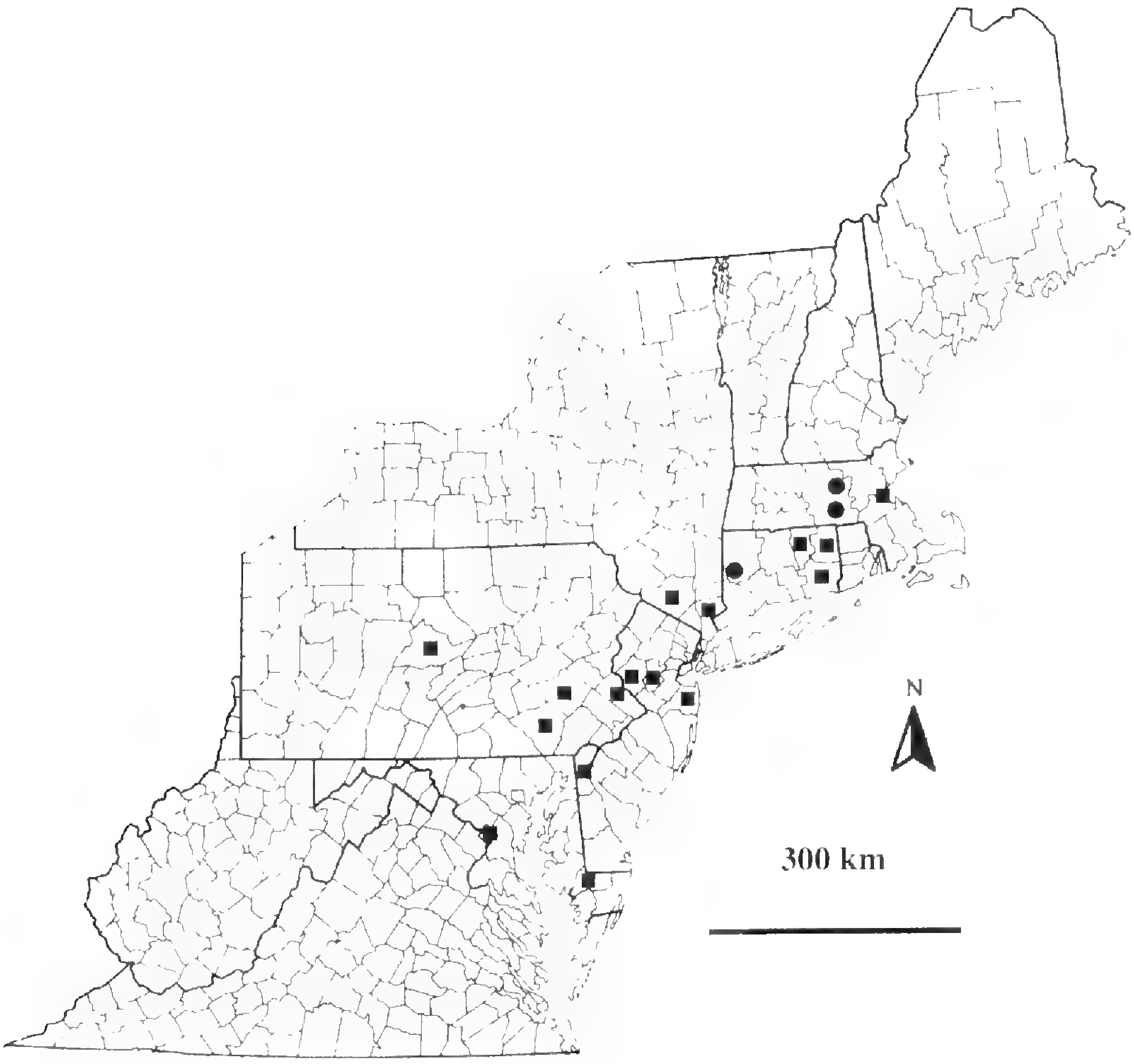

Figure 1. Historical distribution of *Desmodium humifusum* by county (■), and extant populations (●); redrawn from Rawinski 1990.

able information is insufficient to make a decision. *Desmodium humifusum* was placed in this category partly because Rawinski, in the Final Status Survey Report for the species, theorized that the plant could be a hybrid (Rawinski 1990). The Category 2 candidate list was discontinued by act of Congress on December 6, 1996 [Federal Register 61(235): 64481].

Desmodium humifusum was never common, based on a survey of herbarium specimens by Rawinski (1990) that yielded only 35 historic collections from four major herbaria (New York Botanical Garden, Gray Herbarium of Harvard University, New England Botanical Club, and Philadelphia Academy of Natural Sciences). These collections indicated a historical distribution roughly from Boston, Massachusetts to the District of Columbia, with 19 sites representing 16 counties in seven states and the District of Columbia (Figure 1). Although field surveys by Rawinski and others

Table 1. Morphological differences among *Desmodium paniculatum*, *D. humifusum*, and *D. rotundifolium*.

Trait/Species	*D. paniculatum*	*D. humifusum*	*D. rotundifolium*
Habit	Upright	Trailing	Prostrate
Stem pubescence	Glabrous or sparsely strigose	Sparsely long pilose and uncinulate	Densely long pilose and uncinulate
Stipules	Subulate and often deciduous	Lanceolate and persistent	Broadly ovate and persistent
Leaflet shape	Lanceolate	Rhombic	Suborbicular

failed to re-locate this species at any of the historic locations, three new populations were discovered, two in Worcester County, Massachusetts, near Clinton and Oxford and a third near New Milford, Litchfield County, Connecticut (Figure 1). The Clinton population was estimated to contain 50–100 plants, whereas the other two populations had approximately 10 plants each. The general occurrence of *D. humifusum* in dense clusters of stems limited the precision of population estimates. Rawinski (1990) hypothesized a hybrid origin for *D. humifusum* involving *D. paniculatum* (L.) Alph. de Candolle and *D. rotundifolium* (Michx.) Alph. de Candolle based on morphological intermediacy and the invariable occurrence of the three species together.

Hybridization in *Desmodium* has been well-documented among several species used as forage crops in tropical climates (e.g., Chow 1982; Chow and Crowder 1972, 1973, 1974; Hutton and Gray 1967; Imrie and Blogg 1983; McWhirter 1969; Park and Rotar 1968; Rotar and Chow 1971; Rotar et al. 1967) and has been invoked to explain cases of intermediate morphologies among North American species of the genus (e.g., Isely 1953, 1983, 1990, 1998; Steyermark 1963; Vail 1892; Voss 1985). Furthermore, experimental crosses have demonstrated interfertility between several North American species [e.g., *D. viridiflorum* (L.) Alph. de Candolle × *D. perplexum* B. G. Schub. and *D. laevigatum* (Nutt.) Alph. de Candolle × *D. perplexum*; Raveill 1995] but no attempt has been made to cross *D. paniculatum* and *D. rotundifolium*.

The morphological differences between *Desmodium paniculatum* and *D. rotundifolium* are pronounced, with *D. humifusum* having roughly intermediate morphology (Table 1). The putative parental species are broadly sympatric with the entire range of *D.*

rotundifolium, from Massachusetts, Vermont, Michigan, and Kansas south to Florida and Texas (Great Plains Flora Association 1986) contained within the broader geographical range of *D. paniculatum.* However, the two species are generally separated ecologically. *Desmodium rotundifolium* is generally found in the interior of woodlands, while *D. paniculatum* occurs in more sunny habitats, including woodland openings and edges. The two species most often occur together when natural or man-made disturbance opens a woodland canopy and *D. paniculatum* moves into habitat previously occupied only by *D. rotundifolium* (Raveill, pers. obs.).

The proposed hybrid origin for *Desmodium humifusum* is supported by: 1) the close proximity of the three species at each location where *D. humifusum* occurs, 2) similar floral structure, 3) similar floral phenology, and 4) identical chromosome numbers. All three species are diploid with $2n = 22$ or $n = 11$ (Young 1940). The count for *D. humifusum* was reported for *D. glabellum* Michx. [= *Meibomia glabella* (Michx.) Kuntze] following the nomenclature at that time (Britton and Brown 1913; Robinson and Fernald 1908; Small 1933). Little variation in chromosome number has been found in *Desmodium*; all reported species have $2n = 22$, except for a few species from South America and Africa with $2n = 20$ (Rotar and Urata 1967; Turner and Fearing 1959). Polyploidy has never been reported in *Desmodium* or related genera (Ohashi et al. 1981).

Although morphological intermediacy is usually the initial criterion on which to base a hypothesis of hybrid origin, other explanations exist (Gottlieb 1972). Allozyme analysis can be used to test hypotheses of hybridization (Crawford 1990). The simple co-dominant inheritance of allozymes allows for the detection of additive profiles in hybrid taxa where parental taxa are fixed for different alleles or where allele frequencies differ significantly (Aparicio et al. 2000; Gallez and Gottlieb 1982; Hollingsworth et al. 1995; Johnson et al. 1998; Werth 1989). Although lack of differentiation between putative parental species can limit hypothesis testing, proposed parental species can sometimes be conclusively excluded (Harris and Abbott 1997).

In this study, allozyme analysis was used to test the null hypothesis that the three species were genetically discreet. The alternative hypothesis was a hybrid origin of *Desmodium humifus-*

um with *D. paniculatum* and *D. rotundifolium* as the putative parental species.

MATERIALS AND METHODS

Leaf tissue for protein extraction and electrophoresis was obtained from *Desmodium humifusum, D. paniculatum,* and *D. rotundifolium* plants at each of the three extant locations of *D. humifusum* (Figure 1). For comparison, a site in Lenawee County, Michigan, was chosen at which *D. paniculatum* and *D. rotundifolium* grew intermixed over an extensive area. At this site, neither *D. humifusum* nor any plants that seemed intermediate between *D. paniculatum* and *D. rotundifolium* occurred.

Sampling strategies varied because of the distribution of the species at each location. *Desmodium humifusum* occurred either as individual stems or in dense clusters of intertwined stems. Within clusters, determination of individuals was difficult. All isolated *D. humifusum* stems were sampled and several stems were sampled from each cluster of stems.

At the Clinton and Lenawee locations, plants of *Desmodium paniculatum* and *D. rotundifolium* were present throughout forested areas that had been heavily logged. Hundreds of plants of each species were present, with no apparent pattern to the fine-scale distribution of the two species. Sampling at these locations was confined to a roughly circular area of about 20 m in diameter.

The Oxford and New Milford locations were in powerline cuts, with sampling limited to these rights-of-way. The Oxford *Desmodium humifusum* population was about 20 m from a road and consisted of one cluster of about 10 stems and two isolated plants several meters away. Sampling of the other two species was done between the *D. humifusum* plants and the road. At the New Milford location, a single patch of about 50 stems of *D. humifusum* was present. The powerline right-of-way was heavily overgrown, with individuals of the other two species widely scattered; samples were obtained from an approximately 100 m length of the right-of-way.

The upper portion of each plant sampled was placed into an individual Zip-Lock® plastic bag and kept on ice during transport to Vanderbilt University, where all protein extractions and electrophoresis were performed. A voucher for each plant used in electrophoresis was deposited at the herbarium of Central Missouri State University (WARM).

Horizontal starch gel electrophoresis followed procedures summarized in Wendel and Weeden (1989) and Werth (1985). Enzymes were extracted by hand-grinding approximately equal volumes of fresh leaf material and the simple buffer of Werth (1985) fortified with 10% (w/v) polyvinylpyrrolidone, average molecular weight 40,000, and 0.5% 2-mercaptoethanol. The crude extract was absorbed into wicks of Whatman No. 1 filter paper and inserted directly into 12% starch gels. Ten enzyme systems encoded 15 putative loci: aspartate aminotransferase (*Aat-1, Aat-2*), colorimetric esterase (*Est*), isocitrate dehydrogenase (*Idh-1, Idh-2*), leucine aminopeptidase (*Lap*), malate dehydrogenase (*Mdh-1, Mdh-2*), menadione reductase (*Mnr*), peroxidase (*Per*), phosphoglucomutase (*Pgm-1, Pgm-2*), 6-phosphogluconate dehydrogenase (*6-Pgd*), and triosephosphate isomerase (*Tpi-1, Tpi-2*). Visualization of enzymes followed Soltis et al. (1983), with the use of agar overlays and frozen premixed "zymecicles" (Werth 1990). Five buffer systems were used to resolve the loci:

1. lithium borate/tris citrate pH 8.3 (Soltis et al. 1983) resolved *Mnr* and *Tpi*;
2. tris citrate pH 8.0 (Werth 1985) resolved *Aat* and *Per*;
3. histidine-citrate pH 5.7 (Soltis et al. 1983) resolved *Est* and *Lap*;
4. tris maleate pH 7.4 (Werth 1985) resolved *Pgm* and *Mdh*;
5. morpholine citrate pH 8.0 (0.04 M citric acid titrated to pH 8.0 with n-3 aminopropyl morpholine), modified from Clayton and Tretiak (1972) was used to resolve *Idh* and *6-Pgd*.

All enzymes migrated anodally except *Per*, which migrated cathodally. Alleles were designated by letters, with the most anodally migrating allozyme denoted "*a*." Allele nomenclature was based on a more extensive study of *Desmodium*, with some alleles found in species or sites not reported here (Raveill 1995). The Mendelian inheritance of all variable loci has been reported for *D. paniculatum*, or for the related *D. perplexum*, using either controlled crosses or progeny arrays from single plants (Raveill 1995). No gene duplication was indicated, and all banding patterns and inheritance were consistent with the expectations of diploid species.

Allozyme data were used to determine various genetic attributes of each species and population. BIOSYS-1 (Swofford and Selander 1981) was used for all calculations except for the t-test of means, which followed Sokal and Rohlf (1981). Calculations for mean observed and mean expected heterozygosity per locus used direct counts and unbiased estimates, respectively. Wright's fixation index (F_{IS}) was used to express heterozygosity of individuals relative to the population in which they were found. Levene's correction for small sample size (Levene 1949) was employed in chi-square analysis. Allozyme similarity was assessed using Rogers similarity (Rogers 1972).

RESULTS

Seven of 15 loci were polymorphic in at least one of the putative parental species (Table 2). The only fixed difference discriminating these two species involved *Tpi-1,* at which *Desmodium paniculatum* contained alleles *b* or *c* while *D. rotundifolium* was fixed for allele *e*.

Genetic similarity obtained from pairwise comparisons of co-occurring *Desmodium paniculatum* and *D. rotundifolium* populations ranged from 0.705 at New Milford, Connecticut, to a maximum of 0.819 at the Oxford, Massachusetts site, with a mean of 0.797. The site at Lenawee County, Michigan, without *D. humifusum*, had a similarity of 0.800 indicating that the presence of *D. humifusum* did not cause the potential parental species to be genetically more similar.

All samples within each cluster of *Desmodium humifusum* stems consisted of a single allozyme genotype and was considered to represent a single clone. The actual number of genets of *D. humifusum* was far below previous estimates, being one, three, and four at New Milford, Oxford, and Clinton, respectively, for a total of eight genets known in 1992. Although some plants consisted of only a single stem, the largest clone, "Clinton-4," consisted of an estimated 100 stems over a roughly oval area of about 8 m^2.

No unique alleles were found in *Desmodium humifusum*; instead the alleles of *D. humifusum* were a composite of those of the putative parental species, *D. paniculatum* and *D. rotundifolium.* At the critical *Tpi-1* locus, seven of the eight *D. humifusum* individuals were heterozygous, combining the *e* allele of *D. ro-*

Table 2. Allele frequencies for polymorphic loci for populations of *Desmodium paniculatum* and *D. rotundifolium* from New Milford, Connecticut (NM); Oxford, Massachusetts (OX); Clinton, Massachusetts (CL); and Lenawee Co., Michigan (MI). Loci not listed were monomorphic for all sites. Mean allele frequencies for each species and sample sizes for each population are also included.

		D. paniculatum					*D. rotundifolium*				
Locus	Allele	NM	OX	CL	MI	Mean	NM	OX	CL	MI	Mean
Aat-1	*a*	0.0	0.0	0.0	0.167	0.042	0.0	0.0	0.0	0.0	0.0
	b	1.0	1.0	1.0	0.833	0.958	1.0	1.0	1.0	1.0	1.0
		N=8	N=29	N=43	N=37	N=117	N=11	N=18	N=20	N=17	N=66
Est-1	*a*	0.938	0.0	0.207	0.068	0.303	0.0	0.0	0.0	0.0	0.0
	b	0.063	0.882	0.638	0.932	0.629	0.0	0.0	0.0	0.0	0.0
	c	0.0	0.118	0.155	0.0	0.068	1.0	1.0	1.0	1.0	1.0
		N=8	N=17	N=28	N=37	N=90	N=11	N=7	N=6	N=17	N=41
Idh-1	*a*	1.0	0.086	1.0	0.676	0.690	1.0	1.0	0.275	1.0	0.819
	b	0.0	0.914	0.0	0.324	0.310	0.0	0.0	0.725	0.0	0.181
		N=8	N=29	N=43	N=37	N=117	N=11	N=18	N=20	N=17	N=66
Idh-2	*a*	1.0	1.0	0.333	0.865	0.800	1.0	1.0	1.0	1.0	1.0
	b	0.0	0.0	0.667	0.135	0.200	0.0	0.0	0.0	0.0	0.0
		N=8	N=29	N=43	N=37	N=117	N=11	N=18	N=20	N=17	N=66
Pgm-1	*a*	1.0	0.0	0.372	0.417	0.447	0.0	0.0	0.0	0.0	0.0
	b	0.0	1.0	0.628	0.583	0.553	1.0	1.0	0.950	1.0	0.988
	c	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.050	0.0	0.012
		N=8	N=29	N=43	N=37	N=117	N=11	N=18	N=20	N=17	N=66

Table 2. Continued.

		D. paniculatum					*D. rotundifolium*				
Locus	Allele	NM	OX	CL	MI	Mean	NM	OX	CL	MI	Mean
6-Pgd	*a*	0.0	0.0	0.0	0.0	0.0	0.455	0.0	0.0	0.0	0.114
	b	1.0	1.0	1.0	1.0	1.0	0.545	1.0	1.0	1.0	0.886
		N=8	N=29	N=43	N=37	N=117	N=11	N=18	N=20	N=17	N=66
Tpi-1	*b*	1.0	0.897	1.0	1.0	0.974	0.0	0.0	0.0	0.0	0.0
	c	0.0	0.103	0.0	0.0	0.026	0.0	0.0	0.0	0.0	0.0
	e	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	1.0	1.0
		N=8	N=29	N=43	N=37	N=117	N=11	N=18	N=20	N=17	N=66

Table 3. Allozymic genotypes of all individuals of *Desmodium humifusum* (e.g., MN-1, OX-1, etc.) for loci polymorphic in either *D. paniculatum* or *D. rotundifolium* at each site (Table 2). The number of stems examined for each clone is given.

	Individual							
	NM-1	OX-1	OX-2	OX-3	CL-1	CL-2	CL-3	CL-4
Locus	23	4	1	1	2	3	1	6
Aat-1	*bb*	*bb*	*bb*	*bb*	*bb*	*bb*	*bb*	*bb*
Est-1	*bc*	*cc*	—	—	*bc*	*bc*	*cc*	*cc*
Idh-1	*ab*	*ab*	*bb*	*bb*	*ab*	*ab*	*ab*	*ab*
Idh-2	*aa*	*aa*	*aa*	*aa*	*aa*	*aa*	*aa*	*aa*
Pgm-1	*bb*	*bb*	*bb*	*bb*	*bb*	*ab*	*bb*	*bb*
6-Pgd	*bb*	*bb*	*bb*	*bb*	*bb*	*bb*	*bb*	*bb*
Tpi-1	*be*	*be*	*be*	*ce*	*be*	*be*	*bb*	*be*

tundifolium with either the *b* or *c* alleles of *D. paniculatum* (Table 3).

When compared with the two putative parental species, *Desmodium humifusum* had a significantly higher percentage of polymorphic loci ($p < 0.05$, t-test of means for planned comparisons) and mean number of alleles per locus ($p < 0.01$) than did *D. rotundifolium,* but was not significantly different from *D. paniculatum* for these measures (Table 4). Mean number of alleles per polymorphic locus did not differ between *D. humifusum* and either of the parental species. However, *D. humifusum* did have a significantly higher mean observed heterozygosity per locus and mean expected heterozygosity than either *D. paniculatum* or *D. rotundifolium* ($p < 0.001$, for each comparison). When the data for the Michigan population of the putative parental species were dropped from the calculations, because they could not directly contribute to the *D. humifusum* populations in New England, then *D. humifusum* had higher values for each measure of genetic variability than either putative parental species.

For both *Desmodium paniculatum* and *D. rotundifolium,* nearly every polymorphic locus showed a significant deficit of heterozygotes (Table 5). In sharp contrast, *D. humifusum* had an excess of heterozygotes at every polymorphic locus, although small sample sizes precluded calculations of statistical significance. The fixation index for the New Milford site was, by definition, −1.0 for all polymorphic loci (Table 5) since only one individual was present. Assuming that deviations were random, the chances of a

Table 4. Percentage of polymorphic loci, no criterion (P), mean number of alleles per polymorphic locus (A_P), mean number of alleles per locus (A), mean observed heterozygosity per locus (H_O), and mean expected heterozygosity for populations of *Desmodium paniculatum*, *D. rotundifolium*, and *D. humifusum*. Site abbreviations in Table 2.

Site	P	A_P	A	H_O	H_E
D. paniculatum					
NM	6.67	2.0	1.07	0.008	0.008
OX	20.00	2.0	1.20	0.015	0.038
CL	20.00	2.3	1.27	0.038	0.097
MI	33.33	2.0	1.33	0.056	0.106
Mean	20.00	2.08	1.22	0.029	0.062
D. rotundifolium					
NM	6.67	2.0	1.07	0.000	0.035
OX	0.00	—	1.00	0.000	0.000
CL	13.33	2.0	1.13	0.003	0.034
MI	0.00	—	1.00	0.000	0.000
Mean	5.00	2.0	1.05	0.001	0.017
D. humifusum					
NM	20.00	2.0	1.20	0.200	0.200
OX	13.33	2.5	1.20	0.089	0.071
CL	26.67	2.0	1.27	0.167	0.119
Mean	20.00	2.2	1.22	0.152	0.130

positive deviation were equal to those of a negative deviation at any given locus. Considering only populations with more than one plant, drawing six consecutive values that deviate in the same direction by chance is extremely unlikely ($p < 0.02$, sign test; Sokal and Rohlf 1981).

DISCUSSION

The alleles found in *Desmodium humifusum* are a subset of those in the other two species, which would be possible with three genetically isolated species. Neutral genetic polymorphisms may be shared among closely related species (Klein et al. 1998). Therefore, each of three diverged species could have independently received a portion of the allozyme variability of their most recent common ancestor. By chance, certain alleles might have been lost in both the *D. paniculatum* and *D. rotundifolium* lineages, but maintained in the lineage leading to *D. humifusum*.

Table 5. Wright's fixation index (F_{IS}) for all polymorphic loci from populations of *Desmodium paniculatum*, *D. rotundifolium*, and *D. humifusum*. Location abbreviations are given in Table 2. Chi-square test with Levene's correction for small samples was employed with values that statistically deviate from 0 ($p < 0.05$) indicated with an asterisk (*). Monomorphic loci in each population are indicated with a dash (—).

	D. paniculatum				*D. rotundifolium*				*D. humifusum*		
Locus	NM	OX	CL	MI	NM	OX	CL	MI	NM	OX	CL
Aat-1	—	—	—	1.000*	—	—	—	—	—	—	—
Est-1	–0.067	0.433*	0.803*	0.357*	—	—	—	—	1.000	—	–0.333
Idh-1	—	0.781*	—	0.260	—	—	0.875*	—	–1.000	–0.200	–1.000
Idh-2	—	—	0.679*	0.306*	—	—	—	—	—	—	—
Pgm-1	—	—	0.303*	0.429*	—	—	1.000*	—	—	—	–0.143
6-Pgd		—	—	—	1.000*	—	—	—	—	—	—
Tpi-1	—	0.628*	—	—	—	—	—	—	–1.000	–0.636	0.600

While this possibility cannot be excluded, it seems unlikely and could not be easily tested.

However, the high level of heterozygosity in *Desmodium humifusum* would be difficult to explain if it were a lineage perpetuated by sexual reproduction. The ratio of observed to expected heterozygosity in *D. humifusum* exceeds that of the putative parental species and even that of a panmictic population. One generation of sexual reproduction would reduce the level of heterozygosity to that predicted by Hardy-Weinberg.

It would be surprising for an exceedingly rare species, such as *Desmodium humifusum,* to be as genetically diverse as its common and geographically widespread congeners. Geographically widespread species generally have higher levels of genetic diversity than species with restricted distributions (Baskauf et al. 1994; Karron 1991; Rieseberg et al. 1989). A loss of genetic diversity would be expected in *D. humifusum* because of its occurrence as a limited number of scattered populations, all of which have extremely small population sizes (Ellstrand and Elam 1993).

Clearly, the alternative hypothesis of hybridization is a more parsimonious explanation of the allozyme data, as this would explain both the high heterozygosity and the composite nature of the alleles of *Desmodium humifusum*. The excessive heterozygosity of *D. humifusum* was expected since the possible parental species were genetically differentiated. The most informative locus for assessing hybridization was *Tpi-1* because of fixed differences between the possible parental species. All individuals of *D. humifusum* except one were heterozygous at this locus, combining alleles unique to the parental taxa.

The *Tpi-1*^{c} allele is of interest because it was not encountered elsewhere in a rangewide survey of *Desmodium paniculatum* (Raveill 1995). Because this allele occurred at the Oxford location in both *D. paniculatum* and in one of the three individuals of *D. humifusum,* observations support local hybridization, rather than long-distance dispersal as the source of this hybrid.

However genotypes of half of the *Desmodium humifusum* plants did not match the composites expected of F_1 hybrids based on the alleles of the parental species at each site. Three examples, the "Clinton-3" plant, homozygous at the *Tpi-1* locus, and "Oxford-2" and "Oxford-3" plants, homozygous at the *Idh-1* locus, could be explained if they were sired either by selfing or backcrossing to *D. paniculatum.*

The single *Desmodium humifusum* plant at New Milford did not match the expected composite profile at two loci, *Pgm-1* and *Idh-1*. The homozygous *Pgm-1* locus can be explained by selfing or backcrossing with *D. rotundifolium* but the *Idh-1* locus is more difficult to explain. The *D. humifusum* plant was heterozygous even though both parental species were fixed for the same allele. Hypothetically, the "missing" *Idh-1*^{b} allele could have come from either parental species, since both species contained this allele at other locations. Several hypotheses could be advanced, including dispersal from a distant location, inadequate sampling, or loss of alleles in the parental species. Details of the New Milford location tend to support one of the latter two. Much of the powerline cut was heavily overgrown with young trees, making it difficult to locate *Desmodium* plants. While all individuals of the parental species encountered were sampled, additional plants could have been missed. Also the dense woody growth greatly reduced available habitat for all herbaceous species, including *Desmodium*. Alleles may have been lost as the populations decreased.

In an early and insightful discussion of hybridization, Wiegand (1935) commented that ". . . hybrids seem like swarms of bees, buzzing around for a time, only to disappear, leaving the fundamental species to continue through the ages." Such may be the case with *Desmodium humifusum;* however several traits—such as fertility, perennial habit, and clonal growth—increase the potential for hybridization to have a more profound evolutionary role (Arnold 1997; Burke et al. 2000). The present study provides limited information relevant to the evolutionarily consequences of hybridization, such as introgression or diploid speciation. Introgression may be absent or if it is occurring, then the level of gene flow between the parental species must be low, based on allele frequency differences at several loci. Also genetic similarities between parental species were no greater at sites where *D. humifusum* was present than at the site where the hybrid was absent. However, the failure to detect introgression at a few allozyme loci is not conclusive evidence against introgression (Rieseberg and Wendel 1993).

Because of its hybrid status, *Desmodium humifusum* cannot receive federal listing. The endangered species act has no provision for the listing of hybrids between species that are not themselves rare, even if the hybrid is extremely sporadic in its occurrence [Federal Register 61(26): 4710]. This public policy fails to recognize the uniqueness of sites of rare hybridization events and their potential scientific significance (Whitham et al. 1991). Hybridization and subsequent backcrossing with the parental species can form a genetic bridge between species (Arnold 1994). The unique gene combinations created have the potential of allowing for the exploitation of habitat not suitable to either of the parental species (Cade 1983) and, thus, may be especially important in an evolutionary context (Levin 1970; Stace 1987).

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VARIETIES OF *ASTRAGALUS PULSIFERAE* (LEGUMINOSAE)

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ABSTRACT. Described as new is *Astragalus pulsiferae* var. *coronensis.* This new variety is distinguished by its superficial root crown and longer pod trichomes, as well as by more subtle differences in the type of internode pubescence. In addition, the stipules in the new variety are all distinct, correlating with the above-ground stem.

Key Words: *Astragalus,* new variety, taxonomy, California

Gray (1874) named *Astragalus pulsiferae,* ascribing it to "Phaca, *Inflati.*" Subsequently a second plant, *A. suksdorfii,* was described by Howell (1893). Barneby (1958) treated the later-named plant at varietal rank within *A. pulsiferae.* The species as broadly interpreted by him (Barneby 1964: 965) is an ". . . enigmatically variable species with decidedly bladdery pods more often than not unilocular but sometimes provided with a rudimentary septum; its lower stipules vary from free to connate and its root-crown from superficial to buried." Barneby (1964: 969) also noted:

> "Occasional populations found in the same area [as var. *pulsiferae*], at least sometimes in stiffer soils, combine the characteristic vesture and calyx with a superficial root-crown and stipules all free to the base; samples from these, judged in isolation from the whole species, cannot be excluded on technical grounds from sect. *Inflati.*"

From the 1964 tentative placement with sect. *Monoenses,* the species was realigned, in its entirety, to sect. *Humistrati* subsect.

Micromerii (Barneby 1984: 171), where it was compared to *A. tiehmii* Barneby. That placement was followed subsequently in the treatment of the Fabales in the *Intermountain Flora* (Barneby 1989), and tentatively by Welsh (unpubl. manuscript).

Plants with a superficial root crown but with spreading stem pubescence of var. *pulsiferae* were regarded, at least tentatively, by Barneby (1964: 972), who had seen the plants in the field and of which he had made a collection, as being products of habitat differences; ". . . but plants from stiffer soils, which are composed of sand compacted with basalt pebbles, have a superficial root-crown and stipules not or at least less strongly connate." These latter plants, which Barneby included within var. *pulsiferae,* differ in other respects, also. The plants tend to be erect and tufted, not prostrate-reclining from where they protrude from the soil, and while they have the spreading or spreading-ascending pubescence on stems and petioles, the pod trichomes are decidedly longer than in those plants with a subterranean caudex. Additionally, the stipules in those plants with the superficial root crown are all distinct. Despite the differences, a part of which might still be related to different microhabitats, the relationship of the tufted versus prostrate plants is clearly evident.

Co-authors Ondricek and Clifton have studied the plants in the field for several seasons; Welsh made observations on some populations during June of 2001. These observations, added to those made by Barneby and to information derived from the examination of a rather more complete set of specimens at BRY, CAS, ORE, RSA, UC, and WTU from throughout the range of the species, give indication that there are at least three taxa in the *pulsiferae* complex, as discussed below. In addition to the representative specimens listed below, there are specimens of all three taxa at CHSC.

Astragalus pulsiferae A. Gray, Proc. Amer. Acad. 10: 69. 1874. TYPE: U.S.A. California: Sierra and Plumas Cos., *Pulsifer-Ames & Lemmon s.n.* [LECTOTYPE designated by Barneby (1964: 972): California: Plumas Co., Aug 1874, *Pulsifer-Ames 33* GH!].

Perennial, caulescent, (4) 10–25 (30) cm long, from a branching subterranean (or nearly or quite superficial) caudex, the branches slender. Pubescence basifixed, strigose-strigulose, villous-hirsute, or villosulous. Stems slender, prostrate to decumbent or erect or erect-ascending, buried for a space of (0) 2–9 cm. Leaves 1–4.5 (5.5) cm long; leaflets (3) 7–13, 2–12 mm long, 1–4 (4.8) mm wide, oblanceolate- or obovate-cuneate, retuse or truncate and more or less apiculate, almost flat to loosely folded, rather thinly villous below, less so above; stipules 1–4.5 (5) mm long, either all distinct or some of the buried ones connate. Peduncles 0.4–2.5 cm long, very slender, shorter than the leaf; racemes (2) 3–13 flowered, the flowers spreading at anthesis, the axis (2) 4–12 mm long in fruit; bracts 0.8–2.4 mm long; pedicels 0.7–1.8 mm long, disjointing in age; bracteoles 0; calyx 3.2–5.8 (6.2) mm long, the tube 1.3–2.6 mm long, shallowly campanulate, villous or villosulous, the teeth 1.4–3.6 mm long; flowers (5.2) 6–8.5 mm long, whitish, the banner lilac-veined and keel tipped with lilac, the banner abruptly recurved through 90–100°; ovules (3) 5–9. Pod spreading or declined (often humistrate), sessile, 8–20 mm long, (5) 6–11 (13) mm thick, bladdery-inflated, somewhat dorsiventrally compressed, half-ovoid or ovoid-ellipsoid, unilocular or subunilocular, strigulose to thinly villous, villosulous, or pilosulous.

The species is confined, except for an outlier in Klickitat County, Washington, to the adjacent Shasta, Lassen, Modoc, Plumas, and Sierra Counties, California, and Washoe County, Nevada.

KEY TO VARIETIES OF *ASTRAGALUS PULSIFERAE*

1. Caudex subterranean or less commonly superficial, the stems foliose only to ground level, the subterranean caudex branches lacking leaves; stems strigulose or villous to villous-hirsute; stipules all distinct or the lowermost connate around the stem; pods strigulose or hirtellous, the hairs 0.4–0.9 mm long .... (2)
    2. Stem (at least distally), leaf-rachis, and peduncle villous or villous-hirsute with widely spreading or spreading-ascending hairs; stems subterranean for 6–10 cm .... var. *pulsiferae*
    2. Stem, leaf rachis, and peduncle strigose to loosely strigulose with ascending and subappressed, sinuous hairs; stems subterranean for (0) 1–2.5 (4) cm .... var. *suksdorfii*

1. Caudex superficial, the stems foliose to the base; stems villosulous; stipules all distinct; pods villosulous, the hairs 1–1.7 mm long . . . . var. *coronensis*

Astragalus pulsiferae var. pulsiferae

Tragacantha pulsiferae (A. Gray) Kuntze, Rev. Gen. Pl. 947. 1891.
Phaca pulsiferae (A. Gray) Rydberg, N. Amer. Fl. 24: 357. 1929.

Plants with root crown commonly subterranean. Stems mostly buried for a space of (0) 2–9 cm, commonly branched at emergence from soil, the foliose internodes villous-hirsute. Calyx teeth (1) 1.4–3.6 mm long. Pod pubescence 0.6–0.9 mm long.

Flowering May to August. Loose sandy sites and interdune valleys, often with sagebrush, on the east side of the northern Sierra Nevada. Mostly on sand derived from weathered granitic rocks at 1310–1798 m in Lassen, Plumas, and Sierra Counties, California, and Washoe County, Nevada.

This variety has a rather narrow geographic distribution, from Sierra Valley (Plumas County) and Long Valley (Lassen and Sierra Counties), California, and generally due east about 16 km in Washoe County, Nevada (Antelope and Red Rock Valleys). The individual plants appear as tufts arranged in a circle around a central area filled level with sand. This circular pattern is not evident at sites where the plants are in competition with *Bromus tectorum* L. The tufts arise from the ends of prostrate, subterranean, naked caudex branches, which arise from a central, deeply set taproot. The longest hairs (these spreading or spreading-ascending) of stems and foliage are more than 0.7 mm long, and with pod hairs less than 1 mm long.

REPRESENTATIVE SPECIMENS: California: Lassen Co., ca. ¾ mi. SW of Hallelujah Junction, 2 Jul 1999, *Ondricek-Fallscheer 195* (BRY); Beckwourth Pass (E side), 19 Jul 1955, *Howell 30,818* (ORE); Plumas Co., ca. 8 mi. ESE of Frenchman Lake and 3 mi. due NE of Beckwourth, 8 Jul 1999, *Ondricek-Fallscheer 197* (BRY); Beckwourth Pass, W side, 13 Jun 2001, *Welsh & Atwood 28,120* (BRY); Beckwourth Pass, 19 Jul 1955, *Rose 55,152* (BRY); Sierra Co., Long Valley, 1874, *Lemmon 515* (photo at JEPS). Nevada: Washoe Co., Red Rock Valley, 21 mi. N of Red Rock exit from Reno, 1 Jun 1982, *Lavin, Williams & Barneby 4125* (BRY).

Astragalus pulsiferae var. suksdorfii (Howell) Barneby, Aliso 4: 131. 1958.

Astragalus suksdorfii Howell, Erythea 1: 111. 1893. TYPE: Washington: Falcon Valley, 3 Jun, 21 Jul 1883, *Suksdorf* [LECTOTYPE designated by Barneby (1964: 971): 3 Jun 1883, *Suksdorf 481* ORE!; ISOTYPES: GH!, NY!, US, WS].

Phaca suksdorfii (Howell) Piper, Contr. U.S. Natl. Herb. 11: 369. 1906.

Plants with caudex commonly subterranean for (0.5) 1.5–2.5 cm, or the caudex rarely exactly superficial. Stems mostly simple, sometimes branched or spurred at 1 or 2 nodes preceding the first peduncle, the foliose internodes strigose-strigulose. Calyx teeth 1.4–2.5 mm long, subequal to the tube. Pod pubescence 0.4–0.7 mm long.

Flowering May to July. Open pine forest in loose volcanic substrates at 1380–2005 m, in northwest Plumas and adjacent Lassen and Shasta Counties, California, and also in Falcon Valley, Klickitat County, Washington, at approximately 605 m.

Materials from the main body of the variety in northeastern California tend to average smaller, especially in overall stature (7–10 vs. 20–33 cm tall) and leaf (1.3–2 vs. 3.5–4.7 cm) and leaflet size (1.5–5 vs. 4–12 mm; and the leaflets are more definitely conduplicate) than those in the disjunct type locality in Klickitat County, Washington. Additionally, the California representatives appear to have a more definitely subterranean caudex than those from Washington. The size of the vegetative parts appears to be definitive. However, the floral measurements appear to be identical, and the pod size seems to form a continuum. The difference in size between the disjunct plants in Washington versus those in California within var. *suksdorfii* is matched by a similar size range within individuals of var. *pulsiferae,* a main difference being the geographic disjunction of specimens from the type locality of var. *suksdorfii* in Washington and the body of the variety in northern California. The species is evidently missing in Oregon. Despite qualitative differences, it seems best at the present to maintain both of the morphological variants from Washington and California within the concept of var. *suksdorfii.*

REPRESENTATIVE SPECIMENS: California: Lassen Co., ca. 6.5 mi. W of Crater Mt. and 7.5 mi. due ENE of Lassen Volcanic National Park, 14 Jul 1999, *Ondricek-Fallscheer 205* (BRY); Plumas Co., gravelly plain about the airfield west of Chester, 22 Jun 1938, *Heller s.n.* (RSA); Shasta Co., Bunchgrass Valley, 6 Aug 1911, *Eggleston 7531* (NY); Bunchgrass Valley, 6 mi. due N of jct. Hwy. 44 and 89 (jct. is near NW corner of Lassen Volcanic National Park), 14 Jul 1999, *Ondricek-Fallscheer 202* (BRY). Washington: Klickitat Co., W of Conboy Lake National Wildlife Refuge, 7 Jul 2000, *Ondricek-Fallscheer 208* (BRY); Falcon Valley, 16 Jul 1908, *Suksdorf 6293* (ORE).

Astragalus pulsiferae var. **coronensis** Welsh, Ondricek & Clifton, *var. nov.* TYPE: California. Lassen Co., E of Hwy. 395, rd. to Rams Horn Spring Campground, 40°41.500′N, 120°16.931′W, silty sand, in juniper, sagebrush, and *Purshia* community, at 1540 m (5050 ft.), 14 Jun 2001, *Welsh & Atwood 28,158* (HOLOTYPE: BRY; ISOTYPES: CAS, ISC, NY, POM, UC, and others to be distributed). Figure 1.

Similis var. *pulsifera* et var. *suksdorfo* in habitu generali sed in caudicibus superficialibus internodiis villosulosis et pilorum leguminibus longioribus differt.

Plants with root crown superficial. Stems branching at soil level, foliose to the base, the internodes villosulous. Calyx teeth 1.5–2.5 mm long. Pod pubescence 1–1.7 mm long.

The new variety is named for the type locality near the Rams Horn Spring campground, the Latin *corona* being one possible translation of "horn." Plants appear as low tufts, with no hint of a subterranean caudex. The branches arise from the root crown where it emerges from the soil. The presence of the superficial caudex, a subtle difference in internode pubescence, and definitely longer pod hairs are evidently diagnostic. Perhaps of less importance are the free stipules in this variety. Union of lowermost stipules in plants with a subterranean caudex is a common condition.

HABITAT, DISTRIBUTION, AND PHENOLOGY. *Astragalus pulsiferae* var. *coronensis* flowers May through July, and is found growing in sandy silt, friable at the surface, hard-packed beneath, among basalt cobble and gravel with juniper, sagebrush, bitterbrush, and Jeffrey pine at 1345–1890 m. Plants of var. *coronensis* grow on the Modoc Plateau in Modoc and Lassen Counties and on volcanic inclusions in the Sierra Nevada Range in Plumas County, California. It is evidently rare in Washoe County, Nevada, approximately 30 mi. (ca 42 km) east of the California border.

Discussion by Barneby (1964: 969) of the racial subunits of this complex species aggregation is pertinent. After delimiting the typical phase of the species, he points to "Occasional populations found in the same area, at least sometimes in stiffer soils, combine the characteristic vesture and calyx with a superficial root-crown

Figure 1. *Astragalus pulsiferae* var. *coronensis.* Plant drawn from *Ondricek-Fallscheer 200* (BRY); fruits drawn from *Holmgren & Holmgren 9500* (BRY).

and stipules all free to the base. . . " The presence of connate stipules has been thought useful not only as a diagnostic tool, but as an indicator of relationships. Perhaps connation is at least partly in response, however, to the subterranean habit, an adaptation that allows overwintering of the plant below ground and survival in times of water stress. Whether this taxon would maintain its superficial caudex and distinct stipules in more friable substrates is not known; the microhabitat of var. *coronensis* is on stiffer substrates. All of the plants of var. *coronensis* lack the elongate caudex branches characteristic of the other two varieties, although those varieties occasionally have the caudex branches greatly shortened. The plants of var. *coronensis* appear as small tufts with the humistrate, pink-suffused pods arranged crown-like around the periphery. They are never ring-like around a patch of sand obscuring the buried taproot and caudex branches as in the other varieties.

ADDITIONAL SPECIMENS EXAMINED (PARATYPES): California: Lassen Co., Observation Peak, S side of mountain, 18 km (11 mi.) airline distance E of Ravendale, T34N R16E S34, 1890 m (6200 ft.) elev., 4 Jul 1980, *Holmgren & Holmgren 9500* (BRY); ca. 27 mi. due NE of Susanville, ca. 9 mi. due SSE of Ravendale, 0.5 mi. due NW of Rye Patch Spring, ca. 0.5 mi. E of Hwy. 395, N side of Ramhorn Springs Campground Rd., T33N R15E S28, 9 Jul 1999, *Ondricek-Fallscheer 199* (BRY); ca. 11 mi. due SE of Adin, E edge of Hunsinger Flat Road (U.S.F.S. Rd. 38N04), 1 mi. S of jct. with U.S.F.S. Rd. 39N08, T38N R10E S35, 9 Jul 1999, *Ondricek-Fallscheer 200* (BRY); E of Hwy. 395, rd. to Rams Horn Spring Campground, 40°41.54′N, 120° 16.870′W, sandy silt, in juniper, sagebrush, and *Poa* community, 1541 m (5053 ft.), 14 Jun 2001, *Welsh & Atwood 28,150* (BRY); Modoc Co., S of Alturas, near Jones Lane, T41N R12E S16, 12 May 1981, *Schoolcraft 385* (NY); 2 mi. S of Yankee Jim Ranch, 1 Jul 1981, *Ganio 5* (NY); Plumas Co., E end of Squaw Valley and W end of Dixie Valley, 30 May 1998, *Clifton 36,000* (BRY). Nevada: Washoe Co., Granite Range, Leadville Canyon, T37N R23E S22, 30 Jun 1983, *Tiehm 8015* (CAS, NY, RSA).

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THE IMPACT OF FLOWER HARVESTING ON SEEDLING RECRUITMENT IN SEA LAVENDER (*LIMONIUM CAROLINIANUM*, PLUMBAGINACEAE)

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ABSTRACT. Flowers of *Limonium carolinianum* are harvested for use in dried flower arrangements and various crafts. The increasing commercialization of this harvest has led to concerns regarding its sustainability. We quantified the extent of the harvest on four marshes on the Bay of Fundy coast of Nova Scotia, Canada. Over a four-year period from 1996 to 1999, flower stalk removal averaged 32% on easily accessible portions of these marshes (i.e., within 100 m of a road) compared to 5% on inaccessible portions (greater than 500 m from a road). In 5 × 5 m plots where flowers were experimentally removed, no seedlings emerged the following year, whereas seedlings always emerged in unpicked control plots. This rapid and dramatic impact of localized harvesting on seedling emergence is due to the limited dispersal and short life span of *L. carolinianum* seeds. Sampling in concentric circles around isolated adults revealed that 50% of seedlings emerged within 34 cm of the parent and 90% emerged within 61 cm. Tethered seed experiments revealed that seeds that did not germinate in the first spring after production did not survive to the next spring. Our results suggest that unregulated harvesting has the potential to dramatically impact recruitment into local populations. To reduce the likelihood of local extinction we recommend that harvesters do not reduce flower stalk densities below 1 per m^2.

Key Words: *Limonium carolinianum*, flower harvesting, salt marsh, seed bank, seed dispersal, local extinction, sustainable harvesting

Limonium carolinianum (Walter) Britton, Plumbaginaceae (sea lavender) is a long-lived perennial herb that ranges the entire eastern coast of North America from Newfoundland to Texas (Roland and Smith 1983). Inflorescences of this species are collected and dried for use in floral arrangements and various crafts. Small-scale harvesting by individuals has a long history within

Atlantic Canada. Given that *L. carolinianum* is fairly common on salt marshes and beaches, such small-scale harvesting may have little impact on populations. However, due to the current popularity of the flowers and recent larger-scale commercial harvest of them, there is a growing concern about the effects of harvest (see article by Jim Wolford in the May 26, 1996 edition of the Advertiser and article by Jodi Delong in the September 3, 1996 edition of Shunpiking). Local landowners have suggested to us that there have already been population declines on some heavily exploited salt marshes in Nova Scotia.

The historic loss of salt marsh habitat has also impacted on *Limonium carolinianum* populations. In Nova Scotia it is estimated that 57% of all salt marsh has been lost due to dyking for agricultural use and erosion caused by dredging and filling (Hatcher et al. 1981). Much of what remains is highly fragmented with many pockets of salt marsh being less than 10 hectares in size (Eaton et al. 1994). Depending upon how widely this species disperses, this fragmentation has the potential to further exacerbate the effects of local harvesting.

Because of these concerns, we conducted a study to determine: 1) the current level of harvest in salt marshes along the Bay of Fundy coast in Nova Scotia, and 2) the impact of this harvest upon recruitment into the local population. We addressed the first objective by enumerating flower stalks in permanent plots before flower opening, and again after seed set, in four relatively accessible and four relatively inaccessible salt marshes over a period of four years. Since the impact of flower harvesting upon recruitment in any one location and in any one year will vary depending upon how widely seeds are dispersed and the extent to which seeds may be stored in the seed bank, we collected basic data on both these parameters. Finally, we experimentally assessed the impact of harvesting on seedling emergence by removing flower stalks from controlled plots and examining the impact the following year.

Although the focus of this study was on the effect of harvesting on seedling recruitment, it should be recognized that the importance of seedling recruitment in determining population growth rate has yet to be determined in this species. However, regardless of how closely seedling recruitment is linked to population growth rate, an understanding of the effect of harvesting on this parameter is important as it is the primary mechanism by which this species disperses, and by which genetic diversity within the population is generated.

MATERIALS AND METHODS

Study species. *Limonium carolinianum* inhabits salt marsh and both rocky and sandy beaches. Individuals have leathery, succulent leaves, arranged in a basal rosette around a compressed stem that is attached to a central taproot. Inflorescences are produced on scapose stems. They first appear in early July and develop into highly branched stalks with many small purple flowers by mid-August. Flowering can continue as late into the fall as October. Breeding experiments have shown *L. carolinianum* to be self-compatible, and individuals bearing both selfed and outcrossed seeds are found in the wild (Hamilton and Rand 1996). Each flower can produce up to four seeds, but normally produces only one. *Limonium carolinianum* is also capable of limited clonal growth through the addition of ramets to the underground stem. However, ramets remain permanently attached to the central taproot and never give rise to physiologically independent clones. As a result, individual plants vary widely in size and can have from 1 to 20 or more inflorescences.

Study sites. The individual studies described below were conducted at one or more of the following salt marshes: Kingsport (45°09′N, 64°22′W), Avonport (45°7′N, 64°16′W), Annapolis Royal (44°44′N, 65°32′W), Porter's Point (45°08′N, 64°23′W), and Wolfville (45°05′N, 64°21′W). These five marshes were chosen for three reasons: 1) based upon their floristic composition and zonation patterns they are typical of salt marshes in Nova Scotia (Davis and Browne 1996), 2) they were large enough to allow replication of the study plots, and 3) they provided a range of geographic locations along the Bay of Fundy coast of Nova Scotia. Due to time constraints, those studies that required frequent visits to the field were all conducted at a single site, the Wolfville salt marsh. We make the assumption that the data collected at this one site is representative of the remaining sites.

Extent of harvest. To assess the extent that harvesters were exploiting populations of *Limonium carolinianum* at the time of the study, we established plots in Kingsport, Avonport, Annapolis

Royal, and Porter's Point. Plots were established on parts of the marsh that were either easily accessible or relatively inaccessible to harvesters. A plot was considered accessible if it was within 100 m of the nearest road, and inaccessible if it was greater than 500 m from the nearest road. Plots were 5 × 10 m in size and were marked by wooden stakes at each of the four corners. The stakes extended only 30 cm above the surface of the ground and were largely hidden by the surrounding vegetation. Therefore, it is unlikely that they were conspicuous enough to discourage people from harvesting in that area. Three plots were established on both accessible and inaccessible sites on the Kingsport, Avonport, and Annapolis Royal marshes in 1996. Two additional plots were established at each of the original sites, and another five plots established on accessible and inaccessible sites on the Porter's Point marsh in 1997. From 1996 to 1999, the number of flower stalks in each plot was counted prior to flower opening (late July/ early August) and again after flowers had withered (September/ October). During the latter census we also noted whether there were any indications that flower stalks had been harvested, by looking for the remains of cut flower stalks still attached to the plants. Due to time constraints not all of the inaccessible sites were sampled in all years.

Seed dispersal. Ten adult plants were selected on the Wolfville salt marsh in June 1999 after natural emergence in the field had terminated (see below). Circular, 2 cm wide belt transects were set up at 10 cm intervals from the adult plant and the number of seedlings in each transect was counted. Sampling continued outward from the mother plant until three consecutive transects without seedlings were sampled. The seedling density for each band was calculated and the total number of seedlings at a given distance from the parent was determined through interpolation between bands.

The above procedure assumes that all seedlings encountered in the circular transects were the progeny of the single adult at the center of the plot. To help ensure the validity of this assumption, only adult plants that were a minimum of 3 m from their nearest neighbor were chosen for this study. This distance was chosen on the basis of preliminary observations of the diameter of the seedling "shadow" surrounding individual plants.

Seed longevity in seed bank. To help interpret the results of the seed longevity experiment (see below), the pattern of natural seedling emergence over the course of the growing season at the Wolfville salt marsh was examined. In May 1997, twenty 15 × 15 cm plots were established at randomly selected points in a subsection of the marsh with a high density of adult *Limonium carolinianum.* At first emergence, all seedlings in each plot were counted and removed on an approximately weekly basis until emergence ceased. The plots were censused again in 1998 and 1999. In 1997 and 1998, the plots were also censused in October/ November to determine if any emergence occurred in the fall.

To assess how long *Limonium carolinianum* seeds can remain viable under field conditions, naturally ripened seeds were collected from the Wolfville salt marsh in the spring and fall of 1998, and placed in 10 × 10 cm fine-mesh nylon bags (25 seeds per bag). Bags were placed back on the salt marsh for varying lengths of time under one of three conditions:

1. tied to a wooden stake at a height of 30 cm to simulate seeds that fail to shatter and remain in the seed stalk;
2. fastened to the surface of the soil, using nails placed at each of the four corners of the bag, to simulate seeds that shatter and remain on the soil surface;
3. buried at a depth of 2.5 cm to simulate shattered seeds that have been buried by mud washed in by the tide.

Seeds collected in the fall of 1998 were stored dry in the laboratory at 3.5°C until being placed back on the marsh on December 10, 1998 or June 22, 1999 (i.e., after natural emergence had terminated). Seeds collected in the spring of 1998 (i.e., from seed stalks that had overwintered) were placed back on the marsh on June 4, 1998, again, after natural emergence had terminated. In the case of seeds placed on the marsh in June, the treatment simulating seeds that failed to shatter was omitted, as by this time all seeds had naturally shattered. Seeds placed on the marsh on June 4, 1998 and December 10, 1998 were collected on April 10, 1999, and seeds placed on the marsh on June 22, 1999 were collected on July 7, 1999. There were 20 seed bags (replications) per treatment per date of collection.

At the time of collection, the number of seeds in each bag that had already germinated was noted and the remaining seeds placed in petri dishes on moist Kimwipes soaked in distilled water. The petri dishes were wrapped in parafilm to minimize water loss and placed in a growth chamber that provided a 14 hr. photoperiod and a 20/15°C day/night temperature. Germination was monitored daily until a period of five days had passed in which there were no new germinates, at which time the remaining seeds were tested for viability using tetrazolium chloride (Delouche et al. 1962).

None of the seeds that failed to germinate in the growth chamber were found to be viable using the tetrazolium test. Therefore total viability was calculated as the sum of germination in the field and in the laboratory expressed as a percentage of the total number of seeds originally placed in the field. As the resulting percentages were not normally distributed, a Kruskal-Wallis test was used to examine differences in field germination and total viability among treatments.

Effects of bloom picking on seedling recruitment. On July 15, 1998, twenty 5 × 5 m plots were established in an inaccessible region (i.e., > 500 m from the nearest road) of the Wolfville salt marsh that also had a high density of *Limonium carolinianum*. Ten plots served as unmodified controls, while in the other 10 plots all flower stalks were removed. Treatments were assigned randomly to plots. The following spring after seedling emergence was complete (see above), seedling density was sampled as described in the seed dispersal survey. A point was randomly selected within each plot and the nearest adult was used as the center for the circular belt transects. In most cases the nearest plant was part of a cluster of several plants. In these cases, the focus for the circular transects was the center of the entire group of plants and the total number of plants in the cluster was determined. Sampling was done at 10 cm intervals from the center to a distance of 100 cm. These data were used to estimate the total number of seedlings within the sampled area (i.e., a circle with a radius of 100 cm). The effect of bloom removal on seedling density was examined using analysis of covariance with the number of adults in the plots as the covariate.

RESULTS

Extent of harvest. Averaged across sites and across years, 32% of flower stalks were harvested from accessible plots com-

Table 1. Extent of *Limonium carolinianum* harvest on accessible versus inaccessible parts of four marshes along the Bay of Fundy coast in Nova Scotia from 1996 to 1999. Harvest was quantified by counting the number of flower stalks in permanent plots prior to flower opening in the summer and again in the fall after flowers had withered. There were 3 plots per site in 1996 and 5 plots per site in all other years. Not all sites were censused in all years. Asterisks indicate that the remains of cut flower stalks were observed.

	Percent of Flower Stalks Removed (±SE)			
Marsh	1996	1997	1998	1999
Avonport				
Accessible	91 ± 3*	15 ± 7*	35 ± 12*	33 ± 10*
Inaccessible	—	14 ± 15	16 ± 11	17 ± 21
Annapolis Royal				
Accessible	29 ± 11*	48 ± 14*	28 ± 9*	42 ± 15*
Inaccessible	—	—	−8 ± 7	—
Kingsport				
Accessible	5 ± 3	29 ± 13*	15 ± 11*	8 ± 3
Inaccessible	4 ± 4	1 ± 3	3 ± 5	—
Porter's Point				
Accessible	—	39 ± 12*	23 ± 9*	33 ± 9*
Inaccessible	—	—	−6 ± 7	—

pared to 5% from inaccessible plots (Table 1). Direct evidence of bloom harvesting in the form of cut flower stalks was observed in the accessible portions of all four marshes (13/15 plot-year combinations), but was never observed in the inaccessible portions (0/8 plot-year combinations). The level of harvest on accessible plots varied substantially from marsh to marsh and from year to year. The greatest range among years was observed at Avonport where the level of harvest ranged from 15 to 91%. The range in harvest levels for accessible plots at Annapolis Royal (28–48%), Kingsport (5–29%), and Porter's Point (23–39%) was less than that observed at Avonport, but still substantial. The range in harvest levels on the inaccessible plots was much less than that observed for the accessible plots. At the two sites where we sampled the inaccessible plots over multiple years, Avonport and Kingsport, the ranges in harvest levels were 14–17% and 1–4%, respectively.

Seed dispersal. The highest seedling densities were observed at approximately 20–30 cm from the mother plant (Figure 1). No

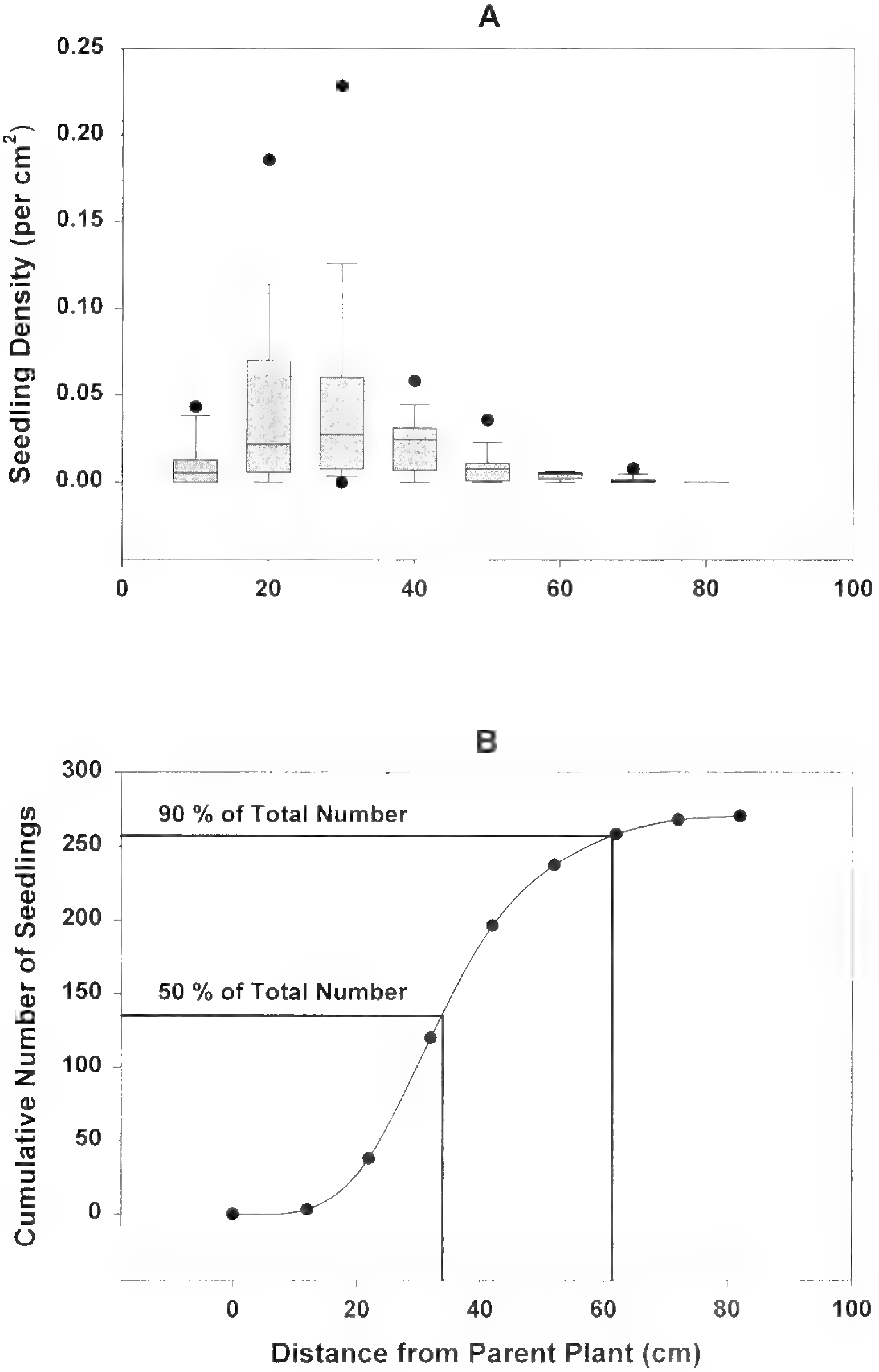

Figure 1. Seedling density (A) and cumulative number of seedlings (B) as a function of distance from 10 isolated parent plants. Densities in (A) are graphed in a box plot that displays the 10th, 25th, 50th, 75th, and 90th percentiles as well as any outliers.

seedlings were observed further than 80 cm from the mother plant. On average, 50% of the seedlings were within 34 cm and 90% of the seedlings were within 61 cm of the parent.

Seed longevity in seed bank. Natural seedling emergence began in early spring, from mid-April to early May depending upon the year (Figure 2). Emergence was highly synchronous within years, with most of the seedlings emerging within a two-week period. Emergence was essentially complete by mid-May in 1998 and 1999, but extended into early June in 1997. We observed no seedling emergence in the fall.

Freshly ripened seed collected in the fall germinated readily under laboratory conditions; on average, 97% of the seeds germinated (Figure 3). Seed viability decreased after overwintering on the marsh, but the extent of this decrease varied depending upon location (Kruskal Wallis test, $X^2 = 15.01$, $p = 0.005$). Buried seed had the highest viability and seeds that were staked above the ground (simulating seeds that remained on the seed stalks) had the lowest viability. Field germination in the spring was even more dependent upon location of the seeds (Kruskal Wallis test, $X^2 = 25.84$, $p < 0.0001$). Most of the buried seeds germinated in the field, while very few of the seeds staked above ground germinated; germination of the seeds placed at the soil surface was intermediate between that in the other two treatments. Seeds that were placed on the marsh after natural emergence ended in the spring did not germinate in the field, but when brought into the laboratory later that summer had a viability only slightly below that of seeds before the flush of spring emergence. However, there was no evidence that the remaining treatments (buried versus soil surface) had any effect on viability (Kruskal Wallis test, $X^2 = 0.19$, $p = 0.6646$). Seeds that were placed on the marsh after the flush of spring emergence were no longer viable the following spring.

Effect of bloom picking on seedling recruitment. No seedlings were found on the 10 picked plots, but seedlings were observed on all 10 unpicked plots (Figure 4). Seedling densities in the unpicked plots were highly variable. An analysis of covariance revealed that much of this variability was correlated with the number of adults in the plots ($F = 5.57$, $p = 0.0313$).

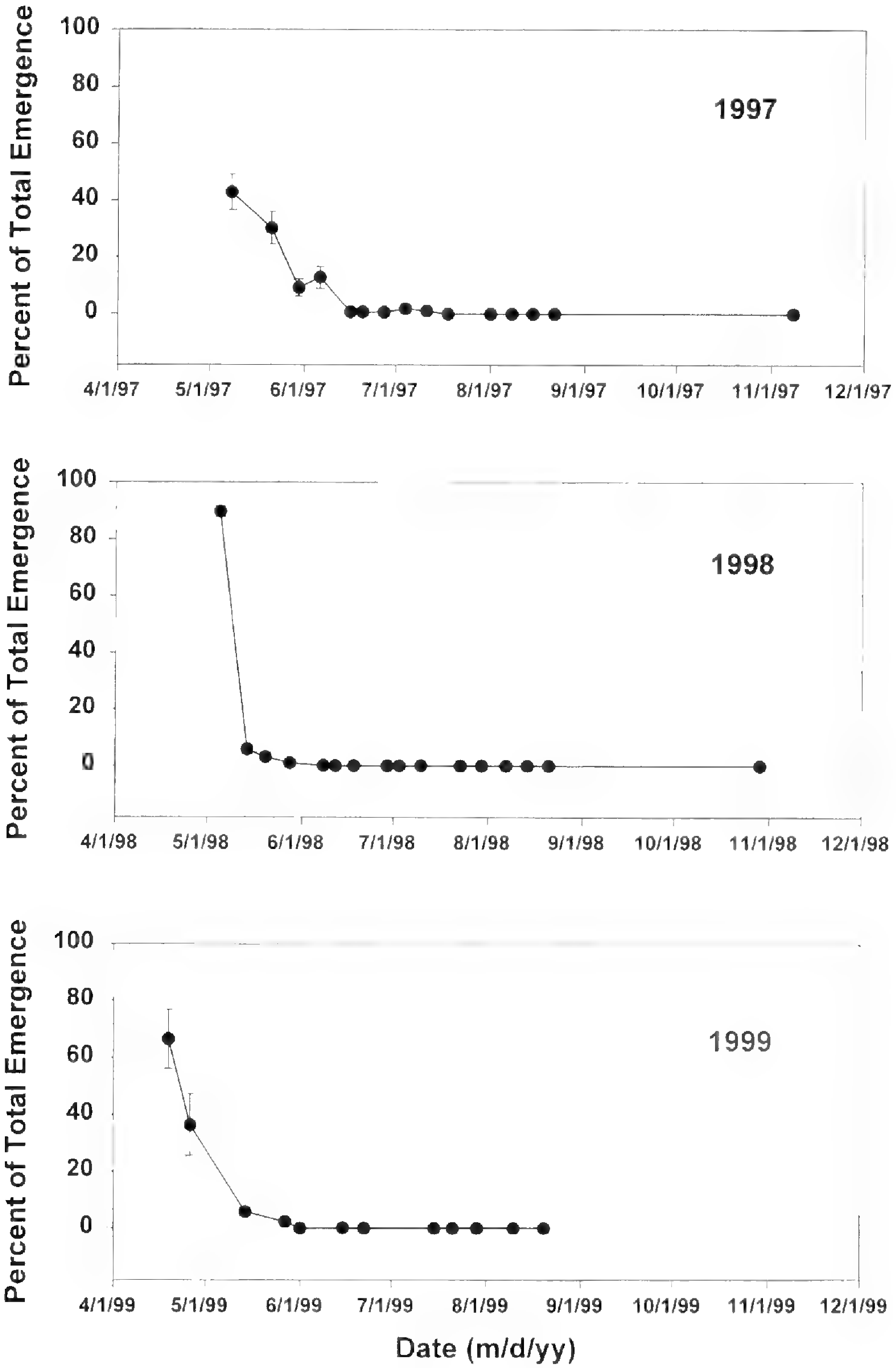

Figure 2. Percent of total seedling emergence over the course of the growing season on the Wolfville salt marsh in 1997, 1998, and 1999. Points are the mean of 20 plots (± 1 SE).

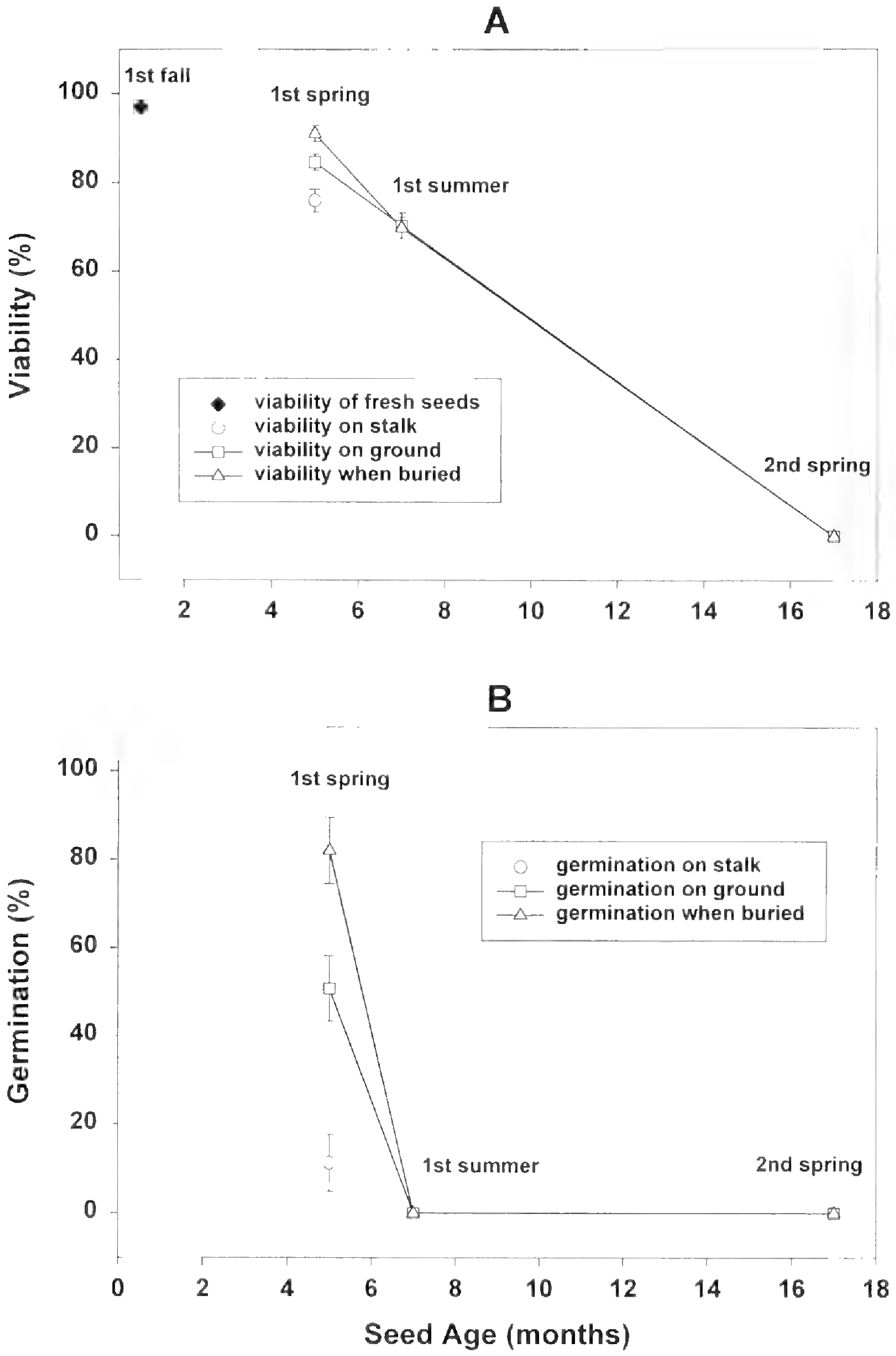

Figure 3. Percent viability (A) and percent germination in the field (B) of seed collected from the Wolfville salt marsh, placed in fine-mesh nylon bags, and returned to the marsh for various lengths of time. To simulate the environment of seeds still attached to the seed stalk, seeds on the ground surface, and seeds buried beneath the ground, the bags were placed at one of

It also revealed that the effect of picking on seedling density was highly significant (F = 9.45, p = 0.0073).

DISCUSSION

The current harvest of *Limonium carolinianum* flower stalks is variable in both time and space, varying from year to year, marsh to marsh, and even within a marsh depending upon accessibility to harvesters (distance to the nearest road). Importantly, the level of harvest at a particular time and location can be extensive, in one particular case exceeding 90%. The long-term impact of such a harvesting regime on a local population will depend, at least in part, upon how well the species is able to disperse through time and space. If the scale at which seeds disperse is greater than the scale of the harvested patches, or if seeds remain viable within the seed bank for a length of time greater than the average time between harvests, periodic heavy harvesting may have relatively little impact on the local population. This does not appear to be the case for *L. carolinianum*.

The scale over which *Limonium carolinianum* seeds disperse is relatively small. No seedlings were found further than 80 cm from the parent plant. Given that many of the seeds remain attached to the inflorescence over winter (pers. obs.), this limited dispersal is not surprising. Most seeds appear to simply fall in a small area directly underneath the seed-bearing portion of the inflorescence. The inflorescences tend to bend to one side prior to shattering, probably due to tidal action, resulting in a seed rain displaced to one side of the mother plant, with maximum seedling density occurring approximately 30 cm from the plant. This distance corresponds well with the height of the seed stalk.

Although the seedling distribution data suggest dispersal on a very limited scale, this species is likely capable of dispersing to much greater distances under some circumstances. A sample of 100 seeds threshed by hand from inflorescences collected in the

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three locations: 1) tied to a stake at a height of 30 cm, 2) tacked to the ground surface, or 3) buried 2.5 cm beneath the surface. In calculating seed age, it was assumed that all seeds matured on November 10. Points are the mean of 20 values (± 1 SE).

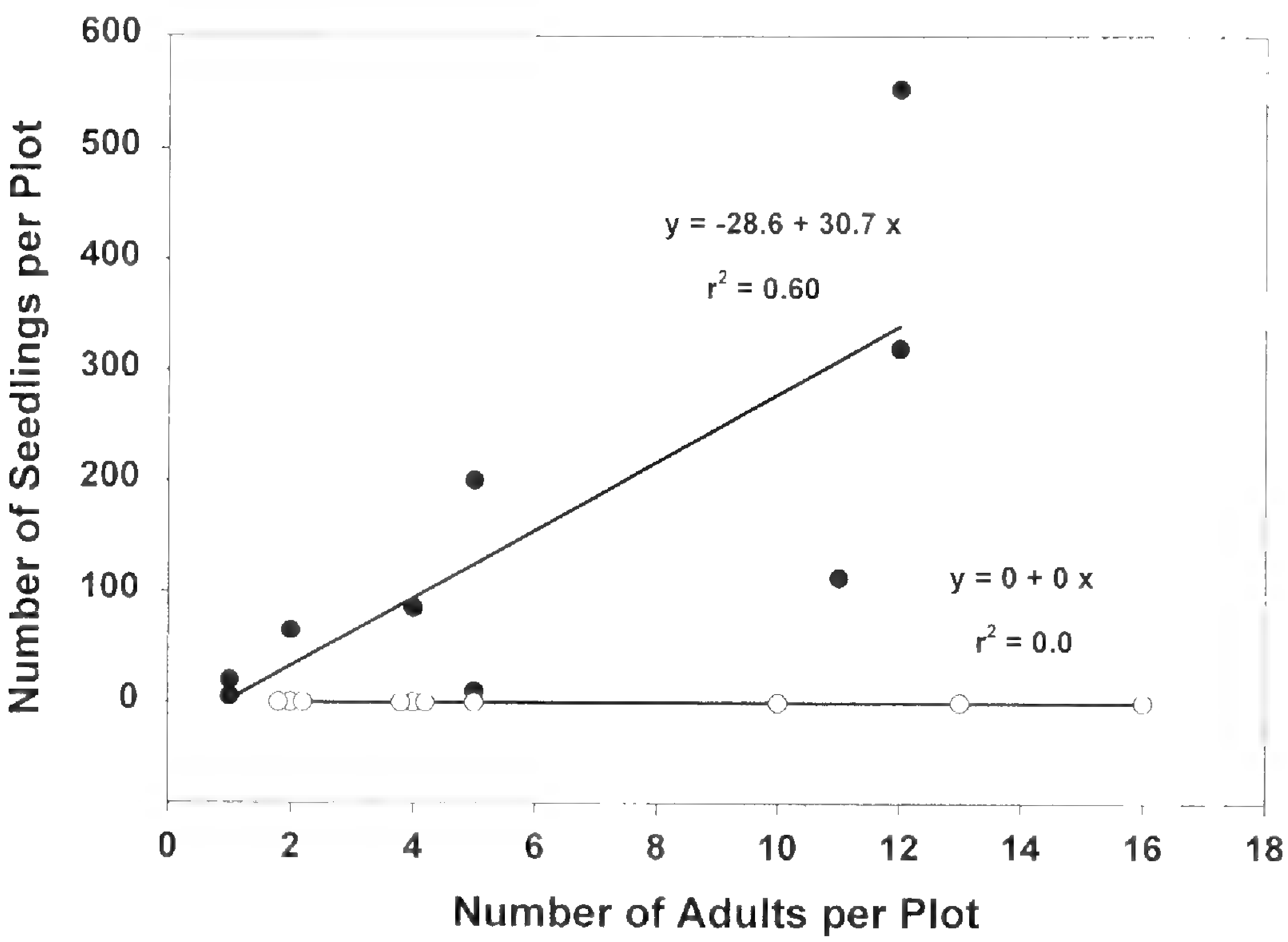

Figure 4. Number of seedlings per plot as a function of the number of adults per plot for control (closed symbols) and harvested (open symbols) sites. X-axis points are jittered for clarity.

spring was found to float on water from 1.5 to more than 7 hours before sinking (unpubl. data). This suggests that seeds carried by the tide could travel many hundreds of meters before coming to rest. Further, a study of seed dispersal on four waterfowl species by Vivian-Smith and Stiles (1994) found *Limonium carolinianum* on the feet and feathers of these birds. Long-distance seed dispersal by animals or by tidal action may be important in founding new populations, either on a new site in the same marsh, or in an entirely different marsh. However, successful colonization due to long-distance dispersal is probably a relatively rare event. The vast majority of the seeds carried by the tide for example, will likely be deposited in water too deep for successful establishment. Only occasionally will the seeds settle in a site suitable for colonization. Long-distance dispersal, although potentially important in founding new populations, will be of little consequence in maintaining local populations in the short term. This was clearly illustrated in the flower harvest experiment by the total lack of seedlings in the picked plots. It is worth noting that these plots were in fact relatively small (5 × 5 m), and in all cases surrounded by plants that successfully set seed. If immigration from long-distance dispersal (i.e., dispersal further than 1 m) is important for local population dynamics, one would expect at least some seedlings to appear in the picked plots. The limited dispersal ability of *L. carolinianum* has also been confirmed by studies of gene flow. Using molecular markers, Hamilton (1997) examined gene flow within and between two *L. carolinianum* populations on Narragansett Bay, Rhode Island. These two populations, located approximately 5 km apart, were genetically distinct. Further, Hamilton observed within-population genetic subdivision at a spatial scale of less than 100 m.

Freshly ripened seeds collected in the fall displayed no innate dormancy; complete germination was achieved when these seeds were placed in a suitable environment in the laboratory. Yet, no germination was observed in the field at this time, suggesting that dormancy was enforced by environmental conditions. Low temperatures are perhaps the most obvious limitation to germination in the fall, but the fact that many seeds remain attached to the inflorescence until spring is probably also important. Seeds attached to the inflorescence will not be able to imbibe sufficient water and will therefore not germinate even with suitable temperatures. Germination in the spring was rapid and synchronous and again, there was no indication that the seeds had any innate dormancy; all seeds that failed to germinate in the laboratory were found to be nonviable. However, viable seeds placed on the marsh after the spring flush of germination failed to germinate in the field, but did germinate (though viability was lower) when brought back into the laboratory. This suggests that any seeds that do not germinate in the spring are prevented from germinating during the summer due to unfavorable environmental conditions, perhaps high salinity levels. Soil salinities increase as the summer progresses in most salt marsh systems (Ungar 1987) resulting in germination inhibition in most halophyte species (Ungar 1994). Snowmelt and periods of precipitation in the spring lower soil salinities, allowing germination to occur for a few weeks in the spring. This pattern of germination is common in halophyte species (Ungar 1994). Given that seeds do not germinate under field conditions in the summer or fall, seeds that do not germinate in their first spring, but are still viable, will not have another opportunity to germinate until their second spring. Our data indicate however that seeds do not survive to their second spring under field conditions. Effectively this means that if a seed does not germinate in the first spring after production it will never germinate. As a result, this species lacks a persistent year-to-year seed bank. This conclusion is supported by the fact that no germination was observed in experimental plots that were completely harvested.

Implications for conservation. The lack of a persistent seed bank and the very limited dispersal of *Limonium carolinianum* means that harvesting has an immediate and dramatic effect upon recruitment into the local population. However, whether this in turn would result in significant population declines or lead to the extinction of local populations is as yet unknown. Variation in adult survivorship and growth is often more important than variation in seedling recruitment in determining population growth rate in long-lived species (Caswell 1986). The removal of blooms will divert resources from seed maturation and has the potential to increase adult survivorship and growth. Therefore, it is conceivable that in spite of its marked effect on seedling recruitment, harvesting may in fact have no negative effect on population growth or viability. In addition to information on seedling recruitment, resolution of this question requires long-term data on the effect of harvesting on adult demography and the summarization of these data in the form of a population growth model. We are currently conducting such a study. In the meantime, given that there are anecdotal reports of population declines, it is worthwhile to explore how the results of the present study could be used to help reduce any possible negative effects of harvesting on population viability.

Presently there are no legal means, or voluntary guidelines in existence for managing the harvest of this plant. However, there is growing interest in, and concern over, the sustainable harvest of wild species (Prescott-Allen and Prescott-Allen 1996). Based upon our data we can make two simple recommendations that will help reduce any impact of flower harvesting on *Limonium carolinianum* populations. First, harvesters should never harvest the last inflorescence in a clump of plants. With such a guideline, a population would still have at least one flower stalk per square meter after harvesting. This would ensure that there is some seed available to recolonize a site if the adult(s) in the immediate area should die. Second, periodic closures (voluntary or enforced) of marshes to flower harvesting would provide pulses of recruitment into a population. If these pulses occur frequently enough relative to the life span of the adults, this would reduce the possibility that local populations would go extinct. Sites where the local population has been extirpated would eventually be recolonized by long-distance dispersal, but our study suggests that natural recolonization would be extremely slow.

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NEW ENGLAND NOTE

A NEW COMBINATION IN *LYCOPODIELLA* (LYCOPODIACEAE)

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Lycopodium L. *sensu lato* is currently considered to contain several distinct elements best treated as genera. Evidence for recognition of these segregate genera is provided by sporophyte, gametophyte, and spore morphology, anatomy, analysis of chromosome numbers, and phytochemicals (Bruce 1976; Ollgaard 1987; Pedersen and Ollgaard 1982; Towers and Maass 1965; Wagner and Beitel 1993). *Lycopodiella* Holub is a small group of wetland species with elongate horizontal shoots, unbranched upright shoots, apically leaf-like sporophylls, and photosynthetic gametophytes. A new combination is proposed for this genus.

Richard J. Eaton began a series of collections in 1928 of an unusual bog clubmoss from Concord, Massachusetts. The new *Lycopodiella* was robust with upright shoots commonly 14–17 cm tall. The margins of both the leaves and the sporophylls were toothed. The horizontal shoots were noteworthy in that they arched above the substrate. The strobilus represented a large proportion of the total upright shoot height (25–53%). Eaton (1931) noted that over a period of several years the colony increased in size. Using available evidence—unique combination of morphological characters and persistence of the colony—Eaton provided the new bog clubmoss with the name *Lycopodium inundatum* L. var. *robustum* R. J. Eaton (he used the genus *Lycopodium* because *Lycopodiella* was not held generically distinct at that time). Eaton probably chose to ally the new plant with *Lycopodium inundatum* on the basis of the relatively tall strobilus.

Gillespie (1962) and Kartesz (1994) considered the plants described by Eaton conspecific with *Lycopodiella* ×*copelandii* (Eiger) Cranfill, the hybrid of *Lycopodiella alopecuroides* (L.) Cranfill and *Lycopodiella appressa* (Chapm.) Cranfill. That nothospecies has ascending sporophylls and leaves of the upright shoot, strobili 4–11 mm thick, and each horizontal shoot segment commonly produces more than two upright shoots (Bruce 1976; Eiger 1956). Eaton's new plant, in contrast, had horizontally spreading sporophylls, spreading-ascending leaves of the upright shoot, thicker strobili (14–17 mm), and each horizontal shoot produced only one or two upright shoots (Eaton 1931; A. Haines, pers. obs.).

Throughout the description of the new bog clubmoss, Eaton (1931) compared various aspects of its morphology to *Lycopodiella alopecuroides* and *Lycopodiella inundata* (L.) Holub, but he never considered the plant to be of hybrid origin. The new taxon was, in fact, intermediate in many features, including the number of teeth on sporophyll and leaf margins, ratio of strobilus height to total upright shoot height, and length the stem arches to distal contact point. Further evidence for a hybrid origin of the variety described by Eaton is provided by examination of two sympatric populations of *L. alopecuroides* and *L. inundata* in south-central Maine (Haines 2001 and unpubl. data). Individuals intermediate between these two orthospecies were found at both locations and are conspecific with the plants from Concord, Massachusetts [29 Nov 2000, *Haines s.n.* (MAINE); 2 Sep 2001, *Haines s.n.* (MAINE, NEBC)]. Both Bruce (1976) and Tryon and Moran (1997) also considered the plants described by Eaton (1931) to be hybrids between *L. alopecuroides* and *L. inundata.* A new combination is needed under *Lycopodiella.*

Lycopodiella ×robusta (R. J. Eaton) A. Haines, *comb. et stat. nov.*, pro variety. BASIONYM: *Lycopodium inundatum* L. *var. robustum* R. J. Eaton. Rhodora 33: 202, 1931. TYPE: UNITED STATES, Massachusetts: Middlesex Co., Concord, 28 Sep 1930, *Eaton s.n.* (NEBC).

As previously stated, *Lycopodium inundatum* var. *robustum* has been considered to be a synonym of *Lycopodiella ×copelandii.* This erroneous synonymy may be the result of Eaton's interpretation of the former taxon. Approximately half of the Harvard University Herbaria specimens cited in the protologue of Eaton (1931) are in fact *L. ×copelandii,* as evidenced by the ascending sporophylls, narrow strobili, multiple upright shoots, thicker horizontal stems, and relatively few teeth on the sporophylls and leaves of the horizontal shoots. The following specimens are entirely *L. ×copelandii*: *Eames 5860* (GH); *Fernald 8381* (NEBC); *Fernald 15,851* (NEBC); *Fernald & Long 15,939* (NEBC). It should be noted that one of the paratypes [*Hoffman s.n.* (NEBC)] contains two taxa, only one of which is *L.* ×*robusta* (the other is *L. inundata*). Also, one of the isotypes at GH contains three taxa, only one of which is *L.* ×*robusta* (the others are *L. alopecuroides* and *L.* ×*copelandii*). The type is, however, wholly and unambiguously *L.* ×*robusta*.

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NEW ENGLAND NOTE

RECENT PLANT COLLECTIONS—MASSACHUSETTS

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The following report describes two taxa that are new additions to the flora of Massachusetts. Verification that the taxa are new to the state was accomplished by consulting *The Vascular Plants of Massachusetts: A County Checklist* (Sorrie and Somers 1999) and by personal communication with the curators of the New England Botanical Club Herbarium (NEBC) and the University of Massachusetts Herbarium, Amherst (MASS). Nomenclature follows that of Gleason and Cronquist (1991).

Erysimum hieraciifolium L. (Brassicaceae). Massachusetts: Hampden Co., West Springfield, Mittineague Park, edge of woods along grassy roadside of entrance road to park, 4 Jun 1999, *Lovejoy 1440* (WSCH); West Springfield, Bear Hole Watershed, Prospect Ave., disturbed moist roadside bank adjacent to open shrub swamp, acid sandy loam, locally common, 23 May 2001, *Zebryk 7299* (NEBC, MASS).

Significance: A common and widely distributed plant species in Europe (Hulten 1971; Tutin et al. 1964), *Erysimum hieraciifolium* has been occasionally reported from North America, with known occurrences from Manitoba, New Brunswick, Newfoundland, Nova Scotia, Ontario, Quebec, and Saskatchewan in Canada, and from Illinois, Indiana, Michigan, New York, Pennsylvania, and Wisconsin in the United States (Gleason and Cronquist 1991; Kartesz and Meacham 1999; Voss 1985). According to Ray Angelo, curator of the New England Botanical Club Herbarium (NEBC), the collections reported here are the first known occurrences not only for Massachusetts, but apparently for New England as well. Associated with *Erigeron annuus* (L.) Pers., *Carex stricta* Lam., *C. stipata* Muhl., *C. cristatella* Britton, *Leersia virginica* Willd., *Polygonum pensylvanicum* L., *Alnus serrulata* (Aiton) Willd., *Cornus amomum* Miller, and *Salix discolor* Muhl. at the Prospect Avenue locality, the plants are conspicuous because of their tall stature, thus the common name "Tall Wormseed-

Mustard." The species is readily identified by the abundant 4-pronged stellate hairs adorning upper leaf surfaces, a feature not shared by other members of the genus occurring in New England. The origin of this plant at the site is unknown. However, Lovejoy's roadside collection site at Mittineague Park occurs only 2.5 miles from the Prospect Avenue locality, leading one to speculate that vehicular traffic may serve as a dispersal mechanism for *E. hieraciifolium.* Interestingly, several companies on the Internet now market this plant as "Siberian Wallflower," and offer its seeds in meadow mixes for naturalizing. Judging by the potential of this non-native species to become at least locally common after introduction, the sale of *E. hieraciifolium* should be discouraged on the domestic market.

Helictotrichon pubescens (Huds.) Pilger (Poaceae). Massachusetts: Berkshire Co. Sheffield, open grassy meadow at rest stop on U.S. Rt. 7 just south of Bowman Hill, adjacent to working dairy farm, moderately acid sandy loam, locally abundant, 2 Jun 2001, *Zebryk 7309* (NEBC, MASS).

Significance: Another common and widely-distributed European species (Clapham et al. 1987; Hulten 1971; Tutin et al. 1980), *Helictotrichon pubescens* is rare in New England, being previously vouchered only from Litchfield County, Connecticut, and from Chittenden County, Vermont (Angelo and Boufford 1998; Ray Angelo, NEBC, pers. comm.). The site in Sheffield, Massachusetts is an infrequently mowed meadow, where apparently naturalized *H. pubescens* occurs with several other native and introduced pasture grasses including *Festuca elatior* L., *F. rubra* L., *Poa pratensis* L., *Phleum pratense* L., and *Bromus hordeaceus* L. Other associated herbaceous species include *Linaria canadensis* (L.) Dum.-Cours. and *Potentilla simplex* Michx. The origin of *H. pubescens* at this site is unclear, but it may be that the plant was introduced as a forage grass at the nearby dairy farm. Subsequent to the discovery of naturalized *H. pubescens* in Sheffield, this taxon was observed for sale as an ornamental plant at two garden centers, one in Connecticut and the other in Massachusetts. As evidenced by the relative abundance of *H. pubescens* compared to other grass species at the Sheffield site, it appears that *H. pubescens* has the ability to become an aggressive competitor without cultivation. Although admittedly an attractive species, sale of *H. pubescens* as an ornamental landscape plant should probably be discouraged.

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NEW ENGLAND NOTE

COTONEASTER DIVARICATUS (ROSACEAE) NATURALIZED IN MASSACHUSETTS

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Cotoneaster divaricatus Rehder & E. H. Wilson (spreading cotoneaster) is native to central China, and planted as an ornamental in eastern Massachusetts. The fruits of *Cotoneaster* are attractive to birds, which disseminate the seed. In Europe this has led to an increasing number of reports of bird-sown naturalized species, spread from garden and roadside ornamental plantings (Fryer and Hylmö 1995, 1997; Stace 1997). Jeanette Fryer (pers. comm.) informs me that some of the European birds involved include waxwings (*Bombycilla garrulus*), blackbirds (*Turdus merula*), and redwings (*Turdus iliacus*). In western North America, I have repeatedly observed American robins (*Turdus migratorius*) and American crows (*Corvus brachyrhynchos*) eating the fruits of five *Cotoneaster* taxa, all of which are easily found as seedlings under crow roosts and other bird perches. Both of these birds are common in Cotuit, Barnstable County, Massachusetts. In light of this frugivorous interaction, it is not surprising that large and old ornamental plantings of *C. divaricatus* near the Cotuit library are the epicenter of widely scattered clusters of apparently bird-sown *C. divaricatus*. Within a one-mile radius of the town library I found ten colonies of adventive *Cotoneaster* scattered among native trees and shrubs in thickets, on roadsides, in suburban yards, and at the edge of second-growth oak woods. Seedlings were common in the vicinity of cultivated plants, and occasional around older wild plants. I would consider this one diffuse population of *C. divaricatus*, with ca. 50–200 wild plants, and probably reproducing outside of cultivation for many years.

VOUCHER SPECIMEN: Massachusetts: Barnstable Co., Cotuit, Barnstable, from thickets near the junction of School Street and Main Street, 8 Jul 2001, *Zika 16,349* (NEBC, WTU).

This colony is representative of the population, found at elevations of 10–25 ft., on dry sandy substrates, and its associates include some aggressive adventives as well as native species: *Acer campestre* L., *A. platanoides* L., *A. pseudoplatanus* L., *A. rubrum* L., *Berberis thunbergii* Alph. de Candolle, *Campsis radicans* (L.) Seem. *ex* Bureau, *Celastrus orbiculatus* Thunb. *ex* A. Murray, *Euonymus alatus* (Thunb.) Siebold, *Lonicera* ×*bella* Zabel, *L. morrowii* A. Gray, *Populus alba* L., *Prunus serotina* Ehrh., *Quercus coccinea* Münchh., and *Rhus typhina* L. This appears to be the first report of the genus as an escape from cultivation in Massachusetts (Kartesz 1999; Sorrie and Somers 1999).

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NOTE

NEW REPORTS OF POACEAE IN THE ROCKY SUBSTRATUM OF MUNICIPALITY OF PEROTE, VERACRUZ, MEXICO

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Despite the constant and longstanding impact of human activities in central Veracruz, México, the native vegetation is considered to be relatively undisturbed. Principally, human activity has taken the form of goat grazing, the felling of wood for timber and fuel, and fires. Nevertheless, the rocky habitat of volcanic and limestone origin has managed to conserve its original vegetation. However, the area is little known, botanically.

Over the course of two years, botanical material was collected from central Veracruz during several exploratory expeditions. Species never before recorded in the state were found during these visits: *Garrya ovata* Benth. subsp. *goldmanii* (Wooton & Standl.) G. V. Dahling and *Beschorneria calcicola* García-Mend. (Castillo-Campos et al. 1998) are among the most noteworthy, along with new recordings of species from the Caryophyllaceae: *Drymaria malachioides* Briq., *D. molluginea* (Lag.) Didr., *D. xerophylla* A. Gray, *Polycarpon tetraphyllum* (L.) L., and *Scleranthus annuus* L. (Escamilla and Castillo-Campos 2000). Because they are characteristic of this type of substrate, it is not surprising that Poaceae are abundant in the study area.

The municipality of Perote is found in the central region of Veracruz State (Figure 1). This region includes a plateau and features the second highest elevation in the state with the Cofre de Perote, at 4282 m (Soto and Angulo 1990). According to Marchal and Palma (1985), the site has three different geological compositions: calcareous rocks, detrital rocks, and basalt filtering accompanied by breach and volcanic ash deposits. The municipality of Perote has two types of climate: subhumid temperate, corresponding to the driest of this subtype, and dry temperate.

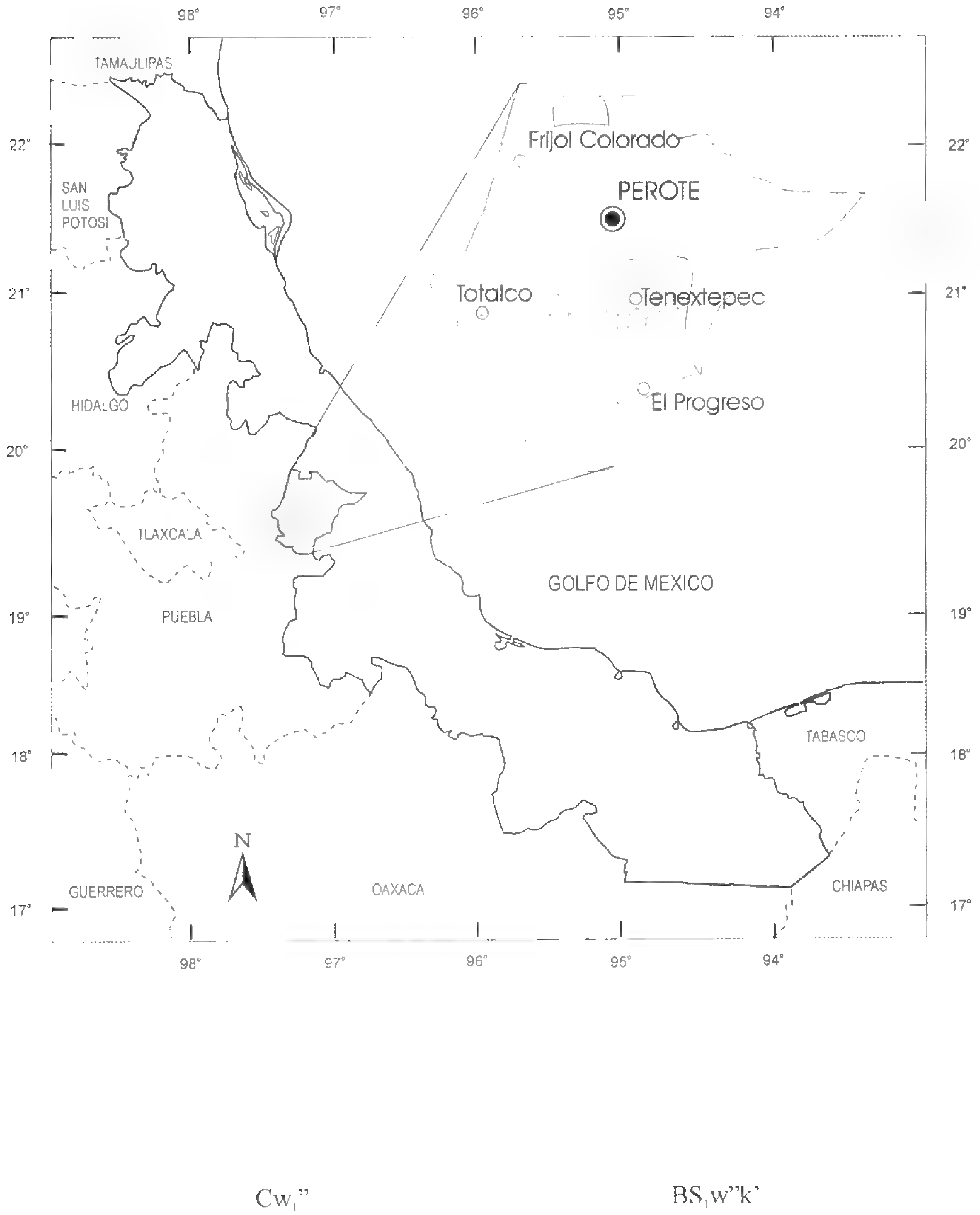

Figure 1. Municipality of Perote, Veracruz (Gobierno del Estado de Veracruz 1988). Climate types follow Soto and Angulo (1990): Cw$_1$'' = subhumid temperature, BS$_1$w''k' = dry temperate.

Following the classification of Miranda and Hernández X. (1963), the types of vegetation present in the rocky area of Perote are either oak and pine forest or *Yucca-Nolina* thicket.

Determination of the material collected yielded the following six new reports for the state of Veracruz: *Aristida purpurea* var. *curvifolia, Bromus diandrus, Calamagrostis pringlei, Erioneuron* *avenaceum* var. *avenaceum, Muhlenbergia glabrata,* and *Setaria reverchonii* subsp. *ramiseta.* The results obtained from this study demonstrate the importance of intensifying botanical exploration in little-known areas such as the rocky areas of central and northern Veracruz. It is possible that these sites feature unknown species, not only from the Poaceae but from other plant families as well.

SPECIMEN CITATIONS

Aristida purpurea Nutt. var. *curvifolia* (E. Fourn.) Allred

Plants from 20 to 40 cm tall; the first glume is shorter than second, obtuse glumes, 7 and 10–11 mm long, respectively.

Plants were growing in xerophytic thickets and rocky soil; abundance was moderate. This variety is endemic to México in the northern states.

VOUCHER SPECIMEN: MÉXICO. Veracruz: Municipality of Perote, 3 km S of Totalco, between Totalco and Alchichica, elev. 2350 m, 19 Nov 1998, *Castillo-Campos, Avendaño & Acosta 18,976* (XAL).

Bromus diandrus Roth

Plants from 20 to 70 cm tall; panicle loose and open; lemma narrow, acuminate, bifid, awn 3–6 cm long.

Bromus diandrus was found growing in xerophytic brush and rocky soil; abundance was scarce. This species was introduced from the mediterranean climates of Europe.

VOUCHER SPECIMEN: MÉXICO. Veracruz: Municipality of Perote, Progreso, elev. 2460 m, 17 Nov 1998, *Castillo-Campos, Avendaño & Acosta 18,853* (XAL).

Calamagrostis pringlei Beal

Rhizomatous plants with simple or tufted culms; leaf blades involute when dry, pilose; panicle narrow, with ascending branches; glumes almost identical, acuminate and scabrous.

Plants were growing in xerophytic thickets with moderate abundance. *Calamagrostis pringlei* has been described from the mexican eastern Sierra Madre.

VOUCHER SPECIMENS: MÉXICO. Veracruz: Municipality of Perote, on the summit of Cofre de Perote, elev. 4180 m, 20 Oct 1998, *Castillo-Campos, Avendaño & Acosta 18,655* (XAL); SW of Tenextepec Hacienda, elev. 2360 m, 5 Nov 1998, *Castillo-Campos, Avendaño & Acosta 18,766* (XAL).

Erioneuron avenaceum (Kunth) Tateoka var. *avenaceum*

There are four varieties of the species, three in South America and one in North America. *Erioneuron avenaceum* var. *avenaceum* is distinguished by the fact that its glumes exceed the lower floret, the second glume is 5–6.5 mm long, and lobes of the lemma are 1.5–2 mm long.

Plants were found growing in xerophytic thickets and rocky soil; abundance varied from scarce for material collected in a wide open valley to abundant for material collected from a limestone slope. Distribution of var. *avenaceum* runs from the southern United States (Arizona and New Mexico) to southern México.

Determination of this species was carried out on the basis of Valdés-Reyna and Hatch (1997) studies, which considered *Dasyochloa avenacea* (Kunth) Willd. *ex* Steud. as a synonym.

VOUCHER SPECIMENS: MÉXICO. Veracruz: Municipality of Perote, 1 km W of Frijol Colorado, elev. 2200 m, 20 Nov 1998, *Castillo-Campos, Avendaño, Palestina & Acosta 16,800* (XAL); Progreso, elev. 2460 m, 17 Nov 1998, *Castillo-Campos, Avendaño & Acosta 18,851* (XAL); 3 km S of Totalco, between Totalco and Alchichica, elev. 2350 m, 19 Nov 1998, *Castillo-Campos, Avendaño & Acosta 18,974* (XAL).

Muhlenbergia glabrata (Kunth) Trin.

Plants more than 1 m tall; glumes from half to the same size as lemma, lemma slightly bifid with an awn that emerges from between teeth.

Abundance of *Muhlenbergia glabrata* was common, with plants growing in xerophytic brush and oak forest and associated with *Astragalus, Bouvardia, Mammilaria, Plantago,* and *Yucca.* This species is endemic to México.

VOUCHER SPECIMENS: MÉXICO. Veracruz: Municipality of Perote, W of Frijol Colorado, elev. 2200 m, 28 Nov 1998, *Castillo-Campos, Avendaño, Palestina & Acosta 16,792* (XAL); S of Totalco, elev. 2360 m, 28 Oct 1998, *Castillo-Campos, Avendaño & Acosta 18,602, 18,637* (XAL); SW of the Tenexptepec Hacienda, elev. 2360 m, 5 Nov 1998, *Castillo-Campos, Avendaño & Acosta 18,749, 18,791* (XAL).

Setaria reverchonii (Vasey) Pilger subsp. *ramiseta* (Scribn.) W. E. Fox

A small plant, 25 cm tall; bristles not exceeding the spikelet; first glume half the length of spikelet.

Abundance of subsp. *ramiseta* was scarce. The plants were found growing in xerophytic brush and rocky soil. This subspecies is native to the United States and México.

Determination of this species was carried out on the basis of the new combinations proposed by Fox and Hatch (1999) in which three taxa are classified in the subgenus *Reverchoniae*: *Setaria reverchonii* subsp. *reverchonii, S. reverchonii* subsp. *ramiseta,* and *S. reverchonii* subsp. *firmula.*

VOUCHER SPECIMEN: MÉXICO. Veracruz: Municipality of Perote, SW of the Tenextepec Hacienda, elev. 2360 m, 5 Nov 1998, *Castillo-Campos, Avendaño & Acosta 18,805* (XAL).

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NOTE

TURION PRODUCTION BY *RUPPIA MARITIMA* IN CHESAPEAKE BAY

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Turions are mechanisms for overwintering and may function as hibernacula that form during autumn when the meristematic tips of rhizomes form a bulb-like structure composed of leaf tissue (Sculthorpe 1967). During spring, new leaves grow from the turions, and the entire structure can break off the parent rhizome and disperse to new habitats. Turions have been described for *Hydrocharis, Myriophyllum, Potamogeton,* and *Utricularia.* Brock (1982) described turions for the two Southern Hemisphere species, *Ruppia tuberosa* J. S. Davis & Tomlinson and *R. polycarpa* R. Mason. In these species, the turions acted as perennating agents. Turions have not been described previously for *R. maritima* L.

DESCRIPTION

Turions of *Ruppia maritima* were discovered in June 1992 at several locations along two transects across a *R. maritima* bed in lower Chesapeake Bay near the mouth of the Rappahannock River (76°20′N, 37°37′W). *Ruppia maritima* was asexually increasing in this area (Orth et al. 1989). The transects were part of a seed reserve study. The turions appeared while digging sediment cores along the Rappahannock River transect. Water temperature was 19°C, and the turions were not incorporated in the sediment core itself, but drifted to the surface when the substrate was disturbed. Drifting turions occurred at four locations along the transect, totaling 10 turions. No turions were found at any other of five transects during the course of this study. Dissection and microscopic inspection showed that the turions possessed leafy aerenchyma, similar to the Type II turions described by Brock (1982). Type II turions contain meristematic tissue enclosed by swollen leaf structures with numerous enlarged starch-filled cells. The dissected tissue contained cells that stained positive for starch with potassium iodide (IKI). All turions were 1–2 cm in diameter and had new leaves developing.

VOUCHER SPECIMEN: Virginia: Lancaster Co., near Weems, 8 Jun 1992, *Rosenzweig s.n.* (VPI).

DISCUSSION

Verhoeven (1979) described the growth habit of *Ruppia maritima* to include horizontal rhizomes and vertical stems. He described vegetative dispersal by fragmented vertical stems that occurred during the growing season. Plants overwintered as rhizomes, and rhizomes or seeds reestablished populations. Silberhorn et al. (1996) noted that in Chesapeake Bay, *R. maritima* shoot and seed production were both very high. We found that *R. maritima* persisted in some areas and in others it was ephemeral. Our studies suggest that factors influencing growth, distribution, and abundance of *R. maritima* include water quality, habitat quality, inter-specific competition for resources (primarily with *Zostera marina* L.), and the success of different life-stages of plants. First-year plants may not become reproductive at some sites (unpubl. data), so that a newly colonized site may be partially or completely devoid of plants the following growing season, depending on water quality or habitat quality stresses in the new stand. Perennial persistence of *R. maritima* depends on a combination of environmental, ecological, and specific biological factors of the plant.

Asexual propagation is an important means of colonization for aquatic plants, and spreading by rhizomes, fragments of rhizomes, stolons, and tubers may contribute to large clonal populations of aquatic species (Sculthorpe 1967). In Chesapeake Bay, turions may provide an additional means of asexual reproduction that contributes the ability to rapidly colonize suitable habitats. Turions, with their high starch content, should be capable of new plant growth at the beginning of the growing season. More research is needed to determine if turions are more wide spread in this species in Chesapeake Bay and elsewhere. Turion production is seasonal (Sculthorpe 1967), so year-round sampling should be done to detect when turions are produced in Chesapeake Bay. If turions are being produced only at certain sites or at certain times, then it will be important to identify what factors influence turion production in this species.

ACKNOWLEDGMENTS. Dr. Robert Orth and the Virginia Institute of Marine Science, College of William and Mary, provided support for this research.

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RHODORA, Vol. 104, No. 919, pp. 312–315, 2002

BOOK REVIEW

Flora of New Brunswick, Second Edition: A Manual for Identification of the Vascular Plants of New Brunswick by Harold R. Hinds. 2000. 695 pp. illus. line drawings. ISBN 1-55131-015-5 CAN$50.00 (softcover) plus CAN$8 s&h. Published by the Biology Department, University of New Brunswick, Fredericton (orders: www.unb.ca/departs/science/biology/Flora.html).

The 2nd edition of the *Flora of New Brunswick* was worth the wait. It was published just in time for the author, a gifted field botanist and teacher, to realize his goal of seeing it in print before his untimely death in his early 60s on May 9, 2001. This 6" × 9" paperback is 1.75 inches thick and will fit handily in the daypack. Users include botanists, ecologists, foresters, and students in New Brunswick and adjacent Maine and other Maritime Provinces. This is a must-have for all academic libraries throughout northeastern North America and for herbaria worldwide.

The *Flora* represents the main focus of the latter part of Hal Hinds' career. His 23 years of teaching botany at the University of New Brunswick (UNB) and in government-sponsored programs gave numerous students a much deeper appreciation for plants, and some took up botany as a profession because of his influence. One of his specialties was the Polygonaceae, and he spent eight weeks at the Missouri Botanical Garden in 1993 to provide important updates for the *Flora of North America.* As Curator of the Connell Memorial Herbarium at UNB from 1979 to 2001, he expanded and improved the collection significantly and enjoyed providing loans and resources to visiting scientists.

His success at finding historic and previously unknown locales for rare plants enabled him to make a major contribution in the protection of many populations. Hal was known for his adventurous and courageous spirit, and he was willing to tackle baffling hybrids that others were willing to list as "sp.," including the wily shadbushes, asters, sedges, grasses, and ferns. He was always ready to help others learn difficult groups, and had many tips for field identification that made expeditions especially fun and informative. For example, to test for scabrous texture on upper culms of some *Carex,* draw the culm across your lower lip. He brought a clear-eyed approach to some long-standing taxonomic challenges by closely observing morphology and ecology of the taxa over their full range of habitats. The 2nd edition reflects this deeper understanding of some difficult species groups.

The 2nd edition of *Flora of New Brunswick* improves over the 1st edition, published in 1986, in that it includes not only the most recent and best data regarding systematic treatments, but has the contributions of many other knowledgeable botanists building upon Hal's original concepts. Hal became ill while still a young man in his 50s and continued his work on the 2nd edition despite bouts with poor health. Friends and associates formed a Revision Committee in 1997, and with support from the UNB Department of Biology, helped him complete the work. Users of this edition can be grateful for their dedication and volunteer efforts. Some contributed in part by writing sections of the *Flora.* An updated chapter on the "History of Plant Collecting" by C. Mary Young is a fascinating account that puts the 2nd edition in the context of a long struggle to understand the New Brunswick flora. Stephen R. Clayden, lichenologist, wrote a 30-page chapter, "History, Physical Setting, and Regional Variation of the Flora," which is a comprehensive and detailed overview with more than 130 references cited for this chapter alone; this is richly expanded from the 1st edition and will doubtless be cited in many future papers. James W. Goltz, with expertise in the flora of Ontario and in Orchidaceae of New Brunswick, updated the treatment of that group, and worked on numerous other keys and species notes as well.

There are many fine features of the *Flora of New Brunswick.* The font for the cover is Arrus BT, and the text font is Helvetica. Varying sizes and some headings in bold make for high readability. The taxonomic treatments follow the first four volumes of the *Flora of North America* and some unpublished revisions from upcoming volumes. A glossary is brightened by some line drawings and the definitions are concise but clear. The family key provides an entrée, though it is probably easiest to use if one already has a rough idea of what the plant in question might be (and aren't all such keys this way?). The keys are prepared so that each couplet references the previous couplet that brought one to a certain place, so the user can easily retrace the steps taken if necessary. A dot map and a line drawing accompany every species, on the same page as the species notes. Dot maps are based on specimens in the Connell Memorial Herbarium. The presentation of maps and drawings is an improvement over that of the 1st edition, in which drawings and maps were each in separate appendices. The drawings are mostly from *An Illustrated Flora of the Northern United States and the British Possessions* by N. L. Britton and A. Brown (1913). Additional illustrations were prepared especially by C. Mary Young (the cover, 40 glossary illustrations, 25 larger illustrations), Carol Bayley (some of the glossary illustrations), Mary Sims (ca. 13 smaller illustrations), Chris Sears, and W. A. Hathaway. A few of these illustrations appeared in *Wildflowers of Cape Cod* by Hinds and Hathway (1968). These illustrations, which in my opinion could have been more prominently credited in the book, are what make this *Flora* especially user-friendly as they enable the user to establish whether or not he/she is in the ballpark. They are necessarily small, and lack scale, but they include cogent aspects that help provide a search image.

Species notes include translation of the specific epithet; common names including English, French, Maliseet, and Mi'kmaq; geographic range; chromosome number; frequency; habitat and locale information specific to New Brunswick and also throughout Canada in some cases; synonymy; rarity rankings assigned by the Atlantic Conservation Data Centre and signified by stars; pollination and dispersal information if unusual; edibility; toxicity; status as invasive exotic; and folklore attributes. Wildlife uses are noted where pertinent. If they are relevant, subspecific taxa are included. Recent taxonomic changes are often noted with author and reference so that one can look up recent systematic studies. At the back, there are a 5-page bibliography and appendices that summarize the flora and specify changes. Finally, the 2nd edition is completely indexed, including all common names. A full description for each species is not offered; otherwise the volume would be too unwieldy to take into the field. If necessary, the user can turn for descriptions to other sources such as *Gray's Manual, 8th Edition* (Fernald 1950)—which Hal referred to as the "dinosaur." For errata and addenda, a web site is available (see publication information, above).

Although Hal is much missed by those who worked with him on various plant conservation and taxonomy projects, the *Flora of New Brunswick* is an excellent way to remember his warmth and humor and to benefit from his vast field experience and detailed study. Many in the *Rhodora* readership live beyond the full usefulness of the species included in this *Flora,* but anyone who enjoys looking at plants will appreciate the approach taken here. The 2nd edition sets a standard for state and regional florae and should be studied as a model for other works of its kind. Doubtless the 2nd edition will lead to the planning of some botanical vacations in beautiful New Brunswick, where so many interesting habitats and plants await those who want to appreciate the flora through Hal's eyes.

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—ALISON C. DIBBLE, Research Ecologist, U.S. Department of Agriculture Forest Service, Northeastern Research Station, 686 Government Rd., Bradley, ME 04411.

NEW BOOKS

Aquatic Plants of Palo Verde National Park and the Tempisque River Valley by Garrett E. Crow. 2002. 296 pp. line drawings and color photos. ISBN 9968-702-62-5 US$17.00 (softcover). Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica. [opposing pages in Spanish and English; available at www.inbio.ac.cr/editorial]

The Illustrated Flora of Illinois, Flowering Plants: Pokeweeds, Four-o'clocks, Carpetweeds, Cacti, Purslanes, Goosefoots, Pigweeds, and Pinks by Robert H. Mohlenbrock. 2001. xi + 277 pp. line drawings and county dot maps. ISBN 0-8093-2380-X [price unavailable]. Southern Illinois University Press, Carbondale and Edwardsville, IL.

The Illustrated Flora of Illinois, Grasses: Panicum *to* Danthonia, *Second Edition* by Robert H. Mohlenbrock. 2001. xvii + 455 pp. line drawings and county dot maps. ISBN 0-8093-2360-5 [price unavailable]. Southern Illinois University Press, Carbondale and Edwardsville, IL.

The Illustrated Flora of Illinois, Sedges: Cyperus *to* Scleria, *Second Edition* by Robert H. Mohlenbrock. 2001. xii + 223 pp. line drawings and county dot maps. ISBN 0-8093-2358-3 [price unavailable]. Southern Illinois University Press, Carbondale and Edwardsville, IL.

Peterson Field Guide to Western Medicinal Plants and Herbs by Steven Foster and Christopher Hobbs. 2002. xv + 442 pp. color photos. ISBN 0-395-83806-1 $22.00 (flexi-cover). Houghton Mifflin, Boston and New York.

Shrubs and Vines of New Jersey and the Mid-Atlantic States by Christopher T. Martine. 2002. 114 pp. line drawings. $10.00 (softcover, spiral-bound). New Jersey Forest Service, Forest Resource Education Center, Jackson, NJ. [available from NJFS Forest Resource Education Center, 370 East Veterans Highway, Jackson, NJ 08527; phone 732-928-0029; e-mail njfsfrec@bellatlantic.net]

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NEBC MEETING NEWS

March 2002. Incoming President Paul Somers introduced the evening's speaker, outgoing President Dr. Lisa A. Standley. Lisa first became interested in nature as a child attending Massachusetts Audubon Society Day Camp programs. Although a premier interest in birds led her to matriculate at Cornell University, she was soon introduced to botany there by Dr. R. T. Clausen. She received a Master's degree from Cornell, her thesis being on the systematics of *Carex* sect. *Cryptocarpeae* (*C. crinita* and *C. gynandra*). She then received a Ph.D. from the University of Washington where she studied under Dr. Melinda Denton. Her doctoral thesis on *Carex* sect. *Acutae* (now better known as sect. *Phacocystis*) in the Pacific Northwest was published in the series *Systematic Botany Monographs* by the American Society of Plant Taxonomists. It is still the best-selling volume in the series. Following receipt of her doctorate, Dr. Standley taught at Wellesley College for several years before leaving academia to become a consultant with the firm of Vanasse Hangen Brustlin in Watertown, Massachusetts.

Lisa's talk, entitled "Botanizing the extremes," grew out of several visits over the past decade to two outstanding natural areas, the Anza–Borrego Desert State Park (ca. 800 square miles) in the Sonoran Desert of southern California, and the Arctic National Wildlife Refuge (ca. 28,000 square miles) in northeastern Alaska. Both refuges present extreme environments that are challenging to plants. Ranging back and forth between the two, however, shows that they are similar in some important ways.

California's Anza–Borrego Desert State Park is a harsh desert environment where extremes of heat and drought strongly control plant communities, and plants exhibit many adaptations to cope with the problems. The flora is strongly controlled by microhabitat, from cacti (species of *Mammillaria* and *Opuntia*) on parched rocky slopes to maidenhair fern (*Adiantum capillus-veneris*) near a surprisingly permanent waterfall named, appropriately, "Maidenhair Falls." Although the dryness and heat control plant distributions, some mesophytes such as desert palm (*Washingtonia filifera*), ash (*Fraxinus*), and sycamore (*Platanus*) occur in a few protected seeps and along the bottoms of moist ravines. The palms do not appear to be reproducing well at present and studies are underway to better understand the reason.

When in bloom in early spring, desert flats are extremely lush with a wide array of very showy flowers. In years when it rains, every inch of the flats has something in bloom, including species of *Pholisma,* known as "fiesta flower," *Justicia, Penstemon, Mimulus, Phacelia,* and *Abronia.* Composites are abundant, as are the legumes *Oxytropis* and *Astragalus.* Desert poppies (*Argemone*) and *Sphaeralcea* add bright flowers in abundance. Large specimens of *Agave* and *Yucca* are common.

Anza–Borrego is characterized by sedimentary bedrock but there are numerous granite outcrops and badlands. Dry-adapted shrubs such as creosote bush (*Larrea*), smoke-bush (*Dalea*), and mesquite (*Prosopis*) characterize large areas, as do ocotillo (*Fouquieria*) and junipers (*Juniperus*).

The plant communities of the Arctic National Wildlife Refuge have a comparable diversity, even though they occur at a high latitude and endure bitterly cold winters. Shrubby species are lacking except for a few patches of willows (*Salix*) in protected east-west valleys; down-sloping winds in the north-south valleys appear to be inimical to any woody growth other than ground-hugging species of willow (*Salix minima*) and the ubiquitous dryas (*Dryas octopetala* and *D. integrifolia*). In mid-June, the arctic meadows are filled with spectacular wild flowers in a show comparable to the spring extravaganza of the Anza–Borrego Desert State Park. There are meadows of poppies, buttercups, anemones, and lupines, and rocky uplands are characterized by "little rock gardens" with such bright flowers as purple mountain-saxifrage (*Saxifraga oppositifolia*), phlox (*Phlox sibirica*), and groundsels (*Senecio* spp.). Legumes, including the same genera found at Anza–Borrego, *Oxytropis* and *Astragalus,* are abundant. There are numerous brightly-flowered species of lousewort (*Pedicularis* spp.). Grand views of towering mountains and broad river valleys open onto the broad coastal plain and distant views of the Beaufort Sea ice pack.

Both sites have abundant wildlife. In the Sonoran Desert, the fauna is characterized by reptiles, including tortoises, rattlesnakes, and iguanas. The Arctic ecosystem features large herds of caribou, along with ermine, grizzly bears, and muskox, aptly described by Lisa as "fringed sofas on legs." Birds of the desert are few but include roadrunner (*Paenopepla*) and several species of hummingbird. In the arctic, birds are abundant and readily observed, from gyrfalcons to long-tailed ducks to red phalaropes.

The two locales are alike in the fragility of their ecosystems, poised at the extreme edge of viability because of the harsh climatic conditions. The Anza–Borrgeo is most threatened by recreational activities of people from nearby cities, especially off-road vehicle use. The Arctic National Wildlife Refuge is too remote for that particular threat, but drilling for oil on the arctic coastal plain, where caribou calve and waterfowl nest, would threaten the basis of much of the ecosystem.

—ARTHUR V. GILMAN, Recording Secretary *pro tempore.*

June 7 Field Trip. Glenn Motzkin of the Harvard Forest and Dr. William Patterson of the University of Massachusetts, Amherst, led more than 45 Club members and guests (surely a record!) on an ecological tour of Montague Plain, Montague, Massachusetts, most of which is a preserve held by the Massachusetts Division of Wildlife and Fisheries. After Glenn's introduction to the post-glacial and human history of the site, the group examined soil pits just meters apart, but separated by an old ditch-and-mound fence. One pit had a deep plow layer of homogeneous soil; it had been plowed for decades and was abandoned as a field 75–100 years ago. The overstory was *Pinus rigida,* and there were no ericads, just a few scattered herbaceous plants. The other pit had a shallow A horizon, shading into a natural B horizon, the product of 10,000 years of postglacial development. There the overstory was a mixture of hardwoods and pines with a dense understory of ericads, including *Gaylussacia baccata, Gaultheria procumbens,* and *Vaccinium angustifolium.* Several factors may have contributed to the limited colonization of old agricultural fields by these ericads, especially poor dispersal or establishment on xeric sites. At another site on the plain near power lines, Bill Patterson described how fire and cutting are being used to prevent succession and to thin the *Quercus ilicifolia.* These operations have had the combined effect of making the habitat more friendly to some rare moths and to human hunters. The group walked through patches that were at different stages of recovery after prescribed burns.

June 2002. Glenn Motzkin, plant ecologist at the Harvard Forest, spoke about "Historical influences on the vegetation of Massachusetts: Ecological and conservation implications." Glenn spoke about his studies and others on Montague Plain and other barren systems in the Northeast, with an emphasis on sand-plain heathlands, grasslands, pitch pine–scrub oak barrens, and ridgetop pine communities in Massachusetts. Conservation of these communities is of particular concern because they support the highest concentration of rare species in the Northeast and because most of the large barrens have shrunk during the historical period in response to succession and residential and commercial development.

Montague Plain is a sandy outwash delta, originally deposited in glacial Lake Hitchcock. Its land-use history is reflected in the soil profile and in today's vegetation (see the report on Friday's field trip). A sample of 120 plots on the plain showed three categories of plants based on their distribution today relative to plowing. Species such as *Lysimachia quadrifolia, Prunus serotina,* and *Lycopodium obscurum* have similar frequencies today on sites that were formerly plowed for agriculture as well as on sites that were never plowed. In contrast, species such as *Cypripedium acaule* and *Polytrichum* mosses occur much more frequently today on former agricultural lands, even though these sites have been abandoned from agricultural use for > 100 years. Areas that were never plowed are virtually the only habitats occupied by several species that are characteristic of pine barrens, including *Gaultheria procumbens, Gaylussacia baccata, Viburnum cassinoides, Pteridium aquilinum,* and *Quercus prinoides.* In particular, *G. procumbens* is almost entirely restricted to never-plowed land, with less than 5% of the former agricultural lands having any *G. procumbens* in the plots. *Polytrichum* species, in contrast, are restricted almost entirely to previously agricultural lands. Similar relationships between modern species distribution patterns and historical land use occur on outwash plains across the Connecticut Valley.

Studies of other barrens systems in coastal Massachusetts (Martha's Vineyard, outer Cape Cod, and Nantucket), Block Island, and Long Island show similar patterns of species segregation with past agricultural use, but several of the plant species differ from the inland barrens. The coastal suite of plants that indicates formerly plowed or otherwise disturbed land includes

Pinus rigida, Deschampsia flexuosa, and *Arctostaphylos uva-ursi.* Sediment cores from several studies suggest that grasslands were less common before European settlement than during the historical period. Ridgetop barrens (such as Mount Tekoa or Mount Everett in Massachusetts) also are dominated by *P. rigida.* Ridgetop barrens typically occur in areas with little soil and harsh growing conditions; whereas some sites have experienced frequent fire, others have been influenced by frequent ice storms.

To maintain or restore barrens systems, active management may be necessary in order to simulate the effects of the disturbances that allowed these communities to develop, including prescribed fire, mowing, and grazing. Although many barrens originated during the historical period from overgrazing or other severe disturbances, they now harbor numerous rare species. As Glenn said, a legitimate question is, "What are appropriate objectives for these systems?" We frequently choose to manage for early successional habitats, although it may not be possible to maintain every rare species or unusual tree form.

—Joann M. Hoy, Recording Secretary *pro tempore.*

June 8 Field Trip. The Saturday field trip to South River State Forest in Conway, Massachusetts, was led by Jesse Bellemare, a graduate student at Harvard Forest. This trip provided the opportunity to explore the flora of the rich mesic forest, and to see the effect of past land use on its herbaceous layer. Jesse just completed his Master's thesis on the effects of historic land use on herbaceous plant diversity in rich mesic forests in western Franklin and Hampshire Counties, and the South River State Forest was one of his study sites. The site is on Waits River Formation bedrock that includes outcrops of limestone and marble and some calcareous seeps. The Conway area was settled in the late 1700s, and by the early 1800s 75–85% of the land was cleared and much of it was converted to sheep pasture. The state park includes land that was maintained as a sugar bush and never cleared, as well as land that was cleared for pasture and then abandoned in the early 20th century, and has since regenerated to secondary forest. The difference in herbaceous species diversity between the areas with different land use histories was dramatic. The area that had never been cleared had an impressive diversity of herbaceous plants while the reverting pasture had very few herbaceous species and those we did see were widely scattered. Jesse suggested that the difference in diversity was due to two factors. Many of the herbaceous plants of the rich mesic woods are either ant-dispersed or drop-dispersed and so have limited dispersal ability. This, combined with their lack of a persistent soil seed bank, makes these plants slow to recolonize secondary forest. He also suggested that a second factor limiting successful colonization was related to the low light levels produced by the almost closed canopy of the young sugar maples.

Although the trip was a little late for the earliest spring flowers, we still saw many of the herbaceous plants that are characteristic of rich mesic forest. The forest was dominated by *Acer saccharum* but included *Fraxinus americana, Carya cordiformis, Betula alleghaniensis,* and *Fagus grandifolia.* We also found one large individual of *Ulmus rubra.* The uncut primary forest area was rich in ferns including *Matteucia struthiopteris, Dryopteris goldiana, Diplazium pycnocarpon,* and *Deparia acrostichoides,* all characteristic of rich mesic woods. Other ferns included *Dryopteris intermedia* and the hybrid *Dryopteris triploidea.* Herbaceous plants included *Carex plantaginea, Laportia canadensis, Osmorhiza claytonii, Tiarella cordifolia, Dicentra canadensis* (identifiable by its yellow corms), *Actaea pachypoda, Caulophyllum thalictroides, Viola canadensis, Trillium erectum,* and *Cardamine diphylla.* We were lucky enough to spot *Panax quinquefolius* and two Massachusetts State Watch-list species, *Sanicula trifoliata* and *Cardamine ×maxima.* The site also had some interesting bryophytes. Susan Williams also found *Freullania bolanderi* at what appears to be its southernmost station and *Cyrto-hypnum minutulum* (*Thuidium minutulum*), which is a new county record.

—Karen B. Searcy, Recording Secretary *pro tempore.*

ANNOUNCEMENT

NEW ENGLAND BOTANICAL CLUB GRADUATE STUDENT RESEARCH AWARD

The New England Botanical Club will offer up to $2,000 in support of botanical research to be conducted by graduate students in 2003. This award is made annually 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. It is anticipated that two awards will be given, although the actual number and amount of awards will depend on the proposals received.

The award will be given to the graduate student(s) submitting the best research proposal dealing with systematic botany, biosystematics, plant ecology, or plant conservation biology. Papers based on the research funded must acknowledge the NEBC's support. Submission of manuscripts to the Club's journal, *Rhodora,* is strongly encouraged.

Applicants must submit three paper copies of each of the following: a proposal of no more than three double-spaced pages, a budget, and a curriculum vitae. Two letters in support of the proposed research, one from the student's thesis advisor, should be sent directly to the Awards Committee by sponsors. All materials should be sent to: Awards Committee, The New England Botanical Club, 22 Divinity Avenue, Cambridge, MA 02138-2020. Proposals and supporting letters must be received no later than Monday, March 3, 2003. The recipient(s) will be notified by April 30, 2003.

This year the Graduate Awards Committee is pleased to announce two recipients of the Graduate Student Research Awards. Lisa Karst of Portland State University received support for her proposal entitled "Phylogeny of *Sisyrinchium* (Iridaceae), genetic and morphological evidence" and Isabel Ashton of the State University of New York at Stony Brook received support for her proposal "Invasive, exotic non-invasive, and native woody vines of the northeastern United States." For abstracts of these research proposals and a listing of the awards from 1985 to the present, consult the Club's web page (http://www.huh.harvard.edu/nebc/).

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NEW ENGLAND NOTE

NOTE

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LOSSES OF NATIVE PLANT SPECIES FROM WORCESTER, MASSACHUSETTS

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ABSTRACT. I recorded the extant vascular flora of Worcester, Massachusetts in seven years of field work beginning in 1994 and obtained historical records from herbarium specimens and the published literature. A detailed vascular flora of the City was published elsewhere. This paper updates the flora with information from an important and previously overlooked collection of specimens, and examines the apparent historic losses of native species in relation to habitat and taxonomy. Overall species losses were about 18% in the past century. Losses were particularly high among species associated with aquatic habitats, bogs, and calcareous or circumneutral terrestrial habitats. I suggest that the first of these reflects extensive alteration of many bodies of water through siltation, chemical pollution, eutrophication, and stream channelization. Losses in the remaining two habitat types may reflect the initial rarity of such habitats within the City combined with habitat destruction. Losses were especially high in several families, including the Orchidaceae, Ophioglossaceae, Caryophyllaceae, Menyanthaceae, Lentibulariaceae, and Lamiaceae. High losses of aquatic and bog species have been noted in other areas, and high losses among orchids appear to be nearly universal. A combination of changing land use, habitat fragmentation, successional changes, species introductions, and climate changes are likely to cause further species losses in the decades ahead.

Key Words: species loss, biodiversity, habitat destruction, Worcester, orchids, flora

Despite the common knowledge that many human activities decrease biological diversity, such changes are only occasionally documented in the literature, and even less commonly subjected to any formal analysis. Documentation and analysis of species losses are, however, critical to efforts to manage for biological diversity and to minimize future species losses.

Vascular plants are probably one of the groups most suited to the evaluation of species losses. In temperate areas, at least, they are relatively well studied. In the eastern United States, recensuses have taken advantage of published floristic records from the 1800s or early 1900s for a variety of study areas ranging from individual plots (Curtis 1959) and single nature preserves or areas of equivalent size (Deane 1896; Pease 1911), to towns, cities, and counties (Darlington 1853; Hollick and Britton 1879; Owen 1888).

Repeated censuses of particular areas can provide various data, including numbers of species lost and rate of species loss. Such data also permit evaluation of losses in relation to life history attributes, habitat type, and taxonomic affiliation. Many studies of species loss report overall losses, but attempt little further analysis. Notable exceptions include the evaluation of species losses in relation to ecological attributes on Staten Island (Robinson et al. 1994) and in Wisconsin (Wiegmann et al. 2001), in relation to habitat and taxonomy in Massachusetts (Drayton and Primack 1996), and in relation to habitat, growth form, and taxonomy in Singapore (Turner et al. 1994).

Evaluation of losses in areas differing in geography and size, and subjected to different intensities and kinds of disturbances are likely to be particularly valuable. We are currently ill-equipped to say how the characteristics of the lost flora differ at the levels of a nature preserve, a town, a county, and a state; how sensitive rates of species loss are to the size of the area sampled; and how different types of disturbances (e.g., urbanization, agriculture, recreational use) influence the kinds of species lost. Only after analysis of a variety of sites will we be able to answer these questions. The present study is one step in this direction. It examines changes in the vascular flora of Worcester, Massachusetts, one of the largest New England cities, over a period of approximately 100 years. I focused especially on species losses in regard to taxonomy and habitat affiliation.

MATERIALS AND METHODS

Description of the study area. The City of Worcester lies in south-central Worcester County, Massachusetts, covering an area of 9740 ha. It falls largely within the drainage of the Blackstone River, which flows to Narragansett Bay, though a small area of northern Worcester is in the drainage of the Nashua and Merrimack Rivers. The City lies along an ill-defined north-south escarpment that separates lower land (~100 m elevation) to the east and south from higher land (~300 m) to the west and north. The bedrock consists largely of highly metamorphosed rocks of Silurian and Devonian age. The bedrock is covered by till in most areas, with smaller areas occupied by glacial outwash.

Perhaps 300 Indians occupied the area of Worcester prior to European colonization. Permanent European settlement began in the early 1700s, and a major increase in population occurred in the middle 1800s (Anonymous 1879). The original forested landscape gave way to agriculture, which then decreased over the past century. Intensive industrial, commercial, and residential development began in the 1800s and continues to the present. Today, Worcester consists of an urban core, with large buildings, extensive paved areas, and occasional landscaped grounds and vacant lots. Fingers of intensive development extend from the core along major roads towards the edges of the City. Surrounding the areas of intensive development are extensive residential neighborhoods, most of which contain scattered parks and undeveloped land. Closest to the City's perimeter, especially on the west side, are larger areas of undeveloped land, mostly forested.

Historical records of the flora. I used a combination of herbarium records and published reports to document the historical native flora of the City. One important collection is housed in Hadwen Herbarium at Clark University (CUW). Most of these specimens were collected between 1920 and 1955 by a group of botanists active in the Worcester region, including Mary Dodge, Burton Gates, W. H. Hodge, David Potter, George Pride, Norman P. Woodward, Burton N. Gates, and Winifred C. Gates. A second important collection includes specimens of the Worcester Natural History Society (unofficially abbreviated WNHS), housed at the Ecotarium in Worcester. These were collected in the late 1800s and early 1900s by a variety of collectors, including Norman P. Woodward, Katherine I. Fish, Mary C. Dodge, and G. E. Stone. These specimens were not cited in the Worcester flora (Bertin 2000) because I was unaware of their existence. New species from this collection are therefore documented in this publication. Additional records came from the Gray Herbarium (GH) and the herbarium of the New England Botanical Society (NEBC), including collections by Hattie Merrifield in 1879–1880 and K. M. Wiegand, collecting in 1911, and from the herbarium of the University of Massachusetts (MASS).

Supplementing the herbarium specimens were several published sources, including Jackson's (1909) *A Catalogue of the Flowering Plants and Ferns of Worcester County,* an addendum to this flora (Jackson 1927), Tucker's (1894) *Trees of Worcester,* Stone's (1899) *Flora of Lake Quinsigamond,* and lists of Potter and Woodward (1935) and Potter et al. (1940). The published sources and herbarium records do not represent a snapshot of one historical time, but rather record species present at some point in the late 1800s or early 1900s.

Records of the current flora. Intensive field work to inventory the current flora ran from 1994–1996, and less intensive work continued into 2001. I made several hundred separate visits to over 70 sites during this period. These sites included the range of natural and disturbed habitats found in the City. Records were kept of all native and introduced species, and herbarium specimens of approximately 70% of the extant flora were deposited at MASS.

Data analysis. In analyzing species loss by habitat, I used habitat descriptions reported in three published floras covering the study area. I used published information rather than my own assessments to prevent possible bias. I used data from more than one flora to allow for the variation in habitat designations in the different publications. The floras were Gleason and Cronquist (1991), Magee and Ahles (1999), and Seymour (1982). I created a spreadsheet data file including names of all native species that have been reported in Worcester and habitat descriptions supplied in each of the three references. I then established several habitat categories (Table 1), and identified a series of terms found in the floras that fitted each category. For example, bog habitat was designated by a single term: "bog." Rock outcrop habitat was designated by the terms: "cliff," "crevice," "ledge," "outcrop," and "rocks." The categories were chosen to represent a variety of habitats that could be distinguished using terms in the floras. Some categories overlap, and some species were present in more than one category. A computerized search permitted the listing of species in each habitat category in each literature source. For a few habitat categories it was then necessary to examine the species list and delete species clearly inappropriate to that category. For example, one search term for aquatic habitat was "stream." However, this term triggered inclusion of species such as spicebush [*Lindera benzoin* (L.) Blume], which was listed in one flora as occurring "along streams."

To determine habitats associated with particularly high losses,

Table 1. Habitat categories examined in this study, along with the habitat terms in floras that were used to assign species to these categories.

Habitat Category	Habitat Terms
Aquatic	Brooks, floating, lakes, pond, pool, rivers, springs, streams, submersed, water (excluding such combinations as "along rivers")
Bogs	Bog
Burned areas	Burn, fire
Calcareous terrestrial	Alkaline soil, basic soil, calcareous, circumneutral soil, limy soil, neutral, sweet soil (excluding aquatic species)
Coniferous	Cedar, conifer, pine, *Thuja*
Disturbed sites	Buildings, compacted soil, cultivated, disturb, dooryards, dumps, dwellings, garden, gravel pits, henyards, lawn, paths, pavement, railroad, roadside, sidewalks, stone walls, waste, weed
Dry herbaceous	Dry field, dry gravelly field, dry meadow, dry open place, dry sandy fields
Grasslands	Field, grass, meadow, pasture, prairies
Herbaceous	Field, grass, marsh, meadow, openings, pasture, prairies
Rich terrestrial	Fertile, rich
Rock outcrops	Cliff, crevice, ledge, outcrop, rock
Sandy substrate	Sand
Shrub swamps	Shrub swamp
Successional	Abandoned field, old field, seral, successional
Swamps	Swamp
Vegetated wetlands	Bog, marsh, miry, mucky, mud, peat, poorly drained sites, sedge mats, swamp, wet
Wet herbaceous	Low meadow, marsh, moist meadows, peaty meadow, springy meadow, swampy field, wet field, wet grassland, wet meadow, wet sunny
Woods	Forest, wood

the number of species lost in a particular habitat category was compared to the overall rate of species loss using exact probabilities based on a binomial distribution. For example, of 797 native species documented by either herbarium specimens or my sight records, 147 (18.4%) have disappeared. Gleason and Cronquist (1991) report 9 of the 797 native species as being associated with rock outcrops. Of these, two have disappeared in Worcester. Randomly sampling nine species from a universe in which 18.4% of species have been lost, one can use the binomial distribution to calculate the probability that 0, 1, 2, 3, 4, 5, 6, 7, 8, or 9 of the nine species will have been lost. By summing the last eight of these individual probabilities, one finds that the probability of losing two or more of nine randomly selected species is 0.52. Losses in a particular habitat were considered significantly different from the overall rate of loss if the likelihood of such a loss occurring by chance was less than 0.05. Because 0.52 exceeds 0.05, I conclude that Worcester's rock outcrop species have not been particularly prone to local extinction.

A similar approach was used to analyze species disappearances by plant family. Here the grouping was by plant family and the question asked was: "Given the overall rate of species loss, which families showed significantly different extinction rates than the flora as a whole?"

All species and family designations were based on Gleason and Cronquist (1991). The rates of loss reported in this paper are based on species documented by an herbarium specimen (the vast majority) or by my sight record (collectively referred to as documented species). I also performed a second set of analyses that included documented species plus those reported in the literature (total species). I report the results of significance tests involving this group of species, but not the data themselves, which paralleled the results for documented species.

Comparisons of species losses in Worcester to state-wide patterns of rarity were made using published data from the Massachusetts Natural Heritage Program (Sorrie and Somers 1999). The Massachusetts species at greatest risk are referred to herein as state-listed species, comprising species that are designated by the state as endangered, threatened, or of special concern. Species referred to herein as watch list species are those species given this informal designation by the Natural Heritage Program. These species are not formally listed, but flagged for monitoring. For each of these two groups (state-listed and watch list), I calculated the likelihood of obtaining as many listed species among the extirpated Worcester species if sampling randomly from the native species originally present in the City using exact binomial probabilities.

Changes in the extent of several habitats in the past two centuries were gauged by examining United States Geological Survey topographic maps drawn in 1935, 1951, 1971, and 1982, along with a hand-drawn map of the City from 1830. Only three habitats could be distinguished from the maps: forest, wetland, and water. I placed a grid of 5 mm squares on a transparency over each map, and recorded the number of grid points falling in each of the three habitats, along with the total number of grid squares within City boundaries. The total number of grid squares was at least 3300 for each map. The proportion of grid squares falling within each of the three habitats was taken as the proportion of that habitat in the City at that time.

RESULTS

The analyses presented herein are based on a total of 820 native species. Of these, 797 were documented species and the remaining 23 species were recorded only in published literature and were not observed by me. Most species on which my analyses are based are listed in Bertin (2000), and are not repeated here. However, examination of Worcester Natural History Society (WNHS) specimens at the Ecotarium and a few others yielded several dozen additions and changes, listed in the Appendix. Of the 820 total species, 170 (20.7%) are no longer found in Worcester. Of the 797 documented species, 147 (18.4%) no longer occur.

The extinction rates for most habitat categories did not deviate significantly from the overall extinction rate (Table 2). However, four habitats showed significantly greater than average extinction rates in at least one analysis. Species losses from bogs were significantly higher than average for both total losses and documented losses no matter which flora was used for habitat classification. Documented species losses from calcareous terrestrial habitats were significantly greater than average for two sources and for aquatic habitats and coniferous forest for one source each. Three habitats showed species losses that were significantly less than overall losses for one source: disturbed sites, herbaceous vegetation, and swamps.

In the taxonomic analysis, six families had documented local extinction rates significantly higher than for the overall flora: Menyanthaceae, Ophioglossaceae, Lentibulariaceae, Orchidaceae, Caryophyllaceae, and Lamiaceae (Table 3). All but the last family also show significantly elevated species losses when undocumented records are included.

The species lost from Worcester reflect at least partly the patterns of species decline in the entire state. This is illustrated by the fact that the proportions of state-listed and watch list species among those extirpated from Worcester are much greater than the

Table 2. Documented proportion of species lost by habitat category. Sample sizes in parentheses represent the presumed original species numbers in each habitat. Significant departures from the overall extinction rate are denoted as follows: * significantly greater, documented species; † significantly greater, total species; # significantly less, documented species; + significantly less, total species.

Habitat Category	Gleason & Cronquist	Magee & Ahles	Seymour
Aquatic	0.28 (79)*†	0.22 (77)†	0.25 (60)†
Bogs	0.35 (66)*†	0.33 (72)*†	0.39 (51)*†
Burned areas	0.25 (4)	1.00 (1)	1.00 (1)
Calcareous terrestrial	0.25 (20)	0.86 (7)*†	0.40 (15)*
Coniferous	0.50 (8)*†	0.23 (31)	1.00 (1)
Disturbed sites	0.16 (83)	0.11 (215)#+	0.13 (68)
Dry herbaceous	0.31 (16)	0.14 (43)	0.11 (35)
Dry open woods	0.09 (11)	0.29 (21)	0.11 (27)
Grasslands	0.18 (139)	0.15 (305)	0.20 (157)
Herbaceous	0.16 (171)	0.15 (337)#+	0.19 (167)
Rich terrestrial	0.24 (50)	0.19 (104)	0.15 (97)
Rock outcrops	0.22 (9)	0.21 (14)	0.20 (20)
Sandy substrate	0.19 (80)	0.25 (71)	0.17 (52)
Shrub swamps	– (0)	0.09 (23)	(0)
Successional	0.05 (20)	0.15 (13)	– (0)
Swamps	0.20 (108)	0.13 (135)#	0.16 (144)
Vegetated wetlands	0.19 (275)	0.17 (285)	0.16 (268)
Wet herbaceous	0.11 (47)	0.17 (160)	0.12 (17)
Woods	0.18 (390)	0.17 (491)	0.16 (313)

proportion of the listed species among the extant flora (Table 4). For example, state-listed species comprise less than 1% of the extant native Worcester flora, but make up 9.5% of the extirpated native Worcester flora. Similarly, watch list species comprise 1.2% of the extant flora, but 12.2% of the extirpated flora. In each case, the proportion of listed species among the extirpated flora is significantly greater than among the group of all native species known to have existed in Worcester ($P < 0.001$, exact binomial probability).

The extent of forested, wetland and aquatic habitats changed in Worcester during the period 1830–1982 (Table 5). Forest habitat was low in the 1800s and early 1900s, increased during the middle 1900s, and decreased again in the late 1900s. Wetland habitat decreased substantially from the 1800s to the 1900s. Aquatic habitats increased from the 1800s into the early and mid 1900s and then decreased in the past 50 years.

Table 3. Proportions of species lost in families having lost more than a third of original species. Families with two or fewer species are excluded. Numbers of species per family are given in parentheses. * denotes significant departures from extinction rates in overall flora.

Family	Total Species Loss	Documented Species Loss
Menyanthaceae	1.00 (2)*	1.00 (2)*
Ophioglossaceae	0.83 (6)*	0.83 (6)*
Ulmaceae	0.67 (3)	0.67 (3)
Fumariaceae	0.67 (3)	0.67 (3)
Lentibulariaceae	0.67 (6)*	0.60 (5)*
Haloragaceae	0.60 (5)	0.50 (4)
Orchidaceae	0.57 (21)*	0.53 (19)*
Caryophyllaceae	0.56 (9)*	0.56 (9)*
Lamiaceae	0.40 (15)	0.40 (15)*
Onagraceae	0.40 (10)	0.40 (10)
Sparganiaceae	0.40 (5)	0.25 (4)
Potamogetonaceae	0.36 (14)	0.25 (12)

DISCUSSION

The overall species loss in Worcester is approximately 18% if one considers only species that have been documented with herbarium specimens and 21% if one additionally considers species listed for the City only in published records. Several sources of error are likely to influence these numbers. Despite the considerable amount of time that I spent in the field, my records are certainly incomplete, and populations of a few species listed here as extirpated probably remain in the City. Studies from other areas are replete with examples of species reappearing that were once thought to be locally extinct (Dickson et al. 2000; Kent 1975). An opposing source of error is the incompleteness of the earlier records. Most of the 64 previously unrecorded native species probably were present but overlooked in earlier work, though a few could be recent colonizations. Subtracting 64 species from the number of total known species (820) and documented species (797), leaves the actual numbers of historical records (756 and 733, respectively) from which the losses are derived. In percentage terms, the losses then represent 22.5% of total species and 20.0% of documented species. The presence of any undiscovered species with historical records would lower these numbers, but they are probably accurate within a few percentage points.

Table 4. Species loss and persistence among state-listed and watch list species. * species represented by specimens; † _Cypripedium calceolus_ is represent by two varieties, recognized as species in Sorrie and Somers (1999), one endangered, one on the watch list; H = historical, E = endangered, T = threatened; SC = special concern. All species are native.

State-listed Species	Watch List Species
EXTANT	
*_Arabis laevigata_ (Muhl.) Poir.; T	_Asclepias tuberosa_ L.
*_Elymus villosus_ Muhl.; T	*_Bidens discoidea_ (Torr. & A. Gray) Britton
*_Potamogeton vaseyi_ J. W. Robbins; E	*_Eragrostis capillaris_ (L.) Nees
	Isotria verticillata (Willd.) Raf.
	Juglans cinerea L.
	*_Polygala verticillata_ L.
	*_Ribes americanum_ Mill.
	*_Sporobolus cryptandrus_ (Torr.) A. Gray
Extant state-listed species = 3/650 = 0.5% of total and documented species	Extant watch list species = 8/650 = 1.2% of total and documented species
EXTIRPATED	
*_Adlumia fungosa_ (Aiton) Greene; T	*_Bidens beckii_ Torr.
*_Arethusa bulbosa_ L.; T	*_Botrychium lanceolatum_ (S. G. Gmel.) Ångstr.
*_Asclepias purpurascens_ L.; T	*_Botrychium matricariaefolium_ A. Braun
Castilleja coccinea (L.) Spreng.; H	*_Botrychium oneidense_ (Gilbert) House
*_Cypripedium calceolus_ L.; E†	*_Cardamine rhomboidea_ (Pers.) Alph. de Candolle
*_Eriophorum gracile_ W. D. J. Koch; T	_Carex diandra_ Schrank
Galium boreale L.; E	_Carex haydenii_ Dewey
*_Habenaria flava_ (L.) R. Br.; T	*_Chenopodium gigantospermum_ Aellen
Isoetes lacustris L.; E	*_Cypripedium calceolus_ L.†
Juncus filiformis L.; E	*_Dryopteris goldiana_ (Hooker) A. Gray
*_Liatris scariosa_ (L.) Willd.; SC	*_Gentianopsis crinita_ (Froel.) Ma
*_Lygodium palmatum_ (Bernh.) Sw.; SC	*_Habenaria hookeri_ Torr.
*_Myriophyllum alterniflorum_; Alph. de Candolle; T	*_Habenaria viridis_ (L.) R. Br.
*_Myriophyllum verticillatum_ L.; E	*_Lupinus perennis_ L.
*_Ophioglossum vulgatum_ (Blake) Farw.; T	_Malaxis unifolia_ Michx.
*_Panax quinquefolius_ L.; SC	*_Polygonum tenue_ Michx.

Table 4. Continued.

State-listed Species	Watch List Species
**Sisyrinchium mucronatum* Michx.; T	*Scirpus polyphyllus* Vahl
Sparganium minimum (Hartman) Fries; E	*Scirpus torreyi* Olney
**Stachys palustris* L.; H	**Selaginella rupestris* (L.) Spring
	**Silene caroliniana* Walter
	**Smilacina trifolia* (L.) Desf.
	**Sparganium angustifolium* Michx.
	**Stellaria borealis* Bigelow
Extirpated state-listed species = 19/170 = 11.2% of total extirpated species and 14/147 = 9.5% of documented extirpated species	Extirpated watch list species = 23/170 = 13.5% of total extirpated species and 18/147 = 12.2% of documented extirpated species

Species losses reported in several other comparative studies of vascular floras ranged from 3% to 46% (Table 6). Several variables might affect the magnitude of these losses, including the time elapsed between first and last censuses, the amount of change in the study area, the size of the study area, and the thoroughness of the surveys. Three studies from the United Kingdom (Sheffield, Glasgow, and Middlesex, including London), show relatively modest losses of 12% in ~100 yr., 11% in ~180 yr. and 10% in 100 yr., respectively. These areas would have been exposed to a long history of human disturbance before the initial censuses, perhaps eliminating some of the most sensitive species before the first survey. The low losses from Chester County, Pennsylvania may be due to the large size of this study area (1974 km^2). The high losses on Staten Island (46%) undoubtedly reflect the extensive landscape changes accompanying the immense

Table 5. Percentage of Worcester occupied by forest, wetland, and aquatic habitats: 1830–1982.

Year	Forest	Wetland	Aquatic
1830	22	5.0	1.2
1935	18	1.0	3.2
1951	28	0.9	3.5
1971	28	0.4	2.8
1982	18	0.7	1.6

Table 6. Rates of species loss among Orchidaceae and all species for different locations.

Orchid loss (%)	Overall loss (%)	Elapsed time (yr.)	Location	Source
53	18	~100	Worcester, Mass.	This study
19	6	~120	Concord, Mass.	Eaton (1974)
67	37	100	Middlesex Fells, Mass.	Drayton & Primack (1996)
33	19	100	Nantucket, Mass.	Sorrie & Dunwiddie (1996)
33	27	80	Three Mile Island, N.H.	Holland & Sorrie (1989)
16	3	150	Chester Co., Pa.	Overlease (1986, 1987)
75	19	50	Wisconsin; upland forest	Wiegmann (pers. comm.)
75	46	100	Staten Island, N.Y.	Buegler & Parisio (1982)
33	11	~180	Glasgow, Scotland	Dickson et al. (2000)
38	10	100	Middlesex, England	Kent (1975)
35	12	~100	Sheffield, England	Shaw (1988)
33	21	110	Auckland, New Zealand	Duncan (pers. comm.)
88	26	~110	Singapore	Turner et al. (1994)

growth in the island's human population. Middlesex Fells and Three Mile Island also have relatively high losses. A contributing factor is certainly the small size of both areas (400 ha and 17 ha, respectively). Beyond this, Middlesex Fells has been subject to intensive recreational use, reduced wood cutting and grazing, and increased isolation from adjacent natural habitats. Habitat losses on Three Mile Island appear to have been much less extensive, and native species losses there may simply reflect the vagaries of small populations on a small island. Losses in Worcester are in the middle of those reported in the cited studies. Compared to the other areas in Table 6, Worcester is intermediate in size (9740 ha). Much of it has been exposed to extensive land use changes, but extensive areas remain in relatively natural habitat.

Losses by habitat. Species losses were 10–25% in most habitats, mirroring the overall rate of species loss. However, a few habitats have more or less frequent extinctions.

The high losses from aquatic habitats could have several explanations. They could be an artifact either of the greater difficulty of sampling aquatic habitats, or of the fact that one major body of water (Lake Quinsigamond) straddles the Worcester/ Shrewsbury town line. G. E. Stone, who collected extensively from this lake in the late 1800s, frequently did not specify in which town a collection was made. I included his records in the Worcester flora, reflecting the fact that about a third (several kilometers) of the lake's shoreline is in Worcester, and that my cursory observations of the Shrewsbury side yielded neither species nor habitats different from those on the Worcester side. Nevertheless, it is possible that a careful examination of the Shrewsbury side would turn up some of the species listed here as extirpated.

The losses of aquatic species have occurred in habitats that have varied both in quantity and quality. There were apparently only three substantial natural bodies of water in Worcester: Lake Quinsigamond, Indian Lake (formerly North Pond), and Bell Pond (formerly Bladder Pond). Undoubtedly there were also many beaver ponds, but these would have been eliminated along with their builders before the earliest plant collections reported herein. The many additional ponds that increased the extent of water in the City from 1.2% in 1830 to 3.5% by 1951 were created by damming of flowing waters. A dam also substantially enlarged the size of Indian Lake, from an original 12–16 ha to its present 89 ha. However, sedimentation, intentional filling, breaching of dams, and the trapping of streams in underground pipes have reduced surface waters by more than half from their 1951 peak. These reductions have undoubtedly had some effect on the flora. One example is *Potamogeton obtusifolius* Mert. & W. D. J. Koch, several specimens of which were collected from Beaver Brook at Chandler Street, a stream that is now underground.

While changes in the extent of surface water have undoubtedly affected the native flora, it seems likely that changes in water quality have had greater effects. Dam construction converts flowing waters to standing water. Other major alterations include sedimentation, chemical pollution, thermal pollution, use of aquatic herbicides, the conversion of relatively oligotrophic waters to more eutrophic waters, and the practice of draining water bodies (such as Indian Lake and Cook Pond) for weed control. The introduction of non-native species, such as *Myriophyllum hetero-*

phyllum Michx., *M. spicatum* L., and *Potamogeton crispus* L., may also have taken their toll. In another comparative study, Kent (1975) reported high rates of loss among aquatic, bog, and marsh species in the vicinity of London, England. He attributed this loss to draining and filling as well as to a general lowering of the water table. Extensive losses of aquatic and wetland species were also reported from Glasgow (Dickson et al. 2000).

The strongest and most consistent pattern in the habitat data is the loss of bog species, with losses amounting to at least a third of the original species in this habitat. This likely reflects the loss of a habitat that was relatively uncommon in the City to begin with. Several collections of now-extinct bog species from the late 1800s refer to "Floating Island" in Indian Lake. These species include *Chamaedaphne calyculata* (L.) Moench, *Larix laricina, Ledum groenlandicum, Sarracenia purpurea* L., and *Smilacina trifolia,* all now extirpated. It seems likely that this flora was erased when Indian Lake was dammed, increasing the water level. Another bog species (*Juncus filiformis* L.) was reported by Jackson (1927) from a "bog recently filled in" in South Worcester. While the lack of a specimen prevents us from confirming this species' identity, the comment indicates another threat to small bogs. Peat extraction was yet another threat to bog species, and was practiced in at least two areas, Broad Meadow Brook and Peat Meadow, in the 1800s (Anonymous 1879). No bogs remain in the City, though a few acidic swamps supporting *Solidago uliginosa* Nutt., *Drosera* spp., *Bartonia virginica* (L.) Britton, Sterns & Poggenb. and sphagnum occur. Compounding the probably limited original extent of bog habitat is the specialized nature of many bog species, apparently precluding their survival in other habitats. Further, if the original bogs were widely scattered, recolonization of locally extinct species would be difficult, even if habitat alterations were only temporary. In contrast with the results reported here, Dickson et al. (2000) were unable to confirm the extinction of even a single species of raised bogs in the vicinity of Glasgow. Unlike the presumed situation in Worcester, however, Glasgow bogs were relatively widespread. Despite extensive alteration, sufficient areas remain to retain the original flora. Dickson et al. do, however, report extensive losses among species of fens.

Given the substantial reductions in the area of wetland habitats in the past century, it is surprising that losses in all wetland categories are not higher. In fact, bogs are the only wetland habitat with above-average losses. All others are at or slightly below overall losses, and losses from swamps, based on the habitat designations of Magee and Ahles (1999), are significantly below overall losses. Several factors may have been operating here, and present information is inadequate to distinguish among them. One possibility is that wetland species, with the exception of bog species, are relatively unspecialized and can persist in a wide range of wet habitats. A related possibility is that wetland habitats are more dynamic than upland habitats as a result of the vagaries of weather and the activities of beavers, and wetland species have evolved resilient life histories to deal with these changes. Perhaps too, a wetland area that was not actually eliminated received less human influence than many upland habitats. For example, a swamp might be harvested for timber, but it could not be plowed, as an upland habitat might. There also may have been an increase in the extent of forested wetlands at the expense of wet meadows as the impact of beavers and fire were reduced. Finally, water may have served as an agent for the movement of plant propagules, thereby minimizing any deleterious influences of habitat fragmentation.

Among upland habitats, two show some evidence of excess species loss: coniferous and calcareous terrestrial. Both of these habitats are likely to have been much less common in the City than the predominant oak forests. The bedrock of southern New England, which generated the till that serves as parent material of the City's soils, is predominantly acidic. The limited extent of less acid soils is emphasized by the infrequency of calciphiles [as designated in the reference floras; e.g., *Adiantum pedatum* L., *Asplenium platyneuron* (L.) Britton, Sterns & Poggenb., *Carex flava* L., *Cerastium arvense* L., *Eupatorium maculatum* L., *Matteuccia struthiopteris* (L.) Tod., *Osmorhiza longistylis* (Torr.) Alph. de Candolle, *Selaginella apoda* (L.) Spring, and *Sparganium eurycarpum* Engelm.].

Several coniferous habitats may have originally occurred in the City, though they were probably uncommon. Cedar (*Chamaecyparis thyoides*) was present, but probably infrequent, as is the case elsewhere in southern Worcester County. Uplands dominated by *Pinus strobus* L. and *Tsuga canadensis* (L.) Carrièrre may have been limited if the Indians regularly burned the landscape, as seems to have been true in other southern New England locales

(Bromley 1935; Day 1953). Today, cedar is absent, hemlock is infrequent and rarely dominant, and pine, though widely distributed, is dominant at only a few sites. The ten most common tree species in the City are all deciduous (Bertin, unpublished). The lack of conifer-dominated habitats may account for the absence of species such as *Goodyera tesselata.* However, most of the losses noted for the coniferous category are of species also found in non-coniferous habitats [e.g., *Smilacina trifolia, Cypripedium calceolus, Pogonia ophioglossoides* (L.) Ker Gawl., *Arctostaphylos uva-ursi*], so the high losses for coniferous habitats may be coincidental.

The past century has seen a reduction in the extent of grassland habitats such as pastures and meadows, which have undergone succession or been lost to development. For example, a reduction in hay fields can be seen by comparing aerial photographs from the 1950s with those taken more recently. A reduction in such habitats is sometimes invoked to explain the reduction or loss of certain species from our flora, such as *Castilleja coccinea, Ophioglossum vulgatum* L., and *Gentiana linearis* Froel. This trend was not obvious in Worcester, however. Species losses from grassland habitats were lower than overall losses based on habitat classifications in two sources and higher in one, but not significantly different in any case. While the extent of pastures and meadows has certainly declined, many of the denizens of such habitats seem to have persisted in other open habitats, such as lawns, roadsides, and power line clearings, and the widespread availability of such modified habitats has perhaps prevented higher extinction rates in grassland species.

Some workers believe that the incidence of fires in recent decades has declined substantially from their incidence in previous centuries (Whitney 1994). Frequent fires probably maintained certain habitat types in greater frequency than at present. For example, fires were likely to have been especially frequent in dry forests and would have maintained open, savanna-like conditions. Certain wetland habitats might also have been subjected to burning, which would probably have tended to increase the extent of marshes relative to that of shrub swamps and swamps. This study provides no evidence that species associated with fires or fire-maintained habitats have been disproportionately lost. Fires or burns are mentioned only in reference to four native species in any of the three sources, and only one of these, *Epilobium an-*

gustifolium L., appears to have been lost from the City's flora. Occasional fires set by vandals may have helped retain fire-maintained oak savanna in several parts of the City (Rawinski, Massachusetts Audubon Society, pers. comm.). Species of dry open woodlands had low rates of loss according to two classifications and high losses according to the third, but none of these differences was significant. Species from wet herbaceous habitats were lost at rates less than or equal to the rates for vegetated wetlands (a category that includes wetlands dominated by woody plants as well as those dominated by herbaceous plants).

Taxonomic pattern of losses. Of the taxonomic patterns of species loss reported here, some appear to be consistent with patterns of loss elsewhere, whereas others are more idiosyncratic. The most consistent pattern is for the Orchidaceae, discussed below. High losses among the Potamogetonaceae are consistent with results from the London area (Kent 1975) and from a 17 ha island in Lake Winnipesaukee, New Hampshire (Holland and Sorrie 1989), but not with results from Glasgow (Dickson et al. 2000) or Sheffield (Shaw 1988). High losses among the Lentibulariaceae were also noted by Dickson et al. (2000) for Glasgow and for two German floras. High losses in the Menyanthaceae and Haloragaceae in the Worcester flora are likely to be related to the aquatic or bog habitats of many of these species and do not necessarily mimic those reported in other studies in the northeastern United States. In examining species losses from a conservation area near Boston, Massachusetts, for example, Drayton and Primack (1996) reported extensive losses in the Lobeliaceae, Scrophulariaceae, Orchidaceae, and Primulaceae. Working on a 17 ha island in Lake Winnipesaukee, New Hampshire, Holland and Sorrie (1989) recorded the highest losses of native species in the Potamogetonaceae, Orchidaceae, Violaceae, Gentianaceae, and Rubiaceae. Most of these families differ from those experiencing the greatest losses in Worcester.

One family showing high losses both in Worcester and elsewhere is the Orchidaceae. About half of the original Worcester orchids have been extirpated, near the middle of the range reported for other sites (Table 6; Lamont et al. 1988). All 13 of the studies in Table 6 show orchid losses greater than overall species losses. The probability that this pattern would occur by chance alone is $0.5^{13} = 0.0001$. The sensitivity of orchids to local extinction in a wide variety of habitats and geographic areas suggests that they may be a good indicator of habitat "health" (Turner et al. 1994).

Several factors could contribute to the disproportionate loss of orchids. One is the rarity of many orchid species even in relatively undisturbed habitat (Hodgson 1986). Other things being equal, rare species are more likely to go extinct than common ones (Primack 1993). Orchids also have extremely small seeds lacking in endosperm and are dependent on external carbohydrate sources, usually provided by mycorrhizal fungi, for establishment and growth (Baskin and Baskin 1998). These traits may reduce their ability to recover rapidly from population decreases, and also expose them to the risk of factors that influence habitat suitability for their associated fungi. Their capacity for vegetative spread seems to be limited. Additionally, several species occur in bogs, and species in this habitat were especially prone to extinction in Worcester and perhaps elsewhere as well (Overlease 1987). Some orchid species have specialized pollination mechanisms that either require a specific pollinator or depend on pollination by deceit. These factors put orchids at risk from any factors that reduce pollinator numbers and may reduce the rate at which these plants can increase from population lows. A further threat to orchids is browsing by white-tailed deer (*Odocoileus virginianus*). A review of rare plants threatened by deer browsing included 21 orchids in a total of 98 species, a much higher proportion than that of orchid species in the overall flora (Miller et al. 1992). The authors were unsure, however, whether the high frequency of orchids reflected feeding preferences of deer or a bias in recording data. It is uncertain whether deer populations in Worcester have been sufficiently high to have had a major influence on vegetation. A final threat is collection by botanists or gardeners. Collecting by these individuals as well as for the horticultural trade may have contributed to high orchid losses in Singapore (Turner et al. 1994).

Conclusions. Apparent local extinctions of native vascular plant species from Worcester, Massachusetts have been considerable, amounting to approximately one in five species over the past century. The major causes have undoubtedly been habitat alterations resulting from human activities. These alterations have had their greatest effects in relatively few habitats, especially bogs and aquatic habitats. Certain plant families have been hit particularly hard, especially the Orchidaceae and a number of aquatic families. While there may be important differences in patterns of loss in urban and rural areas, the patterns described for Worcester are to some degree representative of statewide patterns. This is illustrated by the disproportionate representation of state-listed species among species that have gone extinct locally.

Losses of native species will continue in Worcester, accompanying the continuing alteration of habitats. Over time, the most conspicuous habitat alterations should decline as less undeveloped land remains for human modification. Undeveloped land will persist in the form of land that is protected or that is too wet or steep for development. However, species losses are likely to continue, reflecting in part the time lag between habitat reduction and local extinctions (Primack 1993; Turner et al. 1994). Drayton and Primack (1996) recorded the loss of over a third of native species during a 100 yr. period in a preserve near Boston. These losses were thought to have been caused by relatively subtle land use changes combined with isolation of the preserve from surrounding sources of propagules. An additional factor that may contribute to future species losses is global climatic change, particularly in areas with highly fragmented landscapes, which make colonization and recolonization difficult. While considerable tracts of land have been protected from development in Worcester over the last two decades, inevitable successional changes, more frequent passive recreational use, further fragmentation and isolation, impacts of non-native species, and climatic changes seem likely to cause substantial further species losses in the next century.

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APPENDIX

ADDITIONS AND CHANGES TO THE LIST OF NATIVE SPECIES IN BERTIN (2000).

Taxonomy follows Gleason and Cronquist (1991). *denotes species new to Bertin (2000); other species are those not previously documented with specimens. Specimen locations: WNHS (Worcester Natural History Society), NEBC (New England Botanical Club), MASS (University of Massachusetts).

FERNS AND FERN ALLIES

ASPLENIACEAE

**Dryopteris clintoniana* (D. C. Eaton) Dowell – WNHS no date
**Dryopteris goldiana* (Hook.) A. Gray – NEBC 1878

ISOETACEAE

Isoetes echinospora Durieu – WNHS 1890

LYCOPODIACEAE

**Lycopodium inundatum* L. – WNHS 1890

OPHIOGLOSSACEAE

**Botrychium oneidense* (Gilbert) House – WNHS 1916

POLYPODIACEAE

Polypodium virginianum L. – WNHS no date

GYMNOSPERMS

CUPRESSACEAE

**Chamaecyparis thyoides* (L.) Britton, Sterns & Poggenb. – WNHS 1890

PINACEAE

**Larix laricina* (DuRoi) K. Koch – WNHS 1890

TAXACEAE

Taxus canadensis Marsh. – WNHS 1890

DICOTYLEDONS

ANACARDIACEAE

Rhus typhina L. – WNHS 1885

ASCLEPIADACEAE

**Asclepias tuberosa* L. – WNHS 1890, also observed growing in the City in 2001

ASTERACEAE

**Cirsium muticum* Michx. – WNHS 1914
**Eupatorium pilosum* Walter – WNHS 1894
**Liatris scariosa* (L.) Willd. – WNHS no date
**Vernonia noveboracensis* (L.) Michx. – WNHS 1890

BRASSICACEAE

**Cardamine rhomboidea* (Pers.) Alph. de Candolle – MASS no date

CABOMBACEAE

Brasenia schreberi J. F. Gmelin – WNHS 1890

CARYOPHYLLACEAE

**Stellaria borealis* Bigelow – WNHS 1929

CORNACEAE

Cornus rugosa Lam. – WNHS 1912

ERICACEAE

**Arctostaphylos uva-ursi* (L.) Spreng. – WNHS no date
**Kalmia polifolia* Wangenh. – WNHS no date
**Ledum groenlandicum* Oeder – WNHS no date

FABACEAE

**Desmodium rigidum* (Ell.) Alph. de Candolle – WNHS 1890
**Lespedeza virginica* (L.) Britton – WNHS 1919
**Lupinus perennis* L. – WNHS 1890
**Tephrosia virginiana* (L.) Pers. – WNHS 1890

LAMIACEAE

Stachys palustris L. – WNHS 1927 [the native var. *pilosa* (Nutt.) Fernald]
Teucrium canadense L. – WNHS 1934

LYTHRACEAE

Decodon verticillatus (L.) Ell. – WNHS 1890

NYMPHAEACEAE

Nymphaea odorata Aiton – WNHS 1886

ONAGRACEAE

**Circaea alpina* L. - WNHS 1890
Oenothera parviflora L. – WNHS 1938

POLYGALACEAE

**Polygala polygama* Walter – WNHS 1877

PRIMULACEAE

**Lysimachia hybrida* Michx. – WNHS 1899

PYROLACEAE

**Pyrola secunda* L. – WNHS 1890

ROSACEAE

**Fragaria vesca* L. – WNHS 1885
Potentilla arguta Pursh – WNHS 1918
**Sanguisorba canadensis* L. – WNHS 1890

RUBIACEAE

**Galium trifidum* L. – WNHS 1916

VIOLACEAE

**Viola primulifolia* L. – WNHS 1919

MONOCOTYLEDONS

ARACEAE

Calla palustris L. – WNHS 1878

CYPERACEAE

Carex cristatella Britton – misidentification, species deleted
**Cyperus dentatus* Torr. – WNHS 1918
Eleocharis robbinsii Oakes – misidentification, species deleted
**Eriophorum gracile* W. D. J. Koch – WNHS 1878
**Eriophorum virginicum* L. – WNHS 1891
**Rhynchospora alba* (L.) Vahl – WNHS 1890
Scirpus subterminalis Torr. – WNHS 1890

IRIDACEAE

**Sisyrinchium mucronatum* Michx. – WNHS 1938

JUNCACEAE

**Luzula acuminata* Raf. – WNHS 1878

LEMNACEAE

Spirodela polyrrhiza (L.) Schleid. – WNHS 1890

LILIACEAE

Aletris farinosa L. – WNHS 1890
Smilacina trifolia (L.) Desf. – MASS 1888
Streptopus roseus Michx. – WNHS 1888

ORCHIDACEAE

Cypripedium calceolus L. – WNHS 1880 (both large- and small-flowered varieties)
Goodyera pubescens (Willd.) R. Br. – WNHS 1876
Goodyera tesselata Lodd. – WNHS no date
Habenaria hookeri Torr. – WNHS 1898
Habenaria viridis (L.) R. Br. – WNHS 1912
Spiranthes lacera (Raf.) Raf. – WNHS 1885

POACEAE

Muhlenbergia uniflora (Muhl.) Fernald – WNHS 1890
Poa alsodes A. Gray – WNHS 1878

POTAMOGETONACEAE

Potamogeton foliosus Raf. – misidentification, species deleted

SPARGANIACEAE

Sparganium angustifolium Michx. – MASS 1890

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NEW RECORDS OF VASCULAR PLANTS FOR OHIO AND CUYAHOGA COUNTY, OHIO

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ABSTRACT. Two hundred and thirty-six species and hybrids of vascular plants are listed as new records for Cuyahoga County, Ohio, and twenty-four of these taxa constitute new Ohio records. Three taxa are first reported for North America. Approximately 39% of the 236 taxa are native to the northeastern United States. Twenty listed species are designated by the Ohio Division of Natural Areas and Preserves as presumed extirpated, endangered, threatened, or potentially threatened, collectively. The abundance of new records is surprising and explanations are proposed.

Key Words: Ohio, alien species, native species, new records, hybrids

This paper is a continuation of our efforts to augment knowledge of plant distributions in Ohio overall, with emphasis on Cuyahoga County, Ohio (Wilder and McCombs 1999). It also complements the recent floristic contributions of others (Cusick 1992; Rabeler 1996; Rabeler and Cusick 1994; Vincent and Cusick 1998; Walters 1995). No flora focused solely on Cuyahoga County has yet been published, but major references to the Ohio flora attribute plant taxa specifically to Cuyahoga County (Andreas 1989; Braun 1961, 1967; Cooperrider 1995; Fisher 1988).

Cuyahoga County borders Lake Erie and ranks among the northernmost of Ohio's 88 counties. Repeatedly glaciated during the Pleistocene epoch, Cuyahoga County contains two of Ohio's five physiographic regions: the Glaciated Appalachian Plateau Region (elevated, hilly topography; Bissell and Frank

1979) and the Lake Plains Region (low-lying, relatively flat terrain; Campbell 1979). Urban land (especially Cleveland), suburbs, and rural areas are common. Certain natural areas are protected to different extents, including the Cleveland Metroparks, various smaller parks, and part of the Cuyahoga Valley National Recreation Area.

MATERIALS AND METHODS

All specimens cited were collected in Cuyahoga County within the last 11 years. We collected virtually all specimens, but Mr. Robert Anthony and Mr. Michael T. Loos each provided one additional collection. Almost all specimens belong to the Wilder and McCombs Herbarium, most of which will be stored for an indeterminate period at Florida Gulf Coast University in Fort Myers, Florida. Eventually, the entire collection may be deposited at the Cleveland Museum of Natural History (CLM), where the material of *Cynanchum laeve* is now housed.

Plants were pressed and prepared as ordinary herbarium specimens. Specimens of *Wolffia* were fixed in a formalin-acid-alcohol solution and stored in vials of glycerine alcohol affixed to herbarium sheets.

Nomenclature follows Kartesz (1994), but for some taxa in the Appendix synonyms are given that appear in other relevant publications (e.g., Cooperrider 1995; Cooperrider et al. 2001). Species and hybrids were determined as new to North America, Ohio, and/or Cuyahoga County based on information in Andreas (1989), Braun (1961, 1967), Cooperrider (1995), Cooperrider et al. (2001), Cusick (1992), Cusick and Silberhorn (1977), Easterly (1964), Fisher (1988), Kartesz and Meacham (1999), Rabeler (1996), Rabeler and Cusick (1994), Schaffner (1928), Vincent and Cusick (1998), Walters (1995), Weishaupt (1971), and Wilder and McCombs (1999). Taxa were determined to be either native to the northeastern United States or alien based on information from one or more of the following sources: Bailey (1949), Wagner and Beitel (1993), and Weishaupt (1971).

RESULTS

Two hundred and twenty-two species and 14 hybrids, representing 73 families of vascular plants, are reported as new to

Cuyahoga County, and 24 of these taxa constitute new records for Ohio (Appendix). Three taxa are first reported for North America: *Cardamine bulbifera, Phellodendron lavallei,* and *Lonicera* ×*salicifolia.* Ohio records include 16 species of 13 families (*Actinidia arguta, Bromus catharticus, Cardamine bulbifera, Chaerophyllum tainturieri, Crepis setosa, Cyperus houghtonii, Fraxinus excelsior, Galanthus elwesii, Hordeum brachyantherum, Muscari armeniacum, Phellodendron lavallei, Prunella laciniata, Rubus recurvicaulis, Saccharum ravennae, Sesamum orientale, Tetradium daniellii*) and eight hybrids of five families (*Carex albicans* var. *albicans* × *C. umbellata, Liatris pycnostachya* × *L. spicata, Lonicera* ×*minutiflora, L. ruprechtiana* [= *L.* ×*muscaviensis*], *L.* ×*salicifolia, Narcissus* ×*incomparabilis, N.* ×*medioluteus, Tradescantia ohiensis* × *T. virginiana*).

The following plant families rank highest according to the number of county records per family: Poaceae (31), Brassicaceae (18), Cyperaceae (16), Asteraceae (15), Scrophulariaceae (10), Rosaceae (9), Fabaceae (7), Caryophyllaceae (6), Salicaceae (6), Caprifoliaceae (5), Lamiaceae (5), and Ranunculaceae (5). Only approximately 39% of the 236 species and hybrids (i.e., 93 taxa) are native to the northeastern United States (Appendix). Families with solely native species as county records include all families of pteridophytes as well as the Cyperaceae and Hypericaceae. By contrast, the Brassicaceae and Poaceae include many alien species as county records, and *Cardamine* ×*maxima, Descurainia pinnata,* and *Rorippa sessiliflora* are the sole native taxa of the 18 listed taxa of Brassicaceae.

Twenty species here newly reported for Cuyahoga County are cited in the *Rare native Ohio plants 2000–2001 status list* (Ohio Division of Natural Areas and Preserves 2000). These species are listed as presumed extirpated (*Cyperus houghtonii*; however, see comments below), endangered (*Amelanchier sanguinea, Baptisia australis, Chamaesyce serpens, Dryopteris clintoniana, Hypericum gymnanthum, Nuttallanthus canadensis, Panicum lindheimeri*), threatened (*Carex albolutescens, Descurainia pinnata, Gymnocarpium dryopteris, Helianthus mollis, Passiflora incarnata*), and potentially threatened (*Carex atherodes, C. viridula, Deschampsia flexuosa, Hedyotis nigricans, Hypericum majus, Opuntia humifusa, Spiranthes ovalis*). Each of the 20 species is known from only one to several locations in Cuyahoga County (Appendix).

DISCUSSION

Two state records require explanation: *Cyperus houghtonii* and *Chaerophyllum tainturieri.* Braun (1967) and Weishaupt (1971) attributed *Cyperus houghtonii* to Ohio; however, Braun (1967) specified that *C. houghtonii* is "Represented in Ohio by a single specimen . . ." in the herbarium of Bowling Green State University (BGSU). Braun did not otherwise distinguish the specimen, but we later identified it as 13 Sep 1895, *E. L. Mosely s.n.* (BGSU). Mosely called the specimen *C. houghtonii,* as did N. W. Easterly (annotation of 1958). However, Mr. Allison W. Cusick (Chief Botanist of the Ohio Division of Natural Areas and Preserves) annotated it as "depauperate *Cyperus schweinitzii* Torrey." We examined the specimen and verified Cusick's identification, based partly on the scabrous, sharply-angled fertile culm and the conspicuously mucronate scales (features of *C. schweinitzii* but not of *C. houghtonii*; Voss 1972). Thus, we list *C. houghtonii* as a new state record. Similarly, Weishaupt (1971) listed *Chaerophyllum tainturieri* from Ohio, but Cooperrider (1995) identified all Ohio specimens as *C. procumbens* (not including our material). Dr. Anton Reznicek (MICH) has confirmed our identifications of *Cyperus houghtonii* and *Chaerophyllum tainturieri.* In contrast, Kartesz and Meacham (1999) reported neither species for Ohio, and Cooperrider et al. (2001) deleted *C. houghtonii* and *C. tainturieri* from their species list of the Ohio flora.

Cardamine ×*maxima* and *Tagetes patula* are presently listed as new for Cuyahoga County. They were earlier reported for Ohio by Schaffner (1928; *Dentaria maxima* Nutt.) and Moldenke (1944), respectively. They were also attributed to Ohio by Kartesz and Meacham (1999), but not by Cooperrider et al. (2001). In addition, Kartesz and Meacham (1999) reported *Alopecurus geniculatus* var. *geniculatus* for Ohio, based on a personal communication made to them; however, the source of this communication was unidentified.

We did not find *Lotus tenuis* listed in publications on the Ohio flora, but Isely (1990) attributed *L. tenuis* to Ohio in his treatment of the Fabaceae of the southeastern United States. We consider Isely's report tentative, because he did not cite specimens of *L. tenuis.* Also, Andreas (1989) and Braun (1967) listed *Panicum lanuginosum* Elliott for Cuyahoga Co., but did not specify whether the segregate species *P. implicatum* Britton and *P. lindheimeri*

Nash occur here. Thus, the latter two species are here listed as county records.

Tradescantia ohiensis, T. virginiana, and *T. ohiensis* × *T. virginiana* all grow in Cleveland, and our informal field observations suggest that the hybrid is common in Cleveland. Voss (1972) identified certain Michigan plants as apparently of this hybrid. He also reported white-flowered specimens of *T. ohiensis* from Michigan, as do we of *T. ohiensis* × *T. virginiana* from Ohio (Appendix).

Kartesz and Meacham (1999), but not Cooperrider et al. (2001), reported *Phellodendron amurense* Ruprecht for Ohio; however, our material of *Phellodendron* is *P. lavallei,* not *P. amurense,* based on considerable abaxial pubescence of the foliage leaves (Rehder 1940). Also, Dr. Anton Reznicek annotated our specimens as *P. lavallei.*

Cooperrider et al. (2001), Kartesz and Meacham (1999), Rabeler (1996), and Vincent and Cusick (1998) only recently reported certain species from Ohio that are here listed as records for Cuyahoga County (*Acer campestre, Amaranthus powellii, Cerastium brachypetalum, Gypsophila scorzonerifolia, Mahonia aquifolium, Prunus subhirtella, Sagina japonica, Salix matsudana,* and *Viburnum plicatum*). Thus, these species are not listed in older comprehensive accounts of the Ohio flora (Andreas 1989; Braun 1961; Cusick and Silberhorn 1977; Weishaupt 1971). Other species that Cooperrider et al. (2001) and Kartesz and Meacham (1999) first reported for Ohio are apparently becoming established in Cuyahoga County, being here reported from four locations (*Centaurea debeauxii*) and five locations within the County (*Salix matsudana*; Appendix).

Certain species here listed as new for Cuyahoga County were previously reported from Ohio, but from locations distant from Cuyahoga County (Andreas 1989; Braun 1967; Cooperrider 1995; Cusick and Silberhorn 1977; Easterly 1964). For each such species, the previously reported location nearest to Cuyahoga County is separated from Cuyahoga County by a distance of approximately 120 miles (i.e., nearly half the length of Ohio), or more. The reported ranges of most such species are hereby extended more-or-less northward: *Acer campestre, Agropyron desertorum, Ampelopsis cordata, Aureolaria laevigata, Buddleja davidii, Cerastium brachypetalum, Chorispora tenella, Croton monanthogynus, Ilex opaca, Liquidambar styraciflua, Mahonia* *aquifolium, Microstegium vimineum, Paspalum laeve, Passiflora incarnata, Physalis philadelphica, Rorippa sessiliflora, Sisymbrium loeselii, Spiranthes ovalis,* and *Xanthorhiza simplicissima*; however, other ranges are extended eastward (*Lepidium ruderale*) or both northward and eastward (*Descurainia sophia*). Presently reported plants of *Xanthorhiza simplicissima* were probably garden escapes, because this is a cultivated species, albeit also native to the northeastern United States (Bailey 1949; Gleason and Cronquist 1991), and because our plants grew on parkland, in woods by a dump (Appendix). For Ohio, Braun (1961) listed *Akebia quinata,* and Braun (1961) and Weishaupt (1971) reported *Quercus robur*; however, they listed no localities within Ohio for these species.

Eight species presently reported as Cuyahoga County records were recently listed as new for Lorain County, which borders Cuyahoga County to the west: *Alisma triviale, Betula pendula, Celastrus orbiculata, Cercis canadensis, Hedera helix, Hieracium piloselloides, Narcissus poeticus,* and *Zea mays* (Walters 1995). Also, the present record of *Berberis vulgaris,* an alien species, is significant because Andreas (1989) considered the species "now presumably extirpated from Ohio." Indeed, we observed only a small clump of this species.

Natural assemblages of vascular plants within Ohio characteristically contain much smaller percentages of alien species and hybrids than the approximately 61% reported here. Cooperrider et al. (2001) found that approximately 33% of Ohio species, additional major infraspecific taxa, and interspecific hybrids, collectively, were alien. Cooperrider (1995) considered 25% of "some 700 species" of selected dicotyledonous families of Ohio as alien to the state. Statistics presented by Andreas (1989) indicate that approximately 28% of species and hybrids of vascular plants of the Glaciated Allegheny Plateau region of Ohio are alien. Corresponding statistics for unglaciated Ohio reveal approximately 24% of species to be alien (Cusick and Silberhorn 1977). Wilder and McCombs (1999), in a floristic survey of Fawn Pond and surrounding territory (Cuyahoga County), presented a comparable figure of approximately 26%.

We offer three primary explanations for the abundance of new records from Ohio and Cuyahoga County. First, the inordinately high percentage of presently reported alien species suggests that many species may only recently have entered, or become prominent in, Cuyahoga County. Second, no flora or plant checklist has yet been published for Cuyahoga County, suggesting that previous botanists might have focused insufficient attention on this area. Third, Cleveland, a largely urban area by Lake Erie, manifests abundant shipping, train traffic, and road traffic. Traffic and/or the distinctive habitats of railroad tracks and roadsides may have favored species introductions. Indeed, we have established many new plant records solely along railroad tracks, and present examples include *Acalypha gracilens, Agropyron desertorum, Amaranthus powellii, Bromus catharticus, Buddleja davidii, Bulbostylis capillaris, Cerastium brachypetalum, Chaerophyllum tainturieri, Cyperus houghtonii, Descurainia pinnata, D. sophia, Gypsophila scorzonerifolia, Helianthus mollis, Hordeum brachyantherum, H. pusillum, H. vulgare, Ipomoea hederacea, I. pandurata, Linaria dalmatica, Mahonia aquifolium, Opuntia humifusa, Papaver somniferum, Passiflora incarnata, Phellodendron lavallei, Quercus robur, Saccharum ravennae, Secale cereale, Sinapis alba, Strophostyles leiosperma, Tagetes patula, Vaccaria hispanica,* and *Vulpia octoflora.* Our observations correlate with previous conclusions that railroad lands may support diverse adventive floras (Muhlenbach 1979).

Another reason for our many new records involves the genus *Lonicera.* We identified the three *Lonicera* hybrids new for Ohio, using Green's (1966) key to species and hybrids in the *L. tatarica* complex. These three hybrids, as well as various other *Lonicera* hybrids, are not treated in many comprehensive floristic works (Braun 1961; Cooperrider 1995; Fernald 1950; Gleason 1968; Gleason and Cronquist 1991; Weishaupt 1971); thus, previous investigators may have misidentified them. We have observed that numerous *Lonicera* individuals in Cuyahoga County are hybrids, particularly of *Lonicera ×bella* (previously known from Cuyahoga County).

In recent years, urban Cuyahoga County (especially railroad land) has experienced an apparent increase in disturbances such as bulldozing and the application of herbicides. Thus, plant diversity has been reduced in some of our finest urban plant localities. Unusual alien and native species observed in Cleveland and nearby in previous years are absent or nearly so (e.g., *Acalypha gracilens, Aegilops cylindrica, Amaranthus tuberculatus, Amelanchier stolonifera, Calluna vulgaris, Hedyotis nigricans, Helianthus mollis, Hordeum pusillum, Iva xanthifolia, Nuttallanthus* *canadensis, Prunus mahaleb, Salvia reflexa,* and *Vulpia octoflora*). Muhlenbach (1979), in keeping with present findings, reported that ". . . weed killing has had disastrous effects on railroad vegetation everywhere." Within rural areas of Cuyahoga County overall, continuing rampant development, other exploitation of natural lands (including parks), and excessive browsing by deer seriously threaten biodiversity.

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APPENDIX

SPECIES AND HYBRIDS THAT REPRESENT NEW RECORDS FOR OHIO AND CUYAHOGA COUNTY.

Data are presented in the following order after the name of a species or hybrid: relevant synonym (in brackets); designation, if any, in the *Rare native Ohio plants 2000–2001 status list* (Ohio Division of Natural Areas and Preserves 2000); habitat(s); the collection number of a representative collection together with the municipality of this collection; any additional municipality(ies) represented by collections in the Wilder and McCombs Herbarium (indicated between parentheses). * = alien to the northeastern United States. SR = species and hybrids newly reported for Ohio; remaining species and hybrids are new solely to Cuyahoga County. All collection numbers are those of Wilder and McCombs except where indicated as collected by M. T. Loos or R. Anthony. Abbreviations represent municipalities or railroad tracks (RR): B, Brecksville; Bc, Beachwood; Be, Bedford; BeH, Bedford Heights; Bk, Brooklyn; BkH, Brooklyn Heights; Bn, Bentleyville; BH, Broadview Heights; BP, Brook Park; Br, Berea; Bt, Bratenahl; BV, Bay Village; C, Cleveland; CH, Cuyahoga Heights; ClH, Cleveland Heights; E, Euclid; EC, East Cleveland; FP, Fairview Park; G, Glenwillow; GH, Garfield Heights; GM, Gates Mills; HH, Highland Heights; HV, Hunting Valley; I, Independence; L, Lakewood; Li, Lindale; M, Mayfield; MaH, Mayfield Heights; MH, Maple Heights; MiH, Middleburg Heights; MoH, Moreland Hills; MV, Mayfield Village; NO, North Olmsted; NR, North Royalton; OF, Olmsted Falls; OT, Olmsted Township; P, Parma; PH, Parma Heights; PP, Pepper Pike; RoR, Rocky River; S, Solon; SE, South Euclid; SeH, Seven Hills; SH, Shaker

Heights; St, Strongsville; UH, University Heights; VV, Valley View; W, Westlake; WaH, Warrensville Heights; WH, Walton Hills. Dash(es) between abbreviations signifies(y) collection(s) made by the boundary or boundaries between municipalities.

PTERIDOPHYTES

DRYOPTERIDACEAE

Cystopteris tenuis (Michx.) Desv. – Vertical rock outcrop; *11679,* Be.

Dryopteris ×*boottii* (Tuck.) Underw. – Swamp within gorge; *8455,* B.

Dryopteris clintoniana (D. C. Eaton) Dowell – Endangered; vertical rock outcrop; side of creek; *11680,* Be.

Gymnocarpium dryopteris (L.) Newman – Threatened; vertical rock outcrop; *11639,* Be.

EQUISETACEAE

Equisetum ×*ferrissii* Clute – Wetland and slope (both habitats by RR tracks); *4508,* C.

LYCOPODIACEAE

Lycopodium hickeyi W. H. Wagner, Beitel & Moran – Woods; fields; *10349,* HH (B, BV-W, GH-VV).

MONOCOTYLEDONS

ALISMATACEAE

Alisma triviale Pursh – Near creek; water along railroad tracks; in ditch; *6066,* B (C, L).

AMARYLLIDACEAE

**Galanthus elwesii* Hook. f. – SR. Along trail on forested ridge; *12723,* C.

**Narcissus* ×*incomparabilis* P. Mill. SR. Along railroad tracks; woodlands; *13158,* C (ClH, MoH).

**Narcissus* ×*medioluteus* P. Mill. – [*Narcissus biflorus* W. Curtis] SR. By railroad tracks; field; woodland; *13309,* P (Bk-C, ClH-EC).

**Narcissus poeticus* L. – Along RR tracks; clump in woodland; *10651,* BV-W (GM).

COMMELINACEAE

Tradescantia ohiensis Raf. × *Tradescantia virginiana* L. – SR. Three formas are represented, as follows:

a. Forma with blue flowers comparable in size to flowers of typical *T. ohiensis* and *T. virginiana*; by RR tracks; along alley by RR tracks; *7090,* C.

b. Forma with blue flowers much larger than those of typical *T. ohiensis* and *T. virginiana,* apparently a garden escape; along railroad tracks; *11959,* RoR.

c. Forma with white petals, green sepals, and blue stamen hairs, the flower size comparable to that in typical *T. ohiensis* and *T. virginiana*; behind urban cemetery and by RR tracks; *11995,* C.

CYPERACEAE

Bulbostylis capillaris (L.) Kunth *ex* C. B. Clarke – In highly insolated cinder along RR tracks and where RR tracks were removed; *11523,* C-E (C, MH).

Carex albicans Willd. *ex* Spreng. var. *albicans* × *Carex umbellata* Schkuhr *ex* Willd. – [*C. albicans* var. *albicans* = *Carex artitecta* Mack.] SR. Upland bordering Rocky River; *10740,* NO.

Carex albolutescens Schwein. – Threatened; land-locked region between RR tracks; meadow; swamp; *5163,* E (B, St).

Carex atherodes Spreng. – Potentially threatened; insolated swamp; *14851,* MiH.

Carex careyana Torr. *ex* Dewey – Woods; *10733,* B.

Carex conjuncta Boott – Along tow path of Ohio and Erie Canal; along creek; along road; *11947,* WH (Be, CH).

Carex hitchcockiana Dewey – Near path in woodland; *14658,* BP-NO-OT.

Carex molesta Mack. *ex* Bright – Wetland along RR tracks; abundant in field; *4056,* C (I, MH).

Carex pellita Muhl. *ex* Willd. – [*C. lanuginosa* Michx.] Wet ditch along road; *4274,* B.

Carex texensis (Torr.) Bailey – Base of shaded hill; *14752,* B.

Carex viridula Michx. – Potentially threatened; grassy area by railroad tracks; *13814,* C.

Cyperus houghtonii Torr. – SR. Presumed extirpated; in highly insolated dry substrate along RR tracks; *11530,* C-E.

Cyperus squarrosus L. – [*C. aristatus* Rottb. and *C. inflexus* Muhl.] Cracks in pavement of parking lot; *14146,* C.

Eleocharis rostellata (Torr.) Torr. – Field; *14096,* Bc.

Rhynchospora capitellata (Michx.) Vahl – Wet meadow; *8642,* HH.

Scirpus acutus Muhl. *ex* Bigelow – In ditch; *3813,* B.

DIOSCOREACEAE

**Dioscorea oppositifolia* L. – [*D. batatas* Decne.] Ravine; disturbed urban land; *7564,* ClH-EC (C).

LEMNACEAE

Wolffia brasiliensis Wedd. – [*W. papulifera* C. H. Thomps.] Beaver pond; lagoon; *11168,* GM-M (BP-NO-OT; I).

Wolffia columbiana H. Karst. – Pond; edge of lake; *11287,* NR (SH).

Wolffia punctata Griseb. – Pond; *14003,* I.

LILIACEAE

**Allium cepa* L. – Embankment along RR tracks; *4244*, C (WaH).

Allium schoenoprasum L. – In garden debris dumped within woodland; *13541*, P.

**Muscari armeniacum* Leichtlin *ex* Baker – SR. In piles of dirt and debris in vacant lot and along RR tracks; *7935*, C (MH).

**Scilla siberica* Haw. *ex* Andr. – Woods; edge of gorge; *7963*, vicinity GM (ClH-SH).

NAJADACEAE

Najas guadalupensis (Spreng.) Magnus – Pond; *14892*, I.

ORCHIDACEAE

Spiranthes ochroleuca (Rydb.) Rydb. – Shaded area along power lines; portion of old field bordering forest; *11776*, I (S).

Spiranthes ovalis Lindl. – Potentially threatened; disturbed land; field by RR tracks; *11554*, S (B).

POACEAE

**Aegilops cylindrica* Host – Ballast between RR tracks; along road; eroded slope beneath terminus of RR bridge; *4027*, C (BkH).

**Agropyron desertorum* (Fisch. *ex* Link) J. A. Schult. – Clearing by terminus of railroad bridge; *13978*, BkH.

**Agrostis stolonifera* L. – In park; *2933*, ClH-EC.

**Alopecurus geniculatus* L. – Dense population in depressed grassy area along parkway; insolated land by power lines; *10721*, St (Bk-C, P).

**Alopecurus pratensis* L. – Fields, swamp, embankment along RR tracks; *12133*, W (B, BH, CH, S, SH).

**Apera interrupta* (L.) P. Beauv. – Insolated urban field; dry, highly insolated substrate along RR tracks; *11050*, C (B, BkH-C).

**Bromus catharticus* Vahl – SR. Eroded slope at terminus of railroad bridge; *13639*, BkH.

**Bromus racemosus* L. – Disturbed, insolated urban land by Cuyahoga River; entrance ramp to I-90; along RR tracks; under bridge; on jetty extending into Lake Erie; along trail; *3972*, C (BkH, C, G).

**Chloris verticillata* Nutt. – Along urban sidewalks and tree lawn; *4831*, C.

Danthonia compressa Austin *ex* Peck – Field, woods; *14311*, P (ClH-EC; B, EC, HH).

Deschampsia flexuosa (L.) Trin. – Potentially threatened; promontory in woods; *4420*, ClH-EC.

Eragrostis capillaris (L.) Nees – Along RR tracks; along alley; vacant disturbed urban land; by wall in disturbed area; *2537*, C (BeH; EC; MH).

**Eragrostis curvula* (Schrad.) Nees – Urban field bordering RR tracks; *11583*, C-EC.

**Eragrostis pilosa* (L.) P. Beauv. – Vacant, highly insolated urban land; tree lawn; overgrown garden; ballast between RR tracks; *4838*, C.

**Hordeum brachyantherum* Nevski – SR. Meadow along RR tracks; *14778,* Bk-C.

Hordeum pusillum Nutt. – Solitary plant between RR tracks; *3930,* C.

**Hordeum vulgare* L. – Terminus of railroad bridge; *13809,* BkH.

**Microstegium vimineum* (Trin.) A. Camus var. *imberbe* (Nees) Honda – Shaded roadside; *14028,* P.

**Miscanthus sinensis* Andersson – Second-growth woodland; *8982,* BH.

Muhlenbergia tenuiflora (Willd.) Britton, Sterns & Poggenb. – Eroded slopes in woods; *11376,* B-BH (WH).

Panicum implicatum Britton – [*Dichanthelium acuminatum* (Sw.) Gould & C. A. Clark var. *fasciculatum* (Torr.) Freckmann] Field, clearing beneath powerlines, insolated slump, woodland, along railroad tracks, trailside, swamp; *13729,* P (B, BH, Bk, C, ClH-EC, E, FP-RoR-W, MH, OF).

Panicum lindheimeri Nash – [*Dichanthelium acuminatum* (Sw.) Gould & C. A. Clark var. *lindheimeri* (Nash) Gould & C. A. Clark] Endangered; disturbed land; *13730,* P.

**Panicum miliaceum* L. – Along roads; under powerlines; dried portion of creek bed; along RR tracks; *7914,* C (Br, CH, L).

Paspalum laeve Michx. – In insolated lawn; *11519,* B.

**Poa nemoralis* L. – Two formas are represented, the typical forma in which living shoots are green and a forma with blue-green living shoots. Woods, by Rocky River; *3156,* EC (C, ClH, ClH-EC, E).

**Saccharum ravennae* (L.) L. – [*Erianthus ravennae* (L.) P. Beauv.] SR. Along railroad tracks; *14062,* C.

**Secale cereale* L. – Eroded slope at terminus of railroad bridge; *13654,* BkH.

**Sorghum bicolor* (L.) Moench – Along roads; field; lawn; urban waste areas; among boulders; dried-up portion of creek bed; along RR tracks; *4903,* C (Be, BV-W, ClH-EC, GH, SH).

**Vulpia myuros* (L.) K. C. Gmel. – Along RR tracks; disturbed, insolated, urban land; *11174,* L (Bk-C, BkH-C; C, ClH-EC).

Vulpia octoflora (Walter) Rydb. – Between RR tracks; *3931*; C.

**Zea mays* L. - Base of embankment along RR tracks; disturbed land by bank of Cuyahoga River; *11779,* G-S (BkH).

TYPHACEAE

Typha ×*glauca* Godr. – Urban wetland along RR tracks; *10258,* C.

DICOTYLEDONS

ACERACEAE

**Acer campestre* L. – Along railroad tracks, in open sunlight; woodlands; *10652,* RoR (Bt, ClH).

ACTINIDIACEAE

**Actinidia arguta* (Siebold & Zucc.) Planch. *ex* Miq. – SR. Abundant climber on trees at forest edges (along road and by swamp in woodland); *5580,* SH (CH).

AMARANTHACEAE

**Amaranthus blitum* L. – Waste area; overgrown urban garden; bare dirt; emersed portions of beds of Cuyahoga River and of creek; by creek and river; along railroad tracks; *8238,* Bt (C, CH, ClH-EC, E, I, P, RoR).

**Amaranthus powellii* S. Watson – Waste area beneath railroad bridge; *14012,* BkH.

Amaranthus tuberculatus (Moq.) Sauer – Urban flower bed; large flower pot retained outdoors; *9040,* C (ClH).

APIACEAE

**Anethum graveolens* L. – Edge of parking lot at urban farmers' market; *11425,* EC.

**Anthriscus sylvestris* (L.) Hoffm. – Along Big Creek and Cuyahoga River; *13383,* C.

Chaerophyllum tainturieri Hook. var. *tainturieri* – SR. Dry, highly insolated substrate along railroad tracks; *11047,* BV-W.

AQUIFOLIACEAE

**Ilex crenata* Thunb. – Woodlands (including woodland land-locked between RR tracks); *6548,* E (Bc).

Ilex opaca Aiton – Woodlands, field; *12086,* NO-W (HH, P).

ARALIACEAE

**Hedera helix* L. – In woods; *10368,* BV (Bc, Bt, OF, ClH).

ASCLEPIADACEAE

Cynanchum laeve (Michx.) Pers. – [*Ampelamus albidus* (Nutt.) Britton] On hedge along sidewalk; *13003,* C.

ASTERACEAE

Aster subulatus Michx. – Along roads (sometimes in a ditch); under bridge; disturbed urban land near RR tracks; *8856,* C (B, Bc, G).

Bidens aristosa (Michx.) Britton – Fields (along RR tracks and not so); *975,* W (MH).

Brachyactis ciliata (Ledeb.) Ledeb. – [*Aster brachyactis* Blake] Beneath bridges; along roads; along parking lot; disturbed land beneath power lines; *11648,* Be (B, Bc, BH, C, FP, I, NR, P).

**Calendula officinalis* L. – Among boulders by Lake Erie; *8818,* C.

**Centaurea debeauxii* Gren. & Godr. – [*C. pratensis* Thuill.] Along railroad tracks; insolated waste area; forest edge bordering disturbed, insolated land; *14431,* C (BP, MiH, P).

**Crepis setosa* Haller f. – SR. Large population in overgrown lawn; *14081,* UH.

**Dyssodia papposa* (Vent.) A. S. Hitchc. – Eastern edge of I-71; *9297,* St.

Helianthus hirsutus Raf. – Slump and level land along RR tracks; *11497,* B (C).

Helianthus mollis Lam. – Threatened; disturbed area of railroad land; *13948,* MH.

**Hieracium piloselloides* Vill. – Lawn; along and between RR tracks; insolated disturbed areas (including slope); in shade at farmers' market; *10924,* OF (B, BeH, BV, C, E, EC, P, S).

Iva xanthifolia Nutt. – Ballast along RR tracks; highly insolated dirt along urban road; *4980,* C.

**Leontodon taraxacoides* (Vill.) Mérat – Two formas are represented, as follows:

a. Typical forma with yellow ligulate corollas; lawns, cemetery; *4445,* B (C, ClH, GM-M, MV, SE).

b. Forma with cream-colored ligulate corollas; lawn bordering road; 4447, B.

Liatris pycnostachya Michx. × *Liatris spicata* (L.) Willd. – SR. Field; *14101,* Bc.

Rudbeckia fulgida Aiton – Fields; wetland; *1908,* MH (NR-P, SH).

**Tagetes patula* L. – Dry substrate along railroad tracks; exposed portion of creek bed; *11623,* BV-W (P).

BERBERIDACEAE

**Berberis vulgaris* L. – In woods; *7173,* GM-M.

**Mahonia aquifolium* (Pursh) Nutt. – [*Berberis aquifolium* Pursh] Along railroad tracks; *10614,* Bk-C (Bc, C).

BETULACEAE

**Betula pendula* Roth – Meadow; wasteland bordering railroad tracks; *13155,* C (Bc).

BIGNONIACEAE

**Catalpa bignonioides* Walter – Along alley; along RR tracks; edge of field; *6954,* C (P).

Catalpa speciosa (Warder) Warder *ex* Engelm. – Along RR tracks; *6958,* ClH-EC (MH).

BORAGINACEAE

**Asperugo procumbens* L. – Beneath high bridge; *7024,* C-FP.

**Heliotropium europaeum* L. – Highly insolated urban waste land near Cuyahoga River; *4427,* C.

**Myosotis arvensis* (L.) Hill Flood plain of Chagrin River; *7177,* GM.

**Myosotis stricta* Link *ex* Roem. & J. A. Schult. – Urban and rural lawns; *6794,* C (B).

BRASSICACEAE

**Brassica juncea* (L.) Czern. – Lawn and eroded slope beneath RR bridge over Cuyahoga River; *11816,* CH (BkH).

**Cardamine bulbifera* (L.) Crantz – SR. Woods and disturbed area; *10915,* Bt.

**Cardamine flexuosa* With. – Weed in flower bed; by picnic area; *13125,* C (Br).

Cardamine ×*maxima* (Nutt.) Wood – [*Dentaria maxima* Nutt.] Woodland by Chagrin River; *13324,* Bn (MoH).

**Cardamine pratensis* L. var. *pratensis* – Lawns; land by shore of Cuyahoga River; *5104,* EC (C, ClH, SH).

**Chorispora tenella* (Pall.) Alph. de Candolle Along and between RR tracks; *6507,* C.

Descurainia pinnata (Walter) Britton – Threatened; dry, fine ballast along RR tracks; *10666,* BV-W.

**Descurainia sophia* (L.) Webb *ex* Prantl – Between and near RR tracks; land beneath terminus of RR bridge over Cuyahoga River; *4967,* C (BkH).

**Erucastrum gallicum* (Willd.) O. E. Schulz – Along RR tracks (sometimes in railroad ballast); rocky field; *11870,* MH (C, G, L).

**Erysimum cheiranthoides* L. – Muck of exposed portion of bottom of Cuyahoga River; along and between RR tracks; weed in flower bed; *11252,* CH (BV-W, C, E).

**Erysimum repandum* L. – Along and between RR tracks; along roads; cleared land beneath power lines; dump; *5240,* C (B, Bk-C, Br, G, vicinity VV).

**Lepidium ruderale* L. Insolated, recently planted lawn; insolated barren land; emersed portion of stream bed; *8409,* C (Br, P).

**Lobularia maritima* (L.) Desv. – Exposed portion of creek bed; dumped debris along RR tracks; along curb in urban area; *9414,* BV-W (C, P).

**Lunaria annua* L. Escape in lawn along I-90; *6832,* C.

Rorippa sessiliflora (Nutt.) A. S. Hitchc. Shore of Cuyahoga River; *14898,* L.

**Sinapis alba* L. [*Brassica hirta* Moench] Disturbed land by terminus of railroad bridge; *13626,* BkH.

**Sisymbrium loeselii* L. – Edge of apparently vacant building within urban area; *8217,* C.

**Thlaspi alliaceum* L. – Edge of entrance ramp onto I-90; *5311,* C.

BUDDLEJACEAE

**Buddleja davidii* Franch. – Ballast along railroad tracks; *14124,* MH.

CACTACEAE

Opuntia humifusa (Raf.) Raf. Potentially threatened; in ditch near railroad tracks; *14164,* C.

CALLITRICHACEAE

Callitriche terrestris Raf. – More-or-less bare soil of parks and picnic areas; *6238,* EC (B, SH).

CAPRIFOLIACEAE

**Lonicera* ×*minutiflora* Zabel – SR. Along RR tracks; *9627,* L (B).

**Lonicera ruprechtiana* Regel [*Lonicera* ×*muscaviensis* Rehder] SR. Along RR tracks; roadside; *12287,* C (B).

**Lonicera* ×*salicifolia* Dieck *ex* Zabel - SR. High on ridge along Rocky River; *10749,* NO.

**Viburnum plicatum* Thunb. – Woodland; flood plain; along dirt road; *11963,* RoR (C, GM-M).

Viburnum rafinesquianum J. A. Schult. – Woods (land-locked area between RR tracks); *6226,* E.

CARYOPHYLLACEAE

**Cerastium brachypetalum* Pers. – Highly insolated land along railroad tracks; *13313,* C.

**Cerastium glomeratum* Thuill. [*Cerastium viscosum* L.] Lawns; vacant disturbed urban and nonurban land; along RR tracks; *6480,* C (BkH, Br, BV-RoR-W, ClH, ClH-EC, HH, PP, VV).

**Gypsophila scorzonerifolia* Ser. - Dry, insolated substrate along RR tracks; *11380,* C-EC.

**Sagina japonica* (Sw.) Ohwi – Field near forest edge; *10945,* BV.

**Scleranthus annuus* L. – Lawn; dirt pile on vacant urban land; *6625,* C (vicin. SH).

**Vaccaria hispanica* (P. Mill.) Rauschert – Eroded slope by terminus of railroad bridge; *13693,* BkH.

CELASTRACEAE

**Celastrus orbiculata* Thunb. – On fence; along RR tracks; *6975,* EC (C, vicin. MV).

**Euonymus europaea* L. – Woods (some located along Chagrin River); along RR tracks; *7010,* vicin. GM (Br-MiH-St, C, vicin. MaH, MV).

CHENOPODIACEAE

**Chenopodium pumilio* R. Br. Urban land including junction of alley and stone wall, and along curb; shore of Cuyahoga River; muck of exposed portion of bottom of Cuyahoga River; *6028,* C (CH, I).

CONVOLVULACEAE

**Ipomoea hederacea* Jacq. – Along RR tracks; *7071,* C.

Ipomoea pandurata (L.) G. F. W. Mey. – Railroad land; *13954,* BeH.

CRASSULACEAE

**Sedum sarmentosum* Bunge – Rocky ledges along West Branch of Rocky River; on old, overgrown bricks along RR tracks; *11092,* OF (C).

CUCURBITACEAE

**Citrullus lanatus* (Thunb.) Matsumura & Nakai – Waste areas (one urban and containing RR ballast); along creek; exposed portion of creek bed; *5498,* C (ClH-EC, P).

**Cucumis melo* L. var. *cantalupensis* Naudin – Waste area; *8924,* ClH-EC.

**Cucurbita pepo* L. – Vacant urban land; *5497,* C.

DIPSACACEAE

**Dipsacus laciniatus* L. – Along highways; by RR tracks; along shore of Big Creek; *8283,* C (Bk, M, MaH, P).

EBENACEAE

Diospyros virginiana L. – Clump of trees in old field along side of road (probable remnant of cultivation); *11286,* B.

ELAEAGNACEAE

**Elaeagnus umbellata* Thunb. – Old fields; forest edge; shore of creek; along alley within urban area; along RR tracks; *7582,* B (Be-MH, C, E, P, RoR, S, W).

ERICACEAE

**Calluna vulgaris* (L.) Hull – Old field by RR tracks; *11625,* BV-W.

EUPHORBIACEAE

Acalypha gracilens A. Gray – Railroad land; *14119,* MH.
Chamaesyce serpens (Kunth) Small – [*Euphorbia serpens* Kunth] Endangered; on bare dirt; *9224,* C-CH (W).
Croton monanthogynus Michx. – In lawn; insolated land along RR tracks; *9275,* C (Bk-C, MH).
**Euphorbia helioscopia* L. – Farm field; *13350,* VV.

FABACEAE

Baptisia australis (L.) R. Br. *ex* Aiton f. – Endangered; overgrown land at end of city street; *13666,* C.
Cercis canadensis L. – Along RR tracks; *11236,* RoR.
**Lathyrus tuberosus* L. – Disturbed land at terminus of railroad bridge, field by power lines, weed in flower beds; *13627,* BkH (B, C, S).
**Lotus tenuis* Waldst. & Kit. *ex* Willd. – Lawn; highly insolated dry land along RR tracks; beneath power lines; *11101,* HH (C, G, I, P).
**Phaseolus vulgaris* L. – Shallow, insolated ditch; *8819,* C.
Strophostyles leiosperma (Torr. & A. Gray) Piper – Insolated dry substrate along RR tracks; *11545,* C-E.
**Vicia sativa* L. subsp. *nigra* (L.) Ehrh. [*Vicia angustifolia* L.] Field, vacant urban land; garden; by power lines; *3491,* C (BkH, CIH-EC, CH, FP-RoR-W, P, PP).

FAGACEAE

**Quercus robur* L. – Along railroad tracks; *13861,* C.

GENTIANACEAE

**Centaurium pulchellum* (Sw.) Druce – Along alley; damp depression; wetland; lawn beneath bridge; *7258,* C (BH, FP).

GERANIACEAE

**Geranium dissectum* L. – Overgrown dirt pile bordering parking lot; *11070,* W.

HAMAMELIDACEAE

Liquidambar styraciflua L. – Along RR tracks; *11664,* C.

HIPPOCASTANACEAE

**Aesculus hippocastanum* L. – In woods; along path through woods; *12198,* W (EC).

HYPERICACEAE

Hypericum gentianoides (L.) Britton, Sterns & Poggenb. – Very abundant in meadow; *8926,* HH.
Hypericum gymnanthum Engelm. & A. Gray – Endangered; field; *11273,* I.
Hypericum majus (A. Gray) Britton – Potentially threatened; field; *11566,* S (I).

JUGLANDACEAE

Carya ovalis (Wangenh.) Sarg. – Materials were distinguished from *C. glabra* based on nature of fruit dehiscence. Woods; *1058,* GH-VV (B).

LAMIACEAE

**Mentha* ×*gracilis* Sole – By beaver pond; *8472,* B.
**Origanum vulgare* L. – Along RR tracks; vacant, shaded urban land; *11187;* L (C).
**Prunella laciniata* (L.) L. – SR. Along path in woods; *11098,* GM-M.
Salvia reflexa Hornem. – RR ballast; dirt pile; along pond; *4397,* C (W).
Trichostema brachiatum L. – [*Isanthus brachiatus* (L.) Britton, Sterns & Poggenb.] Cinder on urban land; along RR tracks; *3170,* C (C-E, CH, MH).

LARDIZABALACEAE

**Akebia quinata* (Houtt.) Decne. – Woodlands; *7206,* Bt (C, P).

MALVACEAE

**Alcea rosea* L. – [*Althaea rosea* (L.) Cav.] South side of Big Creek; *8414,* C (ClH-EC, MH).
**Malva alcea* L. – Disturbed insolated land; periphery of field; *13766,* C.

MENYANTHACEAE

**Nymphoides peltata* (Gmel.) Kuntze – Pond; *8648,* Bn.

NELUMBONACEAE

Nelumbo lutea Willd. – Center of beaver pond; *8375,* GM-M.

OLEACEAE

**Fraxinus excelsior* L. – SR. At forest edge bordering road; *8450,* SH.
**Syringa vulgaris* L. – Along RR tracks; *12061,* RoR.

ONAGRACEAE

**Epilobium parviflorum* Schreb. – Forest edge; seep in urban area; shore of Euclid Creek; by beaver pond; *8579,* ClH-EC (C, M-GM, P).
Oenothera pilosella Raf. – Wet meadow; *14901,* P-PH.

OXALIDACEAE

**Oxalis corniculata* L. – Crack between pavement and wall of house; *13354,* P.

PAPAVERACEAE

**Papaver somniferum* L. – Waste land at terminus of railroad bridge; *13669,* BkH.

PASSIFLORACEAE

Passiflora incarnata L. – Threatened; insolated soil near railroad tracks; *14184,* C.

PEDALIACEAE

**Sesamum orientale* L. – SR. Emersed portion of bottom of Big Creek; *9059,* C.

PRIMULACEAE

**Lysimachia vulgaris* L. – From dense population within swamp; *13853,* VV.

RANUNCULACEAE

**Clematis terniflora* Alph. de Candolle – Scrambler over low-growing vegetation along RR tracks; *11421,* C-EC.
**Clematis vitalba* L. – Along RR tracks; *11194,* L.
**Ranunculus bulbosus* L. – Lawn along road; yard; *5931,* B.
**Ranunculus sardous* Crantz – Lawn of Metropark polo field; *14211,* MoH-HV.
Xanthorhiza simplicissima Marsh. – Woods by dump in Forest Hill Park; *5495,* EC.

ROSACEAE

Amelanchier sanguinea (Pursh) Alph. de Candolle – Endangered; forest edge at upper edge of slope; *9517,* C.
Amelanchier stolonifera Wiegand – [*Amelanchier spicata* (Lam.) K. Koch] Field by RR tracks; *10730,* BV-W.
**Duchesnea indica* (Andr.) Focke – Along RR tracks; woods; wetland; *9638,* L (B, C, ClH-EC).
**Prunus mahaleb* L. – By dirt embankment in waste area; along RR tracks; *10673,* BV-W (MH).

**Prunus subhirtella* Miq. – Damp woods by Rocky River; *6338,* C.
**Pyracantha coccinea* M. Roemer – Field, insolated slump along Rocky River; *8838,* C.
**Rubus caesius* L. – Woodland; *14905,* GM.
Rubus frondosus Bigelow – Field, along creek in woodland, along railroad tracks; *7038,* BP-NO-OT (C, P, W).
Rubus recurvicaulis Blanch. – SR. Insolated, disturbed land near road; *13737,* P.

RUBIACEAE

**Galium odoratum* (L.) Scop. – [*Asperula odorata* L.] Dry, level woods along RR tracks; abandoned house site; *10711,* BV (B).
**Galium verum* L. – Large population in Great Meadow of Forest Hill Park; terminus of road through Gordon Park; *4024,* EC (C).
Hedyotis nigricans (Lam.) Fosberg var. *nigricans* [= *Houstonia nigricans* (Lam.) Fernald] Potentially threatened; flat, disturbed, highly insolated urban terrain; *4079,* C.

RUTACEAE

**Phellodendron lavallei* Dode – SR. Along railroad tracks; *13673,* C.
**Tetradium daniellii* (Benn.) Hartley – [*Evodia daniellii* (Benn.) Hemsl.] SR. Disturbed land along urban road; *7924,* C.

SALICACEAE

**Salix cinerea* L. – By water along RR tracks; *10640,* Bk-C.
Salix ×*glatfelteri* C. K. Schneid. – Forest edge; *14908,* I.
Salix humilis Marsh. – Along RR tracks; *11830,* G.
**Salix matsudana* Koidzumi var. *tortuosa* Rehder f. – [*S. babylonica* L. var. *tortuosa*] Amid boulders facing Lake Erie; wetland; forest edge; insolated dump; field and waste land bordering RR tracks; *6502,* C (EC, G, I, P).
**Salix pentandra* L. – Swamp; *12378,* GM-M.
**Salix purpurea* L. – Swamp; *14967,* SeH (Be).

SAPINDACEAE

**Koelreuteria paniculata* Laxm. – Along RR tracks; *11716,* C.

SCROPHULARIACEAE

**Antirrhinum majus* L. – Insolated, disturbed urban land; dry slope at terminus of railroad bridge; exposed portion of creek bed; *5078,* C (BkH, P).
Aureolaria laevigata (Raf.) Raf. – Colony along forest edge in Forest Hill Park; *4088,* EC.
**Kickxia elatine* (L.) Dumort. – Damp depression in insolated, vacant, urban land; fill-dirt; along RR tracks; *4115,* C (C-CH, P).
Leucospora multifida (Michx.) Nutt. – Along RR tracks; damp depression in insolated, vacant urban land; *4120,* C (MH).
**Linaria dalmatica* (L.) P. Mill. – Along RR spur; *11507,* E.
Nuttallanthus canadensis (L.) D. A. Sutton – [*Linaria canadensis* (L.) Chaz.] Endangered; near RR tracks; *Loos s.n.,* L.

**Paulownia tomentosa* (Thunb.) Siebold & Zucc. *ex* Steud. – Along RR tracks; *11511*, C-E.

**Veronica anagallis-aquatica* L. – By water along RR tracks; edge of Chagrin River; *4184*, C (vicin. GM, WaH).

**Veronica hederifolia* L. – Rich woods; shaded embankment along RR tracks; *10773*, RoR (C-BkH, CH).

**Veronica polita* Fries – Along railroad tracks; insolated bare dirt; lawn; *4226*, C (Bk-C-Li).

SOLANACEAE

**Physalis philadelphica* Lam. – [*Physalis ixocarpa* auct. non Brot. *ex* Hornem.] Near creek; *14159*, Bk.

ULMACEAE

Celtis occidentalis L. – Along RR tracks; by pond; in forest along Ohio and Erie Canal; *10817*, L (C-BkH, CH, RoR).

**Ulmus glabra* Huds. – Along RR tracks; *6387*, C.

**Ulmus pumila* L. – Along road; along RR tracks; along Rocky River; in woodlands; *12156*, C (BkH, ClH-EC, MH).

VIOLACEAE

Viola bicolor Pursh – [*V. rafinesquei* Greene; *V. kitaibeliana* J. A. Schult. var. *rafinesquei* Fernald] Weed in park; *Anthony s.n.*, C.

**Viola odorata* L. – Includes formas with white flowers, dark-blue flowers, and individual flowers with a combination of blue and white. Waste area; second growth by shed; lawns; *2096*, EC (C, ClH, NR).

VITACEAE

**Ampelopsis brevipedunculata* (Maxim.) Trautv. – Forest edges; along RR tracks; *7788*, C (Be, ClH, C1H-SH, RoR).

Ampelopsis cordata Michx. – Growing on vegetation along side of road; *4912*, C.

Vitis vulpina L. – Overgrown field; *11834*, CH.

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NEW RECORDS WITH ECOLOGICAL NOTES FOR RARE AQUATIC VASCULAR PLANTS IN INDIANA. PART 1

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ABSTRACT. Floristic inventories of lakes in northern Indiana have resulted in the documentation of 22 new localities for eight Indiana state-listed aquatic plant species. Six of these eight species are listed as endangered (*Bidens beckii, Myriophyllum pinnatum, Najas gracillima, Potamogeton epihydrus, P. pulcher,* and *P. vaseyi*) and two are listed as extirpated (*Lemna valdiviana* and *P. bicupulatus*). Many of these species are listed in other states within the Great Lakes region. Each species is discussed in terms of notable characters useful in identification, historical and current information on distribution, and notes on the ecology and species associates for each new site record. Possible explanations for the rarity of these aquatic plant species are discussed in terms of habitat loss, undercollecting, and the "Prairie Peninsula" concept. A brief discussion of problems associated with aquatic plant conservation in the state of Indiana is provided.

Key Words: Indiana flora, aquatic plants, rare and endangered macrophytes, naiads, duckweeds, pondweeds, Prairie Peninsula

Aquatic plants are an integral component of aquatic ecosystems, contributing in many diverse ways to the ecological integrity of lakes (Carpenter and Lodge 1986; Jeppesen et al. 1998). The aquatic plant flora of lakes has been extensively documented for many states within the Great Lakes region, such as Michigan, Illinois, Ohio, and Wisconsin. Despite considerable floristic work in Indiana, the aquatic plant flora of its lakes has remained poorly cataloged.

The first comprehensive flora of Indiana was that by Coulter (1900), which was followed by Deam's (1940) classic volume *Flora of Indiana.* No updated flora has been published since Deam's work. Although both floras list many aquatic plant species and provide site localities by county, the collecting of true aquatic plants was sporadic in its coverage of the state and biased towards emergent species. *Plants of the Chicago Region* (Swink and Wilhelm 1994), which includes six counties in northwest Indiana, is one of the few more recent floristic treatments available for the state. It is noteworthy that the treatment of floating and submersed aquatic plant species in this volume is largely based on limited older herbarium collection data from the region and only minimal field surveys (F. Swink, pers. comm.).

Since Deam's floristic surveys, Indiana lakes, streams, and wetlands have suffered extensive habitat loss and degradation due to development. It is estimated that Indiana has lost 89% of its presettlement wetlands (National Research Council 1992). The Lake District, which includes the three northernmost tiers of counties in the state, contains over 500 small and shallow lakes averaging only 34.4 ha in size and 11.9 m in maximum depth (Frey 1966).

The small total volume and extensive shallow littoral zones of these lakes make them highly susceptible to eutrophication. The major form of impact is nutrient and sediment loading from surrounding farmland within the watersheds. Many lakes are characterized by extensive growths of spatterdock or Eurasian water-milfoil that often choke the vast majority of the lake's surface area.

As part of an effort to better understand Indiana's lake plant flora and provide more current records on the status of species, we began comprehensively surveying Indiana lakes in 1997. During the summer and early fall months of 1997 through 2001, many new localities for over 30 state-listed aquatic vascular plant species were recorded for Indiana during floristic quality assessment surveys of over 100 lakes and ponds. Because we believe that much of the aquatic plant flora of Indiana lakes has been overlooked and undercollected, specific efforts were made: 1) to locate new populations of state-listed species; 2) to determine the rarity of these species on a state-wide basis; 3) to begin the development of conservation strategies for those species of particular concern.

This paper is the first in a series of papers on rare aquatic plant species of Indiana. Information is provided here on eight state-listed aquatic plant species, which are presented in alphabetical order. The following information is provided for each species: a description of distinctive morphological features, including notes on closely related taxa if the discussion has bearing on identification issues; a summary of historical records and current distribution within Indiana; a brief narrative describing each new population, including information on site locality, habitat type, and associated species; and a listing of voucher specimens. Recommendations for conservation strategies will be briefly discussed as well, although a more detailed analysis will be presented in a separate publication.

MATERIALS AND METHODS

Systematics. Taxonomy and nomenclature follow that of the *Flora of North America* (1993+) for the following families: Lemnaceae (Landolt 2000), Najadaceae (Haynes 2000), and Potamogetonaceae (Haynes and Hellquist 2000). For species in families not yet treated in the *Flora of North America*, nomenclature follows Gleason and Cronquist (1991). When appropriate, we have included synonymy where nomenclatural differences exist for the species discussed.

State status definitions. The designated Indiana state status for a given plant species follows the definitions from the Indiana Department of Natural Resources, Division of Nature Preserves (R. Hellmich, pers. comm.):

1. Endangered = plants that currently occur at five or fewer sites in Indiana.
2. Threatened = plants that currently occur at six to 10 sites in Indiana.
3. Rare = plants that currently occur at 11–20 sites in Indiana.
4. Extirpated = plants that are considered native to Indiana, but currently do not occur within the state.

The state status of each species is provided in Table 1 for the Great Lakes states, however, it should be noted that the criteria used to define the status of a species vary considerably from state to state and do not necessarily conform to those that have been outlined here for Indiana.

Element of occurrence records. Element of occurrence records, referred to hereafter as EORs, from the Indiana Department of Natural Resources, Division of Nature Preserves are cited for each species. These records provide both current and historical information on locations for each of the species discussed here. It should be noted that an EOR does not necessarily indicate that a species has been collected, but more often that it has been observed at a particular location. Where available records are

Table 1. Summary of eight imperiled aquatic vascular plant species in the Great Lakes region (modified from a compilation of state checklists: Illinois Endangered Species Protection Board 1999; Indiana Natural Heritage Database 1996; Michigan Natural Features Inventory 1999; Minnesota Natural Heritage Database 2000; Ohio Division of Natural Areas and Preserves 1998; Pennsylvania Natural Diversity Inventory 2002; Wisconsin Natural Heritage Program 1998; Young 2001). State status abbreviations used here: E = Endangered; S = Special Concern; T = Threatened; U = Undetermined; W = Watchlist; X = Extirpated.

	State and Status								No. of list-
Taxon	IL	IN	MI	MN	NY	OH	PA	WI	ings
Bidens beckii	E	E			W	X	E		5
Lemna valdiviana		X	X		E	X	X		5
Myriophyllum pinnatum		E			E				2
Najas gracillima		E		S		E	T		4
Potamogeton bicupulatus		X	T	E			U		4
Potamogeton epihydrus		E							1
Potamogeton pulcher	E	E	T		T	T	E	E	7
Potamogeton vaseyi		E	T	S		X	E	S	6

numerous, we have summarized the distribution of these records and given the most recent EOR.

Collection of aquatic plants. Since an implicit purpose of this study is to identify populations of state-listed species before they are lost, our methods, out of necessity, have been qualitative to allow us to survey individual lakes more efficiently and thus include more lakes in our study. All initial lake inventories were conducted by both authors, during which we attempted to survey the entire littoral zone of the lakes investigated. Proportionately more time was spent at locations that likely harbored the greatest diversity, such as undisturbed shoreline areas or shallow sheltered bays. Relative abundance for each population was determined by visual inspection. In most cases, after a population was discovered the site was revisited annually to check on its status.

Submersed, emergent, and free-floating macrophytes were collected while wading in the shallow water along the lake margin. In areas having moderate depths, the sampling of submersed plant species was carried out by dredging the lake bottom with an extendable rake from the side of a Jon boat. Submersed aquatic plants in areas having a depth > 4.0 m were collected using

SCUBA. By employing multiple methods, a larger proportion of the lake could be comprehensively inventoried and the likelihood of sampling rare species was greatly increased. Voucher specimens have been deposited in either the Aquatic Plant Herbarium of Purdue University North Central (indicated here as PUNC) or the Friesner Herbarium at Butler University (BUT).

Percent seed set was determined by visual inspection of infructescences and estimations of the number of mature seeds per spike versus the total number of flowers. This nondestructive method was used because of concerns over species rarity.

RESULTS AND DISCUSSION

***Bidens beckii* Torr.** *Bidens beckii,* often cited as *Megalodonta beckii* (Torr.) Greene, is commonly referred to as the water marigold. It is the only submersed aquatic member of the genus *Bidens* L., which comprises some 200 species (Gleason and Cronquist 1991), many of which are emergent wetland species. The water marigold exhibits a heteroblastic sequence of development, culminating in the production of emergent leaves associated with flowering. The emergent leaves are simple, opposite, and sessile, having either toothed or serrated margins. In deeper water, plants often lack the bract-like emergent foliage and fail to flower (pers. obs.). The submersed leaves of *B. beckii* are characterized by having finely dissected leaves crowded at nodes with varying degrees of similarity to the leaves of several other aquatic species in the genera *Cabomba* Aubl., *Myriophyllum* L., *Ranunculus* L., and *Utricularia* L., with which it is often confused (Peattie 1930; Voss 1996). Voss (1996) described the leaves as being opposite, but branching, giving the foliage a whorled appearance. Flowers are borne in emergent heads, having the typical yellow ray florets that are characteristic of the genus. Some authors believe that differences in the morphology of the florets, awn lengths of the achenes, and chromosome number warrant the segregation of the water marigold from *Bidens* into the genus *Megalodonta* Greene (see Roberts 1985).

Although *Bidens beckii* is found throughout the Midwest, it is state-listed in over 50% of the Great Lakes states (Table 1). Historical records are somewhat vague as to the distribution and abundance of this species in Indiana. Pepoon (1927) and Peattie (1930) suggested that this species was quite rare in northwestern

Indiana during the early 1900s, having been collected or observed from only a few small intradunal ponds in Lake County. Deam (1940) reported this species from seven counties in northern Indiana and suggested that it was once probably found throughout most of northern Indiana, but had likely been destroyed by lakefront settlement. Swink and Wilhelm (1994) reported *B. beckii* from LaPorte County, based on a single collection from Stone Lake in August of 1983 (*Rowlatt 1297*, MOR). This is the last known collection for the state prior to the current study. Indiana EORs simply refer to the original site records from Deam (1940).

During the fall of 1997, we found *Bidens beckii* along the northwestern littoral zone of Stone Lake, LaPorte County, in water 1.0 m deep with the entire population consisting of less than 60 plants. Plants did not have the emergent foliage associated with flowering. Plants growing in association with *B. beckii* were *Myriophyllum sibiricum* Kom., *Potamogeton robbinsii* Oakes, *P. zosterformis* Fernald, *Ranunculus aquatilis* L. var. *diffusus* With., and *Vallisneria americana* Michx. This site was revisited during the summer of 1998. The number of individual plants had declined to twelve. Signs of habitat degradation were apparent, resulting from landowner development of the shoreline. *Myriophyllum sibiricum, P. robbinsii,* and *R. aquatilis* var. *diffusus* also exhibited a substantial decrease in their population sizes. A search of the sheltered, undisturbed backwaters of Stone Lake revealed no additional plants of *B. beckii.*

Despite the unsuccessful attempt to locate additional beds of *Bidens beckii* in Stone Lake, an investigation during the summer of 2000 of the aquatic plant communities in Pine Lake, which is located directly north of and connected to Stone Lake, resulted in the discovery of another population of the water marigold. This population was larger than the one previously reported for Stone Lake, yet it too was threatened by shoreline development along the northwest shore of the highly populated island. Other species growing in association with *B. beckii* included *Ceratophyllum demersum* L., *Myriophyllum spicatum* L., *Najas flexilis* (Willd.) Rostk. & W. L. E. Schmidt, *Stuckenia pectinata* (L.) Börner, and *Zosterella dubia* (Jacq.) Small.

In June of 1998, a population of *Bidens beckii* (> 500 plants) was found at a second site in LaPorte County in a bay along the southwest shore of Hudson Lake. Plants were found growing in water up to 1.5 m in depth. This population was extensive, forming large dense stands encompassing most of the area within the bay. Like the Stone Lake plants, these plants had neither produced emergent foliage nor flowered. Hudson Lake is a marl lake that is largely dominated by the growth of *Chara globularis* Thuill., which at the time formed large beds that covered much of the littoral zone. Other common submersed species found with *B. beckii* included *Elodea nuttallii* (Planch.) H. St. John, *Potamogeton crispus* L., *P. gramineus* L., *Utricularia purpurea* Walter, and *Zosterella dubia*.

In late August of 1998, the first flowering population of *Bidens beckii* was found in 0.5 m of water off the western shore of Wauhob Lake, Porter County. Yellow emergent flowers could be seen among the floating leaves of *Brasenia schreberi* J. F. Gmel. and *Nymphaea odorata* Aiton subsp. *tuberosa* Wiersema & Hellq. At the time, only seven plants had flowered, but others had floral buds. Although the number of plants present was quite low (< 30), the plants appeared to be secure and quite vigorous in this habitat. Discussions with the lakefront property owner on the status of the species resulted in an agreement by the owner not to rake "weeds" from the littoral zone in this area.

VOUCHER SPECIMENS: Indiana: LaPorte Co., LaPorte, Stone Lake, 41°36′43″N, 86°45′03″W, SW of navigable channel, 10 Jun 1998, *Alix s.n.* (BUT); Lake Park, Hudson Lake, 41°42′43″N, 86°33′00″W, in water 1.5 m deep off SW shore, 22 Jun 1998, *Scribailo & Alix 138* (PUNC); LaPorte, Pine Lake, 41°37′40″N, 86°45′07″W, S shore of upper Pine Lake towards N shore of island and E of intersection of Holton Rd. and Island Dr., 7 Sep 2000, *Alix s.n.* (BUT); Porter Co., Valparaiso, Wauhob Lake, 41°32′01″N, 87°02′40″W, in water 0.75 m deep near boat rental dock, 21 Aug 1998, *Scribailo 155, 156* (PUNC).

***Lemna valdiviana* Phil.** *Lemna valdiviana* (pale duckweed) is one of eight *Lemna* species known to occur in Indiana. Its common name is derived from the pale green appearance of its fronds. The intensity of green color is dependent upon growth conditions, the thickness of the frond, and the content of chlorophyll in the different cell layers (Landolt 1986). The fronds of *L. valdiviana* are often asymmetrical, giving them a distinctive falcate shape (Mohlenbrock 1970), resembling the sole of a shoe. Each frond has a single vein; a character shared with only one other North American *Lemna* species, *L. minuta* Kunth, which also occurs in Indiana. *Lemna valdiviana* can be distinguished from *L. minuta* by the greater length of the vein, which in the former species distally exceeds the extension of air space tissue (Landolt 1986, 2000). Distinguishing between these two species can be very difficult and often requires the clearing and subsequent examination of fronds using light microscopy (Landolt 1986).

Lemna valdiviana was first recorded for Indiana as *L. cyclostasa* (Elliot) Chev. by Deam (1932), who collected this species from Noble County. Hicks (1937) summarized Deam's locality data for this species in connection with the upcoming flora. In his *Flora of Indiana,* Deam (1940) reported *L. valdiviana* as being "local in the lake area." Deam referred to map 582 in the text of his flora regarding the distribution of *L. valdiviana,* however, the correct map citation is actually 578. Without the erratum pamphlet that was subsequently provided for the flora, or the correct distribution map in Hicks (1937) for comparison, it is not possible to determine whether the number cited in the text, the maps themselves, or the species designations are in error. Map 578 indicates *L. valdiviana* from Lagrange, Noble, and Wells Counties in the northeastern part of the state. An examination of herbarium specimens from Indiana University (IND) indicated that this species had been collected from Noble County in 1931 as discussed above (*Deam 50405*), and Lagrange County in 1933 (*Deam 54088*). Swink and Wilhelm (1994) did not report this species for the northwestern counties of Indiana. There is only one EOR for this species, which reports its occurrence from Beaver Dam Lake fen in Steuben County in 1974. This site was visited in 2000, but we were unsuccessful in locating a population of this species. *Lemna valdiviana* is listed as extirpated in 50% of the Great Lakes states (Table 1).

On September 22, 1997, the pale duckweed was found in the eastern backwaters of Long Lake, Porter County, Indiana. Plants of *Lemna valdiviana* were typically found in small tangled masses just below the water's surface. This habit is one quite often observed in the related species *L. trisulca* L. Colonies were rare to occasional and were restricted to the northeastern shoreline and a small backwater pond off of the lake, which largely consisted of patchy stands of *Cephalanthus occidentalis* L. Other associated plant species included *Ceratophyllum demersum, L. minor* L., *L. trisulca, Proserpinaca palustris* L., and *Utricularia vulgaris* L.

On October 4, 2001, an additional population of *Lemna val-*

diviana was discovered at the north end of Kaiser Lake beside the public boat launch in Kosciusko County in northeastern Indiana. Plants were abundant, either floating on or submersed just below the surface, and intermixed with *L. minor, L. trisulca, Spirodela polyrrhiza* (L.) Schleid., and *Wolffia columbiana* H. Karst. Clumps of this species were also found submersed and entangled with the leaves of *Ceratophyllum demersum* and *Myriophyllum spicatum.* Lemnid species covered over 50% of the lake's surface area and harbored an extensive population of *L. valdiviana,* comprising an estimated 30% of the mat.

VOUCHER SPECIMENS: Indiana: Porter Co., Valparaiso, Long Lake, 41°31′31″N, 87°02′49″W, in eastern backwaters of the lake, 22 Sep 1997, *Scribailo & Alix 131* (PUNC); Kosciusko Co., Yellowbanks, Kaiser Lake, 41°18′59″N, 85°39′42″W, large mat E of public access site, 4 Oct 2001, *Scribailo & Alix 506* (PUNC).

***Myriophyllum pinnatum* (Walter) Britton, Sterns & Poggenb.** *Myriophyllum pinnatum* is one of five perennial watermilfoil species occurring in Indiana. It is common throughout the Midwest, though endangered in Indiana (Table 1). This species is quite variable in its morphology and habitat, producing whorled pinnatifid leaves on elongated stems when submersed, and branching more freely with scattered leaves when it is anchored along the shoreline (Correll and Correll 1975). *Myriophyllum pinnatum* is more easily recognized as a terrestrial species (Aiken 1981) and can be confused with *M. heterophyllum* Michx., another native species in Indiana that will often produce a short terrestrial form on exposed mudflats as summer lake levels decline. When available, mature fruits provide the best characters for distinguishing between the two species. Although the fruits of both species are 4-angled and have dorsal ridges, these ridges are smooth in *M. heterophyllum,* but are tuberculate in *M. pinnatum.*

Historical records indicate *Myriophyllum pinnatum* was collected by Deam (1940; as *M. scabratum* Michx.) from Jasper County, Indiana, approximately 0.8 km west of the Teft Bridge in the Kankakee River. Swink and Wilhelm (1994) reported the Deam specimen in *Plants of the Chicago Region,* but did not report any new locations for this species in the northwestern counties of Indiana. An EOR reveals that *M. pinnatum* was collected from Fishtrap Lake, LaPorte County, in July of 1985 by

J. Aldrich and J. Wilhelm (the latter possibly Gerould Wilhelm), who stated that this species was abundant at the time of collection and was found intermixed with plants of *M. heterophyllum.* A comprehensive inventory of Fishtrap Lake in 1998 by the current authors did not result in the discovery of this species, but only verified the presence of *M. heterophyllum.* Because *M. pinnatum* and terrestrial variants of *M. heterophyllum* can be morphologically similar with pinnate leaves, it is our opinion that the report from Aldrich and Wilhelm may be erroneous. No herbarium specimens could be located to evaluate the record from Aldrich and Wilhelm.

In 1997, a small population of *Myriophyllum pinnatum* (20 plants) was found along the northern shore of a small cove of Loomis Lake, Porter County, Indiana, which is the first county directly north from where Deam (1940) collected his specimen. Plants of *M. pinnatum* were found on the muddy shoreline in shallow water (0.20 m). Associated species included *Ceratophyllum demersum, Elodea nuttallii, Lemna minuta, L. trisulca, Polygonum amphibium* L., *Spirodela polyrrhiza, Wolffia borealis* (Engelm.) Landolt, *W. brasiliensis* Wedd., and *W. columbiana.* Although most plants found at this site were terrestrial, some were submersed with emergent flowering and fruiting spikes. The fruits were diagnostic in identification and had very distinct tuberculate dorsal ridges, a purple tinge, and were subtended by coarsely toothed bracts (Aiken 1981).

Two additional populations of *Myriophyllum pinnatum* were subsequently discovered in adjoining counties. The first population was found in 1998 at Chamberlain Lake, St. Joseph County, where both flowering and fruiting plants were present. Like the aforementioned population, plants were found either growing as terrestrial variants exposed on mud flats or in their submerged form in shallow water along the sheltered northwest shore. The most common species associates were *Ceratophyllum demersum* and *Nuphar advena* (Aiton) W. T. Aiton, the latter extending over half the distance across the lake. The second population was discovered in the fall of 2000 on the southern shoreline of Stone Lake, LaPorte County. The population at this site was primarily terrestrial and strictly vegetative, sprawling across the muddy shoreline for nearly 3 m. Species associated with *M. pinnatum* at this site included *Pontederia cordata* L. and *Sagittaria latifolia* Willd.

VOUCHER SPECIMENS: Indiana: Porter Co., Valparaiso, Loomis Lake, 41°31′04″N, 87°03′28″W, northern shore of small cove, 8 Aug 1997, *Alix 67* (PUNC); St. Joseph Co., West Field, Chamberlain Lake, 41°39′22″N, 86°22′00″W, in shallow water along north shore, 7 Sep 1998, *Scribailo 184* (PUNC); LaPorte Co., LaPorte, Stone Lake, 41°36′34″N, 86°44′39″W, on shore across from intersection of Lakeshore Dr. and Craven Dr., 15 Sep 2000, *Alix 341* (PUNC).

***Najas gracillima* (A. Braun *ex* Engelm.) Magnus.** *Najas gracillima* (thread-like naiad) is morphologically similar to *N. flexilis* and *N. minor* All., which also occur in Indiana. These species are easily confused because of the presence of extensive plasticity in vegetative characters. The most definitive characters for positive identification of naiad species are seed shape and seed coat reticulation patterns, which can only be determined microscopically. Fruits of *N. gracillima* have an off-center style at their apex, and the seed coats have areoles that are much longer than broad (Haynes 1979, 2000).

Najas gracillima is a relict coastal plain aquatic plant species in the Great Lakes region (Peattie 1922; Reznicek 1994) and is particularly common in the New England states (Haynes 2000; Stuckey 1983). Stuckey (1983) has commented on the rarity of this species in Ohio, Illinois, and Indiana and has cited macrofossil records (Watts 1970; Wright and Watts 1969) as indicating that the species was once far more common in this region. Stuckey postulated that the xerothermic period (beginning 8000 YBP) that advanced a "Prairie Peninsula" (Gleason 1923; Transeau 1935) eastward for a period of some 3000 years would have resulted in the loss of extensive wetland and aquatic habitat that could have contributed to the loss of populations of this species. Recent evidence however, questions the true extent of the "Prairie Peninsula" xerothermic in the Midwest (Baker et al. 1996). More paleobotanical studies utilizing aquatic plant macrofossils are needed to further determine the impact of the postulated xerothermic period on aquatic plant distributions, particularly in the eastern states of the Midwest.

It is our contention that the apparent scarcity of *Najas gracillima* in the Great Lakes region, and particularly in Indiana where it is endangered (Table 1), may actually be an artifact of undercollecting. *Najas flexilis* is very common in Indiana and is often found growing in abundance with occasional plants of *N. gracillima,* so that the latter may easily be overlooked.

We are aware of a single EOR from Pulaski County in northwest Indiana collected by Kriebel in 1938, although it has been collected from two southern counties within the state. Deam (1940) reported the 1935 specimen collected in Lawrence County (*Kriebel 3477*, IND). Wentz and Stuckey (1971) reported the species from Knob Lake, Jackson County (7 Sep 1958, *Starcs 2123*, BUT; 19 Jul 1970, *Starcs 3100*, BUT).

We first identified this slender and delicate species from the shallow waters of the eutrophic Mink Lake in Porter County. Eighty percent of the water's surface area was choked by *Nuphar advena* and the mean water depth within the littoral zone was less than 1.0 m. Plants of *Najas gracillima* were common, growing along the northeastern and northwestern shorelines at a depth of 0.5 m. Plants had a definite red tinge to their leaves and stems. We have observed distinctive red and green color morph variation in this species at many localities, but do not know the cause of this variation. This red coloration was also observed in plants of *Elodea nuttallii.* Other associated species included *Ceratophyllum demersum, C. echinatum* A. Gray, *Lemna trisulca, Najas flexilis, Nuphar advena, Nymphaea odorata* subsp. *tuberosa, Potamogeton amplifolius* Tuck., *P. crispus, P. pusillus* L. subsp. *tenuissimus* (Mert. & W. D. J. Koch) R. R. Haynes & Hellq., *Utricularia gibba* L., and *U. vulgaris.*

Although it has been suggested that *Najas gracillima* may not have the ability to withstand eutrophic waters (Haynes 1979; Wentz and Stuckey 1971) this does not appear to be the case at the Mink Lake site. The population at Mink Lake could be near its tolerance limits to eutrophication and may decline or disappear with time. Fertilizer runoff from an adjacent golf course is the primary source of nutrients contributing to the eutrophication.

In the latter part of August of 1998, *Najas gracillima* was found in Silver Lake, LaPorte County. This population was quite extensive, forming dense patches from the eastern to the southern shoreline. The plants had a lime-green coloration and many had set fruit. Plants growing in association with *N. gracillima* were *N. flexilis, Nuphar advena, Nymphaea odorata* subsp. *tuberosa, Potamogeton amplifolius, P. diversifolius* Raf., *P. epihydrus* Raf., *P. pusillus* subsp. *tenuissimus,* and *Zosterella dubia.*

VOUCHER SPECIMENS: Indiana: Porter Co., Valparaiso, Mink Lake, 41°31′49″N, 87°02′14″W, in water 0.5 m deep off the northeastern shoreline, 10 Jun 1997, *Scribailo & Alix 60* (PUNC); LaPorte Co., Rolling Prairie, Silver Lake, 41°41′25″N, 86°35′45″W, in shallow water along the southwestern shoreline, 29 Aug 1998, *Scribailo & Alix 179* (PUNC); 7 Aug 2000, *Alix s.n.* (BUT).

Potamogeton bicupulatus **Fernald.** *Potamogeton bicupulatus* (snail-seed pondweed) is one of the most diminutive and delicate pondweeds of North America. Like *Najas gracillima,* this species is another of several coastal plain submersed aquatic plant species represented in the northern Great Lakes region (Peattie 1922; Reznicek 1994). It is one of only three linear-leaved pondweed species in North America having dimorphic inflorescences and embryos with more than one complete spiral; it is restricted to acidic waters (Haynes and Hellquist 2000). *Potamogeton bicupulatus* is morphologically similar to *P. diversifolius,* which occurs in many of the southern and central counties of Indiana, as well as a few localities in northwestern Indiana. Peattie (1922, 1930) actually noted *P. hybridus* (referenced in brackets in his works as *P. diversifolius*) as being found in the intradunal pond region of Indiana. These specimens, which were collected from Dune Park in Porter County (4 Jul 1906, *Hill 132,* F; 18 Sep 1903, *Hill 156,* F), were subsequently annotated as *P. bicupulatus* by both Barre Hellquist and Robert Haynes and are the only known historical records for the species in the state. We are unaware of any EORs for this species.

In midsummer of 1998, four plants of *Potamogeton bicupulatus* were located in a shallow drainage ditch, which flowed into Chamberlain Lake, St. Joseph County. The culvert appeared to have been recently installed and sand within the ditch was part of a pile on top of the pipe. It is quite possible that the sand may have been brought in from another area that contained a small seed bank of this pondweed. Only one of four plants had set seed and seed set for that individual was estimated at 50%. A survey of Chamberlain Lake yielded no other plants of *P. bicupulatus.* Associated species included *Ceratophyllum demersum, Nuphar advena,* and *Sagittaria latifolia.*

VOUCHER SPECIMEN: Indiana: St. Joseph Co., West Field, Chamberlain Lake, 41°39′21″N, 86°21′57″W, near drainage ditch, 7 Jul 1998, *Alix 143* (PUNC).

Potamogeton epihydrus **Raf.** *Potamogeton epihydrus* (ribbon-leaved pondweed) is one of the most distinctive and easily recognized North American species of pondweed. Its thin, translucent, strap-like submersed leaves and elliptic floating leaves readily identify this species. Unlike many pondweeds, there are no intergradations between leaf types present. The only North American species morphologically similar to *P. epihydrus* is *P. tennesseensis* Fernald, which is distinguished by having long-tapering apices in the submersed leaves (Haynes and Hellquist 2000), however the latter species is not found in Indiana.

Potamogeton epihydrus is rare in the lower midwestern states and common in Michigan, Wisconsin, and the eastern states (Stuckey 1983). It is very rare in Indiana where it is listed as endangered (Table 1). This species has previously been collected from only one location (Deam 1940; Tryon 1937; Swink and Wilhelm 1994), at State Line Creek in LaPorte County (8 Aug 1936, *Tryon 30593,* BUT; *014212,* ND). Although a review of EORs indicates that this species has been recorded from Ridinger Lake in Kosciusko County and Loon Lake in Steuben County, no herbarium specimens are available to corroborate these reports. In addition, repeated visits by the authors to both of the aforementioned lakes yielded no populations of *P. epihydrus.* Extensive populations of *P. natans* L. were present at both lakes. Observed plants had both smaller floating leaves and longer stipules than are typically representative of this species in Indiana. The combination of these two characters at the two locations might have resulted in the erroneous reporting of the latter species as *P. epihydrus.* It is noteworthy that these lakes are marl lakes, typically of higher pH and alkalinity, and would not likely support the growth of a softer water species like *P. epihydrus.*

In 1997, *Potamogeton epihydrus* was discovered at Silver Lake in LaPorte County where it grew along the shallow sandy banks of the eastern and southeastern shores. In Silver Lake, the ribbon-leaved pondweed formed small patchy beds in water from 15 to 50 cm deep. Seed set was close to 100% (n = 40) on plants from this population. Associated species included *Najas gracillima* and *P. diversifolius.*

In the summer of 1999, *Potamogeton epihydrus* was found at two additional locations in LaPorte County approximately 1.5 km west of Silver Lake in two small ponds behind the Rolling Prairie Elementary School. The species was also discovered at Clear Lake in Porter County. Plants at Clear Lake were found at greater water depths (1.25 m) than at the LaPorte locations. Seed set of plants at this location was approximately 50% (n = 20). Waters of the LaPorte County lakes were more turbid than those of Clear Lake, which may have inhibited the establishment of the ribbon-leaved pondweed at greater depths.

According to Hellquist (1980), Nichols (1999), and Stuckey (1983) *Potamogeton epihydrus* is a species of circumneutral to soft water lakes and ponds. Habitats of this type are limited in Indiana, where calcareous groundwaters and marl deposits have produced a majority of lakes of alkaline pH. Stuckey (1983) recognized *P. epihydrus* as an additional example of an aquatic plant that may have once been more extensive in range prior to the postulated xerothermic period.

VOUCHER SPECIMENS: Indiana: LaPorte Co., Rolling Prairie, Silver Lake, 41°41′27″N, 86°35′33″W, in shallow water of southeastern littoral zone, 23 Sep 1997, *Scribailo & Alix 132, 133* (PUNC); 7 Aug 2000, *Alix s.n.* (BUT); Prairie Pond, 41°40′57″N, 86°36′34″W, in shallow water off S shore directly in front of observation deck, 7 Aug 1999, *Alix 255* (PUNC); Porter Co., Jackson Township, Clear Lake, 41°33′11″N, 86°55′55″W, in shallow water of small bay near W side of lake, 21 Jun 1999, *Scribailo & Alix 203* (PUNC).

***Potamogeton pulcher* Tuck.** *Potamogeton pulcher* (spotted pondweed) is a coastal plain species with a predominantly southeastern range (Haynes and Hellquist 2000), and is not only endangered in Indiana, but is also one of the rarest pondweeds found in the Great Lakes region (Table 1). The localities of this species in Indiana are few and include: Jasper County (Welch 1931); Sullivan County (Deam 1940); Pine Station in Lake County (Hill 1885); Miller Woods Pond in Lake County in 1982 (*Simonin 26,* MOR); intradunal swales west of Miller in Lake County in 1985 (*Wilhelm 12955,* MOR) and 1991 (*Wilhelm & Wetstein 19722,* MOR); and Little Lake in Porter County in 1991 (*Plampin & Newgent 1-1991,* MOR). In July of 1997, we revisited the Little Lake site in the Indiana Dunes National Lakeshore and found only a single plant of *P. pulcher* growing within a monospecific stand of cattails.

In September of 1997, a small population (< 10 plants) of *Potamogeton pulcher* was found off the eastern shore of Fishtrap Lake in LaPorte County. The black-spotted stems and petioles along with the cordate-based floating leaves were quite prominent in these plants and are distinctive features of this pondweed species. The submersed leaves were lanceolate, up to 9.0 cm in length and averaging 1.2 cm wide, having wavy margins and tapering at the base to petioles 1.0 cm long (e.g., Beal 1977). No flowering or fruiting was observed in these plants.

The population of spotted pondweed was 3 m from the eastern shoreline, growing in water 0.75 m in depth. Associated species included *Nuphar advena, Potamogeton robbinsii,* and *Utricularia vulgaris.* This site was revisited in July of 1998, but no plants of *P. pulcher* were found.

In September of 1999, an extensive population of *Potamogeton pulcher* was found in sloughs along the north and south sides of County Road 700 North within the Jasper-Pulaski Fish and Wildlife Area in Jasper County. Although the population consisted of hundreds of plants, none had flowered. Associated species included *Elodea nuttallii, Myriophyllum heterophyllum,* and *Nymphaea odorata* subsp. *tuberosa.*

In the summer of 2000, two additional populations of this species were found. The first population was located in shallow former sand-mining ponds located in the dune and swale topography of Lake County in an area known as the Bonji Tract. This population consisted of approximately 30 plants growing in association with *Proserpinaca palustris* in water only 0.25 m deep at the base of a small stand of *Scirpus pungens* Vahl. The second population was found within a remnant area of the Great Marsh in the Nature Preserve portion of the Indiana Dunes State Park in Porter County. This population consisted of less than 10 plants growing with *Ceratophyllum demersum, Nuphar advena, Peltandra virginica* (L.) Schott, and *Sparganium americanum* Nutt.

The multiple leaf types observed in *Potamogeton pulcher* largely agree with the descriptions by Robbins (1867), who identified the presence of three kinds of leaves in this species: floating leaves roundish-ovate, cordate, or ovate-oblong, all alternate; upper submersed leaves usually lanceolate, acute at base and with very long acuminate tips, very thin, undulate, short-petioled; lowest submersed leaves thicker, flat, oval or oblong with a rounded base, or spatulate-oblong, on longer petioles. Although we completely agree with these descriptions for floating and upper submersed leaves, we found the lowermost submersed leaves to be either lanceolate or spatulate, but not ovate. In addition, the lowermost submersed leaves of plants at the Jasper-Pulaski Fish and Wildlife Area had distinctive dentate margins with less than ten teeth per side. This observation has not been previously reported for this species.

VOUCHER SPECIMENS: Indiana: Jasper Co., Jasper-Pulaski Fish and Wildlife Area, 41°09′30″N, 86°56′24″W, in road ditch next to gravel pit fishing area, 7 Sep 1999, *Scribailo & Alix 301, 302, 303* (PUNC); 21 Jul 2000, *Alix s.n.* (BUT); Lake Co., Gary, Bonji Tract, 41°37′12″N, 87°23′38″W, in shallow water directly east of Clark and Pine Nature Preserve ca. 100 m after crossing Clark St., 5 Aug 2000, *Scribailo & Alix 315* (PUNC); LaPorte Co., LaPorte, Fishtrap Lake, 41°38′03″N, 86°43′44″W, near E shore, 29 Sep 1997, *Alix 134* (PUNC); Porter Co., Indiana Dunes National Lakeshore, Great Marsh in Dunes State Park, 41°39′29″N, 87°02′49″W, in shallow water next to bridge/observation platform on trail #2, 5 Aug 2000, *Scribailo & Alix 328* (PUNC).

***Potamogeton vaseyi* J. W. Robbins.** *Potamogeton vaseyi* appears to be a species of softer waters (Hellquist 1980; Hellquist and Crow 1980; Hopkins 1919; Nichols 1999). The scarcity of softer water lakes in Indiana is likely a factor contributing to the rarity of this species in the state. This species is state-listed in six of the eight states in the Great Lakes region (Table 1).

Small populations of *Potamogeton vaseyi* (< 50 plants) were discovered at Round and Wauhob Lakes, Porter County, in the middle of June 1997. *Potamogeton vaseyi* was common off the northwest shore of Wauhob Lake and rare in Round Lake. Associated species included *Ceratophyllum demersum, Myriophyllum heterophyllum, M. verticillatum* L., *Potamogeton amplifolius, P. richardsonii* (A. Benn.) Rydb., *Utricularia gibba, U. purpurea,* and *U. vulgaris.*

During the summer of 1997, two additional populations of *Potamogeton vaseyi* were discovered in LaPorte County. The first population was found along the eastern shoreline of Fishtrap Lake, LaPorte County, and was comprised of four beds, having a total coverage area of over 120 m^2. Unlike the plants of Round and Wauhob Lakes, these plants were robust and many were either in flower or had fruited profusely. Seed had set on emergent spikes of individuals closer to shore before the inflorescences on deeper plants had emerged from the water. Individual plants from Fishtrap Lake produced multiple infructescences, whereas individuals from Round and Wauhob Lakes each produced only a single infructescence. Associated species included *P. pulcher, P. pusillus* subsp. *tenuissimus,* and *P. robbinsii.*

The second population from LaPorte County was discovered in Saugany Lake (Alix and Scribailo 1998), approximately 16 km northeast of the Fishtrap population. Plants were few in number (< 25) and were found in a small bay of the lake near the west beach. A majority of these plants were growing in relatively shallow water no deeper than 1.5 m. Although plants at this site were in flower and had produced turions, no seeds were observed. Associated species included *Myriophyllum spicatum, Potamogeton amplifolius, P. foliosus* Raf. subsp. *foliosus, P. praelongus* Wulfen, *Ranunculus aquatilis* var. *diffusus, Utricularia vulgaris,* and *Zosterella dubia.*

VOUCHER SPECIMENS: Indiana: LaPorte Co., LaPorte, Fishtrap Lake, 41°38′04″N, 86°43′48″W, eastern shoreline directly NE of VFW dock, 22 Jun 1997, *Alix s.n.* (BUT); Birchim, Saugany Lake, 41°43′13″N, 86°35′13″W, in shallow water next to W beach area, 13 Aug 1997, *Alix s.n.* (BUT); Porter Co., Valparaiso, Wauhob Lake, 41°32′00″N, 87°02′40″W, off W shore near boat rental dock in water 0.75 m deep, 15 Jun 1997, *Alix s.n.* (BUT); Round Lake, 41°31′57″N, 87°02′27″W, collected from mouth of channel, 15 Jun 1997, *Scribailo 66* (PUNC).

CONSERVATION ISSUES

There are many concerns regarding the conservation of rare aquatic plant species in the state of Indiana. As previously noted, lakes of the state are typically small and shallow, making them more susceptible to anthropogenic impacts. Although efforts have been made to improve land use by adopting better management practices such as no-till farming, many lakes continue to suffer from an accelerated rate of eutrophication due to nutrient loading from agricultural runoff.

Many of Indiana's lakes have extensively developed shorelines consisting of cottages with concrete retaining walls and mowed lawns to the water's edge. Buffer strips, which would protect shorelines, provide habitat, and intercept land runoff, are underutilized in the state. Because of the importance of farming in Indiana, many farmers view ditches and creeks primarily as drainage and irrigation sources without concern for the possible impact of these practices on the waterways involved.

A major problem in assessing the status of rare aquatic plant species in Indiana is the almost complete lack of baseline historical surveys on which to base evaluations of rarity. As a result, it is difficult to ascertain whether species are rare because of habitat destruction, because lake quality has been degraded, or because they have always been rare. Issues of rarity are of particular concern with the coastal plain species discussed here. Populations of these species in the Great Lakes region are widely disjointed from their predominantly eastern ranges and may represent unique genotypes of importance to conservation (Reznicek 1994).

Most assessments of aquatic plant communities in Indiana are carried out through the Lake and River Enhancement (LARE) Program of the Indiana Department of Natural Resources (IDNR), which awards lake diagnostic grants to private consulting firms. Aquatic plant inventories are required as part of these surveys. The consulting firms involved often do not have the personnel or time to comprehensively survey and identify each species. As a result, these surveys are of limited value because they are often based on one day of collecting, during which only the most common species are identified. In addition, voucher specimens are rarely prepared or deposited for proper documentation. Condoning the preparation of voucher specimens of course assumes that the collector would assess the abundance of rare species prior to collection and possibly provide GPS coordinates as an alternative for species that are exceptionally rare.

Personnel from the IDNR are often asked to make decisions on lake projects involving such diverse issues as shoreline development, herbicide application, and dredging that may be based on the aforementioned data. An additional problem is that IDNR biologists do not typically have the necessary training or time to identify populations of rare species that might be impacted. Where herbicide application permits are required and evaluated by IDNR for public lakes, it is often the herbicide applicator that has conducted the aquatic plant inventory, raising the question of vested interest.

Herbicide treatment of aquatic plants in Indiana is a multimillion-dollar industry and is by far the most prevalent form of aquatic plant control utilized in Indiana. Unfortunately, there are no state permit requirements for application of herbicides in private lakes. Approximately 50% of Indiana Lakes are considered public because there is public access of some kind. It is important to note though, that since the larger lakes tend to be those that have public access, approximately 80% of the total acreage of Indiana lakes could probably be deemed as public (Carol New-house, Indiana Department of Environmental Management, pers. comm.).

As of July 1, 2002, changes to Indiana state law will reduce the extent to which a riparian resident can treat aquatic vegetation in a public lake without a permit. Formerly, it was not to exceed 50% of the aquatic vegetation area or one-half acre, whichever was less. The new ruling specifies not to exceed 25 ft. along the legally established, average, or normal shoreline and out to a water depth of 6 ft., which now limits the area of treatment to 625 ft^2. It is important to note that the old ruling only applied to chemical treatment, whereas the new ruling governs any type of control method. Although this change represents a positive step favoring conservation of aquatic plants, the regulation still allows multiple residents along a shoreline to eradicate major portions of the aquatic vegetation without the need of a permit. Even if permits are not required for small-scale herbicide treatment in lakes, prior notification of local DNR biologists should be required of all proposed applications, so they can assess if there might be negative impacts on rare aquatic plant species.

A major issue concerning the success of aquatic plant conservation in Indiana is the apparent lack of understanding by the public of the role of aquatic plants in lake ecosystem dynamics. People in Indiana, as in other states, typically want beaches that look like swimming pools. Few lake residents seem to make the connection between aquatic plants and the health of fish populations. This lack of understanding leads to the misconception that the aquatic plant beds can be eradicated without any effect on desirable game fish or other aspects of lake health. Lakeside residents are also seemingly unaware of the importance of aquatic plant beds in reducing shoreline erosion and trapping sediments and nutrients. Education programs are needed to enhance public awareness of the importance of aquatic plants in the maintenance of lake quality. Fortunately, Indiana recognizes many of these issues as problems, and has a variety of education and volunteer programs designed to enhance the understanding of lake residents. The state is also currently drafting more rigorous requirements for the sampling of aquatic plants during lake quality surveys.

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TAXONOMIC REVISION OF THE GENUS *MYRIOPHYLLUM* (HALORAGACEAE) IN CHINA

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ABSTRACT. A taxonomic treatment of the genus *Myriophyllum* L. (Haloragaceae) from China is presented. The distribution patterns of the species are generalized. Seven species have traditionally been recorded from China: *M. aquaticum*, *M. dicoccum*, *M. humile*, *M. spicatum*, *M. tetrandrum*, *M. ussuriense*, and *M. verticillatum*. Previous identifications of *M. humile* are incorrect and the species that occurs in China is *M. dicoccum*. Specimens previously assigned to "*M. spicatum*" can better be assigned to two distinct taxa, *M. spicatum sensu stricto* and *M. sibiricum*. Newly recorded species are: *M. alterniflorum*, *M. heterophyllum*, *M. oguraense*, *M. sibiricum*, and *M. tuberculatum*. Comments, descriptions, additional notes, specimen citations, distribution, diagnoses, and a key for the Chinese taxa of *Myriophyllum* are provided. The native species of this genus exhibit both strong warm/cool temperate affinities and tropical affinities. Four distribution patterns are generalized as follows: 1. Old World Tropics (3 species), 2. Old World Temperate (1 species), 3. North Temperate (4 species), and 4. East Asia endemics (1 species).

Key Words: *Myriophyllum*, Haloragaceae, China

Myriophyllum L. (Haloragaceae) is almost cosmopolitan. However, the distribution of approximately 60 species has three main centers: Australasia, North America, and India/Indo-China. The highest concentration of species diversity is found in Australasia with 36 species of which 31 are endemic (Orchard 1990). To date seven species have been reported from China (Li and Hsieh 1996; Wan 2000; Yan 1983): *M. aquaticum* (Vell.) Verdc., *M. dicoccum* F. Muell., *M. humile* (Raf.) Morong, *M. spicatum* L., *M. tetran-*

drum Roxb., *M. ussuriense* (Regel) Maxim., and *M. verticillatum* L. The species *M. aquaticum* and *M. dicoccum* were not reported in *Flora Reipublicae Popularis Sinicae* (Wan 2000). The purpose of this contribution is to provide an updated treatment of the genus in China. Through extensive field collections and herbarium studies we have discovered that five additional species occur in China. The discovery of these species necessitates a taxonomic treatment and geographical analysis of the genus within China.

MATERIALS AND METHODS

The present work is based on both extensive field collections and the study of herbarium specimens. We have made over 300 collections throughout China, and vouchers from field collections were deposited in WH. Collections from the following herbaria were studied: CDBI, HAST, HIB, HNR, HNWP, IBK, IBSC, IFP, KUN, N, NAS, NEFI, NTUF, PE, TAI, TAIF, TNM, WH, and WUK (abbreviations for herbaria follow *Index Herbariorum Sinicorum,* Fu 1993).

The distribution data were collected over ten years from field collections throughout China and from herbarium studies. Representative specimens are listed for each species and were selected to illustrate their geographic range in China.

KEY TO CHINESE SPECIES OF *MYRIOPHYLLUM*

1. Emergent leaves pectinate-pinnatifid, never entire nor serrate . . . . (2)
    2. Dioecious; turions not developed (only female plants in China) . . . . 2. *M. aquaticum*
    2. Monoecious; turions well developed . . . . (3)
        3. Floral leaves glaucous or light bluish-green; turions 6–8 cm long . . . . 5. *M. oguraense*
        3. Floral leaves green or light to dark green; turions 1–3 cm long . . . . 11. *M. verticillatum*
1. Emergent leaves or at least the upper ones undivided, margin entire or serrate . . . . (4)
    4. Fruits mainly 2-locular (few 4-locular in bisexual flowers), mericarps smooth or tuberculate on dorsal surface, indistinctly lineolate lengthwise . . . . 3. *M. dicoccum*

4. Fruits strictly 4-locular, mericarps aculeate or smooth on dorsal surface . . . . (5)
    5. Dioecious, fruits up to 0.75 mm long . . . . 10. *M. ussuriense*
    5. Monoecious, fruits (1–) 1.5–3.5 mm long . . . . (6)
        6. Uppermost floral leaves alternate . . . . (7)
            7. Stamens 8; fruits subcylindrical in cross section, 1.5–2.0 mm long, mericarps dorsally rounded, mostly smooth or sparsely verrucate . . . . 1. *M. alterniflorum*
            7. Stamens 4; fruits quadrangular in cross section, 2.5–3.5 mm long, mericarps dorsally acute or ridged, sparsely tuberculate and aculeate 9. *M. tuberculatum*
        6. Uppermost floral leaves verticillate . . . . . . (8)
            8. Stamens 4; floral leaves much longer than fruits in length . . . . (9)
                9. Bracteoles ovate, margin serrate, ca. 1.2 mm long; fruits rounded, longer than broad . . 4. *M. heterophyllum*
                9. Bracteoles palmatifid, lobes subulate, ca. 0.4 mm long; fruits cruciform, as long as broad . . . . 8. *M. tetrandrum*
            8. Stamens 8; floral leaves shorter than or rarely equaling fruits in length . . . . . (10)
                10. Submerged leaves usually with 7–12 pairs of segments; stems below inflorescence almost same as the lower parts in width; bracteoles ovate, longer than broad or of equal proportions; anthers 1.2–1.8 mm long . . . . 6. *M. sibiricum*
                10. Submerged leaves usually with 14–24 pairs of segments; stems below inflorescence almost double the lower parts in width; bracteoles reniform to suborbicular, broader than long; anthers 1.8–2.2 mm long . . . . 7. *M. spicatum*

TAXONOMIC TREATMENT

1. Myriophyllum alterniflorum Alph. de Candolle, Fl. Fr. Suppl. 6: 529. 1815. TYPE: FRANCE.

Perennial aquatic herb, monoecious. Stems unbranched or few-branched. Submerged leaves in whorls of (3–) 4–5, occasionally scattered, pinnate, with 8–10 pairs of 0.5–1.5 cm long, and crowded filiform segments. Inflorescence a simple spike, erect, up to 3–7 (–12) cm long, with the unisexual flowers borne in the axils of the floral leaves, upper flowers male, lower flowers female; uppermost male flowers alternate; floral bracts entire or serrate, less than twice the length of the flowers, the uppermost ones ovate or linear, entire or minutely toothed. Stamens 8. Fruits subcylindrical, 1.5–2.0 mm long; mericarps rounded on the back, sparsely verrucate, with a deep groove between them.

Myriophyllum alterniflorum is newly recorded in China. It has an erect spicate inflorescence with upper male flowers alternate. The species morphology varies considerably with its environment. Plants in China sometimes have inflorescences 6–12 cm long compared to 3 cm in European plants. Variation between North American and European forms of this species were also found. Specimens from Newfoundland have short compact leaves, which were identified as var. *americanum* by Pugsley (1938), but the variety is no longer recognized (Aiken 1981). Leaf length in this taxon is a phenotypically plastic characteristic ranging from 0.3–4.0 cm long, and Aiken (1981) noted that plants with short compact leaves are manifestations of low-nutrient environments. Harris et al. (1992) found that genetic variation exists both within and between populations of this species from northwestern Scotland. Plants from northern parts of Europe have robust stems and look like *M. sibiricum* (Aiken 1979; Aiken and McNeill 1980; Ceska and Ceska 1986). *Myriophyllum alterniflorum* and *M. sibiricum* are two distinct taxa, easily distinguished by upper floral bracts alternate and winter turions absent in *M. alterniflorum,* versus all floral bracts whorled and winter turions developed in *M. sibiricum.* The chromosome number in *M. alterniflorum* is $2n = 14$, while $2n = 42$ in *M. sibiricum.* Differences in pollen grains (e.g., wall sculpture microrugulate in *M. alterniflorum* vs. microverrucate in *M. sibiricum*) have also been recorded (Aiken 1978; Faegri 1982).

DISTRIBUTION. Central China (Anhui, Gansu, Hubei, and Jiangsu). *Myriophyllum alterniflorum* is found in the boreal and temperate zones of the Northern Hemisphere. In Europe it is most frequent in the north and west but extends south to Sicily. It is also recorded from North Africa, Russia (Okhotsk and Kamchatka), Greenland, and North America (from Newfoundland to Alaska, south to Nova Scotia, New England, northern New York, northern Michigan, and northern Minnesota).

REPRESENTATIVE SPECIMENS EXAMINED: CHINA. Anhui: Bohu Lake, 14 Sep 1993, *D. Yu 930937* (WH); Guhe, 18 Sep 1951, *Statio Orientali-Sinensis 3537* (PE, NAS); Huangda Lake, 14 Sep 1993, *D. Yu 930925* (WH). Gansu: Wudu, 21 Jul 2000, *D. Wang and Z. Q. Li 00070006b* (WH); 17 Oct 2001, *D. Wang and Y. K. Li 1079* (WH). Hubei: Baoan Lake, 16 Jul 1994, *D. Yu 947001* (WH); Liangzi Lake, 25 Aug 1993, *D. Yu 938124* (WH). Jiangsu: Yixing, no date, *J. Shen 992* (NAS).

2. Myriophyllum aquaticum (Vell.) Verdc., Kew Bull. 28: 36. 1973. Basionym: *Enydria aquatica* Vell., Fl. Flumin. 57. 1825. TYPE: BRAZIL. *J. M. da C. Vellozo,* not seen, probably lost (LECTOTYPE: *J. M. da C. Vellozo,* Fl. Flumin. Icon. 1: t. 150. 1831, designated by A. E. Orchard, Brunonia 2: 249. 1979).

Myriophyllum brasiliense Cambess., Fl. Bras. Merid. 2: 182. 1829. TYPE: BRAZIL. *A. St. Hilaire 1082* (LECTOTYPE: photograph at MPU, not seen, designated by A. E. Orchard, Brunonia 4: 33. 1980).

Myriophyllum proserpinacoides Gillies *ex* Hook. et Arn., Bot. Misc. 3: 313. 1833. TYPE: ARGENTINA. "Ditches at Buenos Ayres", *L. Gillies s.n.* (LECTOTYPE: K, designated by A. E. Orchard, Brunonia 2: 249. 1979).

Perennial aquatic or marsh-dwelling herb. Dioecious (male plants absent in China). Stems up to 1 m (or more) long, 4–5 mm in diameter, branched mostly at the base only, glaucous, rooting freely from lower nodes, glabrous. Leaves all whorled, pectinate, densely crowded, slightly dimorphic; leaf bases somewhat dilated. Submerged leaves in whorls of (4–) 5–6, oblanceolate in outline, rounded at apex, 3.2–4.0 cm long, with 25–30 linear pinnae up to 0.7 cm long. Emergent leaves glaucous, in whorls of (4–) 5–6, erect near apex, more or less spreading in lower parts, narrowly oblanceolate in outline, rounded at apex, (1.5–) 2–3.5 cm long, (0.3–) 0.5–0.8 cm wide, with (18–) 24–36 pinnae in the upper part, pinnae linear-subulate, tips very shortly apiculate, slightly incurved. Numerous pale hydathodes present at the base of leaves. Female flowers 4-merous, with a short pedicel to 0.2–0.5 mm long, borne in the axils of the middle and upper emergent leaves. Bracteoles white, subulate, with somewhat dilated base, sometimes with 1 (–2) lateral lobes, 1.0–1.5 mm long; sepals 4, white, narrowly deltoid, 0.4–0.5 mm long, 0.2–0.3 mm wide, acute, entire or scarcely serrate; petals reduced. Styles 4, clavate, 0.1–0.2 mm long, stigmas white, densely fimbriate. Ovary pyriform, 0.6–0.7 mm long, ca. 0.6 mm wide. Fruits not found. Reproduction in China is strictly vegetative.

Myriophyllum aquaticum is the most commonly cultivated and nearly naturalized species in Taiwan. It was reported by Li and Hsieh in 1996 but the species is not recorded in *Flora Reipublicae Popularis Sinicae* (Wan 2000). Up to the present, only female plants have been found in China. Several characters readily distinguish this taxon from other Asian species: plants dioecious (only females found); emergent leaves glaucous or light bluish-green; all leaves whorled, never entire, and pinnately divided with linear segments; bracteoles subulate with 1 (–2) lateral lobes; and turions not developed. As far as we know, male plants are unknown outside of its native range, and only female plants have become naturalized elsewhere. It is reported that female plants are cultivated and naturalized in warm temperate and tropical areas elsewhere in South America and in Africa, Asia, Australia, New Zealand, Europe, North and Central America, and Hawaii (Cook 1996; Li and Hsieh 1996; Orchard 1990; Preston and Croft 1997). There are no specialized vegetative propagules, and plants spread mainly by asexual means such as detached stem fragments. The species was probably introduced to China by the aquarium trade, either from Japan or from the Atlantic via the Malay Peninsula.

DISTRIBUTION. Taiwan, native to South America (East Brazil, Uruguay, Argentina, and Chile), often cultivated elsewhere in ponds or aquaria, naturalized in Central America, North America, Europe, Africa, Australia, the Pacific (New Zealand and Hawaii), Malay Peninsula, and Japan.

REPRESENTATIVE SPECIMENS EXAMINED: CHINA. Taiwan: Taipei, 19 Jun 1996, *Z. Y. Li 11005* (female; PE); Nantou, 2 Jul 1996, *Z. Y. Li et al. s.n.* (female; PE).

3. Myriophyllum dicoccum F. Muell., Trans. & Proc. Philos. Inst.

Victoria. 3: 41. 1859. TYPE: AUSTRALIA. Northern Territory: Robinson River, no date, *F. Mueller s.n.* (HOLOTYPE: MEL *62413,* not seen).

Perennial aquatic herb, monoecious or hermaphroditic. Stems 30–50 (–80) cm long, to 2 mm in diameter, sparsely branched, freely floating. Leaves alternate or whorled, dimorphic. Submerged leaves scattered or in whorls of 4–5, broadly ovate in outline, 2.0–3.0 cm long, 1.0–2.0 cm wide, spreading to recurved, with 4–10 (or more) pairs of filiform, brown-tipped, finely mucronate, 5–10 mm long segments; emergent leaves alternate, the upper ones narrowly oblanceolate to linear, 0.7–1.7 cm long, 0.5–1.5 wide, spreading or upward erect-spreading, shortly toothed above the middle or entire. The lower emergent leaves shortly pinnately divided. Bracteoles cucullate, acute, 0.7–0.8 mm long, red-hyaline. Male and bisexual flowers in irregular dichasia of 1–3 (–5), in axils of emergent leaves; female flowers borne on the submerged parts. Male flowers 4-merous, sessile; sepals 4, deltoid, ca. 0.2 mm long; petals 4, ca. 1.8 mm long, tardily caducous, red; stamens 4, anthers stiffly erect, linear-lanceolate, ca. 1.5 mm long, ca. 0.3 mm wide. Bisexual flowers similar to male flowers, ovary 4-celled, styles 4, fimbriate stigmas developing after pollen release. Female flowers 2-merous, sessile or pedicellate; sepals 2, deltoid, ca. 0.1 mm long; petals absent; ovary 2-locular; styles clavate; stigmas capitate, non-fimbriate, red. Fruit sessile, or with a short pedicel to ca. 0.2 mm long, 2-locular (in female flowers) or 4-locular (in bisexual flowers), olive-brown; mericarps cylindrical, 1.0–1.2 mm long, ca. 0.4 mm wide, truncate, smooth but minutely and sparsely tuberculate on dorsal surface, and indistinctly lengthwise lineolate on the surface, styles persistent.

Myriophyllum dicoccum is a species that has female flowers under water and emergent bisexual flowers near the water surface. The development of two types of fruits on the same plant is unique for the genus: 4-locular in bisexual flowers and 2-locular in female flowers. The bilocular submerged fruits make this species readily recognizable.

Li and Hsieh (1996) reported that *Myriophyllum dicoccum* occurs in Taiwan. We found this species also occurs in Guangdong, Guangxi, and Fujian of South China. The species was erroneously treated as *M. humile* in both *Flora of Guangzhou* (How 1956) and *Flora Reipublicae Popularis Sinicae* (Wan 2000). We have examined the original materials (*S. H. Chun 8341,* IBSC), which were cited in the *Flora of Guangzhou,* and other specimens from China which were referred to *M. humile,* and found that the cited specimens belong without exception to *M. dicoccum,* as shown by two types of fruits on the one plant and bilocular submerged fruits characteristic of the species. Furthermore, descriptions and illustrations annotated as *M. humile* by a number of authors (Chun 1964; Diao 1990; How 1956; Wan 2000; Wang et al. 1983; Yan 1983) fit *M. dicoccum.* Thus, the species *M. dicoccum* within China has long been mistaken for *M. humile.* These two taxa are easily distinguished by their fruits. In addition, *M. dicoccum* is bound to a seasonal climate and confined to Australia, East India, North Vietnam, Northeast Java, New Guinea, and northward to South China; *M. humile* occurs mainly in New England and other northeastern parts of the United States (Crow 1993; Muenscher 1944). From the available materials, it seems that *M. humile* does not occur in China.

DISTRIBUTION. South China (Fujian, Guangdong, Guangxi, and Taiwan); also occurring in almost all parts of Australia (especially northern Australia), eastern India, North Vietnam, northeastern Java, and New Guinea.

REPRESENTATIVE SPECIMENS EXAMINED: CHINA. Fujian: Liancheng, near Dongjiang, 7 Oct 1932, *Y. Ling 3775* (PE). Guangdong: Guangzhou, 30 Aug 1934, *Y. Li 10013* (IBSC); Guangzhou, Honam Island, 5 Jul 1953, *S. H. Chun 8341* (IBSC, PE); Boluo, near Luofu Mountain, 3 Oct 1978, *Guangdong Exped.-78 6410* (IBSC); Chaoan, 17 Aug 1980, *Z. C. Zhao 0488* (WH); Suixi, 5 Dec 2001, *D. Wang 1402* (WH). Guangxi: Dongxing, 23–24 Aug 2001, *D. Wang & Y. M. Huang 911, 936* (WH), 20 Nov 2001, *D. Wang 1322* (WH). Taiwan: Taipei, Neihu, 26 Sep 1939, *G. Masamune s.n.* (TAI).

4. Myriophyllum heterophyllum Michx., Fl. Bor.-Amer. 2: 191. 1803. TYPE: NORTH AMERICA.

Perennial aquatic herb, monoecious. Stems up to 100 cm. Leaves in whorls of 4–5. Submerged leaves subverticillate or scattered, crowded, up to 5 cm long, pinnately divided, with 5–12 pairs of pinnae per leaf. Spike 3–35 cm long, with flowers borne in the axils of floral bracts. Floral bracts linear, ovate or lanceolate, margin serrate or rarely entire, much longer than the length of the flowers. Bracteoles ovate, serrate, ca. 1.2 mm long and 0.6 mm wide. Flowers hermaphroditic, or occasionally female at base of inflorescence, male above. Petals 1.5–3 mm long. Stamens 4. Fruits 1.0–1.5 mm long, slightly longer than thick, subglobose, mericarps beaked and with 2 finely tuberculate ridges on the outer face.

This naturalized species is newly recorded for China. The specimen collected from southeast China by Levire (*794*, PE) was erroneously referred to *Myriophyllum verticillatum.* The specimen belongs to *M. heterophyllum* due to its blade shape. *Myriophyllum heterophyllum* has floral leaves linear, ovate or lanceolate, serrate to almost entire, while *M. verticillatum* has floral leaves pectinate or pinnate. The mericarps also differ in that *M. heterophyllum* has mericarps beaked with two finely tuberculate ridges on the dorsal surface, *M. verticillatum* mericarps are dorsally smooth.

DISTRIBUTION. Native to North America, where it extends from southwestern Quebec, Ontario, and North Dakota south to Florida and New Mexico; introduced and naturalized in Europe (southeast Austria, Britain, and Ireland) and South China (Guangdong).

REPRESENTATIVE SPECIMEN EXAMINED: CHINA. Guangdong: Guangzhou, Honam Island, 3 Oct 1917, *Levire 794* (PE).

5. Myriophyllum oguraense Miki, Bot. Mag. (Tokyo) 48: 335. 1934. TYPE: JAPAN.

Perennial submerged herb, monoecious. Stems branched mainly at the base. Leaves 4 (–5) whorled, dimorphic. Submerged leaves, ovate to suborbicular in outline, 2.4–5.7 cm long, 2.3–5.5 cm wide, pectinate with 9–13 filiform pinnae. Emergent leaves glaucous, light bluish-green, oblanceolate in outline, 4.5–6 (–9.5) mm long, 1.2–2.5 (–4) mm wide, pectinate with 7–9 (–13) linear-subulate pinnae, tips reddish brown; scale hairs present near the dorsal axils of the pinnae. Inflorescence a simple spike or sometimes with additional 2–10 lateral inflorescences; both main and lateral inflorescences 2.5–9.5 cm long, with axillary unisexual flowers subtended by two bracteoles, upper ones male, lower ones female. Bracteoles white, trifid to pectinate with 2–3 pinnae. Male flowers 4-merous, sessile; sepals 4, green, deltoid, 0.5–0.8 mm long, 0.4–0.6 mm wide; petals 4, white to pale green, 1.8–2.8 mm long, 0.8–1.2 mm wide, hooded, weakly keeled at the base, caducous at anthesis; stamens 8, filaments lengthening to 1.2–1.6

mm long at anthesis, cream; anthers linear-oblong, yellow, 1.4–2.0 mm long, 0.2–0.4 mm wide; ovary 4-locular, reduced, pale green to reddish. Female flowers 4-merous, sessile; sepals 4, 0.4–0.6 mm long, 0.3–0.5 mm wide, green, deltoid; petals 4, white, slightly hooded, 0.5–0.9 mm long, 0.2–0.4 mm wide, caducous; styles 4, short, less than 0.4 mm long; stigmas shortly fimbriate, white, pinkish after anthesis; ovary 4–locular. Fruits sessile, olive brown, shortly cylindrical; each mericarp with 2 longitudinally smooth ridges on dorsal surface and lateral longitudinal ridges at the junction with adjoining mericarps.

Myriophyllum oguraense is newly recorded in China. Its emergent leaves are glaucous, which is very rare among the native species of Chinese *Myriophyllum* and observed only in the exotic *M. aquaticum* in aquaria (see above). It is very distinct from *M. aquaticum* in floral characters and habit (for details see the key, notes under each species). In appearance *M. oguraense* is similar to *M. verticillatum* but differs in the color of the emergent leaves and the long, cylindrical turion. *Myriophyllum oguraense*, described by Miki in 1934, has been considered an endemic species to Japan since being described (Hara 1954; Iwatsuki 1992; Kadono 1994; Miki 1934, 1937; Ohwi 1953, 1975; Ohwi and Kitagawa 1992). The discovery of this species in China shows that this species is confined to East Asia with its distribution extending from China to Japan.

DISTRIBUTION. China (Anhui, Heilongjiang, Hubei, Jiangsu, Jiangxi, and Zhejiang). Found in the distributaries of the Yangtze River Basin and northeastern China; also occurs in Japan.

REPRESENTATIVE SPECIMENS EXAMINED: CHINA. Anhui: Chaocheng, 22 Sep 1951, *Statio Orientali-Sinensis 3938* (PE); Xuancheng, 18 Nov 1959, *T. Y. Liu 586* (WH); Dangtu, 30 Aug 1959, *T. Y. Liou 1018* (WH). Heilongjiang: Ningan, Jingbohu Lake, 18 Jul 1990, *D. Yu 907102* (WH). Hubei: Wuhan, Donghu Lake, 3 Oct 1993, *D. Yu 931010, 931011* (WH); Shishou, no date, *D. Yu s.n.* (WH); Ezhou, 20 May 2001, *D. Wang 699* (WH), 11 Nov 2001, *D. Wang 1271* (WH). Jiangsu: Suzhou, 13 May 1933, *H. Migo s.n.* (WH); Jintan, 18 Oct 1956, *M. B. Deng 3654* (PE). Jiangxi: Dongxiang, 30 Jul 2001, *D. Wang 808* (WH). Zhejiang: Quzhou, 11 Oct 1998, *Y. X. Chong 9810067, 9810068* (WH); West Lake, 15 Jun 1927, *H. H. Hu 1518* (PE).

6. **Myriophyllum sibiricum** Kom., Repert. Spec. Nov. Regni. Veg. Beih. 13: 168. 1914. TYPE: RUSSIA, Kamchatka River Basin,

no date, *N. F. Komarov 4855* (LECTOTYPE: LE, selected by S. G. Aiken and A. Cronquist in Taxon 37: 958. 1988).

Myriophyllum exalbescens Fernald, Rhodora 21: 120. 1919. *M. spicatum* L. var. *exalbescens* (Fernald) Jeps., Man. Fl. Pl. Calif. 691. 1925. *M. spicatum* L. subsp. *exalbescens* (Fernald) Hultén, Acta Univ. Lund. 43(1): 1159. 1947. TYPE: CANADA. Québec: Gaspé Co., York River, 29 Jul 1905, *Williams, Collins & Fernald s.n.* (HOLOTYPE: GH).

Myriophyllum spicatum L. var. *muricatum* Maxim., Bull. Acad. St.-Pét. 19: 182. 1873. TYPE: JAPAN. Yokoska, *Savatier s.n.* (LE, "syntype, not seen"); AFGHANISTAN. *Griffith 2442* (K, "syntype, not seen"); SICILY. Palermo, *Todaro 471* (K, "syntype, not seen").

Perennial aquatic herb, monoecious. Submerged leaves in whorls of 4–5, pinnately divided, with 7–12 pairs of pinnae per leaf. Inflorescence a simple spike with flowers borne in the axils of floral bracts. Floral bracts acute, shorter than or rarely equaling fruits in length, lower bracts serrate, upper ones spathulate-ovate or oblong-cochloform; bracteoles entire, ovate, longer than broad or equal. Petals absent in the female flowers. Stamens 8; anthers 1.2–1.8 mm long. Fruits 4-sulcate, globate, 1.8–2.6 mm long, 1.8–2.6 mm wide; mericarps dorsally tuberculate or aculeate.

Myriophyllum sibiricum is a newly recorded species to China. It has long been confused with *M. spicatum*. The representative characters that separate these species are, for *M. sibiricum*: 1) submerged leaves with 7–12 pairs of pinnae per leaf; 2) mericarps dorsally tuberculate or aculeate; 3) floral bracts acute and shorter than or rarely equaling fruits in length; bracteoles ovate to longer than broad; 4) anthers 1.2–1.8 mm long; 5) stems below the inflorescence have no conspicuous change in width, straight; and 6) cylindrical turions well developed, and turion leaves dark. For *M. spicatum* the representative characters are: 1) submerged with 14–24 pairs of pinnae per leaf; 2) mericarps mostly smooth or finely tuberculate on dorsal surface; 3) floral bracts rounded and equal to or longer than fruits; bracteoles reniform to suborbicular, broader than long; 4) anthers 1.8–2.2 mm long; 5) stems below inflorescence almost double the lower parts in width, very rigid, characteristically curved; and 6) turions not developed.

Myriophyllum sibiricum and *M. spicatum* have been distinguished as two distinct species by many authors (Aiken 1979; Aiken and Cronquist 1988; Aiken and McNeill 1980; Aiken and Walz 1979; Aiken et al. 1979; Ceska and Ceska 1986; Correll and Correll 1975; Löve 1961; Mathewes 1978). The taxa in North America are not readily separated on pollen morphology (Aiken 1978; Mathewes 1978). However, differences in pollen morphology were described by Faegri (1982). Also, flavonoid patterns in these two taxa are different (Ceska 1977). Both species have chromosome numbers $2n = 42$ throughout their North American range (Löve 1961).

Myriophyllum sibiricum is confined to cold temperate regions (Aiken and McNeill 1980; Ceska and Ceska 1986; Faegri 1982; Patten 1954) while *M. spicatum* is ubiquitous in boreal and temperate regions of the Northern Hemisphere, and ranges from Europe to Asia and from sub-arctic to equatorial latitudes. In their overlapping areas of distribution the species should be studied further.

DISTRIBUTION. China [Heilongjiang, Inner Mongolia, Jiangsu, Jilin, Qinghai, Sichuan, Xizang (Tibet), Xinjiang, and Yunnan]; also occurs in cold-temperate zone of northern Eurasia from Scandinavia to Kamchatka and North America.

REPRESENTATIVE SPECIMENS EXAMINED: CHINA. Heilongjiang: Heihe, 16 Aug 1988, *D. Yu 80071* (NEFI); Xinghua, 20 Aug 1988, *D. Yu 80089* (NEFI). Inner Mongolia: Kuduer, 17 Jul 1990, *D. Yu 907063* (NEFI), 29 Jun 1991, *D. Yu 916011* (NEFI), 21 Jul 1991, *D. Yu 917119* (NEFI); Arongqi, no date, *D. Yu 85030, 86153* (NEFI). Jiangsu: Jingtan, 18 Oct 1956, *M. B. Deng 3657* (PE). Jilin: near Chingpohu, 13 Aug 1931, *H. W. Kung 2063* (PE). Qinghai: Gonghe, no date, *The Geog. Pl. Exped. 487* (PE); Ulan, 9–10 Aug 1982, *Y. D. Chen & R. S. Ni 313, 322, 327, 329* (PE). Sichuan: Xikang, Yanduo, 19 Sep 1951, *Y. W. Cui 5749* (PE); Songpan, 19 Jul 2000, *D. Yu 00075051* (WH); Tangke, 21 Jul 2000, *D. Yu 00075178* (WH); Litang, 29 Jun 1992, *Z. C. Zhao 0417* (CDBI); Luhuo, 5 Jul 1992, *Z. C. Zhao 0480* (CDBI); Hongyuan, 22 Sep 2000, *D. Yu 00075210* (WH); 23 Jul 1991, *Z. C. Zhao 910147* (CDBI). Xizang (Tibet): Bangong Lake, *Y. X. Qu 62576* (NAS). Xinjiang: Chahannuoer Lake, 12 Aug 1965, *T. Y. Cheo 651386* (PE, NAS).

7. Myriophyllum spicatum L., Sp. Pl. 992. 1753. TYPE: EUROPE. Herb. Burser VII (1) 79. (LECTOTYPE: UPS, selected by S. G. Aiken and J. McNeill in J. Linn. Soc., Bot. 80: 216. 1980).

Perennial aquatic herb, monoecious. Submerged leaves in whorls of 4–5, pinnately divided, with 14–24 pairs of pinnae per leaf. Inflorescence a simple spike with flowers borne in the axils of floral bracts, the upper flowers male, the lower flowers female, with bisexual flowers between them. Floral bracts rounded, equal to or longer than fruits; the lower bracts lanceolate, pectinate; the upper bracts rhombic to elongate, entire. Bracteoles entire, reniform or suborbicular, broader than long, 0.5–0.8 mm long. Petals absent in the female flowers. Stamens 8; anthers 1.8–2.2 mm long. Fruits 4-sulcate, globate, 1.8–2.6 mm long, 1.8–2.6 mm wide; mericarps mostly smooth or finely tuberculate on dorsal surface.

Myriophyllum spicatum is found throughout China, except the northern regions of the Chang Tang Plateau (Tibet), making it the most widespread species of *Myriophyllum* in China. Described from Europe, *M. spicatum* has often been confused with *M. sibiricum.* The confused identifications especially exist in the collections from northeast and southwest China. The same result was found in studies on *M. spicatum* in North America and North Eurasia (Aiken et al. 1979; Faegri 1982). However, they are distinct taxa (for differences see the notes under *M. sibiricum*).

DISTRIBUTION. Widely distributed in Eurasia, naturalized in North America, rare in Africa and the Tropics.

REPRESENTATIVE SPECIMENS EXAMINED: CHINA. Anhui: Jingxian, no date, *D. Han 838* (NAS); Bohu Lake, 16 Sep 1993, *D. Yu 930914* (WH); Wuchanghu Lake, 20 Oct 2001, *Z. Q. Li et al. 2001100069* (WH); Huangda Lake, 14 Sep 1993, *D. Yu 930930, 930936* (WH); Quanjiao, 14 Sep 1951, *Statio Orientali-Sinensis 3705* (PE); Congyang, 23 Oct 2001, *Z. Q. Li et al.* 2001100096 (WH); Chaohu Lake, 25 Oct 2001, *Z. Q. Li et al. 2001100107* (WH). Gansu: Wudu, 21 Jul 2000, *D. Wang & Z. Q. Li 00070006a* (WH). Fujian: Xiamen, 20 Nov 1978, *G. L. Cai 00665* (PE). Guangdong: Yingde, Wentongshan, 19 Oct 1931, *H. Y. Liang 61408* (PE); Yingde, Hengshitang, 19 Aug 2001, *D. Wang & Y. M. Huang 909* (WH); Shantou, no date, *Y. D. Chen & R. S. Ni* 309 (PE). Guangxi: Yanshan, 15–17 Nov 2001, *D. Wang et al. 1275, 1295* (WH); Guiping, 28 Nov 2001, *Z. Q. Li et al. 20011100114* (WH); Luocheng, 2 Dec 2001, *Z. Q. Li et al. 20011100191* (WH). Guizhou: Danzhai, 13 Aug 2001, *Z. Q. Li & Y. Q. Yang 20010126* (WH); Duyun, 14 Aug 2001, *Z. Q. Li & Y. Q. Yang 20010147* (WH); Longli, 17 Aug 2001, *Z. Q. Li & Y. Q. Yang 20010169* (WH); Qingzhen, 19 Aug 2001, *Z. Q. Li & Y. Q. Yang 20010188* (WH); Caohai Lake, 24 Aug 2001, *Z. Q. Li & Y. Q. Yang 20010202* (WH). Hebei: Beijing, Western Hills, 20 Apr 1930, *T. N. Liou 6924* (PE); Beidaihe, 20 Aug 1951, *F. T. Wang 0116* (PE); Hsiaowutaishan (Xiaowutaishan), 17 Jun 1930, *H. W. Kung 393* (PE), 28 Jun 1931, *T. P. Wang 423* (PE); Anxin, Baiyangdian Lake, 26 Jul 1979, *Y. D. Chen & R. S. Ni 66* (WH, PE); Anxin, Beihezhuang, 18–19 May 1961, *Y. Z. Chao 48, 63* (PE); Chengde, 16 Sep 1962, *W. Wang 3011* (IFP); Miyun, *Y. D. Chen 516* (PE); Rehe, 13–17 Sep 1952, *T. N. Liou 5041, 5368* (PE, IFP); Fanshan, 28 May 1971, *Beijing Med. Exped. Fangshan-group 174* (PE); Baoding, 6 Jul 1989, *Botany teaching and research sect., Hebei Agric. Univ. 4146* (PE); Changping, 9–10 Jun 1952, *N. Y. Liu & Z. S. Zhang 5, 12,* *17* (PE). Heilongjiang: Wudaliangchi Lake, 10–15 Sep 1990, *D. Yu 908043* (NEFI); Kengka (Xingkai) Lake, 9 Aug 1987, *D. Yu 00103* (NEFI); Anda, 8 Jul 1991, *D. Yu 917066* (NEFI); Fulaerji, no date, *Jernakov 1784, 2532* (HNR); Haerbin, 28 Aug 1951, *Skvortzov & G. Z. Wang 1237* (PE); Mishan, 23 Sep 1952, *G. Z. Wang 736* (PE). Henan: Xuchang, 27 28 May 1932, *K. S. Hao 3272, 3317* (PE); Huaiyang, 24 Apr 1935, *T. S. Hwa 24* (PE); Huangchuang, 31 Jun 1959, *Henan Institute, Acad. Sin. 29183* (PE). Hubei: Donghu Lake, 29 Aug 1956, *Z. H. Qian 1640* (WH), 23 Oct 1957, *Z. H. Qian 2686* (WH), 19 Aug 1993, *D. Yu 938094* (WH); Liangzi Lake, 16 Jun 1993, *D. Yu 936101* (WH); Yunihu Lake, 21 Oct 1993, *D. Yu 931067* (WH); Honghu Lake, 30–31 Aug 1993, *D. Yu 938128, 938145* (WH); Changhu Lake, 14 Aug 1993, *D. Yu 938074, 938075* (WH); Futouhu Lake, 16 Jul 1993, *D. Yu 937168* (WH); Baoan Lake, 3 Aug 1993, *D. Yu 938014, 938036* (WH); Huangjia Lake, 28 Jul 1993, *D. Yu 937191* (WH); Qingling Lake, 30 Jul 1993, *D. Yu 937210, 937221* (WH). Hunan: Baojing, 28 Sep 1958, *L. H. Liu 09982* (PE); Dongting Lake, 23 Jun 1993, *D. Yu 936123* (WH); Lianyuan, 2 Aug 2001, *Z. Q. Li & Y. Q. Yang 20010047* (WH); Huaihua, 4 Aug 2001, *Z. Q. Li & Y. Q. Yang 20010051* (WH); Loudi, 1 Aug 2001, *Z. Q. Li & Y. Q. Yang 20010035* (WH); Liling, 16 Nov 2001, *Z. Q. Li et al. 2001110003* (WH); Youxian, 17 Nov 2001, *Z. Q. Li et al. 2001110018* (WH); Chaling, 20 Nov 2001, *Z. Q. Li et al. 2001110062* (WH); Daoxian, 24 Nov 2001, *Z. Q. Li et al. 2001110077* (WH). Inner Mongolia: Wulan, 24 Aug 1956, *X. Z. Lang 75* (PE); Xixinbaqi, 29 Jun 1951, *Z. Wang 1007* (PE). Jiangsu: Nanjing, Qixia Mt., 27 Apr 1929, *Y. L. Keng 2147* (PE); Yuntai Mt., 3 Sep 1958, *F. Y. Liu 10968* (PE); Changsu, 20 Aug 1958, *W. X. Wu 0738* (PE); Xuanwuhu Lake, no date, *S. L. Chen 26* (NAS); Hongzehu Lake, 5 Sep 1993, *D. Yu 939001* (WH); Taihu Lake, 28 Oct 2001, *Z. Q. Li et al. 2001100136* (WH); Yixing, 28 Oct 2001, *Z. Q. Li et al. 2001100146* (WH); Wuxian, 28 Oct 2001, *Z. Q. Li et al. 2001100156* (WH); Liyang, 27 Oct 2001, *Z. Q. Li et al. 2001100121* (WH). Jiangxi: Dongxiang, 31 Jul 2001, *D. Wang & Y. M. Huang 817* (WH), Pingxiang, 9 Nov 1954, *Jiangxi Exped. 2938, 2939* (PE, NAS); Poyanghu Lake, 16 Oct 2001, *Z. Q. Li et al. 2001100006* (WH); Shahu Lake, 17 Oct 2001, *Z. Q. Li et al. 2001100023* (WH); Banghu Lake, 18 Oct 2001, *Z. Q. Li et al. 2001100053* (WH). Jilin: Linjiang, no date, *Noda 824* (IFP). Liaoning: Xinmin, no date, *Y. C. Zhu 1159* (IFP); Zangwu, no date, *Z. Wang 2566* (IFP); Beizhen, no date, *Y. L. Zhang 2786* (IFP); Faku, no date, *Y. C. Zhu 581* (IFP); Panshan, no date, *C. F. Fang 128* (IFP); 26–28 Jul 1981, *Q. Y. Li & M. Q. Pan 221, 227* (WH); Benxi, no date, *Q. L. Wang 404* (IFP). Qinghai: Ulan, 11 Aug 1982, *Y. D. Chen & R. S. Ni 347* (PE); Kelukehu Lake, 7 Aug 2000, *D. Wang and Z. Q. Li 00080071* (WH). Shaanxi: Wugong, 30 Apr 1938, *S. T. Wang 405* (PE); Hsin-an, 27 Jul 1933, *C. W. Wang 61145* (PE); Yulin, Qixing River, 8 Aug 1953, *Y. W. Tsui 10420* (PE); Zhouzhi, 2 Aug 1998, *D. Wang 980802* (WH); Taibaichi, no date, *T. N. Liou & P. C. Tsoong 2408* (PE); Yulin, 19 Jul 1953, 17 Jul 1938, *K. J. Fu 6962* (PE); Hanzhong, 12–25 Aug 1998, *D. Wang 980812, 980825* (WH); Chenggu, 4 Jun 1999, *D. Wang 990604* (WH); Nanzheng, 25 Aug 1998, *D. Wang 980825* (WH). Shandong: Weishan, 9 Aug 1959, *T. Y. Cheo 6911* (PE), 19 Jul 1980, *Y. D. Chen & R. S. Ni 119* (PE), 30 Jun 1983, *G. S. Jiu 02* (PE). Shanghai: Pudong, no date, *J. X. Tan 341* (NAS); Caohe, no date, *Y. W. Law 1638* (NAS). Sichuan: Guanghan, Lianshan, 1 Sep 1939, *T. N. Liou & C. Wang 555* (PE);

Shunching, 10 May 1930, *K. S. Hao 153* (PE); Rongxian, 28 Aug 2001, *Z. Q. Li & Y. Q. Yang 20010247* (WH); Muchuan, 31 Aug 2001, *Z. Q. Li & Y. Q. Yang 20010253* (WH); Litang, 29 Jun 1992, *Z. C. Zhao 0420* (CDBI); Kangding, 24 Jun 1992, *Z. C. Zhao 0370* (CDBI); Daofu, 13 Aug 2000, *S. L. Xia & Z. H. Wu 00086031* (WH); Daochen, 28 May 1973, *Sichuan Vegtation-Exped., Daochen-group 1712* (PE); Le-po-Hsian, 28 Jul 1934, *T. T. Yu 3290* (PE); Xichang, Qionghai, 29 May 1964, *L. N. Zhao 2196* (PE). Taiwan: Taipei, NTU Campus, 2 Oct 1974, *C. M. Kuo 5897* (TAI); Taipei, Shenkeng, 12 May 1907, *T. Kawakami 5742* (HAST); Yingko, 9 Sep 1908, *S. Sasaki s.n.* (TAI); Taoyuan, Tachi, 2 Aug 1960, *L. S. Liao s.n.* (TAI); Taoyuan, 23 Oct 1990, *C. I. Peng 13,526* (HAST); Hsinchu, Hsinfeng, 6 Feb 1984, *C. I. Peng 6391* (HAST); Chiayi, 10 Feb 1969, *C. E. Devol 9014, 9016* (TAI); Chiayi, Potzu, 24 Jul 1913, *M. Kitashima s.n.* (TAI); Taitung, 8 Aug 1913, *Y. Yamamoto s.n.* (TAI). Xinjiang: Bositenghu Lake, 1 Oct 1980, *F. K. Yi 378* (PE), 11 Sep 1998, *D. Yu & S. L. Xia 98096636* (WH), no date, *Y. H. Guo X027* (WH); Buerjing, Ganasihu Lake, 14 Aug 1998, *D. Yu & S. L. Xia 9808134* (WH); Fuhai, 15 Aug 1998, *D. Yu & S. L. Xia 9808163* (WH); Akesu, 30 Aug 1998, *D. Yu & S. L. Xia 9808450* (WH). Xizang (Tibet): Lasha, 27 Aug 1965, *Y. T. Zhang & K. Y. Lang 2163* (PE); Yigong, 19 Jul 1965, *J. S. Ying & D. Y. Hong 0652* (PE); Cuomei, Zheguhu Lake, 29 Sep 2001, *D. Wang et al. 1046* (WH); Payang, 10 Sep 2000, *D. Wang & Z. Q. Li 90267* (WH); Dangxiong, 24 Aug 2000, *D. Wang & Z. Q. Li 80112* (WH); Linzhou, 18 Sep 2000, *D. Wang & Z. Q. Li 90295* (WH); Linzhi, 20 Sep 2000, *D. Wang & Z. Q. Li 90306* (WH); Dazi, 22 Sep 2001, *D. Wang 982* (WH). Yunnan: Kunming, no date, *B. Y. Qiu 70088* (HIB), 29 Jul 1982, *Q. Xia & Y. L. Ma 00003* (PE); Dianchi, 27 May 1957, *B. Y. Qiu 54048* (PE); Dali, May 1935, *C. W. Wang 63491* (PE); Jianhu Lake, 2 Nov 2000, *D. Wang 00010427* (WH); Lijiang, Jun 1935, *C. W. Wang 70588* (PE); Lashihai Lake, 3 Nov 2001, *D. Wang 00011442* (WH); Zhongdian, 31 Jul 1937, *T. T. Yu 12517* (PE); Deqin, 30 Aug 1999, *D. Wang & Z. Q. Li 990103a* (WH); Yongning, Lugu Lake, 4 May 1937, *T. T. Yu 5263* (PE); Dongchuan, 2 Sep 1932, *H. T. Tsai 51967* (PE); Zhaotong, 26 Aug 2001, *Z. Q. Li & Y. Q. Yang 20010226* (WH). Zhejiang: Ling-an, Hualong, 18 Aug 1929, *K. K. Tsoong 721* (PE); West Lake, 18 Sep 1927, *K. K. Tsoong 1505* (PE); Wuxing, no date, *F. X. Liu 1685* (NAS); Huzhou, 10 Sep 1959, *Zhejiang Exped. 29756* (PE); Yongkang, 9 Nov 1993, *Q. F. Wang 109* (WH).

8. Myriophyllum tetrandrum Roxb., Fl. Ind. 1: 470. 1820. TYPE: EAST INDIA. W. Roxburgh, Icones Roxburghianae, pl. 551 (HOLOTYPE: plate 551 at K, not seen).

Perennial aquatic herb, monoecious. Stems few branched. Submerged leaves in whorls of (4–) 5(–6), 3.0 4.0 cm long, 10–11 mm wide, pinnately divided, with 10–16 pairs of pinnae per leaf. Lowermost emergent leaves pinnate with 9–13 pairs of short lobes, rather stiffly spreading, lobes 0.4–0.6 mm long; middle and upper emergent leaves in whorls of 5, lanceolate to linear-lanceolate in outline, 4.0–5.0 mm long, 1.0–1.5 mm wide, with 6–12 pairs of erect-spreading, subulate, brown-tipped, very acute lobes. Inflorescence a simple spike with axillary, unisexual flowers, upper ones male, lower ones female. Bracteoles digitately lobed, 0.6–1.0 mm long. Sepals triangular, 0.15–0.2 mm long, 0.1–0.15 mm wide, entire or finely serrate, acute. Petals spatulate, 1.0–1.5 mm long, ca. 0.4 mm wide, entire, caducous after anthesis. Stamens 4, anthers oblong, 0.6–0.8 mm long. Fruits cruciform, ca. 2.0 mm long, ca. 2.0 mm wide, mericarps ovate, with convex back and flattened sides, irregularly and finely tuberculate to smooth.

The Chinese *Myriophyllum tetrandrum* was first reported by Chun (1964); no fruit description was given. Based on the specimens collected by S. K. Lau (*5743*, IBSC), the fruit is cruciform, mericarps ovate and smooth, with convex back and flattened sides.

Myriophyllum tetrandrum and *M. indicum* Willd. are closely allied but distinct species. Their similarities are: monoecy, pinnately or digitately dissected bracteoles, fruits ca. 2 mm long, ovate mericarps, finely tuberculate to smooth. They differ in that *M. tetrandrum* has 4 stamens, oblong anthers 0.6–0.8 mm long, petals 1.0–1.5 mm long, and is confined to Northeast India and Indo-China; *M. indicum* has 8 stamens, linear anthers 1.5–1.8 mm long, petals 1.5–2 mm long, and is found in Ceylon and South Deccan (Cook 1996; Meijden and Caspers 1971). Differences in pollen grains also exist (Praglowski 1970).

DISTRIBUTION. Hainan Island; also occurs in the eastern and northern parts of India, South Thailand, North Vietnam, and Malay Peninsula.

REPRESENTATIVE SPECIMEN EXAMINED: CHINA. Hainan: Yai-hsien District (Yaxian), 19–29 Mar 1935, *S. K. Lau 5743* (IBSC).

9. Myriophyllum tuberculatum Roxb., Fl. Ind. 1: 471. 1820. TYPE: EAST INDIA.

Perennial aquatic herb, monoecious. Stems much branched. Leaves usually heterophyllous; submerged leaves in whorls of 4–5, 2.5–4.0 cm long, 1.0–1.5 cm wide, pinnately divided, with 8–25 pairs of filiform lobes, the lobes 1–2 cm long; emergent leaves in lower part like the submerged ones but smaller, the upper ones ultimately alternate, with less and shorter lobes, the uppermost ones entire, spathulate to linear, 5–20 mm long. Floral bracts leaf-like; bracteoles rhomboid, serrate, 1.2 mm long, 0.8 mm wide, acute. Flowers borne in axils of emergent leaves, the lowest sometimes female, followed by bisexual ones, with male ones above. Sepals orbicular, 0.1–0.25 mm long and wide, finely serrate or entire. Petals 4, 0.5–1.5 mm long, white. Stamens 4; anthers elliptical to oblong, 0.5–1.0 mm long. Fruits quadrangular, 2.5–3.5 mm long and wide, with sharp longitudinal ribs, both ribs and furrows with pointed tubercules.

Myriophyllum tuberculatum is a newly recorded species to China. *Myriophyllum tuberculatum* may be confused with *M. indicum*. They differ in that *M. tuberculatum* has: 1) stamens 4; 2) anthers elliptical-oblong, 0.5–1 mm long; 3) the upper floral leaves alternate; 4) bracteoles rhomboid, serrate, acute; and 5) fruit quadrangular in transverse section, with sharp longitudinal ribs, both ribs and furrows with pointed tubercules, mericarps dorsally acute. *M. indicum* has: 1) stamens 8; 2) anthers linear, 1.5–1.8 mm long; 3) upper floral leaves whorled; 4) bracteoles pinnate or digitate; and 5) fruit cruciform in section, mericarps ovate, finely tubercled or smooth. *Myriophyllum tuberculatum,* in addition, is confined to South and Southeast Asia. Records of *M. tuberculatum* from Australia (Aston 1977; Cook 1996; Meijden 1969; Meijden and Caspers 1971) have proven to be erroneous (Orchard 1990).

DISTRIBUTION. South China (Guangdong); also occurs in India, Bangladesh, Myanmar, the northern Malay Peninsula, southeast Borneo, and Sunda Islands.

REPRESENTATIVE SPECIMENS EXAMINED: CHINA. Guangdong: Ying-Tak (Yingde), Wentongshan, 19 Oct 1931, *H. Y. Liang 61409* (PE); Yingde, Hengshitang, 18 Aug 2001, *D. Wang & Y. M. Huang 883* (WH).

10. Myriophyllum ussuriense (Regel) Maxim., Mélanges Biol. Bull. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 19: 182. 1873.

Myriophyllum verticillatum L. var. *ussuriense* Regel, Fl. Ussur. 60. 1861, tab. 4, fig. 2–5. TYPE: RUSSIA. between Songacha River and Kengka (Xingkai) Lake, Aug 1859, *R. Maack s.n.* (HOLOTYPE: LE, not seen).

Perennial aquatic or marsh herb, dioecious (very rarely monoecious). Stems weak, 5–20 cm high, emergent parts with crisped hairs. Leaves in whorls of (2–) 3 (–4). Emergent leaves entire or serrate with 1–2 pairs of lobes, linear or lanceolate, the lower ones pinnately parted with 3–13 pairs of laciniae. Flowers sessile, borne in axils of emergent leaves; bracteoles 2, elliptic, 0.4 mm long, 0.15 mm wide, entire or serrate; sepals tubular with 4 lobes; petals 4, obovate, concaved, pale reddish; stamens 8, filaments 0.4 mm long, anthers 1.3 mm long, 0.3 mm wide; styles 4, stigmas white, long-fimbriate. Fruits subglobate, 4-sulcate, olive-brown, ca. 0.75 mm long, 0.6 mm wide; mericarps rounded on the back, finely tuberculate or rugulate.

Regel (1861) published the variety *Myriophyllum verticillatum* var. *ussuriense,* based on specimens from Kengka (Xingkai) Lake; the taxon was raised to specific level by Maximowicz (1873). This species occurs from the cold temperate areas of northeastern China south to subtropical areas of eastern and southeastern China. Collections from northeastern China are typical. They differ from those of southeastern China in being smaller in almost all of their parts. The species is variable throughout its range and in China is probably a complex. Further detailed studies are needed to understand fully the variations both within and between populations of this species. Meijden (1969) and Meijden and Caspers (1971) stated that *M. ussuriense* differs from *M. propinquum* only in minor vegetative characters and treated the taxon as a synonym of *M. propinquum.* Aston (1977) and Wan (2000) followed the same treatment. However, Orchard (1979) found these taxa to be separate species. *Myriophyllum propinquum* is typified by a New Zealand collection and occurs in Australia and New Zealand while *M. ussuriense* is found in China, Russia, Korea, and Japan. *Myriophyllum ussuriense* differs from *M. propinquum* in the shape and size of its bracteoles and smaller flowers, which are often hermaphroditic. In recognizing two distinct taxa we are following Huang (1977), Li and Hsieh (1996), Maximowicz (1873), Orchard (1979, 1990), and Yu (1992).

DISTRIBUTION. China (Anhui, Guangdong, Heilongjiang, Hubei, Jiangsu, Jiangxi, North Taiwan, and Zhejiang); also occurs in the Far East of Russia, Korea, and Japan.

REPRESENTATIVE SPECIMENS EXAMINED: CHINA. Anhui: Anking, 22 Jun 1941, *Migo s.n.* (NAS). Guangdong: Dinghu Mountain, 12 Apr 1966, *G. L. Shi & K. M. Zhang 2711* (PE); Guangzhou, 22 Jun 1953, *S. H. Chun 8335* (IBSC).

Heilongjiang: Hebei, 5 Nov 1990, *D. Yu 901364* (NEFI); Luobei, near Fengxiang, Aug–Sep 1955, *C. S. Wang 286* (IFP); Huma, 15 Jul 1950 *Y. C. Zhu 137, 138* (WH, PE); Hongxing, no date, *T. Y. Ding 56* (IFP). Hubei: Liangzi Lake, 25 Aug 1993, *D. Yu 938101, 938102* (WH); Baoan Lake, 6 Jul 1994, *D. Yu 947004* (WH). Jiangsu: no date, Suzhou, *Migo s.n.* (NAS). Jiangxi: Feng Dezhen, 25 Jun 1963, *M. X. Nie 07497* (stamens 6, 2 reduced; PE); Tsoongjen, 10 Jul 1932, *Y. Tsiang 10246* (NAS). Taiwan: Taipei, 19 Jun 1996, *Z. Y. Li 11006* (male; PE); Taoyuan, 21 Apr 1929, *S. Sasaki s.n.* (male and female; TAI); Taoyuan, Nankan, 5 May 1929, *Y. Kudo 578* (male; TAI), 5 May 1929, *Y. Yamamoto s.n.* (male; TAI); Hsinchu Co., Hukou, no date, *H. Simada 4343B* (female; TAI). Zhejiang: Jiangshan, Jianglang, 8 Nov 1929, *Y. Tsiang 3133* (IBSC); Quzhou, 10 Oct 1998, *Y. X. Chong 9810053* (WH).

11. Myriophyllum verticillatum L., Sp. Pl. 2: 992. 1875. TYPE: EUROPE. (LECTOTYPE: the left-hand specimen on Linn. 1123. 3, designated by S. G. Aiken and J. McNeill in J. Linn. Soc., Bot. 80: 219. 1980).

Perennial aquatic or marsh herb, monoecious. Stems robust, branched or unbranched. Leaves in whorls of 4–6. Submerged leaves pectinate with 8–16 pairs of filiform pinnae. Inflorescence a simple spike 7–25 cm long, erect, with flowers borne in the axils of floral bracts, with males in the upper, females in the lower, and a few hermaphrodite flowers between them. Floral bracts pinnate or pectinate, never entire, 1–5 times as long as the flowers, the lower as the submerged leaves, the upper lanceolate to linear-lanceolate with 8–10 pairs of rather stiff lobes; bracteoles pectinate or absent. Petals ca. 2.5 mm in male flowers, strongly reduced in female flowers. Stamens 8. Fruits ovoid or subglobose, ca. 3 mm long, smooth.

Myriophyllum verticillatum is widespread in the temperate regions of the northern hemisphere. Variability exists, especially in plants from south, north, and west China. Plants can persist as a terrestrial form for brief periods, and in this state the plants may be as small as 3 cm in length, leaves ca. 1 cm long with as few as 4 leaf-segments. Such terrestrial specimens from China can be mistaken for *M. ussuriense.* Diao (1990) discovered two variations in this species from Lijiang county, Yunnan Province in China; one with petals elongate, tardily caducous, stigmas coarsely papillose; the other, with petals not elongate, soon caducous, stigmas feathery. These variations require reinvestigation and should be treated with caution, as this species is phenotypically plastic. In North America, some varieties that had long been applied to this species are no longer recognized (Aiken 1979, 1981). Some authors state that the best field characters for identifying this species are floral bracts that are always divided, and the clavate winter turions that are formed along the stem during the late summer (Crow and Hellquist 1983; Weber and Nooden 1974). In Asia, *M. verticillatum* is easily distinguished in that all floral bracts well surpass the flowers and are laciniate-pinnatifid to the top of the spike.

DISTRIBUTION. Found in central, north, and southwest China. In Asia: east to Kamchatka and Japan, south to Afghanistan and Kashmir; North America: Canada, from British Columbia to Newfoundland, south to Maryland and California; Europe: north to Lapland, not in Iceland and Greenland; found in mediterranean Africa, as well.

REPRESENTATIVE SPECIMENS EXAMINED: CHINA. Hebei: Beidaihe, 20 Jun 1930, *W. Y. Hsia 1914* (PE); Fanshan, 18 Aug 1971, *Beijing Med. Exped. Fanshan-Group 657* (PE); Beijing, Summer Palace, 3 Jul 1953, *F. Zhao 0355* (PE); Beijing, 6 Sep 1935, *S. T. Wang 264* (PE), 18 Aug 1953, *F. Zhao 0433* (PE), 8 Oct 1951, *S. Y. Li & L. W. Xu 0145* (PE); Pinggu, 13 May 1972, *Beijing Med. Exped. 119* (terrestrial form; PE); Beijing, Prince Park, 17 Jun 1930, *T. N. Liou 6925* (PE), 8 Jun 1931, *T. P. Wang 210* (PE), 4 Oct 1930, *T. N. Liou 6927* (PE); Baiyangdian Lake, 27 Jul 1979 *Y. D. Chen & R. S. Ni 68* (PE, WH), 14 Jul 1959, *Botany teaching and research sect., Hebei Agricult. Univ. 4221* (PE). Heilongjiang: Jiayin, 13 Aug 1988, *D. Yu 80054* (NEFI); Maoershan, no date, *D. Yu 85023* (NEFI); Dailing, 24 Jul 1988, *D. Yu 80016* (NEFI); Huma, 20 Aug 1988, *D. Yu 80240* (NEFI); Meixi, 10 Aug 1988, *D. Yu 80042* (NEFI); Ning-an, Jingbo Lake, 10 Sep 1981, *G. S. Zhou & Y. D. Chen 513* (PE), 15 Jul 1990, *D. Yu 907063* (NEFI); Dongjingcheng, 16–19 Jul 1990, *D. Yu 907075, 907112* (NEFI); Daqing, 8 Jul 1991, *D. Yu 917064* (NEFI); Qiqihaer, no date, *Z. S. Qin 104* (IFP); Mishan, no date, *G. Z. Wang 736* (IFP); Acheng, 10 Aug 1951, *Skvortzov & G. Z. Wang 1082* (PE). Inner Mongolia: Arongqi, no date, *D. Yu 85006, 85058* (NEFI); Erkenaqi, 24 Aug 1951, *Z. Wang 2061* (PE, IFP); Yimengzhashakeqi, Daerhute, 9 Jul 1956, *Huanghe Exped. 7295* (PE); Kuduer, 4–21 Jul 1991, *D. Yu 917055, 917105* (NEFI); Zalantun, no date, *Z. S. Qin 86* (IFP), no date, *Skvortzov 3485* (IFP); Wushentai, 5 Jul 1963, *Geog. Dept. of Peking University IM-164* (PE). Jiangsu: Nanjing, no date, *F. X. Liu 210* (NAS). Jilin: Huichun, no date, *C. S. Wang 2391* (IFP); Helong, 8–11 Sep 1959, *Yianbian-Group II 664, 769* (terrestrial form; PE); Antu, 27 Aug 1959, *Yianbian-Group II 393* (IFP). Liaoning: Faku, no date, *Y. C. Zhu 579* (IFP); Xinmin, no date, *Y. C. Zhu 1165* (IFP); Zhengjiatun, 6 Jun 1950, *Noda 113* (terrestrial form; PE, IFP). Shaanxi: Yulin, 26 Aug 1957, *T. P. Wang 18246* (HIB); Shanxi: Yongji, 25 Apr 1964, *C. G. Li 130* (PE). Sichuan: Ganzi, 8 Jul 1992, *Z. C. Zhao 0494* (CDBI); Hongyuan, 22 Jul 2000, *D. Yu 00075319* (WH); Ruergai, 20 Jul 2000, *D. Yu 00075102* (WH); Ruergai,

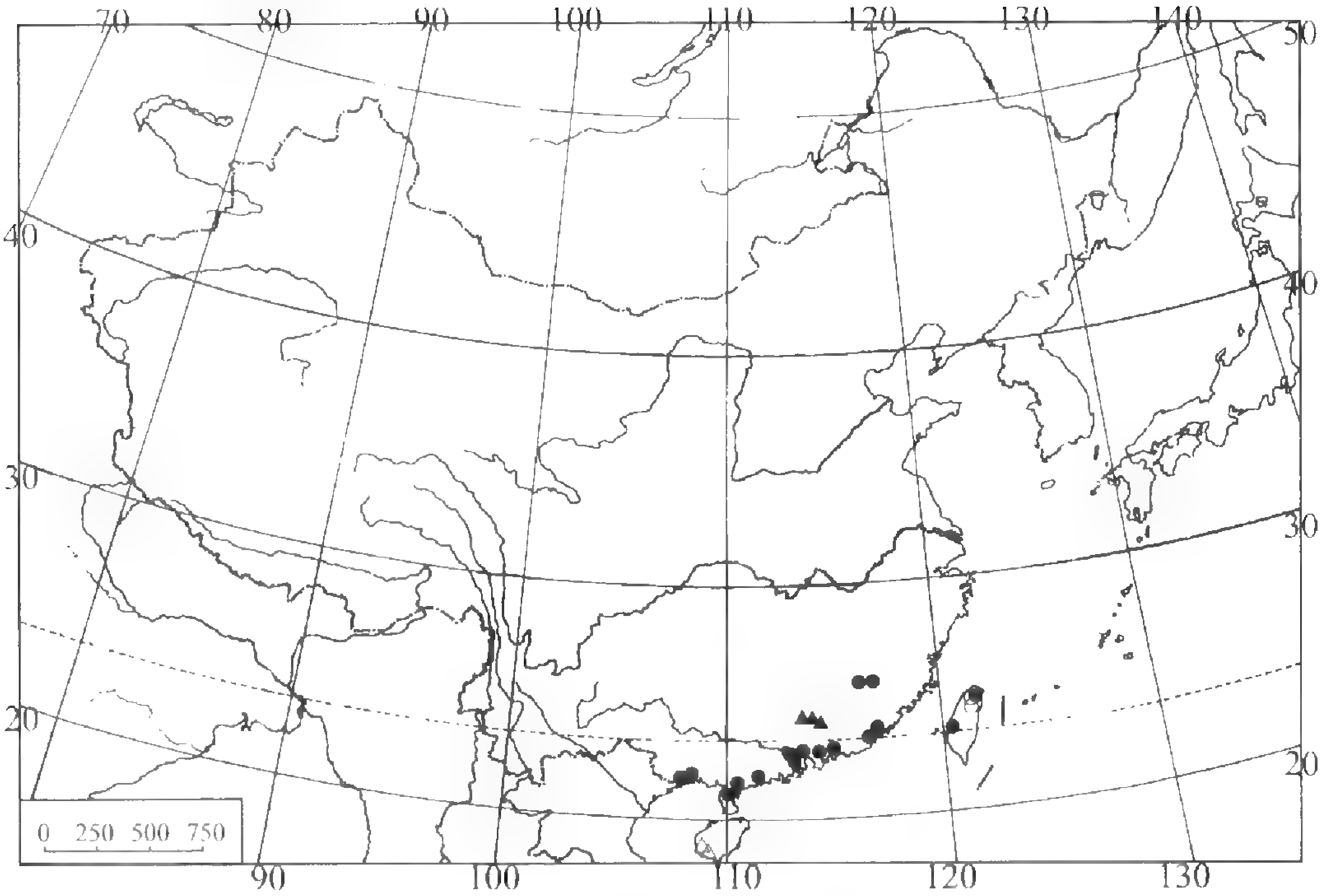

Figure 1. Distribution of Old World Tropical *Myriophyllum* in China. *M. dicoccum* (●), *M. aquaticum*, naturalized (○), *M. tuberculatum* (▲), and *M. tetrandrum* (△).

23 Oct 2001, *D. Wang & Y. K. Li 1152* (WH); Waqie, 22 Jul 2000, *D. Yu 00075228* (WH). Xinjiang: Cahannuoer Lake, 13 Aug 1965, *T. Y. Cheo 651412* (NAS); Tacheng, 16 Aug 1998, *D. Yu & S. L. Xia 9808221* (WH); Habahe, 10–11 Aug 1998, *D. Yu & S. L. Xia 9808032, 9808038, 9808058* (WH); Fuhai, 15 Aug 1998, *D. Yu & S. L. Xia 9808164* (WH); Zhaosu, 26 Aug 1998, *D. Yu & S. L. Xia 9808377* (WH); Kuche, 28 Aug 1998, *D. Yu & S. L. Xia, 9808414* (WH). Xizang (Tibet): Ritu, 15 Aug 1976, *Qinghai-Xizang Exped. 9071, 9079* (PE); Ali, 6 Sep 2000, *D. Wang & Z. Q. Li 00090239* (WH). Yunnan: Lijiang, Jul 1935, *C. W. Wang 71181* (PE), 1 Sep 1999, *D. Wang & Z. Q. Li 990128* (WH), 4 Sep 2001, *D. Wang 946* (with flowers and fruits; WH); Heqing, Caohai Lake, 14 Nov 2000, *D. Wang 114796* (WH); Kunming, Apr 1935, *C. W. Wang 62948* (PE). Zhejiang: Ningbo, 22 Jun 1934, *P. J. Tsoong 309* (PE); Hangzhou, 15 Jun 1927, *H. H. Hu 1518* (PE).

DISTRIBUTION PATTERNS

Following Takhtajan's (1978) regionalization of the world flora, and referring to Good's (1974) scheme, the species distribution patterns of Chinese *Myriophyllum* (excluding the naturalized species *M. aquaticum* and *M. heterophyllum*) can be generalized as: 1) Old World Tropics (Figure 1), *M. dicoccum, M. tetrandrum,* and *M. tuberculatum*; 2) Old World Temperate (Figure 2), *M. ussuriense*; 3) North Temperate (Figures 2 and 3), *M. alterniflo-*

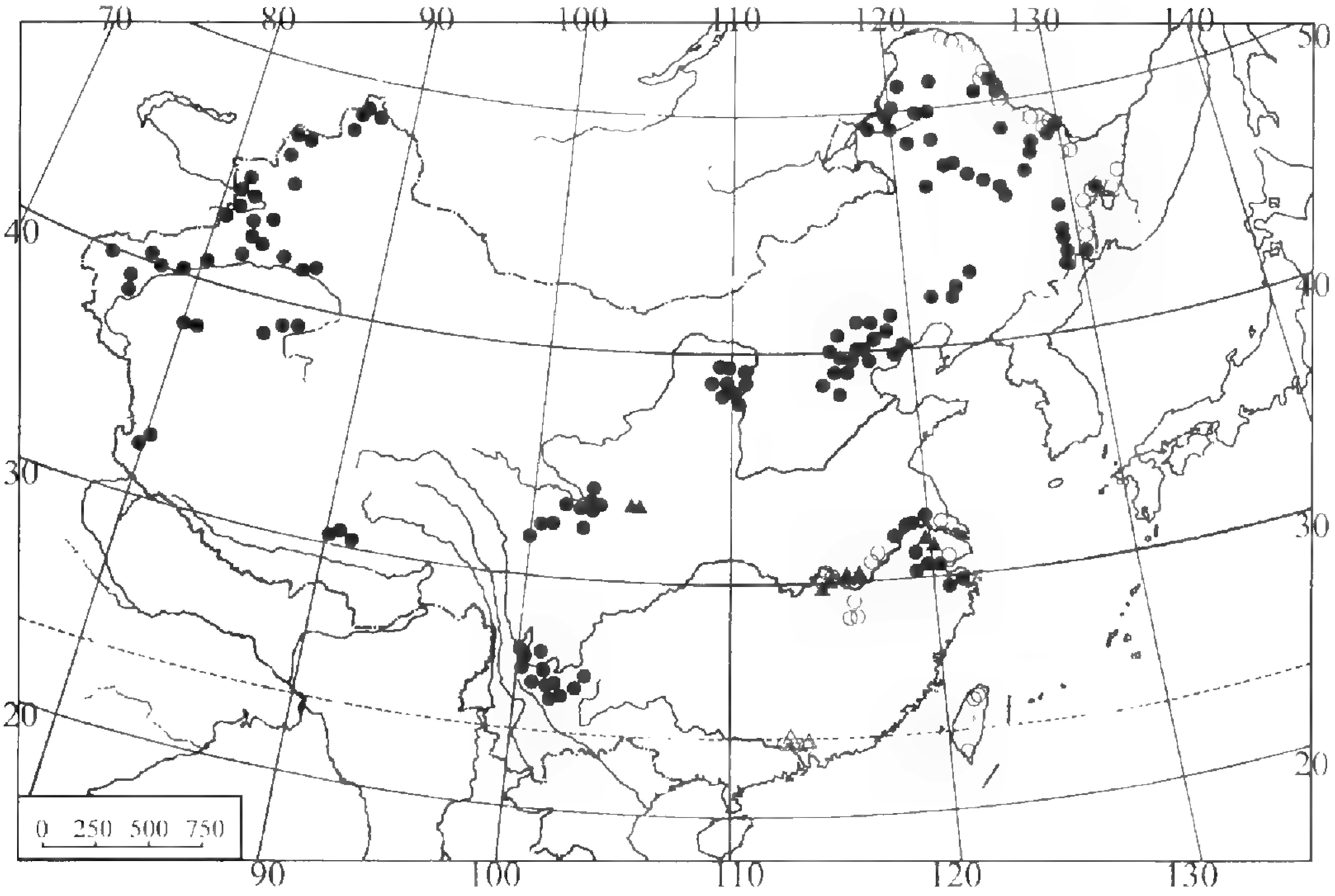

Figure 2. Distribution of Temperate *Myriophyllum* in China. *M. verticillatum* (●), *M. ussuriense* (○), *M. alterniflorum* (▲), and *M heterophyllum*, naturalized (△).

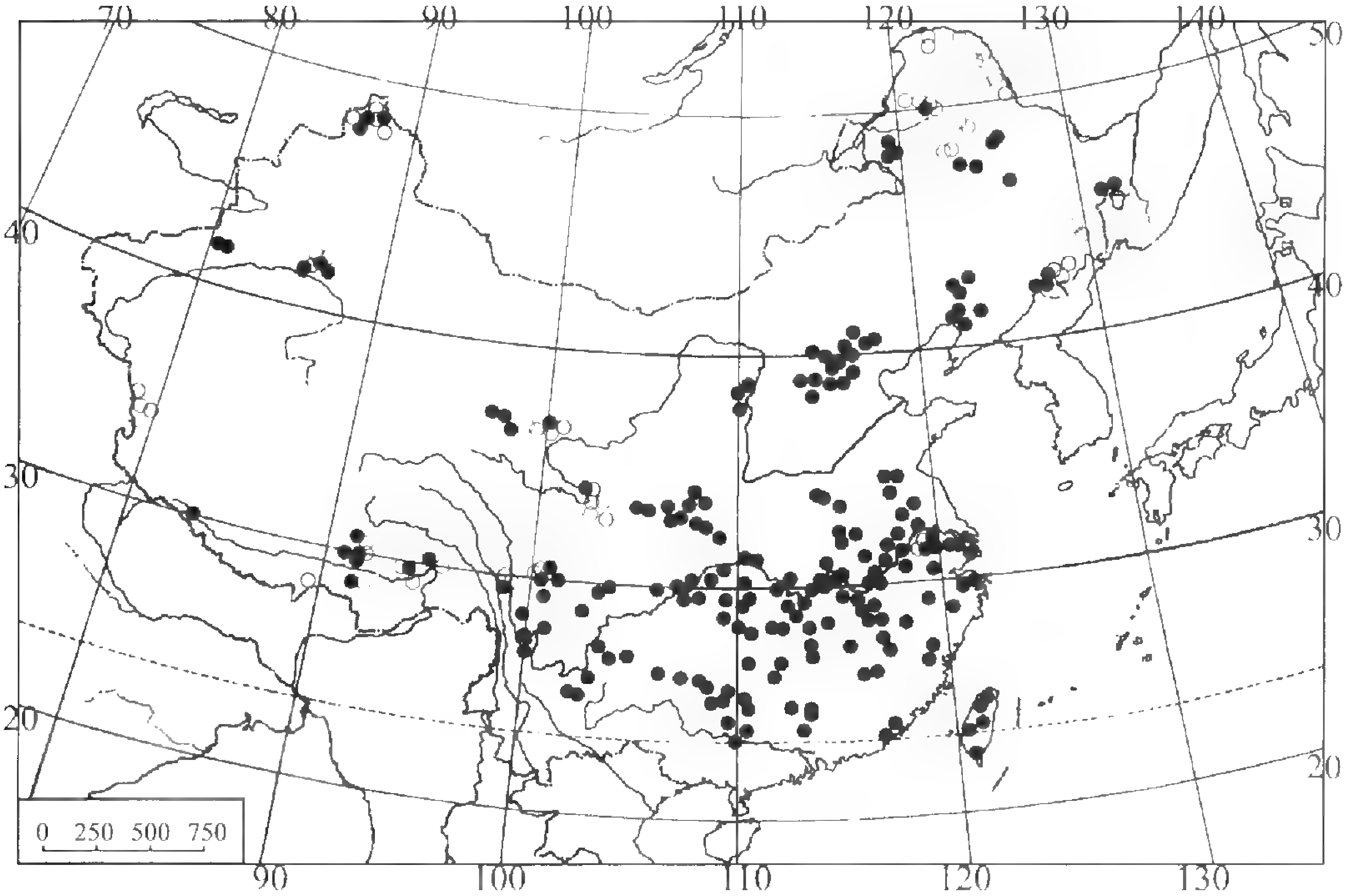

Figure 3. Distribution of the widespread species, *Myriophyllum spicatum* (●), and its allied species, *M. sibiricum* (○). Both species have North Temperate affinities in China.

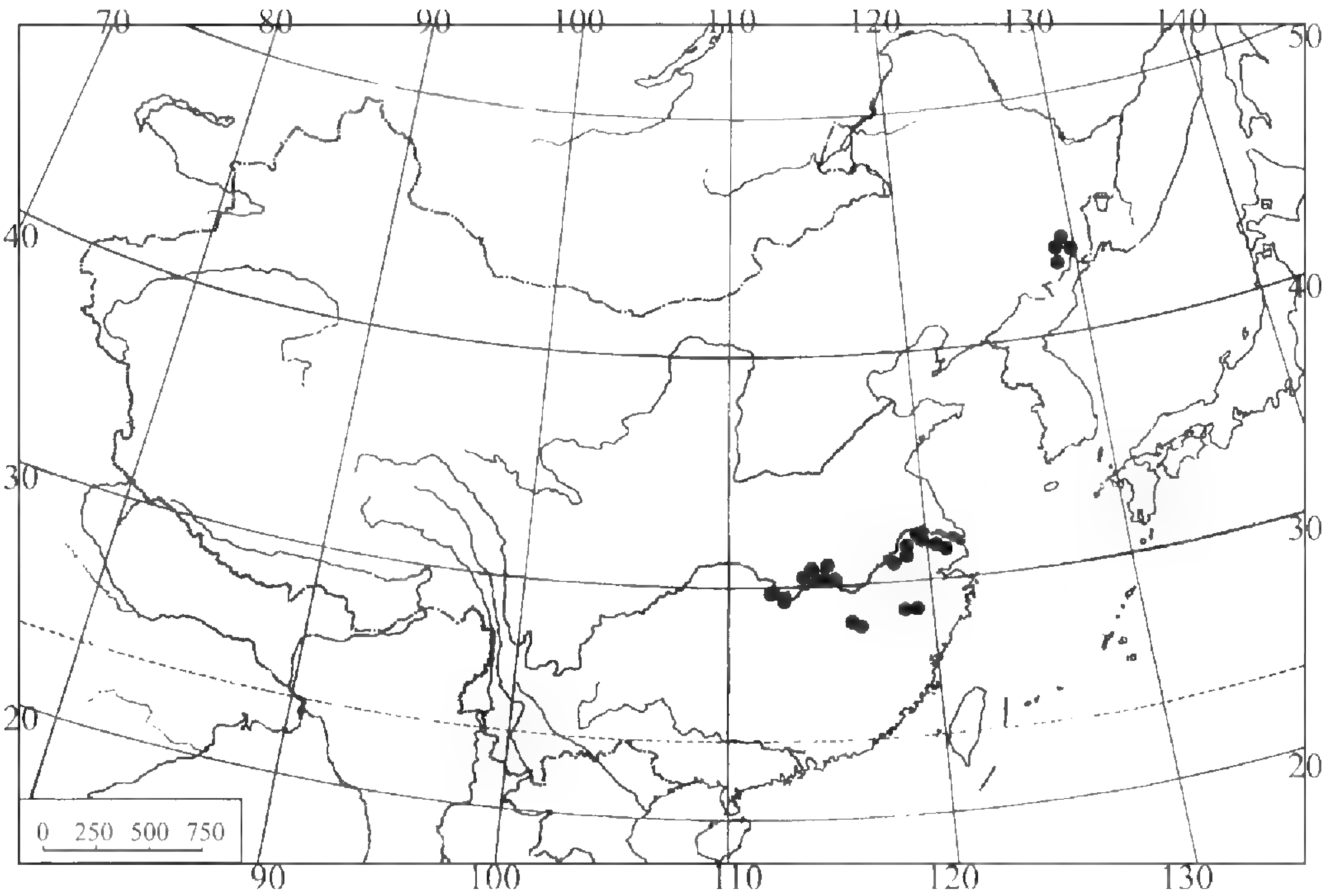

Figure 4. Distribution of East Asian endemic, *Myriophyllum oguraense* (●), in China.

rum, M. sibiricum, M. spicatum, and *M. verticillatum*; and 4) East Asia endemics (Figure 4), *M. oguraense.* Thus, *Myriophyllum* is found in four major regions of China, and the distribution of Chinese *Myriophyllum* consists of North Temperate, Old World Tropical, and East Asia endemic elements.

The species exhibiting strong tropical affinities and having an Old World Tropics distribution are on the northern borders of their geographical ranges. Of them, *Myriophyllum dicoccum* occurs in Tropical Asia and Tropical Australasia, while *M. tetrandrum* and *M. tuberculatum* occur in Tropical Asia (Indo-Malesia).

The remaining six species are of strong warm/cool temperate affinities that belong to Old World Temperate, Temperate Asian, and East Asia distributions. Of the six, *Myriophyllum ussuriense,* has an Old World Temperate distribution and occurs in Temperate Asia, and *M. oguraense* is an endemic species to East Asia and has a Sino-Japanese disjunct distribution. The others are confined to a North Temperate distribution. Among them, *M. spicatum* and *M. verticillatum* are almost widespread in the temperate regions of the northern hemisphere and have much wider geographical distributions than the others. The species *M. sibiricum* is confined to cold temperate regions and *M. alterniflorum* to the boreal and temperate zones of the northern hemisphere.

ACKNOWLEDGMENTS. We express our sincere thanks to the curators of the following herbaria for access to specimens: CDBI, HAST, HIB, HNR, HNWP, IBK, IBSC, IFP, KUN, N, NAS, NEFI, NTUF, PE, TAI, TAIF, TNM, WH, and WUK. We are indebted to two anonymous reviewers for constructive comments on the manuscript, and to Susan G. Aiken for helpful critiques on the original manuscript. This work was supported by the State Key Basic Research and Development Plan of China (G2000046801-1) and the Natural Science Foundation of China (39830060, 30070061, 30170172, and 30270098).

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NEW ENGLAND NOTE

NEW RECORDS FOR *CHENOPODIUM FOGGII* IN NEW ENGLAND

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Chenopodium foggii Wahl is a rare annual herb native to eastern North America. It currently possesses a global rank of G3Q (fewer than 100 world occurrences, questionable taxonomy; Pennsylvania Natural Diversity Inventory 2001). Unlike many familiar species of goosefoots, such as *C. album* L., it occurs in non-anthropogenic habitats. *Chenopodium foggii* is frequently located on rock outcrops, at cliff bases, and along sparsely wooded slopes (Wahl 1954). It is closely related to, and sometimes included in, western *C. pratericola* Rydb. (Clemants 1992; Gleason and Cronquist 1991). *Chenopodium pratericola,* however, is adventive in the east where it is found in open, disturbed, often saline soil (e.g., coastal beaches, salted roadsides; Seymour 1982). Although Basset and Crompton (1982) recognized *C. foggii* in their review of the genus in Canada, they apparently confused important morphological characters, as suggested also by Clemants (1992). *Chenopodium foggii* will be recognized as a distinct species in the upcoming *Flora of North America* contribution (Clemants and Mosyakin, in prep.). This paper presents results of recent field and herbarium surveys for *C. foggii* in New England.

Chenopodium foggii is a relatively recent addition to the flora of North America. It was described by Wahl (1954) during a North American revision of the genus. *Chenopodium foggii* is typically a short, sparingly branched plant with moderately farinose surfaces, keeled sepals, horizontally oriented fruits, and a loose or irregularly rupturing, minutely echinate pericarp that detaches from the body of the lustrous black seed. It shares these character states with *C. pratericola. Chenopodium pratericola,* however, has thicker, less often toothed, and narrower leaves than *C. foggii.*

Historic New England occurrences. Along with his description, Wahl (1954) documented nine occurrences of *Chenopodium foggii* in New England (summarized in Table 1 and discussed below). Sites were identified by herbarium specimen review and not by field survey. Since its description, *C. foggii* has not been reported from New England.

Both of the specimens Wahl cited from Maine are old records (i.e., prior to 1900) and were found in areas of the state that have been heavily developed since. Furthermore, the herbarium label data are vague and no detailed location information was recorded.

Historic New Hampshire stations of *Chenopodium foggii* were mainly in open, rocky woods and cliff bases. Three of the sites reported by Wahl are in the northern half of the state, and one collection (Walpole, Chesire County) is from extreme southwestern New Hampshire. The most recent collection reported by Wahl was from 1920. Examination of specimens at NHA by the first author yielded three additional collections of *C. foggii* from Mount Stanton, in Bartlett (6 Jul 1965, *Hodgdon et al. 14504*; 2 Aug 1960, *Steele s.n.*; 26 Aug 1954, *Steele 1531*). All three collections had been misidentified as *C. boscianum* Moq., a frequently used and inappropriate name for the eastern *C. standleyanum* Aellen. No extant sites of *C. foggii* are known from the state, and recent surveys of the Harts Ledge have not re-located the species (Bill Nichols and Dan Sperduto, New Hampshire Natural Heritage Inventory, pers. comm.).

Wahl cited a single record from Vermont, and no other occurrences are known (Bob Popp, Vermont Nongame and Natural Heritage Program, pers. comm.). Vermont is currently the only state in New England to list this plant as a species of conservation concern (Vermont Nongame and Natural Heritage Program 2000), though it is listed incorrectly under the name of *Chenopodium desiccatum* A. Nelson.

Wahl listed only two sites for Massachusetts, though a third site is known from Hampden County by a 1916 collection annotated by Wahl in 1963 (Karen Searcy, University of Massachusetts Herbarium, pers. comm.). Weatherbee (1996) considered *Chenopodium foggii* to be uncommon in Berkshire County. Bruce

Table 1. Collections of *Chenopodium foggii* attributed to New England by Wahl (1954). Collection numbers are not provided in the table as they were not cited by Wahl and Harvard University Herbaria collections were not available during research for this manuscript.

County	Town	Location	Date	Collector and Herbarium
Massachusetts				
Berkshire	New Marlboro		28 Aug 1920	*Hoffman* (NEBC)
Berkshire	Mount Washington	Bash Bish Falls	9 Sep 1919	*Hoffman* (NEBC)
Maine				
Androscoggin	Auburn		21 Jun 1896	*Merrill* (NEBC)
York	South Berwick		3 Sep 1898	*Parlin* (GH, NEBC)
New Hampshire				
Carroll	Bartlett	Whites Ledge	8 Sep 1915	*Pease* (NEBC)
Cheshire	Walpole	Fall Mountain	31 Jul 1900	*Fernald* (GH)
Coos	Hadleys Purchase	Harts Ledge	9 Sep 1915	*Pease* (NEBC)
Grafton	Haverhill		18 Aug 1917	*Fernald* (NEBC)
Vermont				
Orange	Fairlee		4 Aug 1928	*Pease* (NEBC)

Sorrie (formerly of the Massachusetts Natural Heritage and Endangered Species Program, pers. comm.) considered this species to be very rare in Massachusetts and did not encounter it during floristic work in the state.

It is surprising to note that given the lack of current records for this species in New England, *Chenopodium foggii* has received very little conservation focus and has been formally listed by only one of the six states. Confusion with the adventive *C. pratericola* has likely contributed to its being overlooked in the northeast.

Field observations. On 3 October 1999, the primary author visited Bartholomew's Cobble in Sheffield, Berkshire County, Massachusetts. This well-known feature adjacent to the Housatonic River comprises low outcrops of dolomitic marble (DeLorme 1998). Both mesic and xeric substrates occur, supporting a large number of calciphilic plants. A relatively small *Chenopodium* was observed on a dry, open terrace with southwest aspect. Morphology, in particular keeled, moderately farinose sepals, small leaves (less than 4 cm long) with few or no teeth, and horizontally oriented fruits in the calyx, suggested the population could be *C. foggii*. Examination of the fruits at 20× confirmed this, and the identification was verified by Steven Clemants (Brooklyn Botanic Garden). The site was characterized by exposed bedrock and sparse, stunted *Juniperus virginiana* L. Associated species included *Aquilegia canadensis* L., *Rubus occidentalis* L., *Schizachyrium scoparium* (Michx.) Nash, *Carex cephaloidea* (Dewey) Dewey, *Woodsia obtusa* (Spreng.) Torr., *Hypericum perforatum* L., and *Achillea millefolium* L. The location was approximately 195 m above mean sea level. This is the only known extant site in Massachusetts.

Bartholomew's Cobble is owned by the Commonwealth of Massachusetts and managed by the Trustees of Reservations. State employees have been made aware of the occurrence of *Chenopodium foggii* and its rarity in New England. The specimen, which includes a color image of the plants *in situ*, has been deposited at the New England Botanical Club Herbarium.

VOUCHER SPECIMEN: Massachusetts: Berkshire Co., Sheffield, Bartholomew's Cobble, 3 Oct 1999, *Haines s.n.* (NEBC).

On 21 July 2000, we visited a *Polygonum douglasii* Greene station on Cedar Mountain in Parsonfield, York County, Maine. The site occurs on a small, open bald of Devonian-Silurian limestone (Osberg et al. 1985). We observed a relatively small *Chenopodium* in flower that did not appear to match any species known to be extant in the state. The plants were generally shorter than 30 cm with moderately farinose surfaces. The leaf blades did not exceed 4 cm in length and were essentially entire. Though characteristics of the sepals could be observed, such as a well-formed keel, fruit size and details of the pericarp were not assessable. The flowering morphology and associated natural community suggested this plant could be *C. foggii.* As this species had not been seen in Maine for 102 years, a return trip was made by the second author to collect a fruiting stem and confirm the identification.

The specimen collected from Cedar Mountain demonstrated the pericarp morphology for *Chenopodium foggii* (e.g., minutely echinate texture, non-adherant). *Chenopodium foggii* is similar, in regard to the freely separable pericarp, to another uncommon eastern forest species that is historically known to occur in Maine, *C. standleyanum.* The keeled sepals and farinose habit, however, distinguished the Cedar Mountain plants from *C. standleyanum,* which has unkeeled sepals and nearly glabrous herbage. The identification was confirmed by Steven Clemants.

The Cedar Mountain site is the only known extant station of *Chenopodium foggii* in Maine. Associated species include *Polygonum douglasii, Carex backii* Boott, *Poa compressa* L., *Rumex acetosella* L., *Aquilegia canadensis, Corydalis sempervirens* (L.) Pers., *Saxifraga virginiensis* Michx., *Stellaria graminea* L., and *Dryopteris marginalis* (L.) A. Gray. The station occurs at ca. 260 m elevation and has southern aspect. The property owners are aware of the plant and plan to conserve the area. The specimen has been deposited in the University of Maine Herbarium.

VOUCHER SPECIMEN: Maine: York Co., Parsonfield, Cedar Mtn., 18 Sep 2000, *Newcomer s.n.* (MAINE).

Herbarium survey. An herbarium survey was initiated by the New England Wild Flower Society to collect information on rare and poorly known native species. The goal of this research, called the Herbarium Recovery Project, is to verify the accuracy of collections in regional museums and gather label information for 532 species in New England. *Chenopodium foggii* is a target species of this project. While examining material at the Harvard University Herbaria, the primary author annotated three specimens as *C. foggii.* The New Hampshire specimen was collected while in flower, and although the morphology and habitat matches that of *C. foggii,* it cannot be identified with certainty. However, the specimen is an apparent duplicate of one cited by Wahl (1954). Steven Clemants has also reviewed these sheets and concurred with the determinations. This represents the first report of *C. foggii* from Connecticut.

SPECIMENS EXAMINED: Connecticut: New Haven Co., New Haven, East Rock, dry rocky wooded waste, 14 Sep 1932, *Eames 11488* (GH). New Hampshire: Cheshire Co., Walpole, Fall Mountain, rocky woods, 31 Jul 1900, *Fernald 423* (GH). Vermont: Rutland Co., West Rutland, Twin Mountains, 15 Aug 1900, *Williams 2077* (GH).

Chenopodium foggii is a poorly known and overlooked species in New England. The premature inclusion of this species in the synonomy of *C. pratericola* has likely reduced the intensity of field efforts that may have resulted in its earlier rediscovery. *Chenopodium foggii* fits criteria for a Division 1 species in New England (globally rare with fewer than 100 world occurrences; Brumback and Mehrhoff et al. 1996). Field surveys should be directed toward locating new and historic populations, particularly in high pH bedrock regions.

ACKNOWLEDGMENTS. The following people contributed to this note and are thanked: Steven Clemants; Bill Nichols, Dan Sperduto, Bob Popp, Karen Searcy, Bruce Sorrie, Thomas Vining, and Pamela Weatherbee. The New England Wild Flower Society is also thanked for permission to use data collected during the Herbarium Recovery Project.

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NOTE

THE DELETION OF *CYPERUS HERMAPHRODITUS* (CYPERACEAE: *TETRAGONI*) FROM THE LOUISIANA FLORA

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Fieldwork in Louisiana produced collections of *Cyperus thyrsiflorus* Jungh. (*Rosen 789, 1084*, NO). We reviewed Thomas and Allen (1993) for information on the distribution of *C. thyrsiflorus* in Louisiana and found this species synonymized under *C. hermaphroditus* (Jacq.) Standl., a putative, yet largely allopatric Neotropical ally of the poorly circumscribed Section *Tetragoni* (Carter and Jones 1997). This classification problem also occurs in the *Manual of the Vascular Plants of Texas* (Correll and Johnston 1970), erroneously extending the range of *C. hermaphroditus* into the southeastern United States. In his revision of the Mexican species of *Cyperus,* Tucker (1994) also included Texas in the distribution of *C. hermaphroditus.* Preparation of the *Vascular Plants of Texas* by Jones et al. (1997) brought to light that the name *C. hermaphroditus* had been misapplied to specimens of *C. thyrsiflorus,* thus necessitating the deletion of *C. hermaphroditus* from the Texas flora. In Horvat's (1941) revision of the subgenus *Mariscus,* she reported a collection of *C. hermaphroditus* from Arizona, and an evident "fugitive" from Alabama, apparently the only collections for North America. The remaining collections are from Central America, South America, and Mexico. We have examined specimens identified as *C. hermaphroditus* from Louisiana (NLU, NO) and found them to be *C. thyrsiflorus* and *C. pilosus* Vahl. We, herewith, wish to continue the clarification of the taxonomic confusion associated with these two species in the southeastern United States by proposing the deletion of *C. hermaphroditus* from the Louisiana flora.

The following key separates *Cyperus thyrsiflorus* from *C. hermaphroditus* and *C. pilosus.* Though *C. hermaphroditus* does not occur in Louisiana, it is included for comparison. *Cyperus pilosus* apparently has often been mistaken for *C. thyrsiflorus* in Louisiana, and therefore is included in the key. Pertinent synonymy following Jones et al. (1997), a brief description modified from Tucker (1994) and Carter and Jones (1997), and an illustration of *C. thyrsiflorus* are also provided.

KEY

1. Rachis glabrous .... (2)
   2. Spikelets remote, 7–9 per 5 mm rachis span in proximal half of rachis; achenes narrowly elliptic to oblong, 0.5–0.65 mm wide .... *C. thyrsiflorus*
   2. Spikelets more congested, 18–26 per 5 mm rachis span in distal half of rachis; achenes elliptic to oblong to narrowly obovate, 0.6–0.8 mm wide .... *C. hermaphroditus*
1. Rachis antrorsely strigose .... *C. pilosus*

Cyperus thyrsiflorus Jungh. Linnaea 6: 24. 1831. Figure 1.

[= *C. anceps* Liebm., *C. dissitiflorus* C. Nees *ex* Torr., *C. pallens* (Liebm.) Standl. & Steyerm., *C. regiomontanus* var. *pallens* (Liebm.) Kük., *C. tribrachiatus* (Liebm.) Kük., *Mariscus dissitiflorus* (C. Nees *ex* Torr.) C. B. Clarke, *M. pallens* Liebm., *M. tribrachiatus* Liebm.]

Rhizomatous perennial, 20–40 cm tall. Mid-culm diameter 0.5–1.5 mm, trigonous, smooth. Leaves 0.8–2.8 (–3.0) mm wide. Inflorescence rays (2–) 3–6; peduncles conspicuous; inflorescence bracts 5–7. Spikes oblong to subglobose; spikelet length 3.4–7.4 (–17.0) mm, mostly divaricate; scale length 2.0–3.0 mm long, veins and margin whitish. Stigmas 3, stamens 3, mature achenes 1.8–2.1 mm long, 0.4–0.45 mm wide, trigonous, brown. Infrequent in dry-mesic woods, more common in waste places and disturbed areas from Florida west to Texas, the Caribbean, Mexico, and South America.

SPECIMENS EXAMINED: Louisiana: Ascension Parish, 18 May 1999, *Rosen 789* (NO); Avoyelles, 11 Oct 1985, *Thomas et al. 94088* (NLU); Cameron Parish, 6 Sep 1984, *Thomas et al. 90803* (NLU); East Baton Rouge Parish, 17 Jul 1934, *Chilton & Trotter 104* (NLU); Iberia Parish, 22 Jun 1983, *Thomas & McCoy 84393* (NLU); Jefferson Parish, 11 Sep 1980, *Darwin 1922* (NLU);

Figure 1. *Cyperus thyrsiflorus.* A. spikelet showing overlapping fertile scales (bar = 1 mm); B. habit (bar = 1 cm); C. spike showing oblong shape and remote, mostly divaricate spikelets (bar = 1 mm). Drawn from *Rosen 789.*

Orleans Parish, 28 Jul 1974, *Thomas et al. 40637* (NLU); Plaquemines Parish, 4 Sep 1978, *Fleming 395* (NO); St. Bernard Parish, 17 Jun 1960, *Lemaire 628* (NO); St. Tammany Parish, 28 Apr 2000, *Rosen 1084* (NO); Terrebonne Parish, 16 Jun 1991, *Thomas et al. 123938* (NLU); Vermilion Parish, 11 Jul 1989, *Slaughter 997* (NLU); West Feliciana Parish, 14 Aug 1972, *Curry et al. 469* (NLU).

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NEW BOOKS

Annotated Checklist of the Vascular Plants of the Washington—Baltimore Area: Part II, Monocotyledons by Stanwyn G. Shetler and Sylvia Stone Orli. 2002. 95 pp. (softcover). Published by Botany Section, Department of Systematic Biology, National Museum of Natural History, Smithsonian Institution, Washington, DC. [complete checklist is available in pdf format at www.nmnh.si.edu/botany/projects/dcflora]

Field Guide to Liverwort Genera of Pacific North America by W. B. Schofield. 2002. viii + 228 pp. illus. line drawings. ISBN 0-295-98194-6 $25.00 (softcover). Published by the Global Forest Society in association with the University of Washington Press, Seattle and London.

Plant Systematics: A Phylogenetic Approach, Second Edition by Walter S. Judd, Christopher S. Campbell, Elizabeth A. Kellogg, Peter F. Stevens, and Michael J. Donoghue. 2002. xvi + 576 pp. illus. line drawings; black & white photos. ISBN 0-87893-403-0 $86.95 (hardcover). Sinauer Associates, Inc., Sunderland, MA. [companion CD-ROM with over 2200 color photographs included]

The Wild Orchids of Arizona and New Mexico by Ronald A. Coleman. 2002. xiii + 248 pp. illus. 32 plates of color photos; dot distribution maps. ISBN 0-8014-3950-7 $39.95 (hardcover). Cornell University Press, Ithaca, NY.

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NEBC MEETING NEWS

September 13 Field Trip. Fourteen NEBC members assembled in a light, misty rain at Kettle Pond in Groton State Forest, Vermont, for a leisurely field trip. Art Gilman introduced the area and pointed out the salient landscape features. Groton State Forest is the largest state-owned parcel in Vermont with nearly 26,000 acres of managed forest lands. The area is underlain by the granitic Knox Mountain pluton, which outcrops in the numerous hills, and the soils are acidic and relatively nutrient-poor, being derived from glacial till of mostly local origin.

Leaving the parking lot, the first item of interest was a severe gall problem noted on the leaflets of *Rhus typhina*; these large (marble-sized) hollow galls were filled with insects that Don Miller tentatively identified as Homoptera (*Aphis*). Further along the trail, the ericaceous shrub community dominant along the shoreline of Kettle Pond included *Kalmia angustifolia, Vaccinium myrtilloides, Chamaedaphne calyculata, Rhododendron groenlandicum,* and *R. maximum.* Also present were typical associates such as *Ilex verticillata* and *Nemopanthus mucronatus,* the latter in particularly handsome fruiting condition. The numerous shrubs of *R. maximum* were observed in healthy condition despite their location near the eastern wind-exposed shore of the pond. They bore numerous capsules and had obviously flowered abundantly this year. Here and at other stations in Groton State Forest the species is disjunct from its main range by approximately 100 miles.

The group next crossed Route 232 to the old railroad bed, now a popular hiking trail. Underneath a large granite boulder along the side of the trail was a small stand of the uncommon luminous moss, *Schistostega pennata.* Due to drought conditions, the typically reflective protonemal mat could not be observed, but the tiny feather-like fronds were readily observed with a hand lens.

A short hop by car brought the group to Owl's Head, by which time the rain had stopped and the clouds lifted to provide excellent views of Kettle Pond and the southern portions of the Forest. The bald granite knob, although highly trampled by hikers and sightseers, nevertheless provided numerous items of botanical interest. *Potentilla tridentata* and *Solidago simplex* subsp. *randii* var. *randii* were evident, and various shadbushes (*Amelanchier* spp.) were discussed without reaching consensus. A highlight for many was a small tree of the high-elevation *Sorbus decora* (here at 1900 ft.) with large orange fruit and short blunt leaflets. This was easily compared to an adjacent specimen of *S. americana* with smaller, slightly redder fruit. A brief search for *Rhododendron canadense,* although known from Owl's Head, failed to reveal this emblem of the Club's official publication.

On the short hike down to the parking lot, Melanie Schori pointed out script lichen (*Graphis scripta*) on the bark of several trees, and Don Lubin was able to find a small stand of *Diphasiastrum habereri.* At the end of the trip, the skies promptly cleared to bright sunshine as members returned to their cars for the trip to St. Johnsbury for the evening meeting.

September 2002. The evening meeting was held at the Fairbanks Museum and Planetarium in St. Johnsbury, Vermont. Vice President Arthur Gilman introduced Marcia Spencer-Famous, who spoke to the Club on "The Feasibility of Peatland Restoration." Marcia and her husband, Norm Famous, have teamed to study the possibility of restoring raised peatlands following extraction, or mining, of the peat. This issue has become of special interest because extraction of horticultural and fuel peat using processes that drain and remove peat over large areas started in the twentieth century. In North America, most of such activity is in Canada, with only limited extraction in the United States.

Marcia began by reviewing the formation of raised peatlands (raised bogs), stressing that the hydrologic regime of these systems results from a peat accumulation process, which takes thousands of years and is an integral part of the resulting ecosystem. Because horticultural peat, being largely the partially decomposed remains of *Sphagnum,* retains water in large amounts, such systems are similar to saturated sponges with the upper layers above the regional groundwater level. They can range from relatively simple systems to large complexes that are a mosaic of multiple domes, secondary ponds, and a variety of other wetland types, as Marcia amply illustrated with aerial photographs. In addition to *Sphagnum,* raised bogs host a suite of plants adapted to acidic conditions, low nutrient availability, and saturated organic soils. In addition to woody ericads, some plants commonly found in raised peatlands include *Rubus chamaemorus, Geocaulon lividum, Calopogon tuberosus,* and *Eriophorum vaginatum* var. *spissum.*

Production of horticultural peat involves developing a bog by excavating perimeter (primary) ditches, installing cross-drains called field (secondary) ditches, removing vegetation over large areas, and crowning the areas between the field ditches to form mining fields. During the summer each year, the surface is scarified to promote air-drying and the top ¼ to ½ inch of peat is mechanically vacuumed or removed using a milling process. Typically, up to 4 inches of peat is removed per year. Until the last two decades, in-kind restoration of peatlands abandoned after mining was not a priority, but today's environmental laws and ethics are forcing a new look at the situation.

When merely abandoned, mined bogs present a variety of environmental problems that make reestablishment of any wetland vegetative cover, not to say restoration to original community, extremely difficult. High soil acidity, low and/or changed nutrient levels, changes to the soil structure and the hydrologic regime, drought-like surface conditions (caused by drainage and crowning of the fields) alternating with seasonally flooded conditions, wind erosion, water erosion during storm events, hydrophobic surface crusting, and frost heaving all are difficult to overcome.

Investigations into natural recolonization patterns have found that plant succession does not follow the pattern of the original bog development. Typical pioneers are cotton grasses (*Eriophorum* spp.) and birches (*Betula* spp.). Cotton grasses typically die after 10–15 years, but their tussocks form moist microniches, sometimes aiding the slow return of *Sphagnum.* However, *Sphagnum,* so critical to the community, is not typically a pioneer genus and may not colonize for several decades. Under good conditions, bog species such as crowberry (*Empetrum nigrum*), leatherleaf (*Chamaedaphne calyculata*), and other ericads, or larch (*Larix laricina*) colonize eventually, but total cover may not happen for an extended period. For example, after 20 years poorer sites may have only 5–10% cover, while sites with better growing conditions may achieve 50–75% cover. The best sites may achieve 100% vegetative cover, but even when this occurs the results are usually not equivalent to the original peatland community. For example, one abandoned extraction area developed a complete cover of leatherleaf (*C. calyculata*), but still had no *Sphagnum* established within it.

To obtain a self-sustaining wetland plant community, a number of conditions, especially soil saturation, are required. Rewetting is sometimes achieved by blocking drainage ditches, leveling crowned fields, creating berms to retain precipitation on site, and flooding, where possible. Even with such manipulation, sites are often not wet enough to support establishment of *Sphagnum.* Studies of a particular system in England found that the community established today, 500 years after the initial extraction of peat, was still dissimilar to the original community. Thus, while plant communities can eventually become established on peat extraction sites, restoration to a state equivalent to the original peatland is not likely to be achieved in the short term, especially if plans for development are not made with restoration principles in mind.

Much research has been conducted over the past two decades in Europe, Canada, and, to a lesser extent, the United States. Investigations into the recolonization of *Sphagnum,* rewetting techniques, and edaphic changes from drainage, among other topics, have led to a better understanding of mined peatland management. This knowledge has facilitated the development of management recommendations for restoring mined peatlands to functional ecosystems, if not to their original condition.

—ARTHUR V. GILMAN, Recording Secretary *pro tempore.*

October 2002. President Paul Somers introduced Past-President C. Barre Hellquist who spoke to the Club on "Dodging crocodiles in tropical Australia for aquatic plants." Barre spoke at length of his tenth trip to Australia since the 1981 Botanical Congress (Sydney), which served as a follow-up trip to his 1997 sabbatical research. Like that past sabbatical endeavor, this two-month expedition included teaming up with Surrey Jacobs of the Royal Botanic Garden – Sydney. This fieldwork focused primarily on the aquatic genus *Nymphaea,* the water-lilies.

Barre's quests for aquatic plants took him from the northernmost point on the mainland, the tip of the Cape York Peninsula in Queensland, through the rugged Kimberley at the northern end of Western Australia. In all, this venture carried him by train, plane, automobile, and helicopter to some of the most remote places for fieldwork.

Australia is home to numerous plants adapted to its permanent or temporary freshwater bodies, and serves as the center of diversity for several groups. The essentially cosmopolitan Menyanthaceae is centered there with three of its five aquatic genera, including *Nymphoides* (water snowflakes). This genus is most diverse in Australia with 20+ species, including *N. exigua, N. cristata,* and *N. indica.* The often-aquatic Haloragaceae is also most diverse in Australia with about 20 species of *Myriophyllum* (water mil-foils) alone, including *M. latifolium* and *M. verrucosum.*

Australia also boasts the world's largest water-lilies and arguably some of the most beautiful tropical water-lilies. The genus *Nymphaea* (Nymphaeaceae) is well represented (subgenera *Anecphya, Brachyceras,* and *Lotos*) in the country and often presents itself as a taxonomic challenge. Unusual flower colors and morphological variations are plentiful, and upon further study may be the basis for the naming of new species or hybrids. For example, the marked floral variation found in *N. violacea* calls into question its current taxonomic limits. Typically this species has fragrant blue flowers with short stipules. However, atypical white flowered, long-stipuled populations have been found lacking fragrance. Other populations have exhibited unusual purple-striped sepals and peduncles, yet with otherwise typical flowers.

Low Lake in Queensland, which serves as a dumping ground for troublesome crocodiles, hosts a remarkable population of *Nymphaea atrans.* This is typically a "changeable" species, in which the flower color gradually changes over the course of blooming from bluish-white to pink to dark red. At this locale, however, the flower color remains constant during the days of anthesis. Other unusual variations include an odorless night-blooming *N. pubescens*; a diminutive, faint-smelling, day-blooming *N. noucheli*; and a white-flowered *N. immutabilis.* There was a special variant discovered in Queensland with less bronze-colored foliage and purple flowers that may be described as a new species.

In the Kimberley region, one of Australia's last frontiers, other notable Nymphaeaceae were observed. An unusual population of "*Nymphaea immutabilis*" was found as well as typical *Ondinea purpurea. Ondinea* is the only monotypic genus in the water-lily family and is endemic to Australia. Attempts to cultivate this genus, as well as other Australian water-lilies, have been largely unsuccessful.

—DONALD J. PADGETT, Recording Secretary *pro tempore.*

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