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EVIDENCE FOR HYBRIDIZATION OF TWO OLD WORLD *RHAMNUS* SPECIES—*R. CATHARTICA* AND *R. UTILIS* (RHAMNACEAE)—IN THE NEW WORLD

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ABSTRACT. A highly variable, fully fertile population of *Rhamnus* that was first established in Ann Arbor, Michigan, circa 1952 was studied to identify the species present and determine whether some individuals were of hybrid origin. Specimens of four taxa hypothesized as being present in the population—*R. cathartica, R. davurica* var. *davurica, R. davurica* var. *nipponica,* and *R. utilis*—were used to establish reference clusters using a canonical discriminant analysis. Results of the discriminant analysis suggest that the population is a hybrid swarm and that only *R. cathartica* and *R. utilis* were involved in the formation of the hybrids at the study site. Additional analyses with the computer program HYWIN corroborated the results of the discriminant analysis, enabled circumscription of putative hybrids, and for each hybrid provided a pair of specimens in the data set that best matches the morphologies of its parents. Utilization of both discriminant and HYWIN analyses in studies of hybrid swarms appears complementary and effective.

Key Words: Rhamnaceae, *Rhamnus, R. utilis, R. cathartica,* introduced species, hybrid swarm, North America, Michigan, discriminant analysis, HYWIN

Rhamnus is a wide-ranging genus comprising up to 150 species of Temperate and Tropical zones of both hemispheres. It is abundant in eastern Asia and southwestern North America and adjacent Mexico (Rehder 1940; Brizicky 1964; Johnston and Johnston 1978; Cronquist 1981; Mabberley 1987). In North America the genus is represented by about 25 species, including several introductions from Europe (Wolf 1938).

A highly variable, fully fertile population of *Rhamnus* was discovered by Reznicek in 1984 in Washtenaw County, Michigan. This population included some plants that clearly were *R. cathartica* L. Yet, some individuals with larger, narrower leaves resembled the Asian species *R. davurica* Pall. var. *davurica* or *R. davurica* var. *nipponica* Makino. Other individuals with larger, longer blades, but short petioles, resembled *R. utilis* Decne. [*R.*

davurica Pall. var. *davurica*—*R. citrifolia* (Weston) W. J. Hess & Stearn var. *citrifolia,* not *R. citrifolia* Rusby (Hess and Stearn 1979, 1981). *Rhamnus davurica* var. *nipponica* Makino—*R. nipponica* (Makino) Grubov (1949a); *R. citrifolia* (Weston) W. J. Hess & Stearn var. *nipponica* (Makino) W. J. Hess & Stearn (1979); *R. davurica* subsp. *nipponica* (Makino) Kartesz & Gandhi (1994)]. A substantial number of plants could not be placed reasonably with any of these species and were suspected of being hybrids. All four taxa are closely related members of subsection *Cervispina* Moench (Weberbauer 1895; Wolf 1938; Grubov 1949a), and all have the chromosome number $2n = 24$, as determined by Dolcher (1963), Mulligan (1961), and Wulff (1939) for *R. cathartica*; Li (1988) for *R. davurica* var. *davurica* and *R. davurica* var. *nipponica*; and Bowden (1945) for *R. utilis.*

Rhamnus cathartica is native in Europe and western and northern Asia east to northwestern China. Though rarely cultivated now, it was introduced to North America presumably as an ornamental woody plant or perhaps for its fruits, which have been considered as having medicinal value. Also, extracts of the drupes at various developmental stages treated with corresponding mordants yield a wide range of colors that can serve as dyes, and the bark is rich in tannins used as tanning agents (Grubov 1949b; Mabberley 1987). *Rhamnus cathartica* has escaped from cultivation, become naturalized in eastern North America, and now is abundant in urban environments and nearby woodlands (Greene 1896; Bailey 1947; Barnes and Wagner 1981). In recent years it has become a serious pest. It is also the alternate host for the oat rust, *Puccinia coronata* Corda (Okane et al. 1990; Swink and Wilhelm 1994). *Rhamnus davurica* var. *davurica* is distributed in eastern Russia, eastern China, and Korea. *Rhamnus davurica* var. *nipponica* is distributed in central and northern Japan (primarily Honshu) as well as eastern China and Korea. *Rhamnus utilis* is distributed in central and eastern China, Korea, and is rare in Kyushu, Japan (Makino 1904; Wolf 1938; Rehder 1940; Steward 1958; Grubov 1949b; Kitagawa 1979; Ohwi 1984; Flora of China Editorial Committee 1996). Grubov (1949a) considered specimens identified as *R. davurica* var. *nipponica* from Korea, western China, and adjacent Russia to represent the segregate *R. ussuriensis* J. J. Vassil., restricting *R. davurica* var. *nipponica* (under *R. nipponica*) to Japan. We have kept them in our analyses under *R. davurica* var. *nipponica. Rhamnus davurica* and *R. utilis* are economically important in the manufacture of dyes (Mabberley 1987).

No pertinent records documenting the introduction of *Rhamnus* into the study site are available. Herbarium specimens of *R. cathartica* in MICH document its presence in Michigan as early as 1914. A collection from a site near the study area in 1980 (*Reznicek 6165,* MICH) was the basis for the first report of *R. utilis* in Michigan (Voss 1985). *Rhamnus davurica* var. *davurica* and *R. davurica* var. *nipponica* are not known from Michigan. Elsewhere in eastern North America *R. davurica* (as *R. citrifolia*) is reported by Gleason and Cronquist (1991) as "sparingly introduced into our range." Swink and Wilhelm (1994) reported both *R. utilis* and *R. davurica* (including var. *nipponica*) for the Chicago region. *Rhamnus davurica* var. *nipponica* also was reported from Massachusetts (Seymour 1982).

The objectives of this study were to: (1) identify the species present at the site, especially to ascertain whether any individuals were, in fact, *Rhamnus davurica* var. *davurica, R. davurica* var. *nipponica* or *R. utilis*; (2) assess the nature and extent of hybridization at the study site; and (3) attempt to circumscribe possible hybrids.

MATERIALS AND METHODS

Sampling of the study specimens. Vigorously grown terminal branches, bearing sun-leaves and drupes, were sampled to represent the variation present at the study site. The plants occur along ca. 150 meters on the southeast-facing edges of a hedgerow of *Gleditsia triacanthos* L. and *Maclura pomifera* (Raf.) C. K. Schneid. (see Appendix 1 for locality and specimen citations). Because fruits offer several characters that distinguish species, only trees bearing drupes were sampled. Additional sampling was done ca. 10 meters east of the hedgerow in clusters of trees and shrubs dominated by *Rhamnus* spp. and surrounded by mowed grass. The clusters were established around trees of *Malus pumila* Mill. surviving from a former orchard. Drupes were preserved in FAA. Thirty-two specimens were collected and deposited in MICH. The principal plant associates were: *Lonicera maackii* (Rupr.) Maxim., *Prunus serotina* Ehrh., *Viburnum opulus* L., *Celastrus orbiculatus* Thunb., and *Ligustrum vulgare* L., with *Morus alba* L., *Acer negundo* L., and *Rosa multiflora* Thunb. as occasional associates. The site is at an elevation of 265–271 meters on a heavy, clay-loam soil derived from glacial till, and is within U.S.D.A. Hardiness Zone 5: minimum temperatures of −29°C to −23°C (U.S.D.A. 1990).

Determination of age. Transverse sections from the nine *Rhamnus* trees having the largest trunks in the sampling area were taken at ca. 30 cm above ground in June 1994, and annual rings were counted. These nine trees were not necessarily the trees sampled for morphology. On the basis of observations on seedling growth in the area, three years were added to the count to cover the period of development to a height of 30 cm. Vouchers and wood samples are deposited in MICH.

Specimens and characters selected. Thirty-eight drupe-bearing herbarium specimens of *Rhamnus cathartica* (MICH), *R. davurica* var. *davurica, R. davurica* var. *nipponica,* and *R. utilis* (A, MICH; Appendix 1) served as reference specimens and were studied with the study specimens.

Seventeen qualitative and quantitative characters were measured on each specimen. The characters selected were those that showed variation among the taxa represented by the reference specimens, including characters used by Schneider (1916), Rehder (1940), and Grubov (1949a). Two to 20 measurements were made for each character, depending on the quality of the specimen. Ten drupes were sampled from each specimen. The mean of each of the quantitative characters was entered into the data set. The characters measured were: (1) maximum length of terminal blade; (2) maximum width of terminal blade; (3) maximum length/maximum width ratio of terminal blade; (4) petiole length of terminal leaf; (5) petiole length/blade length ratio of terminal leaf; (6) sum of the basal angles of terminal blade; (7) gloss of the adaxial surface of terminal blade (scored on a scale of 1–5 where 1 = dull and 5 = very glossy); (8) pubescence on the adaxial surface of terminal blade; (9) pubescence on the abaxial surface of terminal blade (both 8 and 9 scored: 0 = none, 1 = none or along the major veins, 2 = along the major veins, 3 = throughout or only along the major veins, and 4 = throughout); (10) thorn length (apex to the base of the first terminal bud); (11) thorn pubescence (scored: 0 = absent and 1 = present); (12) peduncle length; (13) drupe length; (14) drupe width; (15) drupe length/width ratio; (16) drupe color (scored on a scale of 1–5 where 1 = green and 5 = purple); (17) the number of pyrenes per drupe (scored: **0** = 2 pyrenes, **1** = 2 or 3, **2** = 3, **3** = 2, 3, or 4, **4** = 3 or 4, and **5** = 4). Blade gloss and drupe color of the study specimens were scored while the material was fresh. Characters 7 and 13–16 were not available on the reference specimens and were entered as missing. Raw data are available from the authors.

Statistical analysis. *A priori* groups corresponding to the taxa (*Rhamnus cathartica, R. davurica* var. *davurica, R. davurica* var. *nipponica,* and *R. utilis*) that might have played a role in the hybridization were established using the reference specimens. These specimens were included in the discriminant analysis, described below, as reference points to allow comparison and positive identification of the study site's putative parental species (Appendix 1). Reference specimens 1–10 were *R. cathartica*; 12, 18, 20–22, 24, and 25 were *R. davurica* var. *davurica*; 11, 14, 19, 23, and 26–30 were *R. davurica* var. *nipponica*; and 15–17 and 31–39 were *R. utilis* (specimen 13 was omitted). An additional specimen (40, MICH) was collected near the study site and, suspected of being a hybrid, was included in the analysis with the study specimens. A stepwise linear discriminant analysis was performed to select the characters that are most predictive for distinguishing these groups. It was followed by a canonical discriminant analysis employing the first two canonical variables, using the MIDAS package on the University of Michigan mainframe computer. The derived discriminant function then was used to assess the positions of the study specimens and specimen 40 with respect to the reference specimens. Results were plotted (Figure 1) using the SAS statistical package version 6.08 (SAS Institute, Inc. 1993) on a DOS personal computer.

Although Atchley et al. (1976) note serious problems with the extensive use of ratios in statistical analyses, three ratios that are diagnostic were used in the discriminant analysis so that both it and the HYWIN analyses (see below) use the same suite of characters. This may cause some distortion of the clusters presented in the discriminant function analysis, but facilitates comparisons among the analyses.

Determination of putative hybrids and parental specimens. The complexity of the data set and the limitations of discriminant functions prompted the development of the computer program HYWIN (Estabrook et al. 1996). This program evaluates triplets of specimens in which one specimen is considered the hybrid offspring of the other two, and ranks the hypothesized hybrid according to character intermediacy, parental distance, and equality. The HYWIN analysis of the data set used the default weights (wI = 1, wE = 1, and wP = 1) for the ranking criterion and the 0.95 probability option. Two major HYWIN analyses were conducted. In the comprehensive analysis, 55 specimens (all 32 study specimens, specimen 40, and 22 reference specimens representing *Rhamnus cathartica* and *R. utilis*) were analyzed. The objective was to generate another set of hypotheses on the identity of the specimens and their grouping without *a priori* designation of putative parental species. These hypotheses then can be compared with those generated by the discriminant analysis. In the second analysis, only the study specimens (41–72) were analyzed. This was followed by a third analysis in which the specimens that were suggested as putative hybrids in the second analysis were removed.

RESULTS

Determination of age. Four of the nine trees whose rings were counted were 35–42 years old and ranged from 44.7 to 81.5 cm in circumference (14.2–25.9 cm in diameter). Those trees were a 42-year-old staminate *Rhamnus cathartica,* a 38-year-old carpellate *R. cathartica,* a 36-year-old staminate *R. cathartica,* and a 35-year-old carpellate *R. utilis.* The remaining five trees appeared to be hybrids, were 27–34 years old, and ranged in circumference from 37.6 to 73.7 cm (12–23.5 cm in diameter).

Statistical analysis. Four clusters corresponding to the reference specimens of the four taxa were generated (Figure 1).

Characters 1, 3, 5, and 6 were found to be best for distinguishing *a priori* groups. Ranges of these characters are listed in Table 1.

Study specimens (marked by black dots in Figure 1) were placed in clusters corresponding to the taxa as follows: in the *Rhamnus cathartica* cluster 41, 44, 53, 55, 61, 67, 68, and 72; in the *R. utilis* cluster 42, 46, and 66; and in the *R. davurica* var.

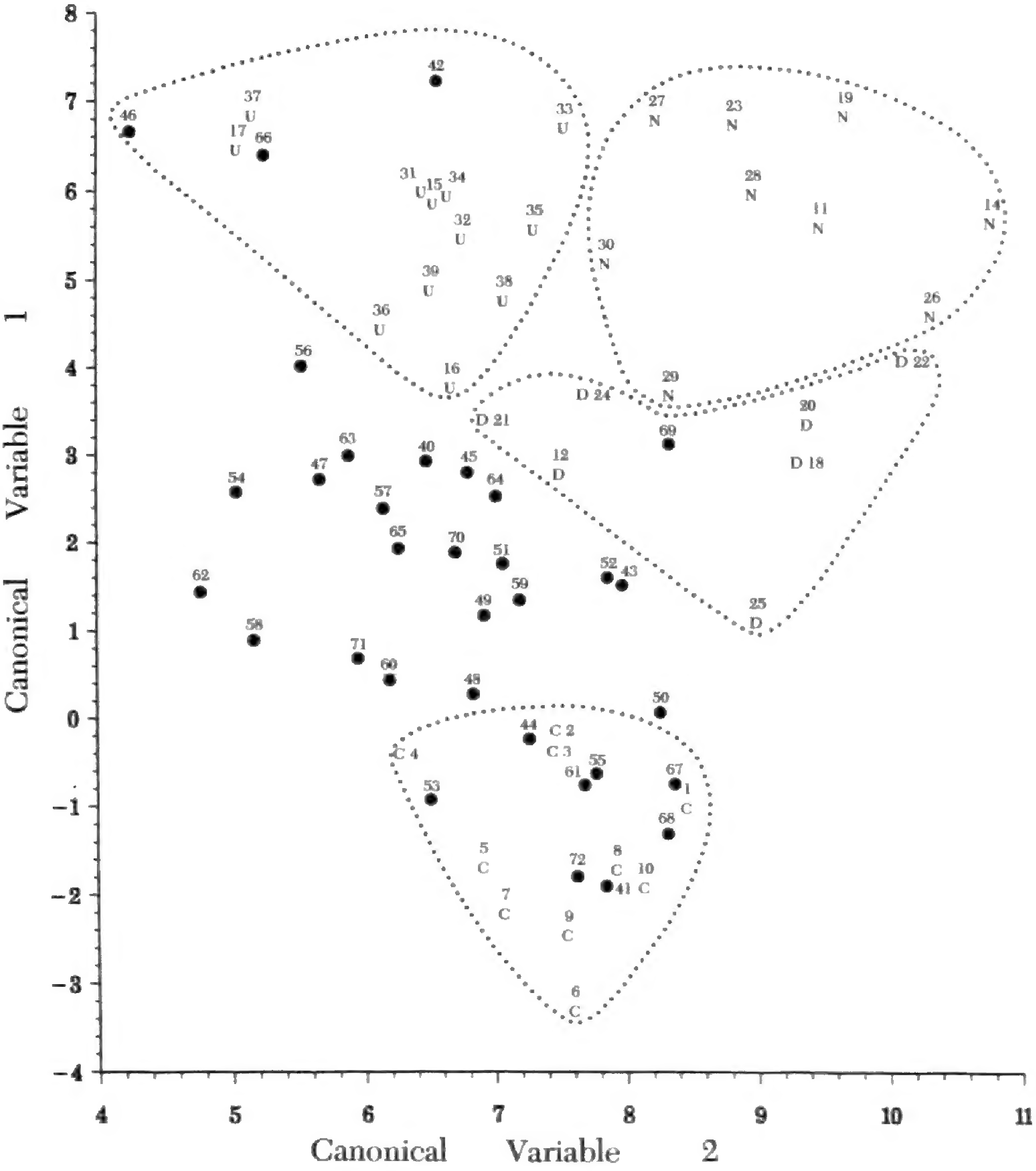

Figure 1. A canonical discriminant analysis of 72 *Rhamnus* specimens employing the first two canonical variables. Letters denote assigned group membership of the reference specimens: C = *R. cathartica*; D = *R. davurica* var. *davurica*; N = *R. davurica* var. *nipponica*; U = *R. utilis*; ● = specimen from the study site (plus specimen number 40). The number above or beside each letter or dot is a case number representing the specimen (see Appendix 1). Dotted outlines of groups are merely an aid to visualizing clusters of taxa and have no statistical significance.

davurica cluster 69. No study specimens were placed in the *R. davurica* var. *nipponica* cluster. Specimen 40 and all other study specimens were arrayed between the clusters formed by specimens referable to *R. cathartica* and *R. utilis*. These included specimens 43, 45, 47–52, 54, 56–60, 62–65, and 70–71.

Table 1. The ranges of characters found best for distinguishing *a priori* groups in the discriminant analysis.

	Taxon			
Character	*R. cathartica*	*R. utilis*	*R. davurica* var. *davurica*	*R. davurica* var. *nipponica*
1. Maximum length of terminal blade (mm)	19–66	66–159	60–125	68–124
3. Maximum length/maximum width ratio of terminal blade	1.2–2.5	2.2–3.4	2.2–3.5	2.9–4.4
5. Petiole length/blade length ratio of terminal leaf	0.08–0.75	0.03–0.23	0.14–0.58	0.01–0.23
6. Sum of the basal angles of the terminal blade	81°–170°	27°–127°	61°–125°	33°–100°

Comprehensive HYWIN analysis. The count for the 0.95 probability option for the specimens examined was the 374 highest ranking triplets. Twenty-one of the 55 specimens never participated in the role of a putative hybrid (reference specimens 2, 4–10, 15, 17, 31–34, and 37; and study specimens 42, 46, 48, and 66–68), and 34 specimens were suggested as putative hybrids (reference specimens 1, 3, 16, 35, 36, and 38–39; specimen 40; and study specimens 41, 43–45, 47, 49–65, and 69–72). Input and output data are available from the authors.

HYWIN analysis of the study specimens. Results are presented in Table 2 and summarized by frequency counts in Table 3. The count for the 0.95 probability option for the specimens examined was the 201 highest ranking triplets. Twelve of the 32 specimens never participated in the role of a putative hybrid (41, 42, 44, 46, 48, 55, 61, 63, 66–68, and 72), and 20 were suggested as putative hybrids (43, 45, 47, 49–54, 56–60, 62, 64, 65, and 69–71). Two specimens, 46 and 68, were suggested as parents in the highest ranking triplets of ten specimens suggested as hybrids, specimens 66 and 68 were suggested as parents in the highest ranking triplets of five specimens, and other combinations of putative parents were each suggested in the highest ranking triplets of the remaining five specimens. A striking feature of Table 2 is that specimen 68 (*Rhamnus cathartica*) was suggested as one of the putative parents of 17 of the 20 specimens that were suggested as putative hybrids. The equality score of eight of these specimens indicates that they are closer in their overall morphology to specimen 68. Of these, specimen 60 is the closest to specimen 68 (NP = 0.176). Specimen 46 (*R. utilis*), the second most frequent putative parent, was suggested as one of the putative parents of 11 of the 20 specimens. The equality score of five of these specimens indicates that they are closer in their overall morphology to specimen 46. Of these, specimen 69 is the closest specimen to specimen 46 (NP = 0.277; Table 2).

Comparisons among the analyses. Results of the discriminant analysis and the comprehensive HYWIN analysis on the status of the reference specimens substantially agree (Table 2). However, a few reference specimens were suggested as hybrids in the HYWIN analysis. In the *Rhamnus cathartica* cluster, the HYWIN analysis generally corroborated the discriminant analysis. Only two reference specimens, 1 and 3, were suggested as hybrids. Specimen 1, collected in England, possesses exceptionally long thorns compared with the *R. cathartica* specimens collected in North America. In a rerun of the HYWIN analysis with the exclusion of character 10 (thorn length), specimen 1 was not suggested as a hybrid. In an additional run of the data set, in which the characters having missing data were excluded, specimen 3 was not suggested as a hybrid. In the *R. utilis* cluster four reference specimens—35, 36, 38, and 39—were suggested as hybrids by the HYWIN analysis. However, the putative hybridity of these specimens should be regarded as inconclusive because of incomplete specimens.

The discriminant analysis, the HYWIN analysis of the study specimens, and the comprehensive HYWIN analysis (see Table 2) all suggested identical status for 23 of the 32 study specimens. Discrepancies between the two HYWIN analyses appeared in six specimens—41, 44, 55, 61, 63, and 72—that are all in the *Rhamnus cathartica* cluster but display some variation in blade shape (Figure 2). These specimens were not suggested as putative hybrids in the analysis using only the study specimens, but were suggested as putative hybrids in the comprehensive HYWIN analysis. Discrepancies between the comprehensive HYWIN analysis and the discriminant analysis appeared in eight specimens: 41, 44, 48, 53, 55, 61, 72 (all in the *R. cathartica* cluster), and 69

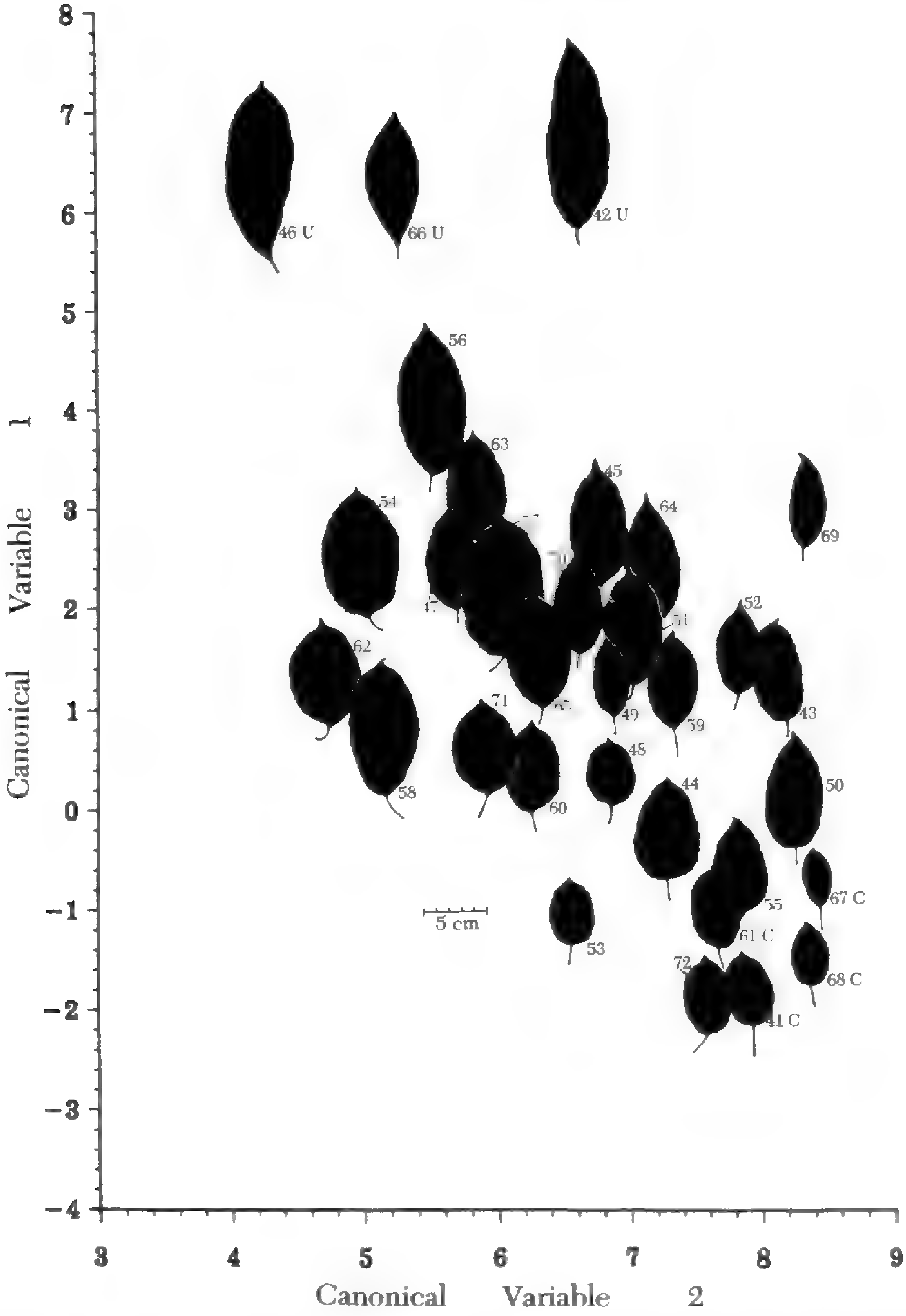

Figure 2. Silhouettes of representative leaves from the *Rhamnus* study collection (case numbers 41–72) arranged according to the coordinates for each specimen as determined by the canonical discriminant analysis. Letters beside numbers mark those specimens that were determined as orthospecies. C = *R. cathartica*; U = *R. utilis*. Scale = 5 cm.

(in the *R. davurica* cluster). Discrepancies between the HYWIN analysis of the study specimens and the discriminant analysis appeared only in four specimens: 48, 53, 63, and 69. Thus, the status of nine study specimens—41, 44, 48, 53, 55, 61, 63, 69, and

72—appeared uncertain as a result of discrepancies among the three primary analyses (see Table 2).

In the third HYWIN analysis of the study specimens, with the putative hybrids of the second analysis removed, specimen 41 was not suggested as a hybrid. The same result was obtained in an additional run of the comprehensive data set from which characters having missing data were excluded. Furthermore, in the third HYWIN analysis of the study specimens, numbers 44 and 55 were suggested as hybrids whose best matches for parental morphologies in the data set were specimens 68 and 42 [the equality scores (EQ) of both indicate that they are closer to specimen 68, and the distance to the nearest parent (NP) of each is 0.250 and 0.179, respectively]. Specimen 48 was suggested as a hybrid whose best matches for parental morphologies were specimens 66 and 68 (its equality score indicates that it is closer to specimen 68, and its distance to this nearest parent is 0.21). Specimen 48 was also suggested as a hybrid in the second run of the comprehensive data set with the putative hybrids suggested by the initial analysis removed. Specimen 61, once again, was not suggested as a hybrid. Specimen 72 was suggested as a hybrid whose best matches for parental morphologies were specimens 55 and 67 (its equality score indicates that it is closer to specimen 55 with a distance of 0.162 to this nearest parent). Specimens 53 and 69 were suggested as hybrids in all HYWIN analyses, but were included, respectively, in the *Rhamnus cathartica* and *R. davurica* var. *davurica* clusters of the discriminant analysis.

Of the 12 specimens that were never suggested as putative hybrids in the HYWIN analysis of the study specimens, only specimen 63 did not appear within the *Rhamnus utilis* or *R. cathartica* clusters of the discriminant analysis (Figure 1). Although specimen 63 was suggested 25 times as a parent, it appeared only once in this role in the highest ranking triplet of a specimen that was suggested as a hybrid (53; Table 2). Specimen 63 also was suggested as a hybrid in the comprehensive HYWIN analysis. In a subsequent run of the data set of the study specimens with the putative hybrids of the initial analysis removed, specimen 63 appeared as a putative hybrid for the first time at rank 5 and was the most frequent specimen (14 times) to be suggested as a hybrid. Its highest ranking triplet suggested that the best matches for parental morphologies in the data set were specimens 42 (*R. utilis*) and 67 (*R. cathartica*). Its equality score indicates that it is closer to specimen 67, and its distance to this putative parent is relatively large (NP = 0.4) compared to the distance of each of the other putative hybrids to its nearest putative parent (NP = 0.1–0.3). This distance is also reflected in the discriminant analysis (Figure 1).

DISCUSSION

Age determination suggests that the site was colonized by *Rhamnus* circa 1952, and perhaps that *R. utilis* arrived at the site shortly after *R. cathartica.* Observations of numerous *Rhamnus* seedlings in the area showed that, under good conditions, fruits may occur as early as 6–8 years after seedling establishment. This would allow 5–7 generations since the introduction of the founding trees. No dead stumps or old, decrepit trees that might suggest an earlier introduction to the site were present. There is no evidence that *Rhamnus* was planted at the site. Abandonment of the orchard at the site probably instigated the proliferation of other plants, including *Rhamnus. Rhamnus* seeds are dispersed primarily by birds (Barnes and Wagner 1981; Brizicky 1964; Hernandez 1993; Catling and Porebski 1994). It is likely that birds, carrying the seeds from nearby *Rhamnus,* roosted on the dominant trees at the site and contributed to the initial establishment of seedlings under and at the edges of the canopy. Later, additional dispersal and establishment of seedlings resulted in the complex population present at the site. The hybrids appear very vigorous and outnumber the parents.

The results of the discriminant analysis are best interpreted as showing a variable hybrid swarm. The spatial arrangement of the clusters in Figure 1 suggests that *Rhamnus utilis* and *R. cathartica* were involved in the formation of the hybrids, and that *R. davurica* and *R. davurica* var. *nipponica* were not involved. The parental species have become connected phenetically by numerous intermediate types, presumably by backcrossing and by the production of F_2 and later hybrid generations, thereby grading one into the other. Leaf size and shape differ considerably between *R. cathartica* and *R. utilis,* but Figure 2 effectively shows that a continuum of morphology has been achieved. The placement of specimen 40—collected near the study site—between the *R. utilis* and *R. cathartica* clusters suggests that it is a hybrid.

Placement of study specimen 69 in the *Rhamnus davurica*

Table 2. Results of the first run of the HYWIN analysis of the study specimens, and a comparison of this analysis to the comprehensive HYWIN analysis and to the discriminant analysis. The highest ranking triplets of each of the 32 study specimens among the 201 highest ranking triplets at 0.95 probability. The weights assigned for the ranking criterion: wI = 1.0, wE = 1.0, wP = 1.0. Abbreviations: Rank = Rank of first time suggested as a hybrid; IN = intermediacy score; EQ = equality score; PD = parental distance score; NP = distance to the nearest parent. When the EQ value is positive, the putative hybrid is closer to putative parent 2; when it is negative, the putative hybrid is closer to putative parent 1. An underlined collection number of a putative parent denotes that the respective putative hybrid is closer to this parent; STUDY HYWIN = the HYWIN analysis of the study specimens only; COMP HYWIN = the comprehensive HYWIN analysis of 55 reference and study specimens; DA = the discriminant analysis of the reference and study specimens; O = a putative orthospecies; H = a putative hybrid; C = *Rhamnus cathartica*; U = *R. utilis*; D = *R. davurica*. The putative species identities listed in the DA column were determined according to the location of the respective specimen in relation to the species cluster in the discriminant analysis (Figure 1) as circumscribed by the dotted lines.

Case Number	Putative Parent 1	Putative Parent 2	Rank	IN	EQ	PD	NP	STUDY HYWIN	COMP HYWIN	DA
41								O	H	C
42								O	O	U
43	$\underline{66}$	68	1	0.479	−0.003	0.677	0.358	H	H	H
44								O	H	C
45	$\underline{46}$	68	21	0.441	−0.101	0.662	0.314	H	H	H
46								O	O	U
47	46	$\underline{68}$	12	0.444	0.047	0.662	0.317	H	H	H
48								O	O	H
49	$\underline{46}$	68	82	0.330	−0.214	0.662	0.313	H	H	H
50	46	$\underline{68}$	31	0.330	0.061	0.662	0.335	H	H	H
51	$\underline{61}$	66	2	0.571	−0.036	0.613	0.333	H	H	H
52	46	$\underline{68}$	3	0.471	0.007	0.662	0.353	H	H	H
53	63	$\underline{68}$	124	0.348	0.234	0.601	0.252	H	H	C
54	$\underline{66}$	68	77	0.157	−0.043	0.677	0.374	H	H	H

Table 2. Continued.

Case Number	Putative Parent 1	Putative Parent 2	Rank	IN	EQ	PD	NP	STUDY HYWIN	COMP HYWIN	DA
55								O	H	C
56	41	46	34	0.371	0.074	0.615	0.314	H	H	H
57	66	68	71	0.185	−0.056	0.677	0.350	H	H	H
58	41	66	135	0.087	0.026	0.636	0.371	H	H	H
59	46	68	11	0.525	0.123	0.662	0.288	H	H	H
60	62	68	165	0.386	0.096	0.375	0.176	H	H	H
61								O	H	C
62	46	68	58	0.211	−0.032	0.662	0.352	H	H	H
63								O	H	H
64	46	68	4	0.492	−0.042	0.662	0.331	H	H	H
65	46	68	10	0.449	0.044	0.662	0.330	H	H	H
66								O	O	U
67								O	O	C
68								O	O	C
69	46	68	62	0.380	−0.208	0.662	0.277	H	H	D
70	66	68	7	0.463	−0.045	0.677	0.343	H	H	H
71	66	68	88	0.106	0.012	0.677	0.398	H	H	H
72								O	H	C

Table 3. The HYWIN summary output of the 201 highest ranking triplets at 0.95 probability of the data set of the study specimens. Note: "—" denotes never suggested as a hybrid or parent.

Case Number	Number of Times Ranked as a Hybrid	Rank of First Time Suggested as a Hybrid	Number of Times Ranked as a Parent	Rank of First Time Suggested as a Parent
51	25	2	0	—
64	18	4	0	—
43	17	1	0	—
52	15	3	0	—
65	14	10	0	—
47	14	12	0	—
70	12	7	0	—
57	11	71	1	166
54	10	77	0	—
56	10	34	0	—
59	10	11	1	166
45	9	21	0	—
49	9	82	0	—
50	6	31	0	—
62	6	58	1	165
69	5	62	0	—
71	5	88	0	—
58	2	135	0	—
53	2	124	2	91
60	1	165	4	112
44	0	—	9	107
42	0	—	24	27
63	0	—	25	33
48	0	—	3	60
41	0	—	40	17
66	0	—	70	1
67	0	—	5	86
68	0	—	58	1
61	0	—	34	2
46	0	—	80	3
55	0	—	17	54
72	0	—	28	8

var. *davurica* cluster (Figure 1) merits consideration. This placement and the resemblance of specimen 69 in its overall morphology to some of the reference specimens in the *R. davurica* var. *davurica* cluster suggest that it is *R. davurica* var. *davurica.* In the context of the study collection, however, this single specimen showing some characters of *R. davurica* var.

davurica is most parsimoniously explained as being a somewhat unusual hybrid. Additional specimens referable to both *R. utilis* and *R. cathartica* are represented both in the study collection and in other areas nearby, but only this single incidence of *R. davurica*-like morphology is known. In addition, there is no evidence in Figure 1 of *R. davurica* var. *davurica* acting as a parent in hybridizations. This morphology, produced in the context of a hybrid swarm, should lead to caution in identifying other collections of introduced *Rhamnus* in North America. The hypothesis that specimen 69 is a hybrid is corroborated by the results of both HYWIN analyses (Table 2). Specimen 69 was not suggested as a parent of any hybrid in either analysis. Its equality score (−0.208) indicates that it is closer to study specimen 46 of the *R. utilis* cluster. Its distance to the nearest parent (NP = 0.277) indicates that it is closer to specimen 46 than specimens 45, 49, 62, and 64 (NP = 0.314, 0.313, 0.352, and 0.331, respectively), which share the same putative parents. Specimen 53 represents a similar case in which both primary HYWIN analyses suggested that it is a putative hybrid, whereas the discriminant analysis placed it within the *R. cathartica* cluster. It appears somewhat removed from the other specimens of the *R. cathartica* cluster and deviates in a number of characters (e.g., blade length/width ratio and gloss) from the specimens circumscribed as orthospecies. The results of the HYWIN analyses strongly support the hypothesis that it is a hybrid.

The third HYWIN analysis of the study specimens with the hybrids suggested by the second analysis removed, the discriminant analysis, and the comprehensive HYWIN analysis all support the hypothesis that specimen 63 is a hybrid of *Rhamnus utilis* and *R. cathartica.*

On the basis of the third HYWIN analysis of the study specimens, specimens 41 and 61 are hypothesized as *Rhamnus cathartica,* whereas specimens 44, 48, 55, and 72 are hypothesized as hybrids. The low NP values of specimens 44 and 55 may indicate that they resulted from backcrossing to *R. cathartica.* The suggestion that specimen 72 resulted from hybridization of plants resembling specimens 55 and 67 reinforces the interpretation of the presence of a variable hybrid swarm at the study site. In addition, this suggestion sheds light on the difficulties in determining whether specimen 72 is an orthospecies or a hybrid since a putative backcross (specimen 55) has most likely hybridized with *R. cathartica* and produced a plant whose morphology is very close to that of *R. cathartica.*

One additional aspect of Figure 1 merits brief mention. The spatial separation of *Rhamnus davurica* var. *davurica* and *R. davurica* var. *nipponica* (Figure 1) is relatively clear, perhaps as clear as that of *R. davurica* var. *davurica* and *R. utilis.* Though very preliminary and based on a small sample size, this result supports the recognition of *R. davurica* var. *nipponica* as a species, *R. nipponica* (Makino) Grubov (1949a). Schneider (1916) postulated that *R. davurica* is most nearly related to *R. cathartica,* and pointed out the difficulty of determining whether *R. davurica* var. *nipponica* is a good variety or even a different species. Choo et al. (1993) discovered significant differences in the pollen grains of *R. davurica* var. *davurica* and *R. davurica* var. *nipponica* and suggested that their taxonomic rank should be amended pending additional, broader investigation. Drawing taxonomic conclusions from these preliminary observations is premature, but we hope that they may point the way to additional research.

The discriminant analysis provides an effective visual presentation of the parental species and putative hybrids. The HYWIN analyses provide "fine tuning" in cases where the results of the discriminant analysis are not clear enough to allow confident placement of specimens at the boundaries of clusters of species. Several study specimens were placed within the orthospecies cluster by the discriminant analysis, but were suggested as hybrids by the more stringent HYWIN analyses. These discrepancies are suggestive of backcrosses closely resembling parents, and here are so interpreted. Thus, comparison of the results of both types of analyses enables the formulation of more precise hypotheses. The utilization of both analyses in studies of hybrid swarms appears to be very effective.

The results of all three analyses allow us to conclude that three study specimens—42, 46, and 66—can be identified as *Rhamnus utilis*; four study specimens—41, 61, 67, and 68—as *R. cathartica,* and 25 specimens—43–45, 47–60, 62–65, and 69–72—can be designated putative hybrids of these two species (Figure 2).

Reconstruction of the actual complex hybridization events that resulted in the full range of variation present at the study site's hybrid swarm is not possible. However, the analyses presented enabled the identification of the orthospecies and their results may serve as the best hypotheses to account for the most recent hybridization event that produced the morphology of each of the putative hybrids.

It is interesting to note that two Old World species that have been brought together to a habitat on a different continent, away from their place of origin, have hybridized naturally and probably produced several generations of fertile hybrids. The first step of this evolutionary progression involved human intervention, but the next steps have occurred without that intervention. The aggressive nature of these new hybrids should be of concern to local stewards and naturalists.

Wagner (1983) pointed out that if the number of taxa involved in a study is large and the characters that separate them are poorly differentiated, the problems of detection of hybrids may be severe. We hope that the methodology and results of this study encourage researchers to conduct morphological analyses of complex hybrid swarms in other taxa.

ACKNOWLEDGMENTS. We wish to dedicate this paper to Prof. Warren H. Wagner, Jr., whose research and teaching have been an inspiration for this work.

We are grateful to the curators of the Harvard University Herbaria for the loan of specimens of *Rhamnus* from Asia. We thank Kenneth E. Guire, Kathleen B. Welch, and Veena Somayaji of the University of Michigan Center for Statistical Consultation and Research for their assistance with the statistical analyses. We also thank Prof. George F. Estabrook for his collaboration on the development of HYWIN, and Prof. Robert Fogel for his generous assistance with computer generated graphics. We are grateful to David Borneman and Nancy Burghardt of the City of Ann Arbor Parks and Recreation Department for granting permission to remove wood samples, and to Susan A. Reznicek for her assistance with the figures. The constructive comments of two anonymous reviewers are gratefully acknowledged.

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APPENDIX 1: SPECIMENS EXAMINED

NOTE: The case numbers (in parentheses below) are used in the text and in Figure 1 to abbreviate the collectors and collection numbers.

STUDY SPECIMENS

U.S.A. MICHIGAN. Washtenaw County: Ann Arbor, Leslie Science Center Park, 6 Sep. 1984, *Reznicek & Reznicek 7462* (41); *7463* (42); *7464* (43); *7465*

(44); *7466* (45); *7467* (46); *7468* (47); *7469* (48); *7470* (49); *7471* (50); *7472* (51); *7473* (52); *7474* (53); *7475* (54); *7476* (55); *7477* (56); *7478* (57); *7479* (58); *7480* (59); *7481* (60); *7482* (61); *7483* (62); *7484* (63); *7485* (64); *7486* (65); *7487* (66); *7488* (67); *7489* (68); *7490* (69); *7491* (70); *7492* (71); *7493* (72) (MICH).

REFERENCE SPECIMENS

***RHAMNUS CATHARTICA* L.**

ENGLAND. Nottingham County: near Newark, Sep. 1890, *Fisher s.n.* (1) (MICH). **U.S.A.** ILLINOIS. Cook County: Burre Woods, 26 Aug. 1960, *Laskowski 187* (6) (MICH). MICHIGAN. Emmet County: on the west bank of Tannery Creek, T35N, R5W, Sec. 28, Oct. 1967, *Tanton s.n.* (4) (MICH). Hillsdale County: west side of Bankers Road, T7S, R3W, Sec. 6, 14 Sep. 1985, *Fritsch 115* (5) (MICH). Oakland County: Broomfield Hills, 3 Sep. 1916, *Billington s.n.* (2) (MICH); waste places and along roads near Birmingham, 29 Aug. 1915, *Chandler s.n.* (3) (MICH). Washtenaw County: Ann Arbor, along the banks of Huron River, 14 Oct. 1949, *Jordal 3339* (7) (MICH). NEW YORK. Cayuga County: Salmon Creek, south of Genoa, 28 Aug. 1919, *Eames & Wiegand 12422* (9) (MICH). Orange County: Black Rock Forest, along Old Point Road near Upper Res., 22 Jul. 1966, *Raup 7668* (8) (MICH). OHIO. Clark County: Springfield Township, Sec. 4, NE ¼, North of Beaver Creek, 0.15 mile S of Tuttle Cemetery and 0.3 mile NW of Redmond Road Bridge, 23 Aug. 1983, *Cusick 22927* (10) (MICH).

RHAMNUS DAVURICA* PALL. VAR. *DAVURICA

CHINA. Jilin Province: lake shore, 27/31 Jul. 1931, *Chen 170* (20) (A). Shanxi Province: Chih-li, 12 Oct. 1924, *Dorsett 967* (21) (A). Zhejiang Province: Hsiao Lin, 30 Aug. 1925, *Dorsett 4110* (24) (A). Manchuria: Halasust, along Yalu River, 10 Aug. 1929, *Skvortzov s.n.* (18) (A). **KOREA.** Kyonggi-Do, Kwangnung, 37°44′N, 128°06′E, 15 Oct. 1947, *Chung 788* (12) (MICH). Kankyo Province: Sempo, 3 Aug. 1917, *Wilson 8827* (25) (A). **RUSSIA.** Manchuria: Khabarovsk area, mouth of the River Kur at the Amur River, 13 Sep. 1895, *Komarov 1072* (22) (A).

***RHAMNUS DAVURICA* PALL. VAR. *NIPPONICA* MAKINO**

CHINA. Hubei Province: Lichuan Xian, Hsien, vicinity of Zhuanjiaowan, 30°10′N, 108°45′E, *Sino-American Botanical Expedition 2024* (23) (A). **JAPAN.** Honshu: near Yamanaka Lake in Kai, 18 Jul. 1956, *Togasi 1365* (14) (MICH). Pref. Nagano. Shinano Province: Mikuni-tooge and Mikuni-tooge Road, Azusayama Kawakami-mura, Minami-saku-gun, 4 Sep. 1960, *Furuse s.n.* (29) (A); Mount Temgu Kawakami-mura, Minami-saku-gun 19 Sep. 1962, *Furuse s.n.* (26) (A); Minami-karuizawa, 18 Aug. 1951, *Mizushima 10209* (30) (A); Minamisaku-gun, Nobeyama, 31 Jul. 1971, *Togashi & Tateishi 73* (27) (A); Nobeyamagahara, East foot of Mount Yatsuga-dake, Minamisaku-gun, 31 Jul. 1972, *Tateishi & Togashi 239* (28) (A). **KOREA.** Kwangnung: Kyonggi-Do, 28 Sep. 1933, *Chung 5588* (11) (MICH). Cholla-Namdo: Mudung San, 35°5′N, 127°E, 2 Oct. 1981, *Meyer & Bristol 164* (19) (A).

RHAMNUS UTILIS **DECNE.**
CHINA. Anhui Province: Siunin, 7 Sep. 1925, *Ching 3318* (35) (A). Fujian Province: Kuliang, 27 Jul. 1926, *Chung 6704* (36) (A). Guangdong Province: Yu-yuen, 20 May 1933, *Ko 52678* (38) (A); Loh Ch'ang District, Chong Uen Shan near Kau Fung, 2–30 Nov. 1932, *Tsang 20642* (17) (MICH). Guangxi Province: Kwei-lin District, Hsi-chang village and vicinity, Ch'i-fen-shan, 1–11 Oct. 1937, *Tsang 28408* (37) (A). Guizhou Province: Jiangkou Xian, along the Yixi River between Guanba and Gaofeng, SW side of the Fanjing Shan mountain range, 5 Sep. 1986, *Sino-American Guizhou Botanical Expedition 912* (16) (MICH); Kiangkou Hsien, Miao Wang, 26 Sep. 1931, *Steward et al. 532* (32) (A); Songtao Xian, NE of Fanjing Shan mountain range, 5–6 Oct. 1986, *Sino-American Expedition 1858* (15) (MICH). Hubei Province: Hsing-shan, Hsien, Nov. 1907, *Wilson 623* (33) (A); Shennongjia Forest District, 31°30′N, 11°30′E, Laojunshan Yaowan Canyon on the W side of the Jiuchong River, ca. 1 km. S of Mucheng, 31 Aug. 1980, *Sino-American Expedition 465* (31) (A). Zhejiang Province: S of Pang Yung, 10 Jul. 1924, *Ching 2054* (34) (A). **U.S.A.** MICHIGAN. Washtenaw County: Ann Arbor, end of Wickfield Court between Traver Road and Pontiac Trail, 25 Aug. 1980, *Reznicek 6165* (39) (MICH).

ADDITIONAL SPECIMEN EXAMINED

U.S.A. MICHIGAN. Washtenaw County: Ann Arbor, Nichols Arboretum, N of Geddes Avenue, 6 Sep. 1984, *Reznicek 7461* (40) (MICH).

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BRANCH INITIATION IN THE LICHEN *CLADONIA CRISTATELLA* (BRITISH SOLDIERS)

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ABSTRACT. Branch initiation in the British Soldier Lichen (*Cladonia cristatella*) follows a sequence of discrete developmental stages. Branches arise from dichotomous divisions of a meristem-like apical bundle of fungal cells. Early ontogenetic phases are predictable and controlled by the activity of the fungal meristem. One source of variability in mature thalli is heterochrony; the branching process may be synchronized differently in different thalli. In some thalli the meristem may divide early in ontogeny, in which case the branches are relatively long and distinct. In other thalli the meristem enlarges but does not divide until later in ontogeny. In this case branching is delayed and the branches may be shorter and less distinct. Both patterns of timing for branch initiation produce mature thalli with a morphology that is unique to *C. cristatella.* The early ontogeny in *C. cristatella* is similar to that of taxa that are presumed to be only distantly related. This suggests that branching may be canalized in *Cladonia* species, and that certain branching patterns represent primitive characters in the Cladoniaceae. Morphological variability in *C. cristatella,* which is based partly on heterochrony, has both taxonomic and evolutionary implications.

Key Words: branching patterns, Cladoniaceae, growth dynamics, lichen evolution

Cladonia cristatella Tuck. is a common endemic lichen species of New England that is characterized by great morphological variability. Thomson (1968) listed 12 forms for this species, most of which were based on morphological differences. While these morphological *formae* are not taxonomically significant, they indicate the range of variation perceived in this species by earlier workers. Some of the variation is based on branching patterns, the interpretation of which has caused taxonomic difficulties in this and other Cladoniaceae species (Hammer 1995). Yet branching in *C. cristatella,* though variable, is predictable in its early stages. In *C. cristatella,* as in other Cladoniaceae species, thallus form is produced by definite developmental patterns that produce simple cuplike structures and branches. The simplicity of thallus form in the Cladoniaceae led systematists in the past half century to consider morphology to be of little utility taxonomically. It has been generally but mistakenly perceived that morphological characters of the species are not informative, and that a solution to this problem might be found in chemotaxonomy. Hale (1984) stated that genera in families with a fruticose habit (such as the Cladoniaceae) had few ontogenetic characters. This statement may have been prompted because of the difficulty in tracing morphogenesis in complex lichens: the relationship of morphology in mature *Cladonia* thalli to early development is often unclear. As a result there has been little work on the comparative ontogeny, anatomy, and architecture of the Cladoniaceae. Subsequently, the evolutionary relationships of *C. cristatella* and other Cladoniaceae are unknown because comparative morphological data are scarce. Early workers such as Robbins and Sandstede (see Evans 1930, 1935) noted and named minor morphological differences in populations of *C. cristatella,* while ignoring the underlying developmental similarities of the various forms they described. Similar to other Cladoniaceae species, the taxonomy of *C. cristatella* was thereby burdened with a complicated nomenclature that did not adequately reflect its biology. But the evolutionary biology of *C. cristatella* is reflected in its development. The goal of this paper is to elucidate the developmental biology of *C. cristatella* through a description of branch initiation.

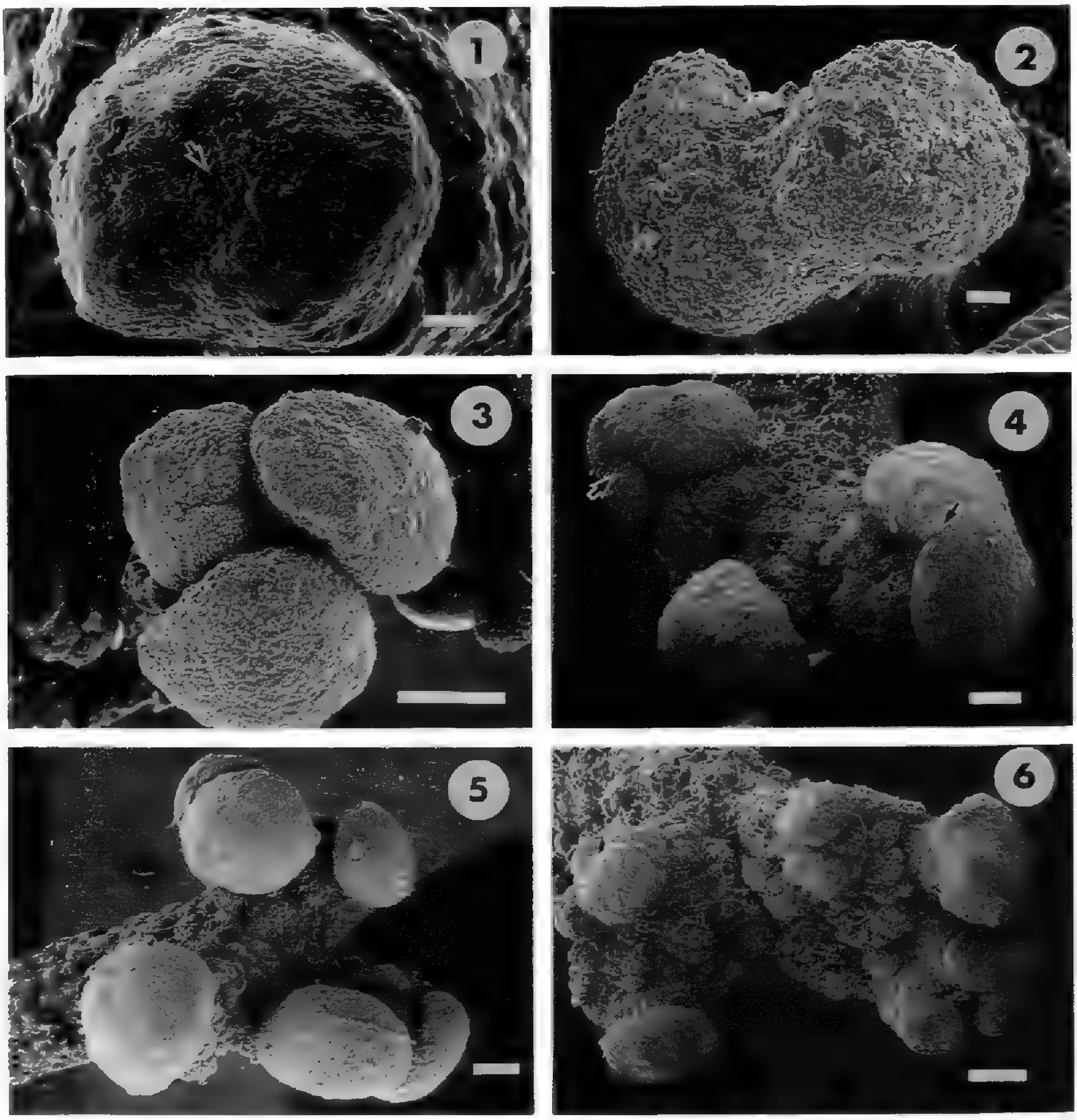
MATERIALS AND METHODS

Several hundred thalli of *Cladonia cristatella* were examined for this study. Particular attention was given to the podetium which is the erect "secondary" thallus of *Cladonia* species. Immature, unbranched podetia, most of which were <1 cm tall, were studied. Mature podetia were examined as well. Most of the podetia and all of the thalli that were dissected came from recently collected specimens. These specimens were collected from a variety of substrates in pine-scrub oak forests in Plymouth and Barnstable Counties, Massachusetts. Many preserved specimens at the Farlow Herbarium (FH) also were examined and annotated. These include (but are not exclusive to) *Ahmadjian 2366, Culberson 6768, Evans 1858, Hammer 6015, Oakes s.n.* (lectotype), *Riddle 208, Robbins s.n.,* and *Sheldon s.n.* Notes were taken, and many of the specimens were sketched under a dissecting microscope. Scanning electron micrographs (SEM) were prepared from approximately 30 freshly collected specimens. See Hammer (1996a) for details on SEM methodology.

The terminology for descriptive studies in lichen morphogenesis is not yet an established convention. This is a problem because lichen form, particularly in Cladoniaceae species, may be plant-like. The shrubby thallus (body) of many of these lichens tempts comparisons with vascular plants, but lichen architecture is based on different units from plants (Hammer 1997). Developmental morphology of lichens is an evolving discipline, and here I follow certain terminological conventions used in previous papers. For example, the cluster of apical cells that comprises *meristem-like tissue* will be called the "*meristem*" or "*meristem bundle.*" "*Bundle*" is a general term for a group of similarly oriented cells that extends parallel with the long axis of the branch (Hammer 1993a, 1996b, 1997; Letrouit-Galinou 1966, 1968). In studies of vascular plants the term "*meristem initial*" sometimes refers to a single apical cell. In this paper the term refers to *the developmental unit* of up to five branch initials, as in Hammer (1996c, 1997). The term "*division*" refers to the splitting of the meristem tissue, and is not associated here with *cell* division. In Hammer (1996a) "division" was used interchangeably with "*split.*" "Division" is used here as a noun (e.g., the division of the meristem tissue) and "split" is used to describe an action, such as when the meristem splits into two parts.

RESULTS

Branch initiation in "early-branching" podetia of *Cladonia cristatella* is determined by the ontogenetic sequence of the apical fungal meristem. The fungal meristem is an aggregation of fungal cells ca. 50 μm in diameter. Before division, the aggregation enlarges to ca. 100 μm and a division furrow forms at the approximate center of the meristem bundle (Figure 1). The bundle later splits along this furrow. The first division produces two more or less equal bundles (Figure 2). The orientation of the bundles changes during development so that the longitudinal axes of the bundles are approximately perpendicular. The next division furrow is oriented approximately perpendicular to the initial division furrow. A division along this furrow, which is the second division to occur in the sequence, produces a meristem initial of three bundles (Figure 3). These

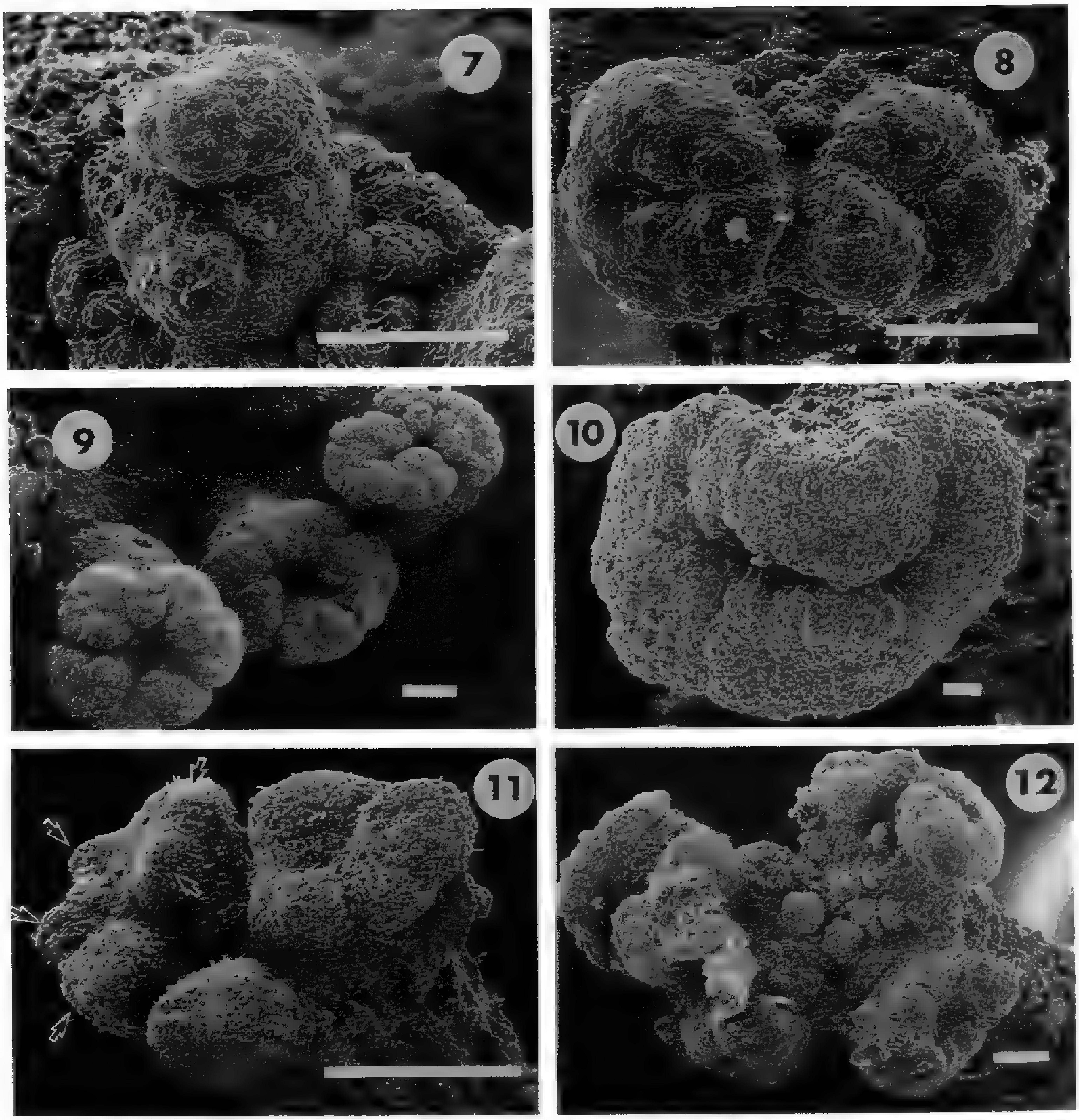


Figures 1–6. Micrographs of fungal meristem in early branching *Cladonia cristatella* (SEM). 1. Apical fungal meristem in earliest stage, before division. Note longitudinal furrow (arrow). 2. Meristem later in ontogeny. First division has occurred but meristem has not split. 3. Three meristem bundles produced by two divisions. 4. Branch initiation by separation of meristem bundles and elongation of thallus beneath them. Note developing division furrows on two bundles (arrows). 5. Further divisions of meristem after elongation. 6. Complete meristem initial with meristem regions that will continue to divide. Scale bars in Figures 1 and 2 = 10 μm. Other scale bars = 100 μm.

bundles may give rise to branches, or they may enlarge and undergo further divisions. Branch initiation occurs when the meristem bundles separate and the lichenized tissue beneath them elongates (Figure 4). Thus, the process that is laid down by the fungal partner is continued in the symbiotic thallus. During any intermediate step (for example, Figure 5), meristem divisions may slow or stop, and branches may be produced. The branches that arise from intermediate steps usually are produced at approximately the same rate. Thus, two to five branches on the same podetium usually are at the same approximate stage of development. The meristem initial is complete when there are five more or less distinct apical meristem bundles (Figure 6). After this point, any meristem bundle of the initial may continue to split, giving rise to branches. Alternatively, it may enlarge without splitting. Finally, any bundle from the meristem initial may remain quiescent. Subsequent divisions may occur at any time and usually are not synchronous. The result is a podetium with five or more branches. In mature podetia with more than five branches, the branches thus may be observed in various stages of development.

In "late-branching" podetia, described below, the meristem tends not to divide as rapidly as in "early-branching" podetia. The initial stage of meristem development may resemble "early-branching" podetia (Figure 7). When the meristem splits, the resulting filial bundles (Figure 8) may continue to grow rather than dividing. They are usually larger than 100 μm in diameter and they may grow to nearly 500 μm. Alternatively, one of the two bundles may split, giving rise to branches while its filial bundle continues to grow (Figure 8). Series of indistinctly divided bundles may be produced in a roughly linear series (Figure 9). These may appear as short protrusions along the margin of a cuplike structure. They also may produce cuplike structures themselves. Any one of these, or part of one, also may split and form branches. The result is that the mature thallus appears to have an irregular branching pattern.

The large bundles appear to have several actively growing areas. There may be some distinct divisions that resemble the furrows described above but the "late-branching" meristem develops as a contiguous, roughly circular, convoluted structure (Figure 10). Branching in mature "late-branching" podetia is indistinct. The characteristic five-bundle meristem initial may or may not be formed in "late-branching" podetia. Where characteristic divisions of the meristem bundle do occur, the five-bundle meristem initial may be the result. The large meristem bundles produce lateral growth (Figures 11, 12) but relatively little vertical growth. Smaller bundles (<100 μm diam.) permit vertical growth.



Figures 7–12. Micrographs of fungal meristem in late branching *Cladonia cristatella* (SEM). 7. Early meristem bundle. Division furrows have formed but meristem has not split. 8. Two filial meristem bundles. Bundle on right has begun to split, initiating branch growth. 9. Series of indistinctly divided bundles in a roughly linear series. 10. A roughly circular, convoluted meristem structure. 11. Indistinct five-unit meristem initial has begun to form in the left-hand structure (arrows). 12. Indistinct meristem initial with short branches. Note four meristematic regions that have not split, or which have partially split. Scale bar in Figure 10 = 10 μm. Other scale bars = 100 μm.

DISCUSSION

Mature thalli of *Cladonia cristatella* have a variable though broadly characteristic morphology. For example, most mature podetia of this species are branched. Branching patterns vary, and podetia may be unbranched, sparingly branched, or abundantly branched. Branching may occur around the margins of a cuplike structure or it may occur independently, with branches arising at the apex of the podetium. Growth seems to be constrained by the size of the continuous meristem bundles. Large meristem bundles either divide or produce cuplike structures but they do not produce branches. By contrast, vertical growth is prevalent where meristem divisions are more frequent and occur earlier in ontogeny, which also was observed in verticillate *Cladonia* podetia (Hammer 1996b). However, the overall variability in *C. cristatella* is constrained by patterns of fungal meristem ontogeny. Branching and vertical growth both are determined by the meristem. The meristem bundle may enlarge and split dichotomously several times in relatively rapid succession, or it may grow rather slowly before splitting. In addition to the variability in mature podetia, early ontogeny in *C. cristatella* is variable. It is unusual to detect this much variation early in ontogeny, as most species in the Cladoniaceae follow a more highly constrained developmental plan. Yet the source of variability in *C. cristatella* is based on different expressions of synchronization. Jahns (1988) may have recognized this when he described the "faulty coordination" of development in *C. cristatella* that was growing in culture.

The varied timing of branch initiation in *Cladonia cristatella,* which occurs early in ontogeny, suggests a source of variation that may be independent of environmental influences. Variability in early ontogeny among thalli growing very close together suggests a heterogenous gene pool within populations of *C. cristatella.* Ahmadjian (1993) found that clones of one thallus were genetically heterogenous. It can be assumed that many genotypes comprise the species complex that is broadly identified as *C. cristatella.* Phenotypic variability among mature thalli is, therefore, a reasonable expectation. Yet certain ontogenetic features unite all of the phenotypes. Their expression at maturity simply depends upon the synchronization of developmental steps. Synchronization of growth in other *Cladonia* species may provide the basis for taxonomic differences (Hammer 1997). If variations in the development of *C. cristatella* are the result of heterochrony, then heterochrony may play a role in the evolution of this species.

It is noteworthy that the early ontogeny of *Cladonia cristatella* is similar to species that are presumed to be only distantly related. For example, the development of the early-branching variant is similar to species in *Cladonia* section *Perviae* (Del.) Matt. (Hammer 1996a). The five-bundle meristem initial also was described in the genus *Cladina* Nyl., for example, in *C. subtenuis* (Abb.) Hale & Culb. (Hammer 1997). While the mature form of these species is different from *C. cristatella,* their pattern of branch initiation is similar. In species in section *Perviae* and in *Cladina subtenuis,* the development of a meristem initial of five fungal bundles through irregular dichotomous divisions is the same as in *C. cristatella.* Branching may continue indeterminately from the meristem initial in all of these species but it is least predictable in *C. cristatella.* In the other taxa, the meristem appears to "rest" after the five-bundle initial has formed. In *C. cristatella* the period of quiescence is short and the meristem initial is indistinct. New divisions form soon after the meristem initial has been established.

The "late-branching" variant of *Cladonia cristatella,* in which the meristem enlarges, becomes convoluted, and slowly splits, has a growth dynamic that is similar to *Cladonia grayi* Merr. While the mature thalli of these species are only vaguely similar (*C. cristatella* may produce cuplike structures while *C. grayi* invariably forms cups), early meristem development in both species is the same. *Cladonia grayi* develops from the same convoluted meristem as *C. cristatella.* These examples provide evidence in lichens to support von Baer's third law (Baer 1828), which states that early developmental stages in related taxa are more similar than later ones (see Wallace 1988).

Ontogenetic information from comparisons of *Cladonia cristatella* with other species has taxonomic and evolutionary implications. Classification is one concern. Generic and infrageneric (sectional) boundaries in the Cladoniaceae are based upon the morphological criterion of "open" vs. "closed" cups and axils (Hammer 1995; Mattick 1938, 1940). But the criterion may not be appropriate for this level of taxonomic distinction. Axillary openings may differ in closely related species (Hammer 1993b, 1996a), a result of differing growth rates. The occurrence of openings is not consistent. They may form in species classified as "closed" axil, and they may not appear in "open" axil species. Finally, this criterion is based on the appearance of mature podetia, which is variable and confusing.

Early ontogeny of branch initiation may provide a robust character upon which to base taxonomic groupings. Branch initiation is the same in *Cladonia cristatella* ("closed" axil) and in *Cladina subtenuis* (an "open" axil species). This leads to questions about the evolution of branching in the Cladoniaceae. Have similar branching patterns arisen more than once? Alternatively, might branching patterns be canalized? The fungal meristem is homologous in *Cladonia* and *Cladina*, and development is the same in both genera. The similar development of the meristem initial in *Cladina subtenuis* and *Cladonia cristatella* suggests that these taxa might not represent two distinct genera.

From an evolutionary standpoint, it is helpful to consider the biogenetic law of Haeckl, which states that general characters are primitive (plesiomorphic) and less general characters are advanced (apomorphic; Nelson 1978). In the Cladoniaceae, the five-part meristem initial is more general (common) than axillary openings. Axillary openings arise from the development of branches, not the other way around, and branched species may not produce openings. May we infer that branched thalli are an evolutionary advance over non-branched thalli in the Cladoniaceae? Evolutionary advance may be inferred from specialization, or from the appearance of autapomorphies. Some lichens, such as *Cladina* species, develop in distinct, highly predictable patterns that Ahti (1961) called "regular." The mature thallus of these species is specialized for photosynthetic and reproductive functions (Hammer 1997). Development in *Cladonia cristatella* is less regular. The mature thallus also is less specialized. *Cladonia cristatella* possesses what can be considered to be a suite of primitive characters. The timing of its early ontogeny is variable. Its unspecialized program of meristem development includes growth patterns that form cuplike structures *and* branches. The early ontogeny of the meristem is similar to other, more specialized species. It seems plausible that species with a related but more specialized growth pattern represent an evolutionary radiation rooted in *C. cristatella* and its relatives. Branching, cup formation, and axillary openings are determined by the early ontogeny of the meristem. The exclusively fungal meristem may prove to be informative about the evolution of morphological characters in the Cladoniaceae.

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CHROMOSOME NUMBERS AND NOTES ON THE TAXONOMY OF SELECTED ALASKAN VASCULAR PLANTS

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ABSTRACT. Chromosome counts are documented and discussed for 44 Alaskan vascular plant taxa. Five of these are either first counts or new numbers for these taxa. A new combination, *Cardamine microphylla* subsp. *blaisdellii* is presented.

Key Words: Alaska, chromosome numbers, *Cardamine microphylla* subsp. *blaisdelli*

Notwithstanding the tremendous advances in plant systematics as molecular data have become more widely available, basic studies of the genome remain important to the circumscription of taxa. The work of many years in arctic Russia by Zhukova and her associates (for example, Zhukova 1966, 1980, 1982; Zhukova and Petrovsky 1971, 1977, 1984, 1985; Zhukova, Petrovsky, and Plieva 1973) and in Alaska by, among others, Dawe (1979), Dawe and Murray (1979, 1980, 1981a, b), Knaben (1968), Johnson and Packer (1968), and Packer and McPherson (1974) demonstrated that there is much more cytological variability within morphological species than previously appreciated. We offer here chromosome counts for Alaskan taxa that provide a) first counts or new numbers for taxa, b) first counts for Alaska, c) counts that document variations of chromosome number, as well as d) examples of chromosomal conservatism over wide geographic areas (Table 1).

MATERIALS AND METHODS

We obtained chromosome counts from root tips prepared by the squash technique. Seeds were stratified on damp filter paper

Table 1. Summary of numbers reported.

	2*n* =	Other Counts
Asteraceae		
Arnica griscomii subsp. *frigida*	ca. 36–38	38, 57, 58, 60, 70, 76
Artemisia borealis	36	18, 36
Artemisia furcata	72	18, 36, 90
Artemisia senjavinensis	36	36, 54
Crepis nana	14	14
Saussurea nuda	26	26
Taraxacum carneocoloratum	ca. 36	32
Tephroseris yukonensis	ca. 46	
Brassicaceae		
Braya glabella	ca. 56	28, 56, 64
Cardamine microphylla subsp. *blaisdellii*	28	28, 42
Cochlearia groenlandica	14	14
Draba cinerea	ca. 48	48, 64
Draba glabella	ca. 64	64, ca. 75, 80
Smelowskia borealis	12	12
Smelowskia calycina var. *integrifolia*	12	22, 24
Smelowskia pyriformis	12	
Caryophyllaceae		
Gastrolychnis involucrata	48	48
Gastrolychnis taimyrensis	48	48
Honckenya peploides	68	66, 68–70, 70
Minuartia arctica	80	ca. 50, 52, 80
Silene williamsii	24	24
Wilhelmsia physodes	70	50–60, 66, 72, 100–110
Fabaceae		
Astragalus aboriginum	16	16, 32
Astragalus nutzotinensis	22	22
Oxytropis arctica	48	48, 96
Oxytropis bryophila	ca. 32	32
Gentianaceae		
Gentiana glauca	24	24
Onagraceae		
Epilobium hornemannii	ca. 36	36
Papaveraceae		
Papaver alboroseum	28	28
Papaver macounii subsp. *discolor*	28	28, 70
Papaver mcconnellii	28	
Papaver walpolei	14	14

Table 1. Continued.

	2*n* =	Other Counts
Polemoniaceae		
Polemonium acutiflorum	18	18
Polygonaceae		
Rumex acetosa subsp. *alpestris*	15	14, 15
Primulaceae		
Androsace septentrionalis	20	20
Primula egaliksensis	36	36, 40
Ranunculaceae		
Ranunculus cymbalaria	16	16
Ranunculus gmelinii	16	16, 32
Ranunculus pygmaeus	16	16
Rosaceae		
Potentilla egedii	28	28
Saxifragaceae		
Boykinia richardsonii	ca. 80	36, 84
Saxifraga nelsoniana	ca. 80	60, 64, 80, 84
Saxifraga nudicaulis	40	40
Saxifraga reflexa	20	20

at 5 to 8°C for four weeks, then germinated under alternating conditions of light and dark at temperatures of 15 and 8°C, respectively. Root tips were pretreated in a 0.002M solution of 8-hydroxyquinoline for 2 to 3 hours at 10°C, then fixed in a 3:1 solution of 95% ethanol:glacial acetic acid. Chromosomes were stained with leucobasic fuchsin dye following the Feulgen procedure in Darlington and LaCour (1975). Voucher specimens have been deposited at the Herbarium of the University of Alaska Museum (ALA).

Synonyms and misapplied names are included when they facilitate cross references to widely used floras and the chromosome atlases cited below, particularly with respect to Löve and Löve (1975), who favored numerous generic segregates. We have tried to incorporate recent information from monographers; hence, the names we use depart in several instances from the nomenclatural foundation provided by Hultén (1968), Porsild and Cody (1980), and Welsh (1974). We also have derived important taxonomic perspectives from the *Arctic Flora U.S.S.R.*, edited over the many years of its production (1960–1987) by A. I. Tolmachev and B. A. Yurtsev, and these instances also are cited below.

Label data for voucher specimens documenting each count contain a reference to Quads. These are the U.S. Geological Survey quadrangle maps (1:250,000 scale topographic series), which serve in Alaska as the equivalent of counties.

RESULTS

ASTERACEAE

Arnica griscomii Fernald subsp. *frigida* (C. A. Mey. ex Iljin) S. J. Wolf

A. louiseana Farr subsp. *frigida* (C. A. Mey. ex Iljin) Maguire, *A. frigida* C. A. Mey. ex Iljin subsp. *frigida*

$2n$ = ca. 36–38: *Kelso 84-398.* U.S.A. Alaska. Seward Peninsula. Darby Mts., Bendeleben Quad.: NE of Death Valley and Tubutulik River.

This amphi-Beringian taxon shows a wide range of chromosome numbers: $2n = 38$, 57, and ca. 76 in North America and $2n = 58$, 60, 70, and 76 in Russia (Downie and Denford 1986). The count reported here provides additional documentation for the diploid cytotype ($x = 19$), which is now known from six localities, all in Alaska (Wolf 1980; Downie and Denford 1986).

The generalization of Wolf (1980) and Downie and Denford (1986), that diploids of this species are primarily restricted to unglaciated areas of central Alaska and that polyploids occur in glaciated areas, holds only as the broadest of regional generalizations, but not in the particular. Four of the five diploids reported by Wolf (1980) are from well within the geographic limits of late-glacial advances, and the one tetraploid count for Alaska (Johnson and Packer 1968) is from an area unglaciated throughout the Quaternary (Hamilton et al. 1986). Whereas the Seward Peninsula as a whole was largely unglaciated (Kaufman and Hopkins 1986), the diploid reported here is from a landscape that experienced local glaciation.

While it is clear that the diploids are restricted to Alaska, surprisingly, they are absent from the adjacent Chukotsk Peninsula, which experienced a similar glacial history where refugial areas persisted throughout the Quaternary. The ancestral stock presumably dispersed from Alaska at some time prior to the last glacial maximum, perhaps as early as the Tertiary, leaving related taxa disjunct in the Canadian Rockies (*Arnica louiseana*) and in the Gulf of St. Lawrence (*A. griscomii* subsp. *griscomii*; Downie and Denford 1986).

Wolf (1989) has determined that the name *Arnica griscomii* subsp. *frigida* must be used when following the treatment of Downie and Denford (1986, 1988) in which *A. frigida* is treated at the rank of subspecies and distinct from the Rocky Mountain taxon *A. louiseana* Farr.

Artemisia borealis Pall.

Oligosporus borealis (Pall.) Polyak.

$2n = 36$: *Kelso 83-278.* U.S.A. Alaska. Seward Peninsula. Teller Quad.: Gold Run Creek.

This is the same tetraploid number as reported from several localities elsewhere in the circumpolar north (Löve and Löve 1975; Dawe and Murray 1979). Korobkov (1981), however, also has mapped numerous diploid ($2n = 18$) cytotypes in western Chukotka and arctic Sakha (Yakutia), which, evidently, he was unable to distinguish morphologically from the tetraploids.

Artemisia furcata M. Bieb.

Artemisia trifurcata Steph.

$2n = 72$: *Kelso 83-236.* U.S.A. Alaska. Seward Peninsula. Kigluaik Mts., Solomon Quad.: near Homestake Creek.

Löve and Löve (1975) reported only diploid ($2n = 18$) numbers for this species, but Korobkov (1972, 1981) has since mapped the occurrence of both diploids and tetraploids ($2n = 36$) in northeastern Asia. The cytotypes are geographically segregated: the diploids are known from the Taimyr Peninsula to approximately Chaun Bay in Western Chukotka and the tetraploids throughout Eastern Chukotka, the Chukotsk Peninsula, and Wrangel Island. The chromosome number is not known for the Asiatic populations disjunct far to the south in the region of Lake Baikal.

The Alaskan counts of $2n = 72$ (this report) and $2n = 90$ (Johnson and Packer 1968, as *Artemisia trifurcata*) show an interesting progression of higher ploidy levels eastward across the Bering Strait. The Alaskan material reported by Dawe and Murray (1979) as *A. furcata* with $2n = 18 + 0–3f$ is *A. globularia* Besser.

Artemisia senjavinensis Besser

$2n = 36$: *Kelso 83-201.* U.S.A. Alaska. Seward Peninsula. Kigluaik Mts., Bendeleben Quad.: Mi. 50 Kougarok Road.

$2n = 36$: *Kelso 83-237.* U.S.A. Alaska. Seward Peninsula. Kigluaik Mts., Solomon Quad.: near Homestake Creek.

$2n = 36$: *Kelso 83-310.* U.S.A. Alaska. Seward Peninsula. Nome Quad.: Dexter Peak.

These three reports, all from the Seward Peninsula in western Alaska, add to the array of diploid counts for the taxon (Dawe and Murray 1981b). Although Korobkov (1981) knew only of $2n = 54$ cytotypes on Chukotka, he noted the existence of smaller (and more coarsely tuberculate) pollen grains on a specimen he saw from the Seward Peninsula, and therefore predicted the existence of diploid plants in Alaska.

In the view of Korobkov and B. A. Yurtsev[1] (pers. comm.), many of the Alaskan plants tend to have a more open growth form than the more consistently pulvinate plants from Chukotka; thus they apply the name *Artemisia senjavinensis* in a narrow sense to the Russian plants only. They then treat the Alaskan taxon as distinct from *A. senjavinensis* and give it the name *A. androsacea* Seem. [or *A. senjavinensis* subsp. *androsacea* (Seem.) Shed.]. Whereas the Chukotkan plants are uniformly $2n = 54$, both $2n = 36$ and 54 are known for Alaskan specimens (Dawe and Murray 1981b), which are without parallel morphological discontinuities; thus the cytotypes cannot be distinguished except by counts. Furthermore, there are Alaskan plants equally pulvinate and indistinguishable from those on Chukotka; therefore, we view these differences as falling within the range of variation of one species, *A. senjavinensis.*

Crepis nana Richardson

$2n = 14$: *Kelso 83-257.* U.S.A. Alaska. Seward Peninsula. Bendeleben Quad.: Kuzitrin River.

This count is consistent with others for the species in North America and Asia (Löve and Löve 1975; Dawe and Murray 1979;

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[1] The surname Юрцев is rendered as Jurtsev and Yurtsev. There is good correspondence in pronunciation between the letters Ю and J in Latin and German, but Yurtsev is the preferred spelling to achieve that same good correspondence in English. B. A. Yurtsev retains the spelling Jurtsev when his name appears Latinized, as an epithet, or as the authority for an epithet or combination.

Krogulevich and Rostovtseva 1984). Contrary to the distribution map given in Hultén (1968), this species is common in the interior of the Seward Peninsula.

Saussurea nuda Ledeb.

$2n = 26$: *Kelso 83-158.* U.S.A. Alaska. Seward Peninsula. Nome Quad.: Nome River estuary.

This same number was obtained from nearby Koyuk, Alaska (Dawe and Murray 1981b), and from western Chukotka (Zhukova 1966).

Taraxacum carneocoloratum A. Nelson

$2n =$ ca. 36: *Parker 1280.* U.S.A. Alaska. Alaska Range. McGrath Quad.: Post Lake.

Until recently this species was known from type specimens alone (Denali National Park). It has since been reported from the Ogilvie Mountains of Yukon Territory, Canada (Porsild 1974), and several additional localities in Alaska (Murray and Lipkin 1987). The chromosome count given by Mulligan and Porsild (1970) for the Ogilvie Mountains is $2n = 32$.

Tephroseris yukonensis (A. E. Porsild) Á. Löve & D. Löve

Senecio yukonensis A. E. Porsild

$2n =$ ca. 46: *Kelso 83-152.* U.S.A. Alaska. Seward Peninsula. Nome Quad.: Newton Peak.

This is the first count, albeit approximate, for this endemic of Alaska and Yukon. The voucher specimen for this count differs from several others at ALA in having less densely floccose pubescence on the involucres and peduncles, and in this respect it approaches *Senecio subfrigidus* Komarov (fide B. A. Yurtsev), which has a number of $2n = 48$ (Zhukova 1980), characteristic of tephroserids (Löve and Löve 1975).

BRASSICACEAE

Braya glabella Richardson

$2n =$ ca. 56: *Kelso 83-209a.* U.S.A. Alaska. Seward Peninsula. Nome Quad.: Teller Road.

This is a relatively common species on the Seward Peninsula and the coastal plain of the Alaskan Arctic Slope, to which Hultén (1968) had incorrectly applied the name *Braya pilosa* Hook. The voucher specimen for this count consists of small plants with narrow leaves and siliques with long styles, attributes that are characteristic of populations on the Seward Peninsula and also specimens we have seen from the opposite site of the Bering Strait on Arakamchechen Island. These specimens resemble *B. bartlettiana* Jordal of the central Brooks Range, which, to us, falls within the range of variability of *B. glabella.*

This species appears to be dibasic (x = 7 and 8), based on counts of $2n$ = 28, 56, and 64 (Dawe 1979). Our specimens also match well those we have seen for *Braya aenea* Bunge subsp. *pseudoaenea* V. V. Petrovsky at LE from Chukotka, for which counts of $2n$ = 28 and 56 have been obtained (Zhukova and Petrovsky 1984).

Cardamine microphylla Adams subsp. ***blaisdellii*** (Eastw.) D. F. Murray & S. Kelso, *comb. et stat. nov.* Based on *C. blaisdellii* Eastw., Bot. Gaz. 33:146, 1902. TYPE: U.S.A. Alaska. Cape Nome, summer 1900, *F. E. Blaisdell s.n.* [HOLOTYPE: CAS (fiche!); ISOTYPE: GH!]

$2n$ = 28: *Kelso, Flock, and Colson 63.* Seward Peninsula. Teller Quad.: Cape Prince of Wales.

This is the first count for this taxon in Alaska. The numerous voucher specimens at LE documenting the counts of Zhukova and Petrovsky (1984) show both $2n$ = 28 and 42 from populations of this taxon in Chukotka.

Among the predominately white-flowered representatives of arctic *Cardamine,* several names have been applied: *C. digitata* Richardson, *C. microphylla* Adams, *C. richardsonii* Hultén, *C. hyperborea* O. E. Schulz, and *C. blaisdellii* Eastw. Most taxonomic accounts agree that 1) there is one taxon with narrow, linear-lanceolate leaflets, and 2) there is a second, variable one with orbicular to elliptic leaflets that shows a distinct tendency in the Bering Strait region toward lobed and toothed forms. The first taxon is *C. digitata*; it is amply distinct from the second morphologically, but the two have been associated nomenclaturally.

The problem began when Schulz (1903) proposed *Cardamine hyperborea* as a new name with the explicit, but mistaken, purpose of providing a replacement for Richardson's *C. digitata,* which he believed to be a later homonym of *C. digitata* (Lam.) O.E. Schulz, based on *Dentaria digitata* Lam. (=*C. pratensis L.*). Unfortunately, some of the specimens Schulz cited as the basis for his *C. hyperborea* are of another species, not Richardson's, a discrepancy noted by Porsild (1938) and Hultén (1945). Hultén believed there still existed a need to replace the so-called later homonym *C. digitata,* for which he proposed *C. richardsonii* as the substitute, typified by Richardson's specimen.

Rollins has written that since the combination *Cardamine digitata* (Lam.) O. E. Schulz was made 80 years after Richardson had proposed his name, there is no impediment to the use of *C. digitata* Richardson. "Since *C. hyperborea* Schulz was a direct substitution for *C. digitata* Richardson, it rests on the same type and whether the description Schulz gave fits or not is not significant in so far as name priority" (Rollins 1952). The name *C. hyperborea* Schulz is superfluous. Hultén's name *C. richardsonii* is, for the same reason, also superfluous, and *C. digitata* Richardson remains the correct name for the taxon.

What name are we to apply to the second element in Schulz's *Cardamine hyperborea*? Porsild (1938) referred these plants to *C. blaisdellii,* which Hultén (1945) placed in synonymy with *C. microphylla.* Petrovsky (1975) recognized *C. microphylla* but continued to recognize another taxon to which he applied the name *C. hyperborea.* This taxon he distinguished from *C. microphylla,* at least in part, by the shape of the leaflets: the terminal one being larger than the lateral and all of them often toothed and lobed. Porsild (1974) also noted a Bering Strait variant within *C. microphylla* in which the basal leaves tend to be lobed, the same taxon to which he had previously applied the name *C. blaisdellii* (Porsild 1938).

Having reviewed the specimens that Porsild (CAN), Hultén (S), and Petrovsky (LE) used as the basis for their treatments, we can see that, in addition to *Cardamine digitata,* two taxa are recognizable: *C. microphylla,* and *C. hyperborea* in the sense it was still being used by Petrovsky. The question is, what name should apply to the latter. *Cardamine blaisdellii* is the correct name, if the taxon is treated at the rank of species. However, because the morphological discontinuity between *C. blaisdellii* and *C. microphylla* is not always clear cut, we propose that it be recognized at the rank of subspecies.

Cochlearia groenlandica L.

Cochleariopsis groenlandica (L.) Á. Löve & D. Löve

$2n = 14$: *Kelso, Flock, and Colson 66.* U.S.A. Alaska. Seward Peninsula. Teller Quad.: Cape Prince of Wales.

This count is consistent with others for this taxon throughout the Arctic (Löve and Löve 1975). Nordal and Laane (1990) and Nordal (pers. comm., 1995) apply the name *Cochlearia groenlandica* to the arctic, autogamous, diploid taxon and *C. officinalis* L. to the self-incompatible tetraploid ($2n = 24$). This breeding behavior of the tetraploid is unusual, for polyplody is often correlated with self-compatibility (Kelso 1992; Molau 1993).

Draba cinerea Adams

$2n$ = ca. 48: *Kelso 84-381.* U.S.A. Alaska. Seward Peninsula. Darby Mts., Bendeleben Quad.: near Death Valley.

Counts of both $2n = 48$ and 64 have been reported by Mulligan (1971) from arctic Canada and by Zhukova and Petrovsky (1984) from northeast Asia.

Draba glabella Pursh

Draba hirta auct.

$2n$ = ca. 64: *Kelso 83-272.* U.S.A. Alaska. Seward Peninsula. Teller Quad.: Gold Run Creek.

Previous counts of $2n = 64$ have been obtained throughout northern Canada and $2n = 80$ at just two localities in the Eastern Arctic (Mulligan 1970), while counts of $2n$ = ca. 75 (Rollins 1966) and ca. 80 (Johnson and Packer 1968) exist from elsewhere in Alaska. When discussing the cytogeography of the taxon for the Eastern Canadian Arctic and Greenland, Mulligan (1970) remarked that the octoploid ($2n = 64$) is more common (that is, it has been counted more often) than the decaploid. It would be interesting to know the distribution and relative abundance of the three Alaskan cytotypes, for *Draba glabella* is common throughout the Arctic Slope and Bering Strait regions.

Smelowskia borealis (Greene) W. H. Drury & Rollins

$2n = 12$: *Parker 1734.* U.S.A. Alaska. Alaska Range. Mt. Hayes Quad.: Rainbow Mt.

This is the third count for this endemic of Alaska and Yukon (Dawe and Murray 1979, 1981a). The reports in Löve and Löve (1975) from Chukotka are based not on *Smelowskia borealis* but a close relative, *Ermania parryoides* Cham., which occurs in both diploid and tetraploid cytotypes.

Smelowskia calycina (Stephan) C. A. Mey. var. *integrifolia* (Seem.) Rollins

S. spathulatifolia Velichkin

$2n = 12$: *Kelso 84-405.* U.S.A. Alaska. Seward Peninsula. Darby Mts., Bendeleben Quad.: Camp Haven.

Löve and Löve (1975) have treated this taxon as synonymous with *Smelowskia porsildii* (Drury & Rollins) Jurtsev (*S. calycina* var. *porsildii* Drury & Rollins). *Smelowskia calycina* var. *integrifolia* is distinguished by its mix of both shallowly lobed and entire, broadly spatulate basal leaves with short petioles, whereas var. *porsildii* consistently has narrow, entire, ligulate basal leaves with long petioles.

Variety *integrifolia* has chromosome numbers of $2n = 12$ (this report) and $2n = 22$ (Dawe and Murray 1979). Tetraploid plants ($2n = 24$) are known on Chukotka (Yurtsev and Zhukova 1972). Its Rocky Mountain relative var. *americana* (Regel & Herder) Drury & Rollins has also been counted at $2n = 12$ in Colorado, Wyoming, and Utah (Drury and Rollins 1952) and at $2n = 22$ in Alberta (Packer 1968). One might think that the $2n = 22$ plants are aneuploids derived from tetraploids, possibly producing seed by agamospermy, but Greene (1978) found normal megagametogenesis in the one Alberta population of var. *americana* he studied.

Variety *porsildii* has a chromosome number of $2n = 22$ in Alaska (Johnson and Packer 1968) and, surprisingly, also $2n = 18$ and 24 (Zhukova and Petrovsky 1984, as *Smelowskia porsildii*) in eastern Chukotka. The more compact forms of var. *porsildii* have been segregated as *S. jurtzevii* Velichkin (Velichkin 1974).

The problem of explaining numbers $2n = 12$, 22, and 24 in var. *integrifolia,* $2n = 18$, 22, and 24 in var. *porsildii,* and $2n = 12$ and 22 in var. *americana* points to the need for more counts to determine the morphologic and geographic limits of these taxa. *Smelowskia calycina* var. *media* Drury & Rollins, an endemic of northeastern Alaska and northwestern Yukon and the fourth member of the North American complex of taxa centered on *S. calycina,* is thus far known only at $2n = 12$.

Smelowskia pyriformis W. H. Drury & Rollins

$2n = 12$: *Parker 1256.* U.S.A. Alaska. Alaska Range. McGrath Quad.: Post Lake.

This is the first count for this rare endemic of Alaska (cf. Murray and Lipkin 1987).

CARYOPHYLLACEAE

Gastrolychnis involucrata (Cham. & Schlecht.) Á. Löve & D. Löve

Gastrolychnis affinis (Vahl) Tolm. & Kozhanch., *Melandrium affine* Vahl, *Silene involucrata* (Cham. & Schlecht.) Bocq., *Lychnis affinis* J. Vahl ex Fries

$2n = 48$: *Kelso 83-265.* U.S.A. Alaska. Seward Peninsula. Bendeleben Quad.: Kougarok Road.

This count is consistent with the one other count from Alaska (Johnson and Packer 1968) and with numerous counts from northeastern Asia (Krogulevich and Rostovtseva 1984).

The species assemblage to which this taxon belongs, although generally placed in *Melandrium, Silene,* or *Lychnis,* is sufficiently distinct from the others to warrant separation as the genus *Gastrolychnis* (McNeill 1978; Kozhanchikov and Tolmachev 1971; Löve and Löve 1975; Czerepanov 1995). The use of *G. involucrata* as the name for this taxon follows Czerepanov (1995).

Regardless of how others reported their numbers, Löve and Löve (1975) restricted to *Gastrolychnis affinis* the number $2n = 24$ and, incorrectly in our view, reassigned all counts of $2n = 48$ to *G. involucrata* subsp. *tenella,* which Czerepanov (1995) has reduced to synonymy under *G. taimyrensis* (Tolm.) Czer. (see below).

Gastrolychnis taimyrensis (Tolm.) Czer.

Lychnis taylorae B. L. Rob., *Melandrium taylorae* (B. L. Rob.) Tolm., *Silene taylorae* (B. L. Rob.) Hultén, *Gastrolychnis involucrata* subsp. *tenella* (Tolm.) Á. & D. Löve, *G. angustifolia* Rupr. subsp. *tenella* (Tolm.) Tolm. & Kozhanch., *G. tenella* (Tolm.) Kuvajev.

$2n = 48$: *Kelso 84-414.* U.S.A. Alaska. Seward Peninsula. Bendeleben Quad.: Kougarok Road near Pilgrim River.

This report is consistent with the two counts (as *Melandrium taylorae*) from interior Alaska (Knaben 1968; Dawe and Murray 1980).

Following Czerepanov (1995), *Gastrolychnis taimyrensis* includes *G. angustifolia* subsp. *tenella* of Eastern Siberia and the

Russian Far East, which has a chromosome number of $2n = 48$ as determined from Sakha (Zhukova, Korobkov, and Tikhonova 1977) and western Chukotka (Zhukova and Petrovsky 1977).

Kozhanchikov and Tolmachev (1971) placed *Melandrium taylorae* in synonymy with *Gastrolychnis angustifolia* subsp. *tenella*, a decision that specimens of both taxa at ALA would bear out. Therefore, what has been regarded as an endemic of Alaska and Yukon (*M. taylorae*) is now seen as distinctly amphi-Beringian.

Honckenya peploides (L.) Ehrh.

Arenaria peploides L.

$2n = 68$: *Meyers 86-9*. U.S.A. Alaska. Seward Peninsula. Nome Quad.: vic. Nome.

There are two additional counts of $2n = 68$ from Alaska (Johnson and Packer 1968; Packer and McPherson 1974.). Other numbers reported for this species from throughout the circumpolar north are $2n = 66$, ca. 66, 68–70, and 70 (Löve and Löve 1975).

Minuartia arctica (Stev.) Asch. & Graebn.

Arenaria arctica Stev., *Lidia arctica* (Stev.) Á. Löve & D. Löve

$2n =$ ca. 80: *Kelso 83-265*. U.S.A. Alaska. Seward Peninsula. Nome Quad.: Dexter Peak.

$2n = 80$: *Kelso 83-302*. U.S.A. Alaska. Seward Peninsula. Nome Quad.: Dexter Peak.

There is another count of $2n =$ ca. 80 (Mulligan and Porsild 1969) from central Yukon and one of $2n = 52$ from arctic Alaska (Johnson and Packer 1968). Löve and Löve (1975) cited the report of $2n =$ ca. 50 by Packer and McPherson [1974, as *Arenaria obtusiloba* (Rydb.) Fern.] under *Lidia arctica*. We have not seen the voucher for the Packer and McPherson count and therefore have not determined if that change of their original determination by Löve and Löve (1975) is justified.

Silene williamsii Britton

S. menziesii Hook. subsp. *williamsii* (Britton) Hultén

$2n = 24$: *Parker s.n.* U.S.A. Alaska. Yukon-Tanana Upland. Circle Quad.: Circle Hot Springs.

This count is consistent with three other counts for this taxon from interior Alaska (Knaben 1968).

Wilhelmsia physodes (Fisch. ex Ser.) McNeill

Arenaria physodes Fisch. ex Ser.

$2n = 70$: *Meyers 86-7.* U.S.A. Alaska. Seward Peninsula. Nome Quad.: vic. Nome.

The chromosome numbers reported for this species are extremely variable; this report adds one more variant to the list: $2n = 50–60, 66, 72, 100–110$ (Löve and Löve 1975; Dawe and Murray 1981a).

FABACEAE

Astragalus aboriginum Richardson

$2n = 16$: *Kelso 83-156.* U.S.A. Alaska. Seward Peninsula. Nome Quad.: Monument Creek.

One previous count for the diploid is from the subarctic interior of Alaska (Dawe and Murray 1979). The count attributed by Löve and Löve (1975) to Johnson and Packer (1968) cannot be found in their paper. There are also two reports of a tetraploid ($2n = 32$) in arctic Alaska (Hedberg 1967; Holmen 1962).

In Löve and Löve (1975), *Astragalus aboriginum* unaccountably disappeared from the list of arctic plants and was replaced by two other names: *A. lepagei* Hultén for the diploid and *A. richardsonii* Sheldon for the tetraploid. According to Yurtsev (1986), *A. lepagei* is a superfluous name for the amphi-Beringian *A. tugarinovii* Basil., which in the Russian Arctic has chromosome numbers of $2n = 16, 32$, and 48.

Astragalus nutzotinensis J. Rousseau

$2n = 22$: *Parker 1735.* U.S.A. Alaska. Alaska Range. Mt. Hayes Quad.: Rainbow Mt.

This count for this Alaska and Yukon endemic is consistent with two others for the species (Dawe and Murray 1979; Ledingham 1960).

Oxytropis arctica R. Br.

$2n = 48$: *Kelso 84-410.* U.S.A. Alaska. Seward Peninsula. Bendeleben Quad.: Darby Mts. near Camp Haven.

The taxonomic disposition of this fruiting material is not an easy matter, but the presence of minute processes on the margins of the stipules favors the determination as *Oxytropis arctica.* Although Löve and Löve (1975) claim the chromosome number to be $2n = 96$, they do report $2n = 48$ for *O. koyukukensis* A. E. Porsild, which is clearly part of the same complex.

Oxytropis bryophila (Greene) Jurtsev

Oxytropis nigrescens (Pall.) Fisch. subsp. *bryophila* (Greene) Hultén

2*n* = ca. 32: *Kelso 83-204.* U.S.A. Alaska. Seward Peninsula. Nome Quad.: Anvil Mt.

This count is consistent with others for the species (Löve and Löve 1975, incorrectly cited therein as *Oxytropis tschuktschorum* Jurtsev).

GENTIANACEAE

Gentiana glauca Pall.

Gentianodes glauca (Pall.) Á. Löve & D. Löve

2*n* = 24: *Kelso 83-299.* U.S.A. Alaska. Seward Peninsula. Solomon Quad.: Big Creek Valley.

This count is consistent with others for the species (Löve and Löve 1975).

ONAGRACEAE

Epilobium hornemannii Rchb.

2*n* = ca. 36: *Kelso 83-178.* U.S.A. Alaska. Seward Peninsula. Nome Quad.: Anvil Mt.

Our count is consistent with others for the species (Löve and Löve 1975).

PAPAVERACEAE

Papaver alboroseum Hultén

2*n* = 28: *Holmes s.n.,* 16 July 1991. U.S.A. Alaska. Denali National Park.

Our count for this North Pacific endemic is only the second to be based on Alaskan material (Dawe and Murray 1981b). The Alaskan counts are consistent with others for the species in the Russian Far East (Zhukova and Petrovsky 1987).

Papaver macounii Greene subsp. *discolor* (Hult.) Rändel ex D. F. Murray

2*n* = 28: *Kelso s.n.,* 1 July 1984. U.S.A. Alaska. Seward Peninsula. Nome Quad.: Glacier Creek Road.

Rändel (1977) proposed that 2*n* = 28 was characteristic of

Papaver macounii on the islands of the Bering Sea (subsp. *macounii*), whereas those on the mainland (subsp. *discolor*) were characterized by $2n = 70$ and ?42 (sic.). She evidently was unaware of the four previous counts at $2n = 28$ for *P. macounii* from localities in interior and arctic Alaska (Knaben 1959, 1968; Johnson and Packer 1968; Packer and McPherson 1974). The count reported here is from near the type locality for subsp. *discolor.*

Mulligan and Porsild (1969) reported (as *Papaver radicatum* Rottb. s.l.) one count of $2n = 70$ for *P. macounii* subsp. *discolor* from a locality in Yukon Territory, Canada. There are several counts of $2n = 70$ for *P. paucistaminum* Tolm. & V. V. Petrovsky on Chukotka and Wrangel Island (Zhukova and Petrovsky 1985), a species clearly very close to *P. macounii* subsp. *discolor,* and more work is needed to resolve this taxonomic relationship.

Horn (1938) reported only a single count of $2n = 28$ based on seed of plants from St. Paul's Inlet (St. Paul Island), which he had obtained from Rolf Nordhagen and, which, according to Knaben (1959), had originated from a collection of Eric Hultén. The count of $2n = 42$ attributed to Horn (1938) by Knaben (1959, Part A, Table 2, p. 22) is clearly the source for Rändel's report for the mainland population (as "?42"), and, equally clearly, it is based on a misprint in Knaben (1959).

Papaver mcconnellii Hultén
P. denalii Gjaerevoll

$2n = 28$: *Parker 1281.* U.S.A. Alaska. Alaska Range. McGrath Quad.: Post Lake.

$2n = 28$: *Kelso 82-66.* U.S.A. Alaska. Seward Peninsula. Teller Quad.: Kigluaik Mts., Crete Creek.

These are the first counts for *Papaver mcconnellii,* an endemic of Alaska and Yukon. Although not mapped for the Seward Peninsula by Hultén (1968), we have found it repeatedly on screes in the Kigluaik Mountains. This has been an enigmatic species, for, until quite recently, our understanding of it has been based on the original description, the type specimen, and two other specimens from Healy, Alaska (Porsild 1951). Abundant material collected in Yukon Territory (Cody 1996) now gives us a clear picture of this species and also shows well the link to *P. denalii* Gjaerevoll, which is fairly common on calcareous screes and summits in the central and southern Alaska Range. The type specimen of *P. mcconnellii* and many specimens from the British Mountains, for example, have leaf lobes that are generally elongate, lingulate or lanceolate, whereas the leaf lobes of *P. denalii* from the type locality in the Alaska Range and the Kuskokwim Mountains can be short and ovate, even orbicular. Numerous plants with intermediate leaf form occur within the Alaska Range.

Papaver walpolei A. E. Porsild

2*n* = 14: *Kelso s.n.,* 16 August 1985. U.S.A. Alaska. Seward Peninsula. Nome Quad.: Cleveland Creek.

This count establishes the chromosome number for an Alaskan population of this Beringian endemic. Zhukova and Petrovsky (1971) have reported two counts of 2*n* = 14 for *Papaver walpolei* from the Chukotsk Peninsula. Their earlier report of 2*n* = 42 for material from Wrangel Island (erroneously reported as 2*n* = ca. 84 in Löve and Löve 1975) was based on *P. gorodkovii* Tolm. & V. V. Petrovsky (Zhukova and Petrovsky 1985).

POLEMONIACEAE

Polemonium acutiflorum Willd.

2*n* = 18: *Kelso, Flock, & Colson 165.* U.S.A. Alaska. Seward Peninsula. Teller Quad.: Cape Prince of Wales.

This count is consistent with others for the species (Löve and Löve 1975; Dawe and Murray 1979).

POLYGONACEAE

Rumex acetosa L. subsp. *alpestris* (Scop.) Á. Löve

2*n* = 15: *Kelso 83-179.* U.S.A. Alaska. Seward Peninsula. Nome Quad.: Anvil Mt.

Two cytotypes, 2*n* = 14 and 15, have been reported for this taxon. Our count is consistent with another for Alaska (Johnson and Packer 1968) and with many others from throughout its broad geographic range [Löve and Löve 1975, as *Acetosa pratensis* Mill. subsp. *arifolia* (Blytt & Dahl) Á. Löve].

PRIMULACEAE

Androsace septentrionalis L.

2*n* = 20: *Kelso 83-116.* U.S.A. Alaska. Seward Peninsula. Nome Quad.: Cape Nome.

This count is consistent with others for the species (Dawe 1979; Dawe and Murray 1979).

Primula egaliksensis Wormsk. ex Hornem.

$2n = 36$: *Holmes s.n.* U.S.A. Alaska. Copper River Delta. Cordova Quad.: Alaganik Slough.

This primarily American species is most closely related to *Primula nutans* Georgi (*P. sibirica* Jacq.), a widespread Eurasian diploid found occasionally in interior and western Alaska (Kelso 1991). A previous Alaskan count was $2n =$ ca. 36 (Johnson and Packer 1968), and one from Colorado was $2n = 36$ (Löve et al. 1971). The Siberian counts, however, have been $2n = 40$ (Zhukova et al. 1973; Zhukova 1982).

RANUNCULACEAE

Ranunculus cymbalaria Pursh

Cyrtorhyncha cymbalaria (Pursh) Britton

$2n = 16$: *Meyers 86-2.* U.S.A. Alaska. Seward Peninsula. Nome Quad.: vic. of Nome.

This count is consistent with others for the species [Löve and Löve (1975), as subsp. *alpina* (Hook.) Á. Löve & D. Löve].

Ranunculus gmelinii DC.

$2n = 16$: *Kelso 83-267.* U.S.A. Alaska. Seward Peninsula. Bendeleben Quad.: vic. of Dahl.

$2n = 16$: *Kelso 83-270.* U.S.A. Alaska. Seward Peninsula. Teller Quad.: Teller Airport.

These are the first counts from Alaska for the diploid cytotype; previous counts for the species have been $2n = 32$ (Johnson and Packer 1968; Packer and McPherson 1974). Diploids are known elsewhere in North America from Manitoba (Löve and Ritchie 1966) and northern Quebec (Hedberg 1967) and from northeastern Asia [Krogulevich and Rostovtseva (1984), together with $2n = 24$ and $2n = 32$].

Ranunculus pygmaeus Wahlenb.

$2n = 16$: *Kelso 83-244.* U.S.A. Alaska. Seward Peninsula. Solomon Quad.: E side Kigluaik Mts., near Homestake Creek.

This count is consistent with others for the species (Löve and Löve 1975).

ROSACEAE

Potentilla egedii Wormsk.

Argentina anserina (L.) Rydb. subsp. *groenlandica* (Tratt.) Á. Löve

2*n* = 28: *Meyers 86-1.* U.S.A. Alaska. Seward Peninsula. Nome Quad.: vic. Nome on Council Road.

This count is consistent with others for the species (Löve and Löve 1975; Dawe and Murray 1979).

SAXIFRAGACEAE

Boykinia richardsonii (Hook.) A. Gray

2*n* = ca. 80: *Kelso 83-299.* U.S.A. Alaska. Seward Peninsula. Nome Quad.: Anvil Mt.

Previous reports for this endemic of Alaska and Yukon are 2*n* = 36 (Knaben 1968) from the interior of Alaska and 2*n* = ca. 84 (Packer and McPherson 1974) and 2*n* = 84 (Johnson and Packer 1968) from two arctic localities.

Saxifraga nelsoniana D. Don

Saxifraga punctata auct.

2*n* = ca. 80: *Kelso 83-313.* U.S.A. Alaska. Seward Peninsula. Teller Quad.: Cape Prince of Wales.

Other counts from Alaska and Yukon are 2*n* = ca. 84 (Johnson and Packer 1968) and 2*n* = 84 (Mulligan and Porsild 1969; Packer and McPherson 1974). Counts of 2*n* = 60, 64, 80, and 84 have been reported from Siberia and the Russian Far East (Löve and Löve 1975; Krogulevich and Rostovtseva 1984).

The report of 2*n* = 28 (Packer 1964), based on material from the Richardson Mountains of Yukon, and several others at 2*n* = 28 and 30 from Siberia and the Russian Far East (Krogulevich and Rostovtseva 1984) should, most likely, be referred to *Saxifraga porsildiana* (Calder & Savile) Jurtsev & V. V. Petrovsky [*S. punctata* L. subsp. *porsildiana* Calder & Savile, *S. nelsoniana* subsp. *porsildiana* (Calder & Savile) Hultén].

Saxifraga nudicaulis D. Don subsp. *nudicaulis*

2*n* = 40: *Kelso 83-233.* U.S.A. Alaska. Seward Peninsula. Nome Quad.: Kigluaik Mts., Nugget Creek.

This is apparently the first count from North America for this Beringian endemic. The same count has been obtained from at least three localities on the Chukotsk Peninsula (Krogulevich and Rostovtseva 1984).

Saxifraga reflexa Hook.

2n = 20: *Kelso 84-380.* U.S.A. Alaska. Seward Peninsula. Bendeleben Quad.: Darby Mts.

The same count was obtained in northwestern arctic Alaska (Johnson and Packer 1968) and the Richardson Mountains of northern Yukon (Packer 1964).

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REPRODUCTIVE BIOLOGY OF *ISOTRIA MEDEOLOIDES* (ORCHIDACEAE)

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ABSTRACT. The contribution of self-pollination to overall reproduction in *Isotria medeoloides* was experimentally assessed. We used insect exclosures and applied three treatments—no floral manipulation; pollinaria removal followed by hand self-pollination; and pollinaria removal followed by hand cross-pollination—and a control. Mature capsule dimensions and total seed weight were measured for each capsule. Analysis of variance revealed no significant treatment effects in mean seed weight, whereas a G-test showed that there were no differences in fruit set among treatments. Capsule length and diameter were strongly correlated with seed weight. Additionally, plant size (measured as leaf whorl diameter) was positively correlated with overall mean seed weight. We conclude that *I. medeoloides* is self-compatible and primarily self-pollinating. We also conclude that while reproduction is not limited by pollen availability, it may be limited by resources, assessed by overall plant size.

Key Words: *Isotria medeoloides,* Maine, autogamy, self compatibility

Isotria medeoloides (Pursh) Raf. has historically been considered the rarest orchid east of the Mississippi except in Florida (Luer 1975), and was included on the Federal List of endangered plant species in 1982 (Federal Register, 1982, vol. 47, p. 39827). However, this species was downlisted to Federally Threatened in 1994 (Federal Register, 1994, vol. 59, p. 50857). As of 1988, there were 81 known populations, the majority of which contain only a few (3–10) individuals (Gregory 1988; Mehrhoff 1983). *Isotria medeoloides* is a sympodial geophyte that produces a single (rarely 2) terminal flower.

The column of *Isotria medeoloides* has a terminal hinged anther which rests above the stigmatic area. The mealy pollen is extruded beyond the pollinia recesses hidden in the adaxial surface of the anther during the second day of anthesis. During pollen extrusion, the hinged anther is forced up, and the pollen is then able to come into contact with the stigmatic area below (Mehrhoff 1980, 1983; pers. obs.). Although this floral morphology enables self-pollination, Mehrhoff (1980, 1983) pointed out that the small populations in his study area precluded experiments to determine the contribution of self-fertilization to overall reproduction. In contrast, the presence of several relatively large populations (greater than 100 individuals) in southern Maine allowed us to study the breeding system of this species as part of an ongoing demographic study.

There has been much anecdotal evidence regarding the breeding system of this species, as well as Mehrhoff's (1980, 1983) field observations that cite the lack of an observed insect vector. Despite the apparent lack of an insect pollinator, *Isotria medeoloides* has consistent, and sometimes quite high, levels of fruit set in natural populations (Vitt 1991). Specific knowledge of the reproductive biology of a rare species enhances our ability to interpret demographic trends, and may help us to predict the underlying genetic structure of a population. This study was designed to determine if *I. medeoloides* is self-compatible and to assess the relative contributions of self- and cross-pollination to overall reproduction.

MATERIALS AND METHODS

Our study site on a Nature Conservancy preserve in southern Maine is typical of the second growth mixed hardwood usually occupied by this species (Gregory 1988). Despite the large population size (200–300 plants), only 52 individuals were flowering when the study was initiated in early June of 1990. We defined an individual (genet) as a stem which occurred farther than 5 cm away from its nearest neighbor. This definition was based upon observations of the underground growth habits of a few individuals, and additionally upon the fact that the vast majority of emergent stems were sparsely dispersed as single stems over the study area. Detailed field observations were carried out from June 5 to June 20, 1989 and from June 1 to June 14, 1990. Approximately 40 hours between 0700 and 1300 hours, and 30 hours between 1300 and 1900 hours, were spent watching for insect visitors over the two field seasons. A preliminary experiment was done in 1989 to assess the occurrence of agamospermy in this species, while the primary experiment to test for autogamy was done in 1990.

The terminal anthers with intact pollinia (the pollinaria) of eight plants were carefully removed at the hinge with forceps in 1989 to test for agamospermy. We subsequently bagged four plants, and let the remainder open-pollinate. In 1990, we randomly assigned 40 flowering plants to one of three treatment groups: (1) no manipulation of the flower; (2) manual self-pollination subsequent to pollinaria removal; (3) manual cross-pollination with nearby individuals after pollinaria removal (Table 1). Pollinaria removal was carried out either before anthesis or during the morning of the first day of anthesis when there was no evidence of pollen extrusion from the pollinia recesses. After treatment, we covered the plants in all three groups with a fine mesh insect exclosure. The 12 plants in the control group were not covered.

Treatment 1 determined if levels of pollination would differ from the control when all insects were excluded (i.e., does autogamy occur in this species), while treatment 2 tested whether this species is self-compatible. Results from treatment 3 were compared with the control to determine if manual cross-pollination increased fruit set relative to open pollination. We expected to detect no differences among the treatments. Despite the lack of evidence of an insect pollinator, fruit set in natural populations can be as high as 89% (Vitt 1991). We reasoned that *Isotria medeoloides* would be highly self-compatible as well as strongly self-pollinating.

We considered pollination successful if the ovary had enlarged and appeared healthy two weeks after treatment. On August 26, 1990, we collected capsules and recorded maximum leaf-whorl diameter of each plant. Fruit set was recorded as negative when an individual initiated a fruit which was subsequently aborted.

We weighed the fresh capsules the day after collection. We used digital calipers and software provided by L. M. Marcus to measure capsule diameter and length. Orchid seeds are too small and numerous to count; therefore, we measured seed set as the total weight of the seeds in each capsule. Individual capsules were air dried in paper bags. The dried capsules remained intact during this process, and were weighed both before and after seed removal. We then calculated the percentage of all individuals that set fruit, as well as the mean total seed weight for each treatment.

RESULTS

In the 1989 preliminary study on agamospermy, 7 of the 8 plants failed to produce fruit. The only plant producing fruit was one that had been allowed to open-pollinate. Although the number of bagged plants from which the pollinaria had been removed in the preliminary study is small (only 4 individuals), the absence of fruit among these suggests agamospermy does not occur in this species. Although fruit set in the open-pollinated individual may have been the result of a cross-pollination event, it is also possible that pollination occurred prior to pollinaria removal.

No insect visitors were detected during our observations in either field season. In 1990, during an informal survey of all flowering individuals found at our study site, only four flowers were found with the pollinaria missing. We never observed pollinaria deposition.

Of the 42 individuals which initiated a capsule, two aborted, one from treatment 1 and one from treatment 2. These were not included in further analysis. Fruit set for the control group (no manipulation, no exclosure) was 83%, whereas fruit set for treatment 1 (no manipulation, exclosure) was 67% (Table 1). Both treatments 2 (hand self-pollination, exclosure) and 3 (hand cross-pollination, exclosure) resulted in 82% fruit set (Table 1), indicating that outcrossing does not increase fruit set, relative to selfing. A G-test of homogeneity between treatment 1 and the control revealed no significant differences ($G = 0.14$; $df = 1$; $0.5 < p < 0.9$), indicating that bagging alone does not significantly affect fruit set, relative to natural levels of pollination. In fact, a G-test for independence across all treatments found that fruit set was independent of treatment ($G = 0.224$; $df = 3$; $0.9 < p < 0.975$). Thus, insects are not necessary to produce fruit in this species, and autogamous pollination can account for observed levels of fruit set in natural populations.

Neither fresh capsule weight nor mean seed weight per capsule differed significantly between treatments using analyses of variance. Bagging (Treatment 1) had a marginally significant effect on capsule length ($F = 2.76$, $p = 0.0570$), compared to the control (Table 1). Correlations between capsule dimensions and overall seed weight were highly significant. Length of capsule was strongly correlated with seed weight (Spearman's $r = 0.86070$, $P < 0.0001$; $n = 37$), as was capsule diameter (Spearman's $r =$

Table 1. Summary of findings for experiments done in 1990. [a] Plants in treatments were covered with a mesh insect exclosure. [b] In grams; reported with Standard Errors. [c] In centimeters; reported with Standard Errors. * Means with different letters are significantly different from each other at the 0.057 level, segregated using Duncan's Multiple Range Test.

Treatment	n	n Fruiting	Fruit Set	Capsule Length[c]*	Capsule Width[c]	Leaf Whorl Diameter[c]	Fresh Capsule Weight[b]	Mean Total Seed Weight[b]
(1) [a]No manipulation	18	12	67%	0.237 ± 0.009[f]	0.068 ± 0.006	13.99 ± 0.575	0.406 ± 0.067	0.011 ± 0.003
(2) [a]Hand self-pollination	11	9	82%	0.253 ± 0.009[fg]	0.078 ± 0.003	14.74 ± 0.565	0.502 ± 0.046	0.014 ± 0.002
(3) [a]Hand cross-pollination	11	9	82%	0.246 ± 0.009[fg]	0.071 ± 0.005	14.13 ± 0.493	0.411 ± 0.054	0.022 ± 0.011
Control	12	10	83%	0.279 ± 0.013[g]	0.082 ± 0.006	15.19 ± 0.669	0.589 ± 0.076	0.018 ± 0.003

0.89899, $P < 0.0001$; $n = 37$). There was also a positive correlation between plant size (measured as leaf whorl diameter) and overall mean seed weight (Spearman's $r = 0.63830$, $P < 0.0001$; $n = 37$). In other words, larger plants produced larger capsules that contained a greater mass of seeds.

DISCUSSION

The fantastic floral forms and complex pollination systems for which orchids are best known presumably have evolved to ensure outcrossing. However, autogamous terrestrial orchids are not uncommon, particularly in habitats that are harsh or where there is a paucity of pollen vectors (Dafni and Bernhardt 1990). The location of the anther above the stigma, coupled with friable pollen and the trend toward self-compatibility, is thought to be an adaptation for mechanical self-pollination (Burns-Balogh and Bernhardt 1985). This arrangement allows extrusion of the mealy pollen directly onto the stigma. *Isotria medeoloides* appears to follow the same morphological pattern (Mehrhoff 1983), and we have shown here that this species is self-compatible.

Although the mealy pollen may be available for outcrossing once it has been extruded from the pollinaria, a pollen vector has not been identified in this study. In the four cases where we assumed the pollinaria had been removed, it is possible that the pollen projection had broken and fallen to the labellum prior to contacting the stigmatic area. This phenomenon was reported by Mehrhoff (1980); pollination was not accomplished in such cases. A pollen vector was not found in the previous study conducted by Mehrhoff (1980), nor in many pieces of anecdotal evidence from others who are monitoring this species from Virginia to New Hampshire, nor was evidence of pollinaria deposition found in the current study. Mehrhoff (1980) concluded that autogamous pollination may have evolved in this species as a response to low pollinator availability, and, given the high levels of fruit set in this species, without apparent benefit of cross-pollination, we conclude that *Isotria medeoloides* reproduces primarily through autogamous self-fertilization. Although it appears that agamospermy does not occur in this species, we cannot rule out the possibility of pseudogamy.

Autogamous pollen deposition appears to be necessary to ensure fruit production. In fact, *Isotria medeoloides* may be thought of as facultatively self-pollinating. However, only 67% of individuals in treatment 1 set fruit, compared with 83% in the control, and 82% in both treatments 2 and 3. Although this difference is not statistically significant, given our sample sizes, it is possible that an increased sample size would either corroborate our findings or might indicate that an as-yet-unobserved pollinator may be responsible for some of the natural levels of fruit set in this and other populations. Further study of the breeding system of this species may be warranted, at the least to determine if cross-pollination does occur as a rare event. This would lend a great deal of insight into the possible genetic structure of natural populations.

Orchid pollination systems are typically thought to be adaptations for low pollinator availability (Montalvo and Ackerman 1987; Ackerman 1989), but resource limitation also may explain the low levels of fruit set which are commonly found throughout the Orchidaceae. If manual pollination does not increase seed or fruit set relative to natural levels, reproduction then is thought to be limited by resources (Willson 1983). As we found no significant differences in capsule production or total seed weight between natural levels of pollination and hand self-pollination, it appears that reproduction in *Isotria medeoloides* is not pollen limited, but may be resource limited.

In fact, reproductive output in *Isotria medeoloides* is closely tied to plant size. The largest individuals produced the largest capsules and highest total seed weight. From our demographic work with *I. medeoloides* in Maine, we know that those individuals which produce fruit consistently belong in the highest size class (Vitt 1991). In addition, we have shown that *I. medeoloides* is self-compatible and primarily self-pollinating. The lack of increased fruit set under our experimental treatments when pollen is presumably not limiting versus the control when pollen may be limiting, indicates that reproduction is limited by resource availability. This conclusion is reinforced by the tight correlation between reproductive output and plant size.

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INFRASPECIFIC DIFFERENTIATION IN THE *AMPHICARPAEA BRACTEATA* (FABACEAE) SPECIES COMPLEX: VARIETIES AND ECOTYPES

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ABSTRACT. Because amphicarpy is strongly associated with heterogeneous habitats, it can be difficult to document and interpret infraspecific differentiation in amphicarpic species. In the woodland annual *Amphicarpaea bracteata,* a canonical variates analysis (CVA) of morphological data from herbarium specimens provided initial support for the recognition of two distinct varieties. Subsequently, common garden and greenhouse studies were conducted with multiple populations of these two well-marked varieties, *A. bracteata* var. *comosa* and *A. bracteata* var. *bracteata.* Because the variety *comosa* is restricted to sunnier habitats while the variety *bracteata* spans a broad range of habitats, these studies included *bracteata* populations from both densely shaded and sunny habitats. CVA of the greenhouse data indicated that the varieties *comosa* and *bracteata* maintained discrete differences in leaf morphology. Thus, varietal differences are, in part, genetically based rather than solely plastic responses to the local environment. Differences between shade- and sun-native *bracteata* populations, although relatively minor, also appeared to be, in part, genetically based. Consistent with its affinity for sunnier habitats, the variety *comosa* achieved superior survivorship and fecundity under high light conditions. However, fecundity was greater in shade-native than in sun-native *bracteata* populations. In combination with trends in leaf morphology, these results support the idea that the variety *comosa* is a sun-adapted ecotype, but not the concept that shade- and sun-native *bracteata* populations are, respectively, shade- and sun-adapted.

Key Words: *Amphicarpaea bracteata,* amphicarpy, canonical analysis, ecotypes, Fabaceae, infraspecific variation, phenotypic plasticity

Amphicarpic plants have dual reproductive strategies, and often one or both reproductive modes are associated with high levels of selfing and limited seed dispersal (Cheplick 1994; Cheplick and Quinn 1988). Consequently, amphicarpic species might be expected to display strong patterns of local population differentiation, reflecting genetic drift in populations with restricted gene flow, perhaps reinforced by local selection (Levin 1981, 1988). Since amphicarpy is strongly associated with spatially or temporally varying environments and phenotypic plasticity (Cheplick and Quinn 1982; Van der Pijl 1982; Schoen and Lloyd 1984), documenting and interpreting such differentiation can be quite difficult.

Amphicarpaea bracteata (L.) Fern. exemplifies these aspects of the amphicarpic habit (Schnee and Waller 1986; Trapp 1988). In this woodland annual, production of flower and fruit morphs depends strongly on overall plant size. Accordingly, across habitats varying in light availability, there is substantial variation in whole-plant morphology and in life history traits (Schnee and Waller 1986). It remains unclear whether variation among populations represents plastic responses to local environments, genetically based differences due to past selection, genetic drift, or some combination of these processes.

Variation among populations is not the only form of infraspecific variation within *Amphicarpaea bracteata.* Turner and Fearing's (1964) taxonomic revision discusses two well-marked varieties, *A. bracteata* var. *bracteata* and *A. bracteata* var. *comosa* Fassett. The monograph illustrates the varieties' coextensive ranges, reiterating previous authors who emphasize "continuous intergradation" (Gleason and Cronquist 1963). More recent evidence, however, suggests that infraspecific taxa matching descriptions of the varieties *bracteata* and *comosa* may grow sympatrically but remain reproductively isolated (Parker 1992, 1994). Also, across a broad geographic range, multilocus enzyme electrophoresis distinguishes two varieties and possibly a third taxon that display distinct allozyme profiles and divergent leaf morphologies (Parker 1996).

Examination of herbarium sheets and observations in the field indicate that it may be fairly common to find specimens or populations corresponding to the two varieties (Fassett 1936, 1939) and possibly to Parker's (1994, 1996) descriptions of a third taxon.

The debate regarding varieties within *Amphicarpaea bracteata* has often mentioned that the varieties tend to differ in their affinities for sunny and shady habitats. For example, circumscription of *comosa* involves not only the tawny pubescence on its leaf surfaces, petioles, and stems, but also a restriction to sunnier habitats (Fassett 1936). In contrast, *bracteata* occurs across a broader range of habitats, from sunnier to very densely shaded habitats (Fassett 1936; Schnee and Waller 1986). Furthermore, there appear to be taxa with leaf morphologies that correspond to classic descriptions of either shade- or sun-adapted ecotypes: (a) a shade-adapted, *bracteata*-like taxon with delicate, thin, broad leaflets and leaves, (b) a more sun-adapted, *bracteata*-like taxon with sparsely pubescent and much narrower leaflets and leaves (Parker 1994), and (c) the sun-adapted variety *comosa* with its dense leaf and stem pubescence and broad but sturdy, thick leaves (Figure 1; Boardman 1977; Givnish 1988).

The studies reported here are based on *a priori* recognition of these three putative taxa within the species complex. These groups are subject to careful scrutiny using multivariate data sets that quantify suites of morphological and life history traits. By comparing patterns of differentiation not only among local populations but also more broadly across the three infraspecific taxa, it may be possible to infer the extent to which these groups reflect varieties and possibly ecotypes adapted to different points along a sun-shade gradient.

To fulfill this goal, morphological differences among groups were assessed at two different spatial scales. First, across the species range, suites of leaf and floral traits were analyzed to determine whether they can consistently distinguish *comosa* from *bracteata,* and possibly a third *bracteata*-like taxon. Second, focusing locally on native populations in south-central Wisconsin, differences in leaf morphology and life history traits were assessed in controlled environments, including both a common garden and a greenhouse. Morphological analyses of native populations address an important ecological question: is variation in leaf morphology consistent with habitat affinity and expectations based on presumed functional adaptations? By incorporating not only leaf morphology but also life history traits, data sets from the common garden and greenhouse address a second ecological question: in high light conditions, are survivorship and fecundity greater in *comosa* and sun-native *bracteata* populations than in shade-native *bracteata* populations?

MATERIALS AND METHODS

Herbarium specimen survey. The 101 sheets from the North American collection at the University of Wisconsin–Madison Herbarium include collections ranging from Winnipeg, Manitoba, south to Gainesville, Florida, and from New Bedford, Massachusetts, west to the Black Hills of South Dakota. For each, varietal designations were verified and unidentified specimens

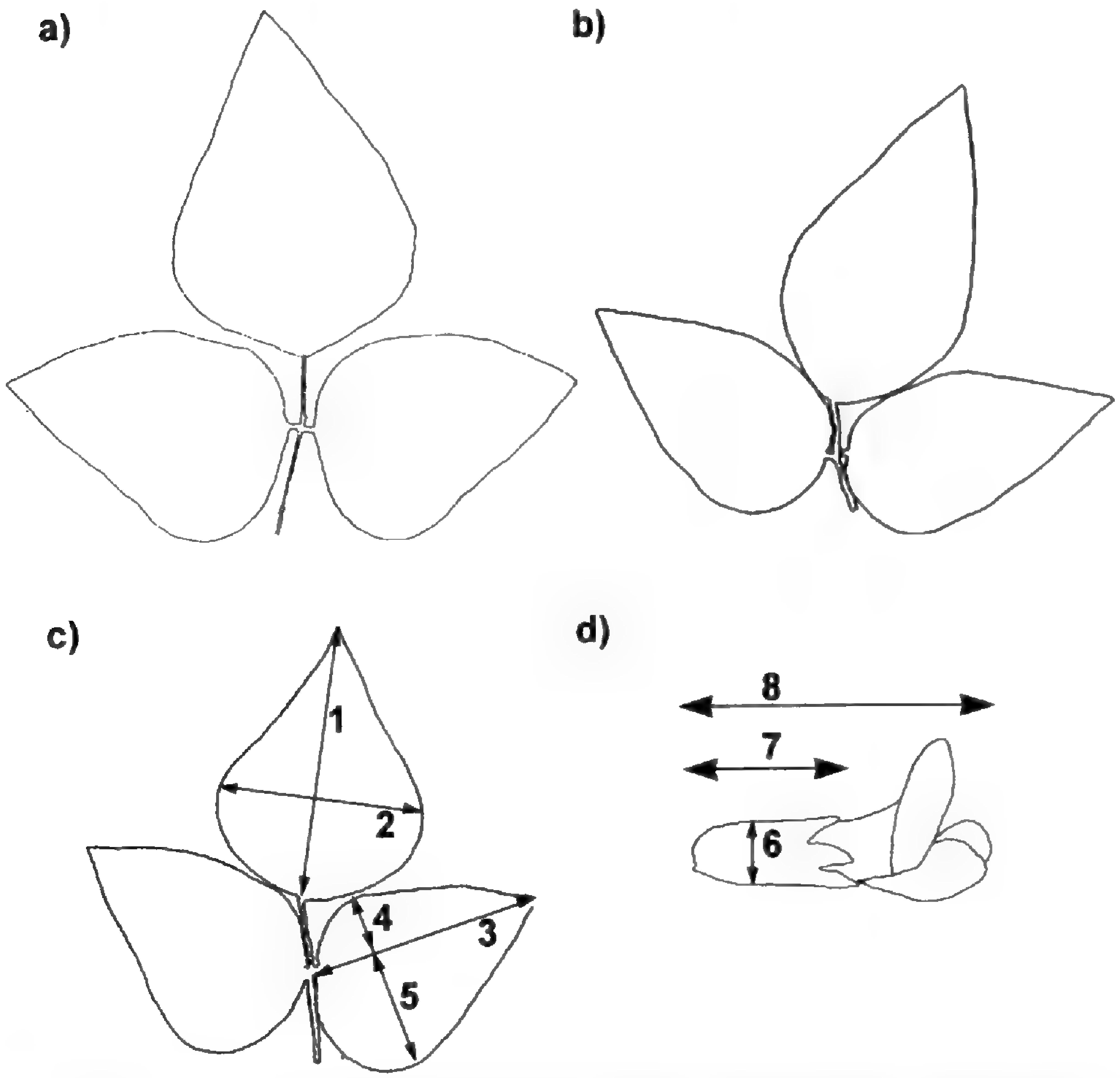

Figure 1. Leaf silhouettes of *Amphicarpaea bracteata* var. *bracteata* with (a) wide and (b) narrow terminal and lateral leaflets, coded as **w** and **n,** respectively, in herbarium specimen surveys. Parker (1991b) proposed that wider leaflets are adaptations for shade while narrower leaflets are adaptations for sun. (c) Leaf silhouette of *A. bracteata* var. *comosa,* coded as **C** in herbarium specimen surveys. Parker (1992) has suggested that despite its broad and truncate leaflets, *comosa* may be a sun specialist based on its high specific leaf area, pubescence of leaves and stems, and narrower habitat distribution. Also shown are (c) leaf and (d) floral traits measured on dried herbarium specimens: 1 = terminal leaflet length; 2 = terminal leaflet width; 3 = right lateral leaflet length; 4 = right lateral leaflet maximum width from midrib to apical edge; 5 = right lateral leaflet maximum width from midrib to basal edge; 6 = calyx width at base; 7 = calyx length; and 8 = corolla length.

were assigned to a variety (*comosa* = **C** or *bracteata* = **B**) based on density and prominence of vestiture on stems, petioles and inflorescences. In addition, all *bracteata* specimens were classified and coded as having either wide leaves and leaflets (**w**) or narrow leaves and leaflets (**n**). This scheme follows Parker

Table 1. Trait descriptions, means (standard errors), and sample sizes for leaf and floral morphology traits recorded from 101 herbarium specimens. All data were approximately normally distributed. Also reported are results of contrasts that combined categories from univariate ANOVAs. **C-B** refers to a contrast of *comosa* and *bracteata* specimens; **w-n** excludes *comosa* individuals and contrasts wide- and narrow-leaflet specimens of *bracteata*. Bonferoni-corrected significance levels are indicated. *** $p < 0.001$; ns = no significant difference.

	Trait Description				
				Contrasts	
Vegetative Traits	*comosa* n = 33	*bracteata* wide-leaflet n = 34	*bracteata* narrow-leaflet n = 15	**C-B** $F_{(1,78)}$	**w-n** $F_{(1,78)}$
Petiole length (cm)	6.40	4.90	4.11	12.569	1.255
	(6.00–6.80)	(4.51–5.30)	(3.51–4.69)	***	ns
Terminal leaflet petiolule length (mm)	1.81	1.34	1.20	27.794	1.049
	(1.74–1.89)	(1.30–1.37)	(1.09–1.32)	***	ns
Right lateral leaflet petiolule length (mm)	0.33	0.33	0.28	0.279	0.726
	(0.29–0.37)	(0.30–0.37)	(0.22–0.33)	ns	ns
Terminal leaflet length (cm)	5.82	4.47	4.80	12.459	0.549
	(5.57–6.08)	(4.22–4.72)	(4.43–5.17)	***	ns
Terminal leaflet maximum width (cm)	4.78	3.40	2.95	21.149	0.912
	(4.52–5.04)	(3.14–3.65)	(2.57–3.34)	***	ns
Right lateral leaflet (RLL) length (cm)	5.41	4.04	4.00	23.188	0.011
	(5.19–5.62)	(3.83–4.25)	(3.68–4.32)	***	ns
RLL max. width, midrib to apical edge (cm)	1.56	1.22	1.11	28.199	1.275
	(1.50–1.61)	(1.16–1.27)	(1.03–1.19)	***	ns
RLL max. width, midrib to basal edge (cm)	2.33	1.66	1.41	40.929	2.313
	(2.24–2.42)	(1.57–1.75)	(1.27–1.55)	***	ns

Table 1. Continued.

	Trait Description				
		bracteata	*bracteata*	Contrasts	
Floral traits	*comosa* n = 22	wide-leaflet n = 26	narrow-leaflet n = 7	**C-B**	**w-n**
Calyx width at base (nearest 0.15 mm)	16.05 (15.39–16.70)	14.39 (13.78–14.99)	14.86 (13.69–16.02)	2.344 ns	0.129 ns
Calyx length from base (nearest 0.15 mm)	37.77 (35.50–39.04)	33.62 (32.45–34.78)	33.86 (31.60–36.11)	5.048 ns	0.009 ns
Corolla length from base (nearest 0.15 mm)	75.18 (73.70–77.07)	68.92 (67.19–70.66)	73.71 (70.37–77.06)	2.101 ns	1.618 ns

(1991a, 1994), who suggested that wider leaves and leaflets may correspond to an adaptation to dense shade, while narrower leaves and leaflets may correspond to an adaptation for sunnier conditions. Parker (1992) also has suggested that, despite its broad leaflets, the pubescent and thicker stems and leaves of *comosa* may indicate adaptation to high light conditions (Figure 1).

Eight leaf morphology traits were scored from a single, fully expanded leaf, choosing the most apical leaf when there was a choice of more than one adequately preserved leaf on an herbarium sheet (Figure 1c; Table 1). Three floral traits also were scored, using the inflorescence with the greatest number of flowers and choosing the most basal aerial chasmogamous (hereafter ACH) flower that could be measured intact on the dried, pressed specimen (Figure 1d; Table 1).

For each of these 11 traits, univariate ANOVAs were conducted, after which planned contrast was used to test whether trait means differed between all *comosa* and all *bracteata* specimens. After excluding the *comosa* plants, a second planned contrast was used to test for differences between the wide-leaflet and narrow-leaflet specimens of *bracteata* (**w** vs. **n**). To adjust for possible error due to multiple comparisons, a Bonferoni procedure adjusted significance levels (to $p < 0.05/22 = 0.002$). To specify and test all hypotheses, the AMATRIX procedure of Systat 5.1 was used (Wilkinson 1990).

Next, a canonical variates analysis (CVA) also took advantage of these *a priori* groups and planned comparisons. The method optimally discriminates among groups based on linear combinations of weighted variables, or canonical variates (CVs). By examining canonical correlations (i.e., correlations between CVs and the original variables), one can interpret which traits are important for delineating groups (Pimintel 1979). To test the statistical significance of the CVA, a multivariate F-statistic was calculated and tested against an appropriate likelihood ratio criterion (here, Wilkes' λ). To facilitate visual examination of group overlap, the CVs of individual specimens were plotted, and group centroids and 50% group ellipsoids were delineated (Wilkinson 1990).

Common garden study. Sun- and shade-native populations of *bracteata* and some *comosa* plants were included in a common garden study conducted during summer 1993. Plants were collected as seedlings on May 18 at two wooded sites in Baraboo, Wisconsin (Devil's Lake State Park and Howard I. Potter Preserve), using a stratified random array of 64 points within four 40 m^2 grids. At each site, two grids were located in a densely shaded area with a closed overstory canopy and another in a sunnier area with a partially open canopy (Callahan 1996). Only *bracteata* seedlings grew in both shady areas and in the sunny area at Devil's Lake. In the sunny area at the Potter Preserve, the two varieties grew sympatrically, and this protocol sampled 22 *comosa* and 42 *bracteata* individuals. Varieties were identified based on presence or absence of dense, tawny pubescence on the elongating apical meristem. Seedlings were transplanted into a random array at a common garden at the University of Wisconsin Arboretum (Lost City Forest site). The semi-open overstory canopy of this garden was similar to the sunny areas at the native sites.

Individuals were monitored for survivorship on 4 dates in 1993: June 10, June 18, June 29, and July 31. During fall 1993, I recorded production of ACH flowers and fruits by all surviving plants. In addition to an analysis of all sun-native and shade-native populations in the common garden study, I also made more detailed comparisons of the 22 *comosa* and 42 *bracteata* individuals transplanted from the sunny area at the Potter Preserve. I used χ^2 statistics to test varietal differences in two life history traits: proportions surviving to particular time points in the growing season and proportion of surviving plants that flowered.

Greenhouse study. A subsequent greenhouse study included populations of both varieties, and both sun- and shade-native populations of *bracteata.* For this study, subterranean (SCL) fruits were collected during October 1994 at both sunny and shady areas at each of five locations in the Eastern Baraboo Hills region of south-central Wisconsin, including the Potter Preserve and Devil's Lake sites. Seeds in SCL fruits are produced by cleistogamous (obligately self-fertilizing) flowers.

The sampling protocol entailed running two perpendicular 25 m transects through the populations. At 1 m intervals, I located the closest *bracteata* and *comosa* plants within 0.5 m (if any), distinguishing source plants as *comosa* or *bracteata* based on presence or absence of dense, tawny pubescence on leaves, stems, and petioles. Only *bracteata* phenotypes occurred in shady areas; both *bracteata* and *comosa* phenotypes occurred in sunny areas.

Table 2. Morphological, overall growth, and life history traits recorded in the greenhouse study (with precision of measurements indicated). Data transformations noted were used to improve normality; otherwise variables were approximately normally distributed.

	Date of Data Collection		
Trait Abbreviation and Description	3/21	4/21	6/12
Ratio of length to width for simple leaf (sl; log transformed; 0.1 cm)	x		
Number of compound leaf (cl) nodes	x	x	x
Proportion of cl nodes with axillary branches (arcsin-square root transformed)	x	x	x
Length of axillary branches from sl node (1.0 cm; log transformed)	x		x
Length of axillary branches from cl nodes (1.0 cm; log transformed)	x	x	
Terminal leaflet length and width (0.1 cm)		x	
Right lateral leaflet length and width (0.1 cm)		x	
Ratio of total dry weight of stem to leaves (1 mg; arcsin-square root transformed)			x
Ratio of number of SCL fruits to total flowers (arcsin-square root transformed)			x
Ratio of number of ACH to total aerial flowers (arcsin-square root transformed)			x

Thus, there was a total of 15 populations, 5 of each type. From each, approximately 25–30 seeds were collected and cold-stratified until the following February. Seeds were planted into standard greenhouse potting medium below a neutral 63 percent shade fabric screen to simulate light levels in sunny habitats. (Average light levels in the sunny area were approximately 30 to 35 percent of full sunlight; Callahan 1996.) Morphological and life history traits were recorded at three times: March 21, April 21, and June 12. Table 2 lists traits and precision of the measurements. With the greenhouse data set, a second CVA was performed, again taking advantage of assignments to groups specified *a priori:* the variety *comosa* (**C**), and sun-native (**H**) or shade-native (**L**) populations of *bracteata.*

RESULTS

The varieties *comosa* and *bracteata* differ significantly for seven of eleven traits examined, all of which are leaf morphology traits. Between the two varieties, differences in floral traits are statistically non-significant or of only marginal significance ($0.05 < p < 0.10$). There are no statistically significant differences between the narrow-leaflet and wide-leaflet groups within *bracteata* for any of the 11 leaf or floral traits (Table 1). However, CVA supports significant separation of group centroids (Wilkes' λ test: $F = 2.695$, d.f. 22, 70, $p < 0.001$).

The first CV axis distinguishes *comosa* from *bracteata,* regardless of whether the latter is considered as two separate groups or as a single group that combines the taxa coded as **n** and **w** (Figure 2a, b). In *comosa,* lateral leaflets are broader with more truncate bases and the terminal leaflet petiolule tends to be longer (Table 3). The second CV axis, which correlates strongly with corolla length (Table 3), provides little additional separation of *comosa* from *bracteata,* but in combination with the first CV it provides moderate separation of the taxa coded as **n** and **w.** This result extends other observations of floral traits by Parker (1996) and Schively (1897), who observed differences in corolla color among *Amphicarpaea bracteata* varieties or populations. In summary, most of the specimens separate cleanly into three groups, but it is not always possible to assign individual specimens with this particular set of quantitative traits.

Different sun- and shade-native populations of *bracteata* did not differ significantly for survivorship. In contrast, focusing on transplants from the sunny area at the Potter Preserve, the two varieties differed in survivorship throughout the 1993 growing season. Of the 22 *comosa* plants at the beginning of the study, 91 percent survived until the end of the growing season. Of the 42 *bracteata* plants at the beginning of the study, about 70 percent survived until the end of June, about 50 percent survived until the end of July, and 43 percent survived until the fall when plants flowered, set fruit, and senesced. Differences in survivorship between varieties on June 27 and July 31 are statistically significant (respectively, $\chi^2 = 6.19$, $p < 0.05$; $\chi^2 = 14.05$, $p < 0.001$). Among the surviving plants, there is no significant difference between varieties in the number of plants that produced ACH flowers ($\chi^2 = 0.26$, $p > 0.50$). However, this statistical test may lack power because the sample size of surviving plants is small.

Greenhouse study. By quantifying numerous morphological and life-history traits in the greenhouse study (Table 2), signifi-

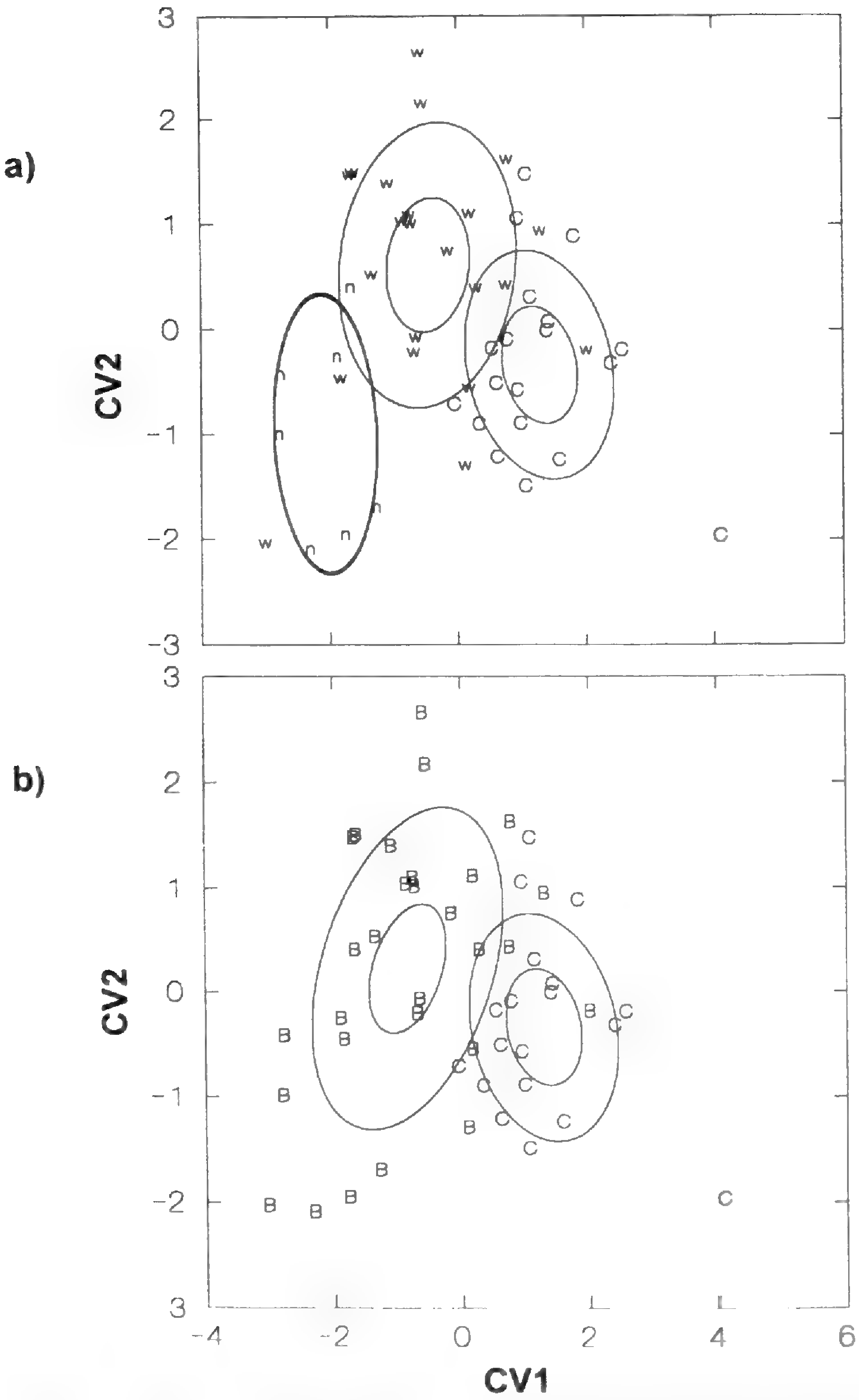

Figure 2. Plots of 95 percent group centroids and 50 percent group ellipsoids based on CVs derived from leaf and floral morphology traits measured on 101 herbarium specimens from across the species range. (a) Codes indicate *Amphicarpaea bracteata* var. *comosa* individuals (**C**; n = 19) and wide-leaflet (**w**; n = 22) and narrow-leaflet (**n**; n = 7) biotypes of *A. bracteata* var.

Table 3. Correlations between dependent variables and dependent canonical variates (CV1, CV2) from herbarium specimen survey. * Indicates three traits that correlate most strongly with each CV.

Trait	CV1	CV2
Petiole length	0.339	−0.074
Terminal leaflet petiolule length	0.592*	−0.100
Right lateral leaflet petiolule length	0.085	0.228
Terminal leaflet length	0.444	−0.433*
Terminal leaflet width	0.494	−0.174
Right lateral leaflet (RLL) length	0.558	−0.310*
RLL max. width, midrib to apical edge	0.564*	−0.081
RLL max. width, midrib to basal edge	0.642*	−0.198
Calyx width at base	0.108	−0.171
Calyx length from base	0.216	−0.273
Corolla length from base	0.157	−0.555*

cant differences were found not only between the two varieties but also between plants from sun- and shade-native *bracteata* populations. The results of CVA support separation of the group centroids (Figure 3; Wilkes' λ test, F = 3.390, d.f. 40, 158; $p < 0.001$).

CV1 separates *comosa* populations from sun- and shade-native *bracteata* populations quite well. More subtle differences between sun- and shade-native *bracteata* populations involve both CV1 and CV2 (Figure 3b). Generally, if plants are grown in a uniform, high light environment, terminal leaflets and lateral leaflets are longest and broadest in *comosa* plants, intermediate in *bracteata* plants from sun-native populations, and shortest and most narrow in *bracteata* plants from shade-native populations. At maturity, number of nodes, number of branches, and production of ACH flowers is greatest in *comosa* plants, intermediate in *bracteata* individuals from shade-native populations, and smallest in *bracteata* individuals drawn from sun-native populations (Table 4). Like the herbarium specimen survey, results of this greenhouse study suggest that there is some overlap among the three groups,

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bracteata individuals described by Parker (1994). (b) The code **B** indicates *A. bracteata* var. *bracteata* regardless of whether the specimen matches descriptions of wide- or narrow-leaflet taxa.

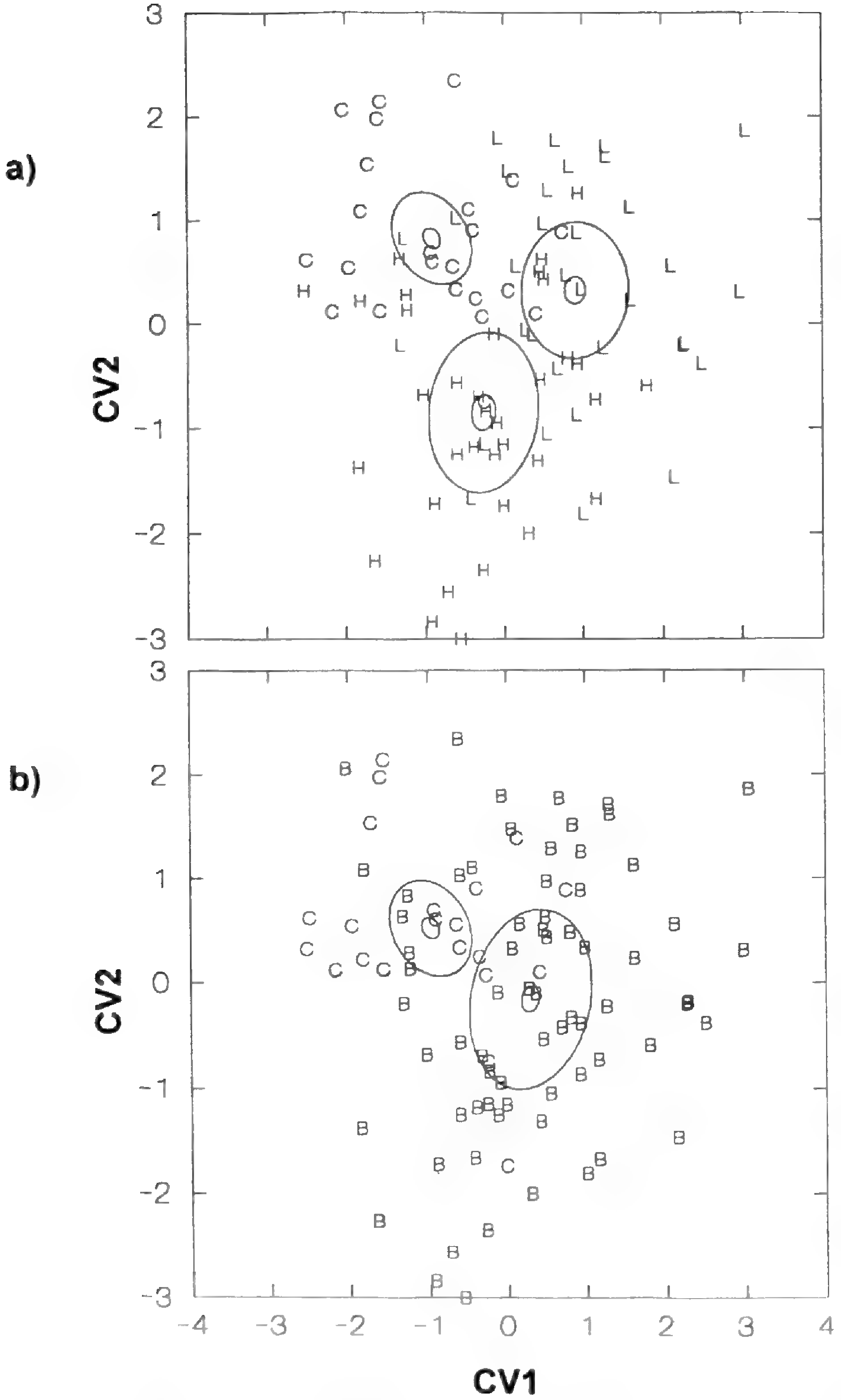

Figure 3. Plots of 95 percent group centroids and 50 percent group ellipsoids based on CVs derived from traits measured on plants cultivated in a greenhouse study. (a) Codes indicate *Amphicarpaea bracteata* var. *comosa* individuals (**C**; n = 23), sun-native *A. bracteata* var. *bracteata* individuals (**H**; n = 35), or shade-native *A. bracteata* var. *bracteata* individuals (**L**; n =

but the majority of individuals can be positively identified as belonging to one of the three groups.

DISCUSSION

Consistent with earlier discussions of varietal differences (Fassett 1936; Turner and Fearing 1964), no single quantitative trait can be used to identify *comosa* or *bracteata* individuals. More often than not, however, by quantifying a suite of morphological traits, one can distinguish two varieties, *comosa* and *bracteata*. A third *bracteata*-like group appears to be relatively indistinct morphologically. However, the weak evidence for divergence of **n** (narrow-leaflet) and **w** (wide-leaflet) taxa may reflect the small number of herbarium specimens that conforms to descriptions of a narrow-leaflet taxon, and associated low power of statistical tests.

Multivariate analysis of data from the greenhouse study successfully detected differentiation between sun-native and shade-native *bracteata* populations. However, morphological differences between sun- and shade-native *bracteata* populations were not concordant with the existence of distinct sun-adapted populations (with narrow leaves and leaflets) vs. shade-adapted populations (with broader leaves and leaflets). Rather, shade-native *bracteata* individuals tended to have the narrowest leaflets and leaves.

Importantly, none of the 128 *bracteata* seedlings transferred from two densely shaded areas to the sunny common garden show leaf or stem pubescence characteristic of *comosa* plants. In the high-light greenhouse environment, individuals from shade-native *bracteata* populations show no obvious pubescence. In contrast, *comosa* plants grown under dense artificial shading (95 percent of full sun) in a related study (Callahan 1996) retained this distinctive vestiture. Both locally and throughout the species' range, the presence or absence of pubescence on stems and leaf

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33). (b) Codes indicate *A. bracteata* var. *comosa* (**C**) individuals or *A. bracteata* var. *bracteata* individuals (**B**), regardless of whether the latter are sun- or shade-native.

Table 4. Correlations between dependent variables and dependent canonical variates (CV1, CV2) from greenhouse study. * Indicates three traits that correlate most strongly with each CV.

Trait	CV1	CV2
Ratio length : width for simple leaf (sl) at first node	0.282	0.089
Early node number	−0.015	−0.111
Mid-season node number	−0.171	−0.211
Final node number	−0.084	0.284*
Early proportion branching nodes	0.236	−0.009
Mid-season proportion branching nodes	−0.298	0.000
Final proportion branching nodes	−0.061	0.284*
Early length of axillary stems from sl node	0.080	0.026
Final length of axillary stems from sl node	−0.022	0.015
Early length of branches from compound leaf (cl) nodes	−0.006	−0.004
Mid-season length of branches from cl nodes	−0.241	−0.092
Terminal leaflet length	−0.384*	0.039
Terminal leaflet width	−0.430*	−0.110
Right lateral leaflet length	−0.316	−0.032
Right lateral leaflet width	−0.330*	−0.136
Ratio of dry weight of stems : dry weight leaves	−0.233	−0.109
Ratio of number of SCL fruits : total flower number	0.261	−0.018
Ratio of number of ACH flowers : total aerial flowers	−0.288	0.432*

surfaces is perhaps the most useful trait for distinguishing two varieties.

The results of common garden work provide no support for the notion that there are distinct shade-adapted and sun-adapted ecotypes within *bracteata,* but superior survivorship of *comosa* supports the idea that *comosa* is a sun-adapted ecotype. However, survival of *comosa* seedlings in the sunny common garden environment may have been mediated by factors unrelated or only indirectly related to light levels. During summer 1993, there were unusually heavy rains and a large population of herbivores (primarily slugs) at the common garden site. Herbivores damaged plants of both varieties, but herbivore stress resulted in mortality much more frequently for *bracteata* plants than for *comosa* plants.

In the more benign greenhouse environment, survivorship was less of an issue. After the first 4 weeks of the study, all *comosa* and *bracteata* plants survived to the end of the study. However, *comosa* plants, distinguishable by leaf morphology traits, also achieved greatest vegetative growth (i.e., number of nodes and number of branches) and fecundity (number of seeds produced) relative to *bracteata* plants, regardless of whether the latter are native to sun or shade.

In their natural habitats, shade-native *bracteata* populations typically are very small in size and produce no aerial flowers. When exposed to higher light availability in the common garden or greenhouse, these populations demonstrated the capacity to respond plastically through vigorous vegetative growth and production of numerous ACH flowers. In addition, although the greenhouse light levels contrasted sharply with light levels in their native, shady habitats, reproductive allocation in shade-native *bracteata* plants was proportionally greater than in sun-native *bracteata* plants. Thus, sun- and shade-native populations of *bracteata* do not appear to be sun- and shade-adapted, based on trends in both leaf shape and life history traits. Related work also has demonstrated that in dense artificial shade, shade-native *bracteata* plants perform poorly in comparison to both sun-native *bracteata* and *comosa* plants (Callahan 1996).

The body of evidence presented here (and previous work, Table 5) suggests that attempting to "split" *Amphicarpaea bracteata* into three distinct infraspecific taxa may be unwarranted. However, the tendency to "lump" or de-emphasize two well-marked and historically recognized varieties within *A. bracteata* probably should be reversed, especially because the two varieties seem to have distinct ecological tolerances (i.e., *comosa* is a sun specialist, while *bracteata* can tolerate environments ranging from quite sunny to very densely shaded). In addition, the varieties *comosa* and *bracteata* distinguished in these morphological and ecological studies are concordant with groups differentiated by multilocus enzyme electrophoresis and by compatibility with strains of symbiotic nodule-forming bacteria (Parker 1996). Although open-pollinated ACH flowers often produce fruits in the field, natural hybridization between the two varieties is probably quite rare in nature, since even hand-pollination seldom produces mature fruits (Wilkinson, pers. comm; pers. obs.), and on average hybrid progeny have reduced vigor (Parker 1992).

It may be taxonomically more convenient to recognize only a single species, but recognizing two varieties within *Amphicarpaea bracteata* may make it possible to use a comparative approach to better understand the evolutionary ecology of *Amphicarpaea*'s rhizobial mutualisms (Parker 1995; Spoerke et al. 1996; Wilkinson et al. 1996), host-specific pathogens (Levin

Table 5. Summary of evidence supporting the recognition of distinct infraspecific taxa within the *Amphicarpaea bracteata* species complex. References: [A] Fassett 1939; [B] Turner and Fearing 1964; [C] Parker 1992; [D] Parker 1994; [E] Parker 1996; [F] this publication.

	Taxa Distinguished	
Type of Evidence	*comosa* from *bracteata*	Within *bracteata*
Habitat distribution	*comosa* restricted to sunnier sites; *bracteata* more widespread; geographic ranges coextensive[A, B, C, E, F]	Taxa within *bracteata* may be differentiated although not necessarily adapted for sun or shade habitats[C, D, E, F]
Vegetative morphology	*comosa* has dense, tawny hairs and stouter stems; *bracteata* is smoother and more slender[A, E, F]	Populations native to low light have narrower terminal leaflets and more rounded, narrower lateral leaflet bases[E]
Floral morphology	*comosa* has flowers with more intense purple pigmentation; *bracteata* has paler to nearly white flowers[C, G]; *comosa* has shorter corollas[F]	Longer corolla length within *bracteata*[F]
Artificial crosses between taxa	Artifical crosses between *comosa* and *bracteata* are possible but difficult; F3 progeny show reduced mean fitness[C]	Not investigated
Multilocus enzyme electrophoresis	A distinct *bracteata*-like lineage exists, showing no overlap with *comosa,* very few heterozygotes and no evidence for hybridization, despite local sympatry[E]	Two lineages can be distinguished, one closely resembling *bracteata* plants, the other showing some affinities to the variety *comosa*[E]

1988; Parker 1991b), or complex and phenotypically plastic reproductive habits (Callahan 1996) within this common but unusual native species.

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RECOLLECTIONS[1]

BOTANICAL REMINISCENCES

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On November first, 1996, at the New England Botanical Club's centennial banquet I was presented with a name tag announcing that I was the member of longest standing in attendance. Then during the festivities I was asked if I would set down some of my botanical recollections for publication in *Rhodora.*

I joined the Club in 1930 as its youngest member, when I was a sophomore at Harvard taking Merritt Lyndon Fernald's course on the taxonomy of vascular plants. The meetings of the Club were held in Boston at the home of the American Academy of Arts and Sciences on Newbury Street. They were attended by a distinguished group of enthusiastic and highly competent amateurs—men who, in the days before automobiles and TV sets, spent their weekends tramping through the countryside from railroad stations and the ends of trolley lines after the tradition of Asa Gray. One of these was Richard J. Eaton, the author of *A Flora of Concord.* These amateurs far outnumbered the professionals. However, it was apparent that Professor Fernald was playing a major role in masterminding the activities of the Club. A fascinating statistic is that up to that time more copies of *Gray's Manual of Botany* had been sold in the United States than any other book with the exception of the Bible.

One of my earliest botanical recollections, when I was six years old, is of an Easter dinner in Cambridge with Uncle Will and Aunt Lilian. Uncle Will was my great uncle, William Gilson Farlow, the father of cryptogamic botany in the United States. He lived on Quincy Street close to the site of the present Harvard Faculty Club. After dinner we were given a tour of the fire-proof wing that housed his rare books and herbarium. This was the core of the Farlow Herbarium, now housed at the end of Divinity Avenue. It was on that visit that I admired a handsome little steel

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[1] This is the first in a series of articles to appear occasionally in *Rhodora.* Contributions will be solicited by the Editor-in-Chief, and suggestions are welcome.—*Ed.*

chest that had a trick way of opening. The Farlows most generously gave this treasure to me.

I entered Harvard in the fall of 1929 with a somewhat nebulous idea that I might become a forester. I loved the outdoors and wild places and had the thought that by entering that field I might be able to contribute toward the rehabilitation of devastated country. Five years earlier I had an experience that strongly influenced this decision. That summer I went West with my family. Our route took us through the Great Lakes by boat, and thence from Duluth by the Great Northern Railroad to Seattle. What I recall most vividly on this trip was a whole day traversing the bleak, burned forests of Minnesota.

In my freshman year I took introductory zoology with George H. Parker, whose lectures I admired for their elegance. Botany came in the second semester with Ralph H. Wetmore. The laboratory assistant was G. Ledyard Stebbins. I enjoyed this course, which launched me on my professonal career. One detail which I recall is anything but academic. Ledyard was an earnest fellow, who did his best to help us find what we were supposed to under the microscope. Some of the athletes in the class used to attach test tube clamps to the tail of his coat as he was leaning over someone's scope. It would have served them right if they had had to carry on without those useful little gadgets when heating test tubes over the burner. None of us imagined that this young man would become one of the world's outstanding evolutionary biologists.

My sophomore year found me taking advanced courses largely peopled by graduate students, which presented challenging competition. It was Fernald's course in particular that strongly developed my interest in plants. His lectures were somewhat rambling, but packed full of bits of folklore, natural history, economic botany, and phytogeography. The lab consisted of drawing mounted specimens of species from representative families, which gave us some facility with a drawing pen. But it was in the field that Fernald's teaching really caught fire. He was short and somewhat roly-poly, but could maintain a vigorous pace. When he spotted an interesting plant on terra firma he would recline on the ground beside it, point out its characteristics and expound on whatever was of special interest. Aquatics were a vital part of the flora for Fernald. He would usually lead us into a swamp right over our boots at the first stop. For the rest of the day we would have no inhibitions about sloshing through the wetlands. The story is told of a time when his enthusiasm for aquatics got him into trouble. He was standing at the end of a small dam where an emergent beckoned from a sheet of duckweed. Stepping forth to collect it, he plopped in over his head. Fernald couldn't swim, but fortunately a football player, standing beside him on the dam, reached over and pulled him out. We understand this student passed the course with a good grade.

The field trips were memorable. I recall my astonishment at finding *Opuntia humifusa* partially smothered by grasses on Cape Cod and the excitement of encountering over eighty species of wildflowers simultaneously in bloom on the slopes of Mt. Equinox. I later participated in a number of forays to Vermont, the purpose of which was to document the ranges of species in northern New England.

In my junior year I started an independent study with Wetmore. He had been working on the cytogenetics of goldenrods and asters, and called my attention to a goldenrod, *Solidago asperula,* that was thought to be a hybrid between two widely distributed species, *S. rugosa* of the uplands and *S. sempervirens,* restricted to sand dunes, salt marshes, and rocky headlands at the edge of the sea. He suggested that I attempt to cross the putative parental types and compare the progeny with *S. asperula.* This I proceeded to do, submitting the results as an honors thesis in the spring of my senior year. My doctoral dissertation, based on developmental studies of these goldenrods, launched me on a research career in experimental plant morphology, which led by steps from plant hormones to growth inhibitors, to effects of light on growth, to fluorescent compounds and finally to patterns of root growth.

Among the problems I faced in carrying on the genetic work with these goldenrods was getting the precious hybrid seeds to germinate. When planted soon after collection only about five percent would start to grow. During an experiment attempting to break dormancy with a freezing and thawing regime, I had some seeds laid out in dishes on my lab table in full sunlight. Suddenly I had nearly one hundred percent germination. I measured the temperature, and it turned out to be about 100°F. This seemed odd, as in nature the seeds germinate in April when the air temperature is about 40°F. Out in the field I measured the temperature of the bare soil, where natural germination takes place. Sure enough, on a sunny day it was 100°F.

A second problem was assuring minimal loss of the delicate seedlings. They were being grown in the greenhouse located on the roof of the Biological Laboratories. I soon discovered that the little pots had to be attended daily and with more tender loving care than that afforded by the fellow in charge of the greenhouse. This was not the kind of lesson learned in undergraduate courses.

Goldenrods are normally biennials. They germinate in the spring, spend the first year getting established, and come into bloom the following year. My third problem was to shorten this cycle in order to speed up the genetic work. Goldenrods are short-day plants, flowering in the fall when the days are short. I discovered that by germinating the plants in the fall and growing them in the greenhouse during the winter, they could be brought into bloom in the spring. Thus it was that several years later I was able to present my fiancée with a bouquet of *Solidago* at our June engagement party.

Later on I became involved with a study of the inheritance of flowering time. Depending upon where they grow along the Atlantic coast, plants of *Solidago sempervirens* respond to different photoperiods, those from the northern portion of the range flowering earlier than those farther south. Plants from Florida, when grown at the latitude of Rochester, New York, remained vegetative and grew to the roof of the greenhouse. In order to cross them with the northern material it was necessary to shorten the day by moving them to the dark. It turned out that several genes were required to account for these differences (Goodwin 1944).

An amusing incident occurred during the spring of my final year at Harvard. I was married by then and Esther and I had spent a morning on the meadow along the Charles River estuary, just across from the Harvard Stadium. We had been making mass collections of goldenrod plants. Formerly a brackish marsh under tidal influence, this area had gradually lost its salinity after the basin had been dammed. Patches of the salt-marsh goldenrod still persisted, but the area had been invaded by the upland species, creating an ideal spot for natural hybridization. While I was collecting the plants, Esther was sitting on a blanket, making tags and placing the specimens in a white vasculum. It rained the following day and late in the morning we were preparing to leave our fourth-floor walk-up to go out to visit my parents in Brookline, as we were feeling the effects of typhoid shots taken in preparation for our imminent trip to central Africa. The doorbell rang and a voice came up through the speaker.

"This is Officer O'Learty. Is Mr. Goodwin there?"

"Yes," I responded, quickly reviewing my recent past activities. Presently a uniformed policeman accompanied by a man in plain clothes appeared at the door.

"Were you up along the river yesterday?" says O'Learty.

"Yes," I replied. "I was up there collecting plants with my wife." At this point Esther puts in an appearance from the back room. The two men exchanged glances and began to grin.

"We had a report that you were burying something; we have had a posse of men up there digging all morning!"

A man who had been picking over a nearby dump had observed our suspicious activity and reported the number of our car to the police. What would have happened if they had found an empty apartment and had caught up with us as we were embarking on our transatlantic voyage to Africa?

While in graduate school I may have had the distinction of taking the first integrated course at Harvard—advanced taxonomy with Fernald. I was the only male who registered; there were three women from Radcliffe. I doubt that there was any consultation on this matter with the Dean. One of the women was Ruth Peabody. She married my classmate, George Rossbach, and stayed on at the Herbarium to help illustrate the eighth edition of *Gray's Manual.* She and I became good friends and have remained in touch. Fifty-four years later Esther and I were invited to join Ruth and her second husband, Ian Berendsen, on a fascinating trip to New Zealand. Ian, a native of that country, worked for many years at the United Nations. He was going home on family business, and they asked us to accompany them and visit some of Ian's favorite haunts. One of my adventures on that trip was walking the famous and very beautiful Milford Track.

As a graduate student I spent several summers in the field. One was collecting plants in the arid Southwest, where I camped in the back country with geology students working on their doctoral dissertations.

In 1935 I spent six weeks at the Atkins Institution of the Arnold Arboretum, a botanical garden established in 1900 by Mr. Edwin F. Atkins of Boston, and located on his sugar plantation at Soledad, Cienfuegos, near the southern shore of Cuba. There I had an opportunity to study the magnificent collection of tropical trees and shrubs that had been assembled, and to make a four-day foray into the Trinidad Mountains, where most of the original vegetation had already been cut over or seriously disturbed. One of my vivid memories was the problem posed by an exotic legume, *Dichrostachys glomerata,* known locally as aroma mala. This woody weed, spreading rapidly from stolons, had completely taken over large areas. It forms impenetrable thickets of spiny stems that are very difficult to eliminate.

From Cuba I sailed to Panama and spent an unforgettable week in the rainforest of Barro Colorado Island. The Island was formed during the construction of the Panama Canal, and is a preserve under the management of the Smithsonian Institution.

My cousin Mary Linder, the sister of David Linder, who served for a number of years as the director of the Farlow Herbarium, married Patrick Putnam. They ran a camp in the Epilu forest of what was then the Belgian Congo. When I became engaged she invited Esther and me to visit them on our honeymoon. We got married in the fall, while I was in the midst of finishing my thesis, but the prospect of going to Africa was an exciting one and we spent our spare minutes during that winter planning an expedition. We obtained lots of sound advice from such seasoned travellers as Thomas Barbour and Arthur Loveridge, both at the Museum of Comparative Zoology.

We set out on this adventure in the summer of 1937—a rather circuitous route to Copenhagen, where we were to spend the winter on an American-Scandinavian Fellowship studying plant hormone techniques with Professor P. Boysen Jensen. By that time we discovered that the Putnams were returning to the States, so we were entirely on our own. We went by sea through the Suez Canal, the Red Sea, and Indian Ocean to Tanga, in what was then Tanganyika, and traveled by stages through that country, Kenya, Uganda, Ruanda, and the eastern edge of the Belgian Congo. Among our special adventures were ascents of Mt. Kilimanjaro and Mt. Elgon. From a botanical point of view we found the cloud forests and open mountain vegetation especially entrancing. I was able to collect among other species some of the huge woody Senecios and Lobelias, which grow at those high altitudes on the equator, and to ship them back to the Gray Herbarium.

It is interesting to note that way back in those days the area where overpopulation appeared most pronounced was Ruanda. There seemed to be a native behind every bush! We drove through Goma, one of the towns that today has been so much in the news—the very site of population dislocations, starvation, and atrocities.

My first academic post was at the University of Rochester. There were only two of us in the Botany Department. As the junior member it fell my lot to become the curator of the University Herbarium which numbered quite a few thousand mounted specimens. Some of these were the property of the University and many were on loan from the Rochester Academy of Science. In addition there were huge piles of unmounted material. It proved to be a fine collection, largely the work of amateurs, notably Milton S. Baxter and Warren Matthews, but also men like Walter Phillips and Ellsworth P. Killip, who had grown up in Rochester and moved away to become professionals. I had the good fortune to meet these men and learn from them about the botanically exciting areas in the vicinity.

During my six years at Rochester I managed to sort through the entire herbarium, getting the collections in order, supervising the mounting of specimens and discarding the inadequately labeled material. One day, while sorting through unmounted specimens, out fell an old letter in brown ink on paper yellowed with age. The author turned out to be John Torrey, writing to his friend at Williams College, Chester Dewey. It was interesting. I copied it before depositing the original in the archives of the University Library. I remember wondering at the time when, if ever, this document would next see the light of day. About nine months later I was reading a newly published life of Torrey by A. Hunter Dupree, when I came upon a familiar passage. Suddenly it dawned on me that it was a quotation from that letter I had salvaged from the herbarium. The biographer must have retrieved it within days of the time I turned it over to the Library!

As curator of the Herbarium I came to meet Royal E. Shanks, an ecologist working on the flora of Monroe County within which Rochester is located. He and I became good friends and collaborated on a list of new records of plants for the county (Shanks and Goodwin 1943). At the same time I put together a flora of Mendon Ponds Park—a botanically rich bit of glacial moraine, dotted with lakes, eskers, and kettles, lying a few miles south of the city (Goodwin 1943). Forty-six years later this list was updated by the New York State Museum (Mitchell et al. 1989). It lists 849 taxa of vascular plants, adding some 86 species to my original list.

Bergen Swamp is a 2000-acre wetland situated about twenty miles west of Rochester. Originally a post-glacial depression underlain by the Niagara limestone, it had become gradually filled in with white marl deposits and invaded by a rich diversity of plant and animal species (Muenscher 1946). Some of these, such as the small white lady's slipper (*Cypripedium candidum*) and Houghton's goldenrod (*Solidago houghtonii*) that grow on the open marl beds, are rare. This wetland had an enormous appeal to me and I soon learned that I shared this interest with a group of local people who, in order to preserve the area, had formed the Bergen Swamp Preservation Society. Although in existence for several years, the Society had not, by the time I joined it, been able to make any headway in acquiring real estate. The land ownership was very complex. The swamp supports extensive stands of white cedar (*Thuja occidentalis*), and every farmer for miles around owned a narrow strip as a source of rot-resistant fence posts.

The Society lacked the resources to finance a survey. Not daunted by this I obtained a free aerial photograph of the area from the Soil Conservation Service, which showed the wooded boundaries of the swamp surrounded by the geometric pattern of the adjacent farms. An old county atlas showed the ownership pattern not only of the farms, but also of the woodlots within the swamp. A passable map was then constructed by superimposing the two. With this as a base I then began to visit farmers in the neighborhood of the swamp and soon encountered one who was willing to sell his five-acre lot on the periphery for $125. The Trustees of the Society approved this initial purchase, which was soon followed by others, including a beautiful 25-acre tract known as Hemlock Knoll. Esther and I made several modest contributions toward these early land acquisitions while I was the Society's treasurer. Today, over fifty years later, the Society owns most of the two thousand acres and employs a full-time warden. The swamp has been designated a National Natural Landmark by the National Park Service. Thus for me began a lifetime involvement in the preservation of natural areas, which later developed into a close association with The Nature Conservancy.

In 1944 we moved to New London, Connecticut, where I joined the faculty of Connecticut College and became the director of its Arboretum. At that time the campus was situated at the northern edge of town and was surrounded on three sides by abandoned farms and wild land. My predecessor, George S. Avery, Jr., had already initiated a land acquisition program which I continued to pursue with vigor. As a result the Arboretum has been expanded from 90 to over 450 acres. In 1952 the College trustees were persuaded to set aside a wild section as the Bolleswood Natural Area, and a long-range ecological study was initiated (Niering and Goodwin 1962). The extensive data set that has been accumulated over the past 44 years has provided generations of students with ecological field experiences and is now being analyzed as a doctoral dissertation by a student at Duke University.

In 1956, as a joint venture with Dr. and Mrs. John M. Ide, we acquired a farm in East Haddam, about 16 miles northwest of New London. Four years later we all made an initial gift to The Nature Conservancy of a piece of the land along Burnham Brook, which traverses the property. We then bought out the Ides' half interest in the remaining property. From this modest beginning the Burnham Brook Preserve has gradually grown through purchases and gifts, in which neighbors have participated, to over 850 acres. Inventories of the biota (published as *Studies in Human Ecology,* Connecticut College) have documented the rich biodiversity of the area, which has now become a part of one of The Nature Conservancy's Last Great Places—the lower watershed of the Connecticut River. It is in the middle of this lovely spot that we are fortunate enough to enjoy retirement.

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BOOK REVIEW

Plants in Changing Environments. Linking Physiological, Population and Community Ecology by F. A. Bazzaz. 1996. ix + 320 pp. ISBN 0-521-39190-3 $74.95 (cloth). ISBN 0-521-39843-6 $29.95 (paper). Cambridge University Press, New York.

One of the major limitations of contemporary ecology is that large amounts of data have been accumulated on a wide variety of systems, but synthesizing approaches have rarely been taken. *Plants in Changing Environments* illustrates one direction from which a synthesis might come, namely the rapprochement between autecology and synecology. In this new book, Fakhri A. Bazzaz uses succession as an integrating theme, beginning with environmental variation and physiological characteristics of plants and searching for connections to the population and community levels. Bazzaz's study is focused through his nearly thirty years of research on old field succession in Illinois, forest disturbance in the northeastern US, forest succession in the tropics, and effects of global change. The text is loosely structured by temporal and spatial scale, working from smaller, shorter scales and events in ecological time toward larger scales and events in evolutionary and successional time.

About two-thirds of the book looks at early- to mid-successional systems, primarily in Illinois. The emphasis is on about a dozen species of annuals and herbaceous perennials, many aspects of whose biology have been studied by Bazzaz and his colleagues. Spatial scales range from individual leaves or roots to patches or entire old fields; temporal scales span instantaneous physiological measurements to a few years. Although some descriptive data on changes in community composition are included in this section, this is background information. The primary themes are the major environmental factors to which the plants are exposed, and proximate responses (e.g., growth, water balance, germination) to these factors. Next, the focus shifts to plant-plant interactions, both competitive and facilitative, and explanations of population turnover in terms of these interactions. I found one of the most interesting themes in this section to be the intricate set of connections among plant architecture, environment (especially as influenced by neighbors), and competition.

The next group of chapters shifts to a longer time scale, looking at the earlier ideas from the evolutionary perspective of niche evolution in early-successional species. An important point made in this section is that early-successional species are exposed to wider environmental variation, both spatial and temporal, than are late-successional species. One would predict early species to have broader niches and greater tolerance of environmental variation; Bazzaz presents some data that support this hypothesis.

Next, the temporal framework shifts to examine the implications of autecological variation among species over successional time. Comparisons of early- and late-successional species show many significant differences in carbon and water economy, growth rates and patterns, and germination. One chapter attempts to predict community species composition from autecological data. This attempt is largely successful, although limited in scope. From data on germination requirements of a number of annuals, Bazzaz was able to successfully predict the dominant in multi-species mixtures over a range of environmental conditions.

The book ends with two chapters that extend the themes of the earlier sections beyond the early-successional venue. The penultimate chapter focuses on disturbances and regeneration in forests. The primary study organisms are species of the genera *Acer* and *Betula,* allowing comparison of gap-adapted versus understory-adapted woody plants. Many of the autecological differences between early- and late-successional species in old field succession crop up again in these comparisons. A chapter on global change as a macro-successional process ends the book. Bazzaz suggests that human-induced changes in atmospheric CO_2, climate, and disturbance frequency will increase landscape dominance by plants with the broad niches and opportunistic dispersal and germination typical of early-successional species.

The focus throughout the book is strongly on systems studied by the author, his students, and collaborators. Of the ca. 670 references cited, about 20% include Bazzaz as an author, a remarkably high figure for a book-length work. This is a tribute to the immense energy and persistence of Bazzaz and his colleagues, whose studies range from physiological ecology and population genetics to global change. Concentration on the work of one research group constitutes both a strength and a weakness of the book. It is a strength because the author has enormous amounts of data on many aspects of the autecology and population biology of his study organisms. This allows a synthetic viewpoint to be taken, and appropriate interspecific comparisons to be made. I found some of the most interesting passages to be the sorts of comparisons that would not be made in shorter, more tightly focused works. However, I found myself frequently wishing for a broader take on how the studies of Bazzaz and his group relate to the work of other researchers. Many references to studies by others are cited, but only rarely are detailed comparisons made.

The illustrations, although abundant (averaging about one figure per two pages) and generally helpful, sometimes seem to have been chosen for their iconic value rather than their information content. Several figures give information that is not used in the text (e.g., Figure 2.4, which gives an elaborate set of definitions of reproductive allocation and effort, none of which are referred to in the text), while others lack important orienting information (e.g., Figure 5.14, which uses various shading patterns to indicate degree of resistance to tree invasion, but lacks a key to indicate which patterns indicate which degree of invasiveness).

In conclusion, *Plants in Changing Environments* provides a wealth of information that is ripe for comparison to species of other geographic regions. I recommend it to succession researchers and, more generally, to those interested in the strengthening of synthetic viewpoints in ecology.

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BOOK REVIEW

Fungi and Environmental Change: Symposium of the British Mycological Society, held at Cranfield University, March 1994, edited by J. C. Frankland, N. Magan, and G. M. Gadd. 1996. xvi + 351 pp. illus. ISBN 0-521-49586-5 $95.00 (cloth). Cambridge University Press, New York.

Rarely does one find a collection of articles being devoted completely to the interactions of the fungi and the environment. Assembled herein are 19 papers drawing on the combined knowledge of 40 scientists. Although the coverage is primarily European in scope, the universal nature of the fungi is documented well.

The most intriguing aspect of the volume lies in the breadth of the materials covered. One might ask, "What is a mycologist?" after reading this book. The vademecum of the mycologist is comprised of many tools—combining the talents of the biologist, chemist, ecologist, pathologist, physicist, etc.—in the quest for a greater understanding of the fungi. The text exemplifies these qualities as the environment is explored from the vantages of the fungi. The reader will find pertinent information on the fungi and biotic interactions. Some of these interactions include forest tree and agricultural plant diseases, activities of the fungi on the surfaces of living leaves and in the litter of leaves, and as components of the soil mycobiota in the form of mycorrhizal and non-mycorrhizal partners. The abiotic interactions are represented through investigations on the roles of ultraviolet light, acid rain components, and several atmospheric pollutants on growth of lichenized and non-lichenized fungi. Readers may be excited with a query into the application of the chaos theory to environmental mycology in the concluding chapter.

The editors are to be congratulated on the publication of the book and thereby bringing these noteworthy articles to the attention of the scientific community. The convenience of the genus/species index adds to the utility of the general index. While some may find the book expensive, certainly the volume should be recommended as an acquisition to the library.

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NEBC MEETING NEWS

January 1997. The January meeting was entitled "Annual Exchange of Botanical Explorations, Exploits, and Excursions" (also known as the annual Show & Tell). Nine members participated in presenting slides showcasing summer travels or recent research.

Pam Weatherbee, Paul Somers, and Ray Angelo showed slides from the Club's Centennial trip to Newfoundland in early July. Club members who did not attend the trip missed spectacular plants (*Cypripedium pubescens* var. *planipetalum, C. reginae, Rubus arcticus, Lychnis alpina, Adiantum aleuticum, Mertensia maritima, Carex pauciflora, Botrychium lunaria, Schizaea pusilla*) as well as caribou, moose, icebergs, outstanding Bed & Breakfasts, and the world's largest blueberry.

Lisa Standley reported on a backpacking trip north of Alaska's Brooks Range, where familiar arctic/alpine species such as rhodora and *Dryas* mingle with western *Pedicularis, Oxytropis,* arctic poppies, and *Saxifraga oppositifolia,* as well as the world's smallest willow. Caribou, grizzly bear, wolves, and wolverine were also highlights of the trip.

Norton Nickerson described a successful wetland mitigation project associated with replacement of salt marsh affected by construction of the MBTA's Neponset River Bridge. He and his team successfully transplanted *Spartina alterniflora* into a mud flat that lacked vegetation and created new high marsh and low marsh by excavating an upland area and transplanting plugs from the adjacent marsh.

David Hunt has been surveying natural communities in the Adirondacks for the NY Natural Heritage Program, attempting to locate and document the best example of each of the 100+ communities in this region. He showed examples of a variety of Adirondack communities, and described a new "sea level fen" community which is located at the upper edge of salt marshes, and contains *Scirpus pungens, Cladium, Eleocharis rostellata, Iris prismatica,* and *Carex hormathodes.*

Neal Sawyer took the Club to Central and South America, showing pictures of his favorite genera (*Deprea* and *Larnax*) in the Solanaceae and their habitats from Costa Rica to Bolivia. Neal showed photos of several taxa in this group, related to *Physalis,* and discussed taxonomic challenges. Neal has collected these plants in cloud forests in Costa Rica, Ecuador, and Bolivia, and traveled through the highlands of Peru, northern Ecuador, and Bolivia's high elevation grasslands.

Barre Hellquist traveled in northern regions in search of water lilies. Enroute, he saw a unique dark pink form of the Great Lakes endemic thistle, *Cirsium pitcheri.* With John Weirsma, Barre succeeded in locating true *Nymphaea tetragona* in Manitoba. The team found a hybrid of *N. tetragona* and *N. tuberosa,* documenting the occurrence of all possible *Nymphaea* hybrids except *N. tetragona* and *N. leibergii* - next year's goal.

George Newman ended the evening with a return to arctic/alpine vegetation, this time at sea level on Brier Island, the westernmost point in Nova Scotia. The island contains the only occurrence of *Geum peckii* outside of New Hampshire, growing with *Sarracenia* in a sea-level bog, as well as the southernmost stand of *Betula michauxii.* George closed with photos of a new large stand of *Veronica alpina* along the Tuckerman's Ravine trail.

February 1997. The speaker was Elizabeth Kneiper, President of the Friends of the Farlow, who spoke on "Boston Lichens: Then and Now." Ms. Kneiper began by providing an excellent overview of the biological diversity and biology of lichens, a taxonomic group much overlooked by most botanists despite their diversity and ecological importance.

Ms. Kneiper described the results of a study she conducted in 1978 and 1979, comparing current lichen diversity in the Boston area with historical diversity during the late 1800s. She developed an historical checklist based on the published and archival records of the many amateur and professional lichenologists who worked in the Boston area in the last century, particularly Edward Tuckerman and Clara Cummings. Results of the study show a dramatic and alarming change in lichen biodiversity over the 100-year interval, with a 50 percent reduction from 237 species in 105 genera to only 124 species in 62 genera. *Peltigera* was reduced to a single species from 6; the *Lobaria* complex, a climax community of mature woodlands, had disappeared; the epiphytic fruticose lichens including *Usnea* and *Ramalina* had virtually vanished, although these were still present outside of the Boston area and in the Berkshires. The species remaining tended to be those demonstrated to be tolerant of poor air quality and crustose species found on calcareous habitats such as concrete and mortar.

Ms. Kneiper's recent Boston inventories show that species not recorded in 1978–79, particularly foliose and crustose species, are now present in the area. It may be that rare species located in the 1978–1979 study were pioneer recolonizers, rather than relict holdouts. Boston lichen diversity may also benefit from experimental (and unintentional) reintroductions from sources that include lichen-covered boulders used to build the Japanese Garden at the Museum of Fine Arts as well as the branches and trunks of the Christmas trees imported from Nova Scotia.

—LISA A. STANDLEY, Recording Secretary.

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CLIMATE CHANGE AND THE DEVELOPMENT OF COASTAL PLAIN DISJUNCTIONS IN THE CENTRAL GREAT LAKES REGION

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ABSTRACT. Paleoecological studies at Portage Marsh in northwestern Indiana provide a Holocene record of local populations of four species disjunct from the Gulf and Atlantic Coastal Plains: *Rhynchospora macrostachya, R. scirpoides, Fuirena pumila,* and *Eleocharis equisetoides.* The populations were established at Portage Marsh when water levels dropped owing to regional climatic drying during the mid-Holocene. They persisted until the late Holocene; only *R. macrostachya* still occurs in the marsh. Populations of these and other Coastal Plain disjuncts probably were established in the southern Lake Michigan region following mid-Holocene drying and formation of extensive shallow wetlands by coastal processes. Seed sources for these populations may have been in the eastern Great Lakes region. We propose that development of Coastal Plain disjunctions in the central Great Lakes region consisted of a sequential series of westward range-shifts in response to climate-induced habitat changes, rather than a single late-glacial migration along a corridor of suitable habitat.

Key Words: biogeography, paleoecology, disjunct populations, climate change, Great Lakes

Scattered populations of plant species with Gulf and Atlantic Coastal Plain affinities occur in the central Great Lakes region (Peattie 1922; Reznicek 1994). These species typically have extensive distributions on the Coastal Plain, ranging from southeastern Texas to southern New Jersey and occasionally southern New England, and are absent or rare through most of the North American interior. In a recent review of the geography, ecology, and conservation biology of the disjunct populations, Reznicek (1994) noted that most of the disjuncts are emergent Cyperaceae and Poaceae that occur in shallow wetlands and lakeshores with fluctuating water levels. Although concentrations of the disjunct species occur in several areas in the central Great Lakes region, the most extensive and diverse is the southern Lake Michigan region of northwestern Indiana and southwestern Michigan (Reznicek 1994). Unfortunately, most Indiana populations have been extirpated owing to extensive wetland destruction during the past century (Wilhelm 1990).

The Coastal Plain disjunctions have long intrigued ecologists and biogeographers (Peattie 1922, 1930; McLaughlin 1932; Cain 1944; Keddy 1981, 1983; Keddy and Reznicek 1982, 1986). Reznicek (1994) reviewed hypotheses proposed to explain the disjunctions, which range from long-distance dispersal to late-glacial migration along a corridor of suitable habitat extending along the ancestral Great Lakes and their outlets. These and other explanations are difficult to test empirically, however.

The difficulty of testing biogeographic explanations based on past events is widely recognized (Wood 1972; Brown and Gibson 1983; Stuckey 1993). Paleoecological studies are a powerful tool for testing disjunction hypotheses, because pollen and plant macrofossils provide direct records of past occurrences and distributions of species (Whitehead 1972). For example, plant macrofossil studies of late-glacial sediments in New England and the eastern Great Lakes region have been used to test explanations for disjunct ranges of high-arctic and cordilleran species in southeastern Canada (Miller and Thompson 1979; Miller 1987, 1989, 1993).

We have completed a paleoecological study of Portage Marsh in northwestern Indiana that provides a long-term record of local populations of four Coastal Plain disjuncts: *Eleocharis equisetoides* (Elliott) Torr., *Fuirena pumila* (Torr.) Sprengel, *Rhynchospora macrostachya* Torr., and *Rhynchospora scirpoides* (Vahl) Griseb. (Singer et al. 1996). That record, combined with recent advances in understanding of the Holocene climatic history of the Great Lakes region (Baker et al. 1992, 1996; R.S. Webb et al. 1993; Singer et al. 1996), provides a framework for evaluating the origin of the disjunction. We describe here our paleoecological results, summarize the postglacial geological, paleoecological, and paleoclimatic history of the Great Lakes region, and discuss potential mechanisms responsible for the Coastal Plain disjunctions.

MATERIALS AND METHODS

Portage Marsh, a shallow, 18 hectare marsh in the towns of Portage and Garyton in northwestern Indiana (Figure 1), is among the few remaining undrained or unfilled marshes in northwestern

Figure 1. Location of Portage Marsh site in eastern North America.

Indiana outside Indiana Dunes National Lakeshore. The site is on shore sediments deposited between 12,200 and 13,000 ^{14}C years Before Present (yr B.P.) during the Glenwood II phase of ancestral Lake Michigan (Chrzastowski and Thompson 1992). The marsh has been disturbed by human activity during the past century. The landscape surrounding the marsh is urban; before the 1950s the landscape was predominantly agricultural. Marsh vegetation is dominated today by *Carex lasiocarpa* Ehrh. and *Calamagrostis canadensis* (Michx.) P. Beauv., with scattered patches of *Typha latifolia* L., *Dulichium arundinaceum* (L.) Britton, and *Cephalanthus occidentalis* L. Open water patches (ca. 0.6 m deep in summer 1994) are occupied by *Proserpinaca palustris* L., *Potamogeton gramineus* L., and *Utricularia vulgaris* L. A complete list of plants observed in the marsh is provided in Singer et al. (1996). Plant nomenclature follows Gleason and Cronquist (1991). Of the Coastal Plain species, only *Rhynchospora macrostachya* has been observed in the modern flora and seed bank of the marsh.

We analyzed pollen and plant macrofossils from two sediment cores (Singer et al. 1996). Core 1 was obtained using a land-based vibracorer (7.6 cm diameter) and included a complete sequence of Holocene and late-glacial sediments. Core 2, which included only the top meter of sediment, was collected using a modified Livingstone piston-corer (10.2 cm diameter). Both cores were taken approximately 75 meters from the northern edge of the basin, where sediments are deepest. Sediment age estimates were based on radiocarbon dating of both cores.

Sediment samples (50 cm^3 each) were dispersed, sieved (710 and 355 μm mesh), and scanned at 6.5× magnification using a stereomicroscope for macrofossil analysis. All well-preserved macrofossils (including fruits, seeds, conifer needles, microsporangia, and oöspores) were identified by comparison with herbarium-documented reference specimens. All specimens were assumed to be constituents of the modern flora of the southern Lake Michigan region (Peattie 1930; Deam 1940; Voss 1972, 1985; Swink and Wilhelm 1979). Notes on morphological criteria used in macrofossil identification are provided in an Appendix in Singer et al. (1996).

Sediment samples for pollen analysis were prepared using standard dispersion and digestion procedures, suspended in silicone oil, and scanned at 400× (Singer et al. 1996). Pollen percentages for terrestrial taxa were calculated based on a sum of all arboreal, shrub, and upland herb types. Cyperaceae pollen was not included in that sum. Pollen percentages for wetland and aquatic plants, including Cyperaceae, were calculated from a sum of all terrestrial, wetland, and aquatic types.

RESULTS

Pollen and plant macrofossils from sediment cores provide a record of regional upland and local aquatic/wetland vegetation for the past 11,000 years (Singer et al. 1996). The pollen percentages for tree taxa, *Ambrosia,* and Poaceae (Figure 2) primarily represent vegetation on the surrounding regional uplands. Some Poaceae and most Cyperaceae pollen probably derives from wetland vegetation in the basin. Plant macrofossils (Figures 3 and 4) record local vegetation within the Portage Marsh basin.

The pollen record during the late-glacial interval (>10,000 yr B.P.) indicates regional vegetation consisting of open forest dominated by *Picea* spp. (Figure 2), together with *Abies, Larix, Populus,* and *Pinus banksiana* Lambert (Singer et al. 1996; Jackson et al. 1986; Webb et al. 1983). During this period, the basin was occupied by an open, hard water lake. Plant macrofossils are rare in the marly sediments of this period.

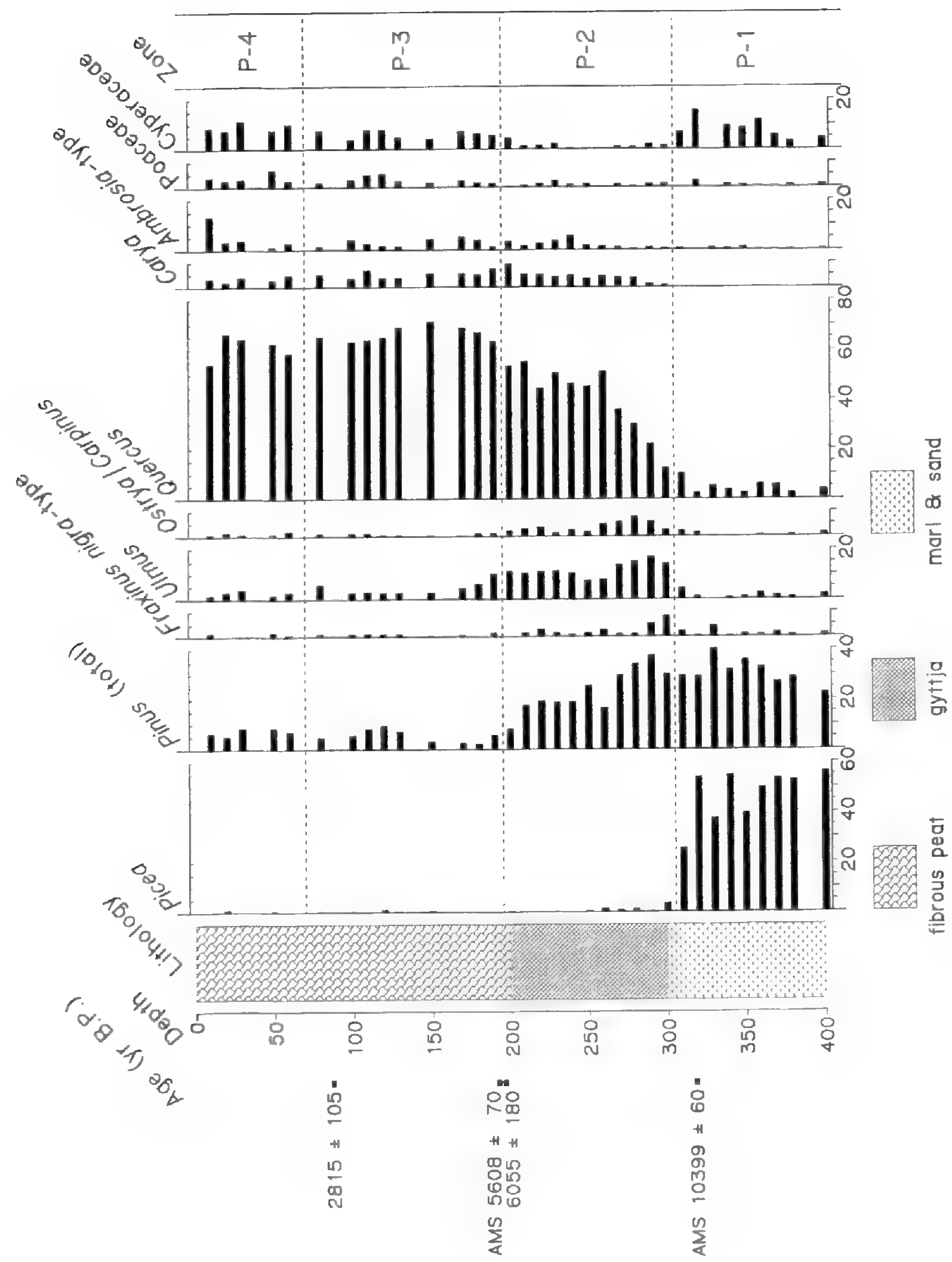
Between 10,000 and 5700 yr B.P., regional vegetation consisted of mixed, mesic forests of *Ulmus, Ostrya/Carpinus, Pinus strobus* L., *Fraxinus nigra* Marshall, *Quercus,* and *Carya* (Figure 2). The basin was occupied by a lake containing submersed plants [*Najas flexilis* (Willd.) Rostk. & Schmidt, *Chara* sp.; Figure 3]. Emergent plants were scarce in the basin, and sediments consisted of fine-textured algal lake mud (gyttja).

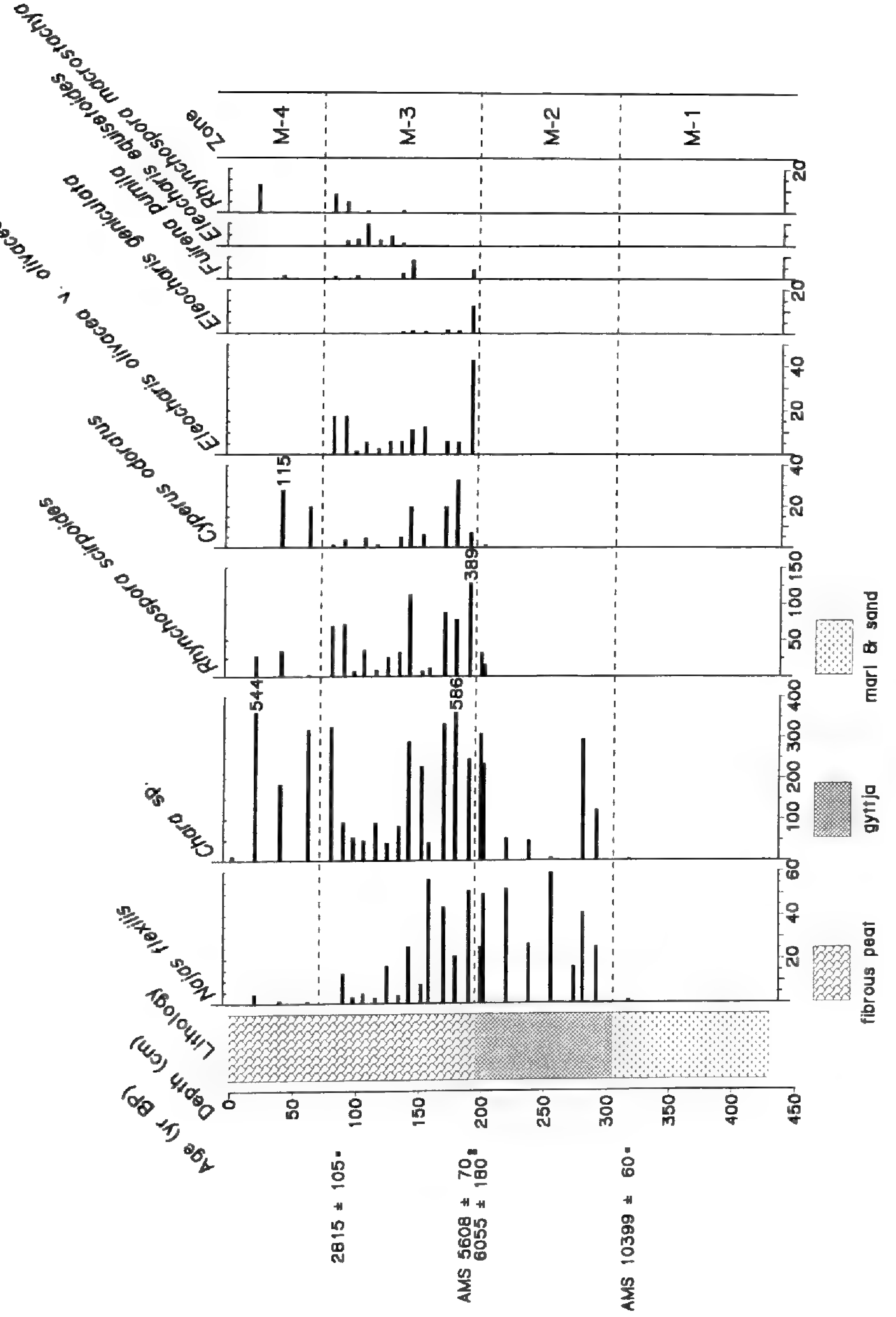
Between 6000 and 5500 yr B.P., the mesic forests of the region were replaced by *Quercus* savanna (Figure 2). At the same time, water levels in the Portage Marsh basin dropped rapidly, leading to development of a shallow, peat-forming marsh with a diverse assemblage of emergent plants (Figure 3). Many of the emergents are annuals or perennials characteristic of exposed shorelines and mudflats during temporary drawdown events. The occurrence of submersed (*Najas flexilis, Chara, Potamogeton* spp.) and floating-leaved plants (*Brasenia*) together with the drawdown emergents in the assemblages indicates a regime of interannual water level fluctuations.

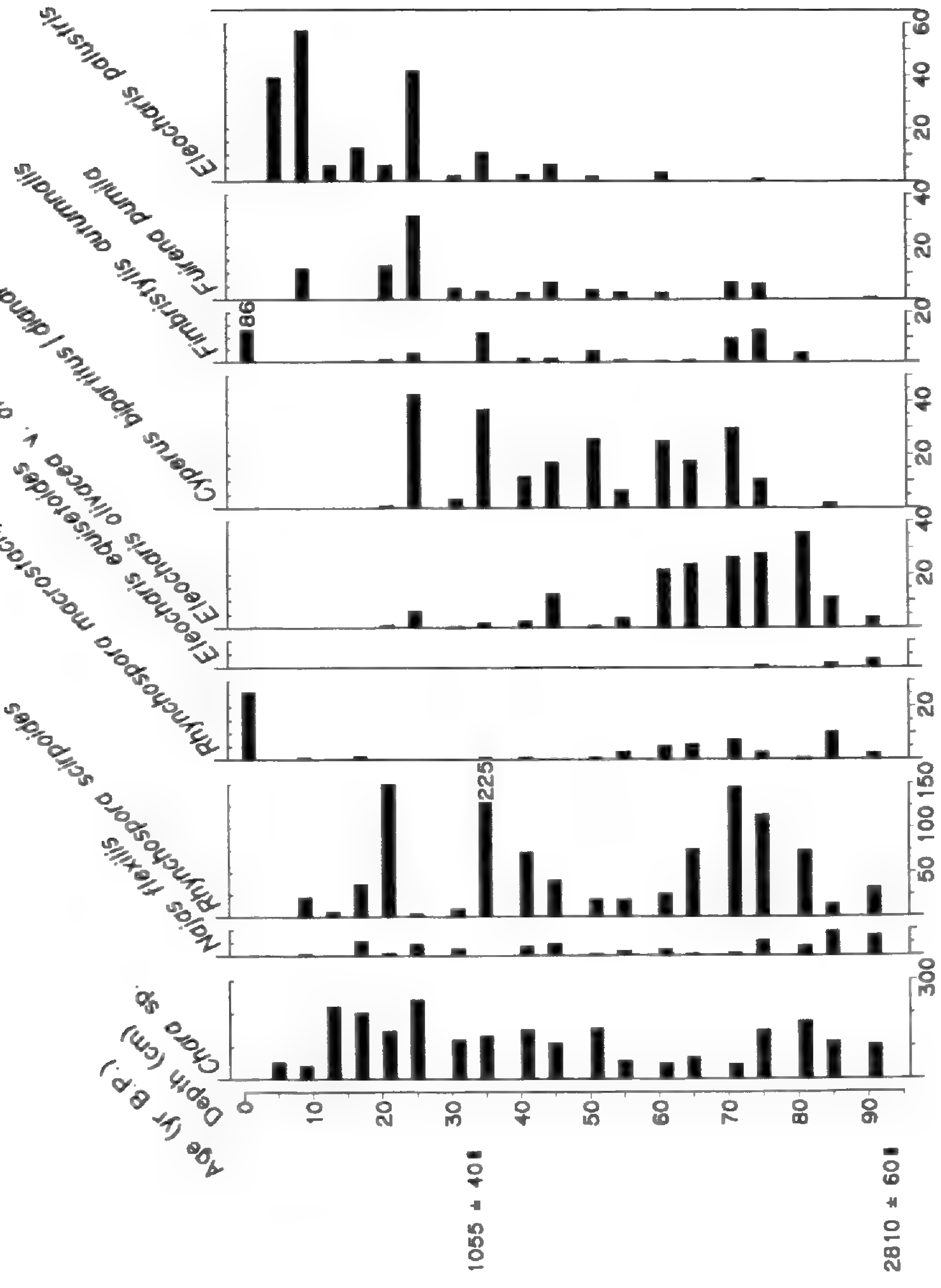
→

Figure 2. Pollen percentage diagram from Portage Marsh Core 1. Only selected taxa are included. Modified from Singer et al. (1996).

Figure 3. Plant macrofossil concentration diagram from Portage Marsh Core 1. Only selected taxa are included. Modified from Singer et al. (1996).


Age (yr B.P.)
Depth
Lithology
Picea
Pinus (total)
Fraxinus nigra-type
Ulmus
Ostrya/Carpinus
Quercus
Carya
Ambrosia-type
Poaceae
Cyperaceae
Zone
P-4
P-3
P-2
P-1
0
50
100
150
200
250
300
350
400
20
40
60
80
2815 ± 105
AMS 5608 ± 70
6055 ± 180
AMS 10399 ± 60
fibrous peat
gyttja
marl & sand


Age (yr BP)
Depth (cm)
Lithology
Najas flexilis
Chara sp.
Rhynchospora scirpoides
Cyperus odoratus
Eleocharis olivacea v. olivacea
Eleocharis geniculata
Fuirena pumila
Eleocharis equisetoides
Rhynchospora macrostachya
Zone
M-4
M-3
M-2
M-1
544
586
389
115
0
50
100
150
200
250
300
350
400
450
20
40
60
100
200
300
400
50
100
150
20
40
20
40
20
20
2815 ± 105
AMS 5608 ± 70
6055 ± 180
AMS 10399 ± 60
fibrous peat
gyttja
marl & sand


Eleocharis palustris
Fuirena pumila
Fimbristylis autumnalis
Cyperus bipartitus / diandrus
Eleocharis olivacea v. olivacea
Eleocharis equisetoides
Rhynchospora macrostachya
Rhynchospora scirpoides
Najas flexilis
Chara sp.
Depth (cm)
Age (yr B.P.)
0
10
20
30
40
50
60
70
80
90
1055 ± 40
2810 ± 60
86
225
20
40
60
50
100
150
300

The four Coastal Plain species (*Rhynchospora scirpoides, R. macrostachya, Fuirena pumila,* and *Eleocharis equisetoides*) colonized the marsh between 5700 and 4500 yr B.P. (Figure 3). Of these, *E. equisetoides* is a shallow-water submersed plant, while *R. scirpoides, R. macrostachya,* and *F. pumila* are emergents of mudflats and other exposed, wet sites. *Rhynchospora scirpoides* and *F. pumila* are annuals.

Quercus savanna persisted on uplands of northwestern Indiana until Euro-American land clearance (Bacone et al. 1980), although mesic forests of *Acer, Betula,* and *Fagus* developed locally on sites with fine-textured soils during the late Holocene (ca. 3000 yr B.P.; Singer et al. 1996; Futyma 1985; Bailey 1972). The mixed assemblage of emergent, submersed, and floating-leaved plants persisted in Portage Marsh until Euro-American disturbance, although the emergent flora underwent some changes after 2800 yr B.P. (Figures 3 and 4). *Eleocharis equisetoides* disappeared ca. 2800 yr B.P., but *Rhynchospora scirpoides* and *Fuirena pumila* may have persisted in the marsh until Euro-American disturbance (Figures 3 and 4). The exact timing of their extirpation is uncertain, owing to a depositional hiatus spanning at least the 19th and early 20th centuries (Singer et al. 1996). *Rhynchospora macrostachya* populations evidently have persisted in the basin throughout the past 4500 years (Figures 3 and 4).

DISCUSSION

Holocene climate change in the Great Lakes region. The changes in regional vegetation, wetland vegetation, and water level observed in the Portage Marsh record show a consistent climatic pattern: (a) cool, moist late-glacial conditions (>10,000 yr B.P.); (b) warm, moist climate during the early Holocene (10,000 to 5700 yr B.P.); (c) rapid transition toward drier climate during the mid-Holocene (5700 to 2800 yr B.P.); and (d) a trend toward cooler, moister conditions in the late Holocene (2800 yr B.P. to

←

Figure 4. Plant macrofossil concentration diagram from Portage Marsh Core 2. Core 2 includes only the top meter of sediments, spanning the past 2800 radiocarbon years. Only selected taxa are included. Modified from Singer et al. (1996).

present). This fits a regional climate pattern documented in eastern Iowa, northern Illinois, southern Wisconsin, northern Indiana, and southern Michigan (Webb et al. 1983; Baker et al. 1992, 1996; Singer et al. 1996).

The Holocene period of highest effective moisture (i.e., precipitation minus evapo-transpiration) in the southern Lake Michigan region, 10,000 to 6000 yr B.P., corresponds to the Milankovitch summer insolation maximum following withdrawal of the Laurentide ice sheet (Kutzbach and Webb 1991). Wright (1992) proposed that higher summer insolation amplified monsoonal flow into the southern Great Lakes region, increasing summer rainfall. Reduction in monsoonal flow as summer insolation decreased after 6000 yr B.P. led to drier conditions. Continuing late Holocene reduction in summer insolation led to cooling and increased effective moisture after 3000 yr B.P. (Wright 1992; T. Webb et al. 1993).

The eastern Great Lakes, St. Lawrence valley, and Hudson–Mohawk lowlands experienced a different sequence of Holocene climatic changes. These regions also were cool and moist during the late-glacial period (>10,000 yr B.P.). However, they were warmest and driest during the early Holocene (9000 to 6000 yr B.P.; Gaudreau and Webb 1986; Webb 1990; R. S. Webb et al. 1993; T. Webb et al. 1993). High summer temperatures were related to the summer insolation maximum. Regional lake levels were low (Webb 1990), and upland vegetation was relatively xeric (R. S. Webb et al. 1993). Summer precipitation may have been low because summer storm tracks were shifted north (relative to today) along the steep thermal gradient at the edge of the Laurentide ice sheet (Webb 1990), which occupied much of eastern Canada from 9000 to 7000 yr B.P. (Dyke and Prest 1987). Effective moisture increased after 7000 yr B.P. (R. S. Webb et al. 1993), and the region has undergone a cooling trend for the past 5000 years (Gaudreau and Webb 1986; T. Webb et al. 1993).

Climate change and the origin of coastal plain disjunctions. Hypotheses proposed to explain the Coastal Plain disjunctions in the Great Lakes region fall into two general categories: (1) Holocene long-distance dispersal from the Coastal Plain populations, and (2) late-glacial migration along the ancestral Great Lakes and their outlets in the St. Lawrence and Hudson–Mohawk valleys and up the Mississippi and Illinois River valleys (Peattie 1922; Keddy 1981; Reznicek 1994). Long-distance dispersal is unlikely in view of the number of species and the magnitude of distances (800–1000 km from the Atlantic Coastal Plain to the central Great Lakes), although it cannot be ruled out with certainty. Plant dispersal events on the order of 10^2 km have been recorded during the Holocene, but plant dispersal over distances of 10^3 km appears to be very rare (Clark et al. 1998).

Peattie (1922) and others have proposed that the Coastal Plain plants migrated inland along a continuous corridor of suitable habitat that existed during the late-glacial. Reznicek (1994) cites geological evidence that such a continuous corridor never existed, but notes that suitable local habitats may have existed intermittently along the migration routes. Thus, the migration would have consisted of site-to-site dispersal events on the order of 10^1–10^2 km. Peattie's original migration hypothesis and its derivatives assume that the migration took place during the late-glacial, and that the disjuncts have occupied their modern ranges during all or most of the Holocene. Local populations persisting along the migration route presumably were extirpated during the Holocene.

The paleoecological record of four of these disjunct species at Portage Marsh, together with a consideration of the postglacial climatic and biogeographic history of eastern North America, suggests an alternative mechanism for the disjunction. These species colonized Portage Marsh between 5700 and 4500 yr B.P., when regional climate change led to the establishment of a marsh with a fluctuating water level. Under the hypotheses of late-glacial migration, mid-Holocene establishment at Portage Marsh would have represented addition of another population to many already existing in the southern Lake Michigan region at the time. However, populations at other wetlands in the region may also have been established after 5700 yr B.P. Most of the wetlands where these species have been observed (Peattie 1930; Wilhelm 1990; Wilcox 1995) were formed during or after construction of the early Toleston Beach complex 4000–5000 yr B.P. (Chrzastowski and Thompson 1992; Thompson 1992). Inland basins that already existed during the early Holocene would, like Portage Marsh, have undergone water level declines 5700 yr B.P. Thus, establishment of most and perhaps all disjunct populations near southern Lake Michigan occurred during the mid- and late Holocene, as suitable habitats were formed by climate-induced shallowing of existing basins and by creation of shallow wetlands by coastal processes.

These species may have colonized the southern Lake Michigan region from the eastern Great Lakes region during the mid-Holocene. Isolated populations of some of these species occur near Lakes Erie and Ontario (Reznicek 1994). Those populations may be remnants of more extensive early Holocene populations. Shallow wetland habitats on suitable substrates may have been more extensive in the eastern Great Lakes region during the relatively dry early Holocene. Such habitats would have disappeared during the mid- to late Holocene owing to increasing effective moisture (T. Webb et al. 1993) and to drowning of coastal wetlands by rising lake levels in the Erie and Ontario basins (Anderson and Lewis 1985; Coakley and Lewis 1985; Coakley and Karrow 1994).

Thus, these disjunct species may have undergone geographic range shifts in response to geographic movements in their "habitat space" (e.g., Huntley and Webb 1989). That "habitat space" is directly linked to regional climate: regional climate constrains local hydrology via precipitation and evapo-transpiration, and the local hydrology constrains the local habitat features experienced directly by the plants (e.g., average and extreme water levels, frequency and magnitude of inundation and drawdown). We hypothesize that populations were established in the eastern Great Lakes region during the early Holocene on shallow wetlands, which were perhaps widespread owing to dry climate and low lake levels. Most of those populations were extirpated in the mid- and late Holocene as effective moisture increased and lake levels rose. To the west, however, increasingly dry conditions and coastal processes created suitable habitats along southern Lake Michigan during the mid- to late Holocene. Dispersal events on the order of 10^2 km led to establishment of populations in these new habitats, which persisted until Euro-American settlement. This hypothesis, like others proposed to explain the disjunction, is speculative. However, it could be tested against alternatives by paleoecological studies of other wetlands in the southern Lake Michigan and eastern Great Lakes regions.

An alternative migration route, proposed by Peattie (1922) and further discussed by Reznicek (1994), is from the Gulf Coastal Plain to the central Great Lakes via the Mississippi and Illinois River valleys. Disjunct populations of several Coastal Plain species occur in the upper Mississippi and Illinois valleys, although none of the four species documented at Portage Marsh are among them. It is possible that the disjunct Coastal Plain flora of the central Great Lakes region consists of a mixture of species that moved westward from the eastern Great Lakes and northward from the Mississippi valley (Reznicek 1994). Unfortunately, Holocene vegetational and climatic changes in the lower and central Mississippi valley and adjacent uplands are poorly documented (T. Webb et al. 1993; Jackson et al. 1997).

Quaternary biogeography and disjunct populations. Late Quaternary pollen and macrofossil records indicate that the postglacial climatic and vegetational history of eastern North America was dynamic and spatially complex. Regional and subcontinental mapping of pollen and macrofossil data indicates spatial shifts in range boundaries and population centers of upland tree and shrub species throughout the Holocene (Gaudreau 1988; Webb 1988; Jackson et al. 1997). These movements were not simply unidirectional migrations from glacial "refugia" in response to postglacial warming. Rather, they consisted of complex and continual adjustments to climatic changes that occurred throughout the Holocene (Webb 1988; Huntley and Webb 1989). Species ranges moved in different directions at different times, and range-boundary expansions of some species were followed by contractions. Studies at finer scales indicate that ranges of tree species shifted along local elevational and edaphic gradients in response to Holocene climatic changes (Brubaker 1975; Jackson 1989; Spear et al. 1994).

Historical explanations of range disjunctions traditionally have emphasized single disjunction-forming events followed by relative stasis. For example, "relict" disjuncts, local vestiges of past regional climate, typically are assumed to have remained *in situ* in locally suitable habitats since the climatic change that led to disappearance of regional populations. Other disjunctions are viewed as remnants of formerly continuous populations that were separated by a unique geological event (e.g., inundation of land bridges, drying of proglacial lakes and outlets). While some disjunct remnants of past climates or events may have persisted in their present locations for thousands of years, direct paleoecological confirmations of such long-term persistence are few. Many disjunct populations probably have complex and dynamic histories, consisting of isolation (via either jump-dispersal or range contraction of the core population) followed by geographic shifts in both the core population and the disjunct populations in response to environmental change. Paleoecological studies are essential to document such shifts and test disjunction hypotheses.

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APPALACHIAN QUILLWORT (*ISOETES APPALACHIANA*, SP. NOV.; ISOETACEAE), A NEW PTERIDOPHYTE FROM THE EASTERN UNITED STATES

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ABSTRACT. *Isoetes appalachiana,* sp. nov., is an element of the *I. engelmannii* complex of North America. Its distinct cytology, spore morphology, and distribution are illustrated and described. Although widely distributed in the eastern United States, it appears to be most common in the Appalachian Mountains. *Isoetes appalachiana* is tetraploid; it is suspected to be an allopolyploid which evolved from the chromosome doubling of *I.* × *altonharvillii,* the sterile hybrid between *I. engelmannii* (*s. str.*) and *I. valida.*

Key Words: *Isoetes appalachiana,* Isoetaceae, pteridophyte, Appalachian Mountains

Isoetes engelmannii A. Br. (*s. lat.*) is widely distributed in the eastern United States, rarely extending into southern Canada. It is considered to be a basic diploid ($2n = 22$), although a single tetraploid population ($2n = 44$) has been reported from northern Florida (Taylor et al. 1993). Although several varieties of *I. engelmannii* were recognized in the 19th and early 20th centuries (var. *fontana* A. A. Eaton, var. *georgiana* Engelm., var. *valida* Engelm., var. *gracilis* Engelm., var. *caroliniana* A. A. Eaton; Engelmann 1867; Eaton 1900, 1905), these were largely ignored by subsequent workers. Morphological and distributional studies combined with cytological data and the application of Scanning Electron Microscopy (SEM) of spores, however, have led to a reconsideration of some of these subspecific taxa, resulting in the description of new species. *Isoetes engelmannii* var. *caroliniana,* for example, was recently recognized as the diploid species *I. valida* (Engelm.) Clute (Luebke 1992; Brunton and Britton 1996), a decision supported by the electrophoretic studies of Duff and Evans (1992). Luebke (1992) also described *I. georgiana* N. Luebke and *I. boomii* N. Luebke from south central Georgia populations previously attributed to *I. engelmannii.* Both are hexaploid ($2n = 66$). *Isoetes engelmannii* var. *gracilis* is widely considered to represent only a larger-than-normal form of *I. engelmannii* (*s. str.*; Taylor et al. 1993).

The discovery of a number of additional tetraploid *Isoetes engelmannii* populations encouraged us to investigate the ecological, morphological, and distributional characteristics of these polyploids and to consider their relationships to previously named taxa in the *I. engelmannii* complex. These investigations indicate that tetraploid populations closely resemble *I. engelmannii* var. *georgiana.* This large-spored taxon was described by Engelmann (1882) from material collected in the 1870s from Floyd County, northwestern Georgia. *Isoetes engelmannii* var. *fontana* described from southeastern Pennsylvania by Eaton (1905) appears to be identical to Engelmann's var. *georgiana* in gross morphology and spore characteristics. Eaton apparently did not consider that the Pennsylvania material could represent the same taxon that was known only from the deep south. We consider these taxa to be synonymous.

In this paper we present evidence for considering tetraploid *Isoetes appalachiana* to represent a previously undetected allopolyploid species.

MATERIALS AND METHODS

Extensive field investigations and collecting throughout the southeastern United States by Brunton since 1990 as part of ongoing systematic studies of *Isoetes* in North America have included efforts to re-locate the locations of type populations of taxa in the *I. engelmannii* complex. Cytological investigation of a selection of southeastern *Isoetes* populations has been conducted by Britton during this period. Over 700 herbarium specimens of the *I. engelmannii* complex from DUKE, GA, NCSC, NCU, FLAS, USF, UNA, FSU, NYS, PH, PSU, UNCC, VDB, VPI and DFB (D.F. Brunton personal herbarium), as well as selected specimens from GH, MO, NY and US, have been studied. Scanning electron micrographs of selected samples were taken using the standard methods of Britton and Brunton (1989, 1992).

Microspores were measured in Euparol, as described by Britton (1991). Megaspore widths (to the outer edges of spore ornamentation) were measured on SEM stubs or in sporewells (Brunton

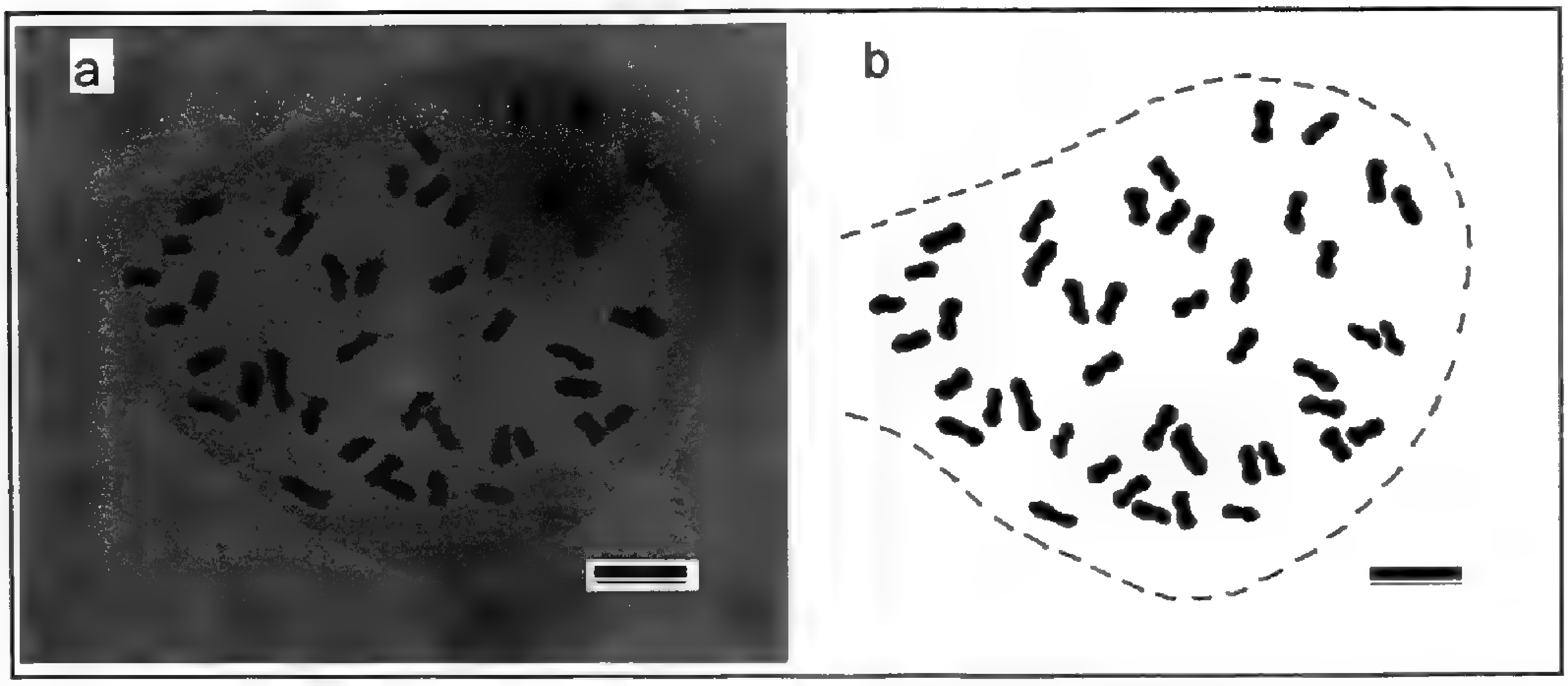


Figure 1. Photomicrograph (a) and interpretive drawing (b) of mitotic root tip plates of *Isoetes appalachiana* (*D.F. Brunton and K.L. McIntosh 11,171,* Huntingdon Co., PA). Scale bar = 5 μm.

1990) by using a binocular stereo microscope at a magnification of 40X or 50X equipped with an ocular micrometer.

Chromosome counts were obtained from *Isoetes engelmannii* (*s. lat.*) populations in Ontario, Pennsylvania, North Carolina, Florida, and Virginia. Plants from each population were grown in distilled water in a growth cabinet. The developing root tips were excised and pretreated in aqueous paradichlorobenzene (PDB) at room temperature for four hours. They then were washed in distilled water, fixed in acetic alcohol (3:1 absolute ethyl alcohol to glacial acetic acid) for 30 minutes or more, hydrolyzed in Warmke's solution (1:1 concentrated HCL to absolute ethyl alcohol) for 7–10 minutes at room temperature, and stained in leucobasic fuchsin (Feulgen) for two hours. The meristems were squashed under a cover glass in 45% acetocarmine stain and examined.

RESULTS

Cytology. Living material from large-spored *Isoetes engelmannii* (*s. lat.*) populations in Pennsylvania, Florida, North Carolina, and Virginia (see listing of type material, below) were confirmed to be tetraploid ($2n = 44$; Figure 1). Specimens from these populations form the sample that was used in the morphological analysis of the tetraploid populations.

Morphology. Tetraploid populations consist of relatively

Figure 2. *Isoetes appalachiana* on shore of Juniata River 8 km S of Huntingdon, Huntingdon Co., PA (6 July 1992).

large quillworts with broad, usually somewhat reflexed leaves (Figure 2) which are curved on their abaxial side and flattened on their adaxial side. Four large lacunal air canals occupy most of the leaf interior. In cross-section, the two abaxial air canals of tetraploid plants from Gadsden Co., Florida, are distinctly smaller than the two adaxial air canals of *Isoetes engelmannii* (*s. str.*) plants from Dinwiddie Co., Virginia. Tetraploid plants are typically more robust than *I. engelmannii* (*s. str.*).

The sporangia of mature individuals usually have a larger proportion of their surface covered by the opaque velum than do plants of *Isoetes engelmannii* (*s. str.*; Table 1). The surface of the sporangium is brown streaked—often heavily so—as opposed to the unmarked or only sparsely marked sporangia of *I. engelmannii* (*s. str.*).

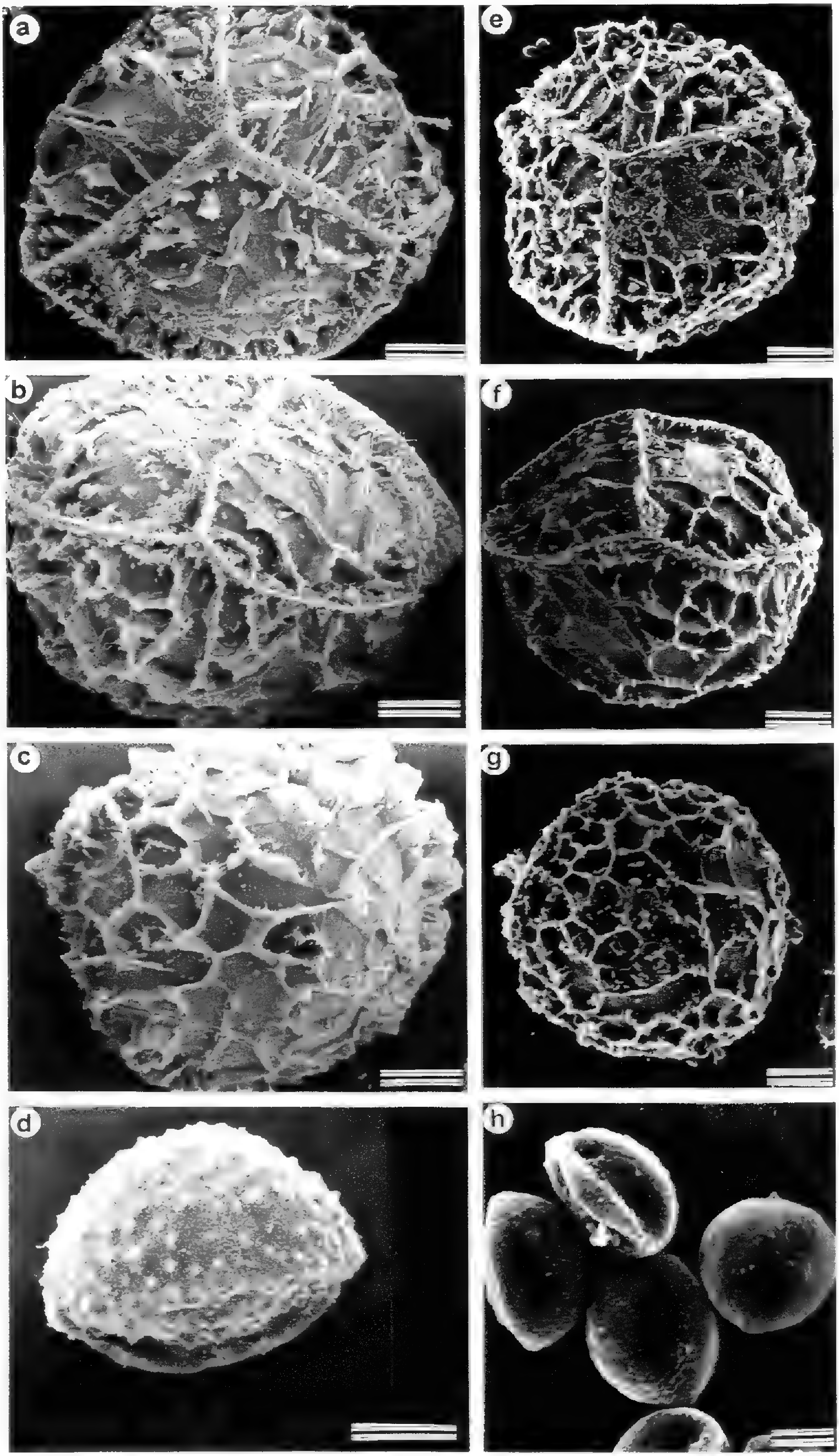
As with virtually all *Isoetes* taxa, spore morphology is critical in the discrimination of these tetraploid plants. Figure 3 illustrates typical tetraploid and diploid *I. engelmannii* spores from various perspectives. Kott and Britton (1983), Britton et al. (1991), Brunton and Taylor (1990), and Musselman et al. (1995) illustrate megaspores and microspores of diploid *I. engelmannii* from throughout the species' range. The megaspores of most tetraploid

Table 1. Comparison of *Isoetes appalachiana* with *I. engelmannii* (Standard deviations and sample size in square brackets).

	I. appalachiana	*I. engelmannii*
Corm	Two-lobed; typically 1.5–2.5 cm wide.	Two-lobed; typically 1.0–1.5 cm wide.
Leaves	Erect to loosely reflexed; narrow to broad, dull green with white basal portion.	Weak, loosely reflexed to sprawling; narrow, dull dark green with paler or white basal portion.
Sporangia		
—pigmentation	Hyaline to white, usually moderately to heavily brown-streaked.	White or pale tan, rarely with scattered brown dots.
—velum coverage	20–25% (rarely to 45%)	10–15%
Megaspore		
—size	(450) **534.1 µm** (611) [SD = 43.41; n = 130]	(380) **461.1 µm** (508) [SD = 29.74; n = 176]
—tri-radial face	Irregular pattern of high, ragged-crested muri.	Regularly reticulate pattern of smooth-crested muri.
—lateral face	Pseudo-reticulate pattern of ragged-crested ridges; short spines distributed individually or as a narrow band along distal side of equatorial ridge.	Continuation of distal face ornamentation to equatorial ridge.
—distal face	Broken-reticulate pattern of ragged-crested, ± thickened muri of variable height.	Reticulate pattern of ± smooth-crested, thin muri of even height.
Microspore		
—size	(28.6) **30.4 µm** (32.0) [n = 100]	(22.0) **25.5 µm** (28.7) [n = 40]
—ornamentation	Sparsely to densely low tuberculate.	Smooth (rarely obscurely tuberculate).
—color	White or pale tan in mass.	White or pale gray in mass.

Table 1. Continued.

	I. appalachiana	*I. engelmannii*
Chromosome Number	$2n = 44$	$2n = 22$
Site Ecology	Submerged to emergent along creek banks, boggy woodland pools and lakes (reservoirs) in acidic sand, clay, or gravel substrate.	Shallow lake and river shores in subacid to calcareous substrate.
Phenology	Leaves well developed by late April (south) or late June (north); spores maturing May (south) to mid-July (north).	Leaves well developed by May (south) or July (north); spores maturing June (south) to August (north).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populations have a ragged-reticulate appearance (Figures 3a–3c), in contrast to the regularly reticulate ornamentation of *I. engelmannii* (*s. str.*) megaspores (Figures 3e–3g). Some cytologically determined tetraploids, however (e.g., the Gadsden Co., Florida, population), have a regular megaspore ornamentation pattern very similar to *I. engelmannii* (*s. str.*). The substantial difference in spore size and microspore ornamentation (Table 1) can be used to separate mature specimens of most problematic populations.

Megaspore muri (ornamentation ridges) of the tetraploid are typically thicker than those of *Isoetes engelmannii* (*s. str.*). They also spread outward at their point of attachment to the megaspore and are more irregular in form than the thin, straight-sided and smooth-topped muri of *I. engelmannii* (*s. str.*; Figures 3c and 3g). A narrow, though frequently obscure, band of short spines distal to the equatorial ridge is often present on tetraploid megaspores (Figure 3b) but has not been observed with *I. engelmannii* (*s. str.*; Figure 3f).

The ploidy level of the tetraploid is reflected in a larger megaspore size. While it averages about 535 μm, individual spores over 600 μm have been observed. *Isoetes engelmannii* (*s. str.*) megaspores average only about 460 μm with individuals larger than 500 μm being rarely observed.

Microspore size is significantly different between the tetraploid and *Isoetes engelmannii* (*s. str.*) as well. Microspore length from a sample of Pennsylvania tetraploid plants averages about 30 μm compared with about 25 μm for diploids (Table 1). Ornamentation on mature tetraploid microspores is strikingly different, exhibiting a low tuberculate pattern (Figure 3d) reminiscent of *I. riparia* Dur. (*s. str.*; Britton and Brunton 1989). In contrast, the surface of *I. engelmannii* (*s. str.*) microspores is smooth (Figure

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Figure 3. SEM composite of *Isoetes engelmannii* (*s. str.*) and *I. appalachiana* spores. a–d: *I. appalachiana.* a–c: holotype, (*D.F. Brunton and K.L. McIntosh 12,274* [OAC]); a: Proximal view of megaspore; b: Lateral view of megaspore; c: Distal view of megaspore; d: microspore (*D.F. Brunton and K.L. McIntosh 11,559* [OAC]). e–h: *I. engelmannii* (*s. str.*) e, g, h: holotype, (*G. Engelmann s.n.,* 1843 [MO]); e: Proximal view of megaspore; f: Lateral view of megaspore (*D.F. Brunton and K.L. McIntosh 11,170* [OAC]); g: Distal view of megaspore; h: Microspore. Scale bar = 100 μm (megaspores), 10 μm (microspores).

3h). Table 1 summarizes the morphological characteristics of the tetraploid and indicates its morphological differences from *I. engelmannii* (*s. str.*).

Some tetraploid populations (in the northern Appalachian Mountains in particular) are strikingly similar to *Isoetes valida.* The much smaller megaspores (450 μm) with more congested, more raggedly reticulate ornamentation, larger velum coverage (50% or more) and unmarked sporangium distinguish mature *I. valida* specimens (Brunton and Britton 1996).

Site ecology. We have observed the tetraploid in a variety of aquatic and emergent habitats. It is found in seeps in mature swamp forest and on emergent clay flats at swamp forest edges (Florida), on emergent clay, silty-sand and/or cobble river shores (Pennsylvania, Virginia), in back-eddies along tributary streams (Georgia, Pennsylvania) and submerged in shallow water in a manmade reservoir (a former mountain stream in Pennsylvania). The flora at these sites appears to be dominated by species preferring acidic substrates. It was the only *Isoetes* taxon present at all but the Jersey Shores, Lycoming County, Pennsylvania, site where it grows with *I. riparia* (*s. str.*). Typically it is found growing with few other vascular plants in the immediate vicinity (Figure 2).

Distribution. The tetraploid is most frequently—almost commonly—found at lower to middle elevation areas of the Appalachian Mountains in Pennsylvania. It also occurs in a number of counties in the southern Appalachians in Georgia, North Carolina, and South Carolina. Inexplicably, it seems to be absent from northern and western Virginia, Maryland, and West Virginia. A similar gap in range was noted initially for *Isoetes valida* (Brunton and Britton 1996). Both may, in part, represent limitations of the floristic record rather than actual distributional gaps. The tetraploid is also known from a number of Coastal Plain counties in the Carolinas, Virginia, and northern Florida. The Florida Coastal Plain stations are found in areas known for their concentrations of regionally uncommon Appalachian disjuncts (Mitchell 1963).

In addition to on-site examination of the populations at which cytological material was collected, between 90 and 100 specimens displaying the morphological features of the tetraploid were noted (and so annotated) in herbaria. Figure 4 illustrates (one per county) the distribution of these specimen records. They include specimens from Florida, Georgia, New Jersey, North Carolina, South Carolina, and Virginia. The material includes those specimens upon which the Florida reports of *Isoetes engelmannii* (*s. str.*) and *I. riparia* are based.

Despite the segregation of these tetraploid populations as *Isoetes appalachiana, I. engelmannii* (*s. str.*) continues to display a widespread distribution across eastern North America. It appears to be particularly concentrated along the Atlantic seaboard from Maine to South Carolina and along the Mississippi River valley into Missouri and Illinois. Stations become increasingly widely scattered inland from the Atlantic, with populations in Ontario and Michigan being components of a disjunct Atlantic Coastal Plain flora (Britton et al. 1991; Reznicek 1994). This revised distribution for *I. engelmannii* (*s. str.*) is similar to that of other riparian deciduous swamp species which are rare in the northern United States, such as *Populus heterophylla* L. and *Fraxinus tomentosa* Michx. f. (McCormac 1993).

The distribution of *Isoetes appalachiana* (Figure 4) overlaps with other swamp and emergent shore quillworts including *I. riparia* (*s. str.*), *I. valida,* and *I. engelmannii* in the north and *I. engelmannii, I. valida,* and *I. hyemalis* Brunton in the south (Taylor et al. 1993; Brunton et al. 1994). It is found in higher, more inland sites in the north and lower, more coastal areas in the south. Additional field studies will be required to clarify this distribution and to evaluate the apparent rarity of stations in the central portion of its range.

DISCUSSION

Taxonomy. We believe that the distinctive cytology, distribution, and morphology of the tetraploid indicate that it is a distinct species and that it probably represents the taxon first recognized as *Isoetes engelmannii* var. *georgiana* by George Engelmann over a century ago. Cytological determination of Engelmann's material is presently impossible, however, and we were unable to re-locate *I. engelmannii* var. *georgiana* at its Floyd County, Georgia, type location. The connection between that taxon and the tetraploid described here, therefore, cannot be established with certainty. Recombination of this name at the species

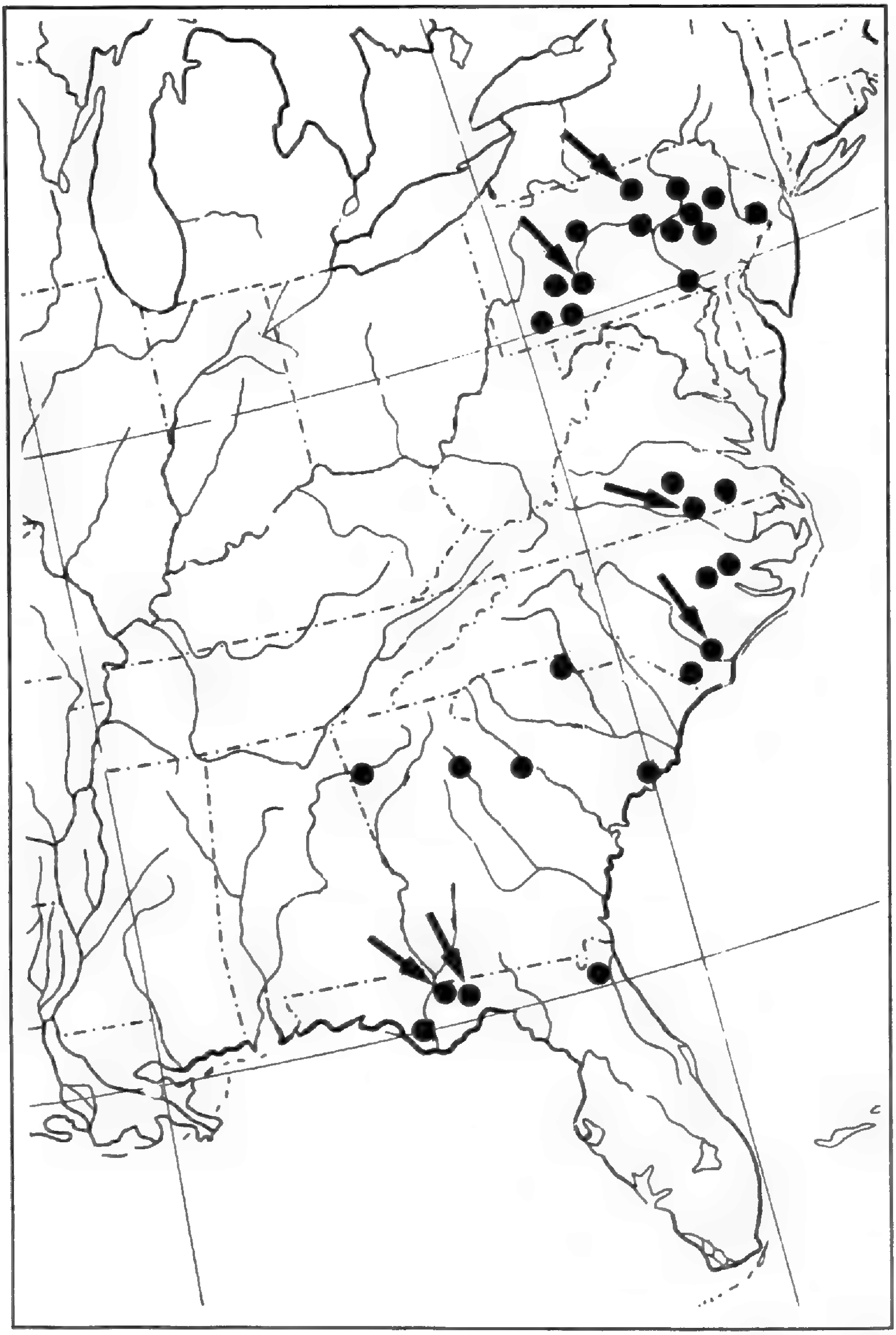

Figure 4. Distribution of *Isoetes appalachiana* (by county) in North America. Arrows point to cytologically confirmed populations.

level, in any event, would be inappropriate due to its previous application to another species (Luebke 1992). Similarly, Eaton's *I. engelmannii* var. *fontana* cannot be cytologically linked to the tetraploid since the type population along the Susquehanna River of southern Pennsylvania has been destroyed by power dam construction (pers. obs.).

We propose the following name and description based entirely on cytologically confirmed type material:

Isoetes appalachiana D. F. Brunton & D. M. Britton, *sp. nov.* (Figures 1, 2, and 3a–3d). *I. engelmannii* A. Braun var. *georgiana* Engelm. (Engelmann 1882); *I. engelmannii* A. Braun var. *fontana* A. A. Eaton (Eaton 1905); TYPE: U.S.A. Pennsylvania: Blair Co., Tipton Reservoir, 6 Aug 1995, *D. F. Brunton and K. L. McIntosh 12,274* [HOLOTYPE: OAC (Plant A); ISOTYPES: MIL, MICH, DAO, GH, VPI, PH, DFB]. The specific epithet reflects the concentration of populations along the Appalachian Mountains.

Isoetes magna et aquatica, emergens foliis colore oleae rigidis vel reflexis, e cormo bilobato exoriens; megasporae similes *I. engelmannii* (*s. str.*), sed majores (plerumque 535 μm), ornatione inique reticulata signatae, quae consistit in muris cum lateribus crassis et fundamentis attenuatis et cristis irregularibus; zona spinarum brevium, densa, angusta vel obscura, secundum latus distale iugi medialis, microsporae ovales, tuberculis humilibus ornatae (plerumque 30 μm); chromosomata $2n = 44$.

FORM: Robust (25–30 cm tall), semi-terrestrial herb arising from a rounded, two-lobed corm 1.5–2.5 cm wide; LEAVES: erect when submerged, reflexed when emergent, dull olive-green with whitish-green to pale brownish-green bases, 1–2 mm wide at mid-length, abaxial side curved, flattened adaxially, four large lacunal air canals conspicuous in cross-section; SPORANGIA: oblong to oval, to 10 mm long, white or hyaline surface moderately to heavily brown-streaked; VELUM: narrow, descending across ca. 20%–25% (rarely to 45%) of the sporangium; LIGULE: delicate, narrowly triangular; MEGASPORES: 535 μm, white, with ragged-reticulate, relatively thick, irregularly crested muri (ornamentation walls) which spread outwards at their point of attachment to the megaspore surface; short spines distributed along distal side of equatorial ridge, often forming a narrow, dense band; MICROSPORES: white to pale tan in mass when mature, 30 μm long, with low tuberculate ornamentation; CYTOLOGY: $2n = 44$.

PARATYPES (all cytologically determined $2n = 44$): FLORIDA: Gadsden Co., Ochlockonee River at Highway 27, 18 Mar 1994, *D.F. Brunton and K.L. McIntosh 11,816* (MICH, FSU, DFB, OAC); Leon Co., Geddies Road, Tallahassee, 15 Mar 1995, *D.F. Brunton and K.L. McIntosh 12,147* (OAC, DFB, MICH); NORTH CAROLINA: Jones Co., north side of Hunters Creek at Highway 58, 2 Jul 1996, *D.F. Brunton and K.L. McIntosh 12,586* (OAC, MIL, MICH, DFB, ODU); PENNSYLVANIA: Huntingdon Co., Juniata River 8 km S of Huntingdon, 6 Jul 1992, *D.F. Brunton and K.L. McIntosh 11,171* (OAC, DFB, MIL, MICH, DAO, WIS, NCSC); Lycoming Co., W channel of West Branch, Susquehanna River, Jersey Shore, 6 Jul 1992, *D.F. Brunton and K.L. McIntosh 11,176* (OAC, DFB); VIRGINIA: Greenville Co., Highway 301, Fountains Creek, Emporia, 9 Jul 1993, *D.F. Brunton and K.L. McIntosh 11,559* (OAC, DFB, DAO, VPI).

Because many specimens of large-leaved quillworts have been collected before megaspores have matured, precise discrimination of herbarium material in the *Isoetes engelmannii* complex is not always possible. The close morphological similarity between *I. appalachiana* and *I. engelmannii* has a parallel with two quillworts in western North America, the diploid *I. echinospora* Dur. and the tetraploid *I. maritima* Underw. Although some specimens of these latter species can be separated confidently only by spore size, the recent description of their sterile triploid hybrid, *I.* × *pseudotruncata* Britton & Brunton, has confirmed that they are cytologically distinct species (Britton and Brunton 1996). Coincidentally, *I. echinospora* and *I. maritima* also can be distinguished by the same microspore characteristic seen with *I. appalachiana* and *I. engelmannii* (*s. str.*). In both cases the diploid has smooth microspores while the tetraploid is conspicuously marked with spines or tubercles.

Origins. *Isoetes appalachiana* likely represents an allopolyploid resulting from the chromosome doubling of a sterile hybrid between two diploids. The involvement of *I. engelmannii* (*s. str.*) is strongly suggested by the morphological similarity of the two taxa and by range considerations. Based on present and fossil distribution (e.g., Taylor et al. 1993; Craig 1969) as well as morphology, the other likely diploid parental candidates might be *I. echinospora* or *I. valida.* Assuming that *I. appalachiana* should reflect the morphological traits of both progenitor species, the absence of elements of the strongly echinate megaspore morphology of *I. echinospora* should eliminate this northern taxon from serious consideration. The morphology of *I. valida,* however, fits well, as this member of the *I. engelmannii* complex displays an even more congested, ragged-reticulate ornamentation and a larger velum coverage than *I. appalachiana* (Brunton and Britton 1996). The distribution of these two species also is similar. *Isoetes* × *altonharvillii* Musselman & Bray, the sterile hybrid between *I. engelmannii* and *I. valida,* has been described recently from Virginia (Musselman et al. 1995) and has also been collected in Delaware and North Carolina. It seems reasonable, therefore, to speculate that *I. appalachiana* evolved from the doubling of diploid *I.* × *altonharvillii* just as it is believed that *I. riparia* has evolved from a comparable doubling of the sterile diploid hybrid *I.* × *eatonii* Dodge (Taylor et al. 1993).

Possible *Isoetes appalachiana* × *engelmannii* (*s. str.*) hybrid specimens have been seen in herbarium collections from Lancaster, Northampton, and Berks Counties, Pennsylvania, Cecil Co., Maryland, and Passaic Co., New Jersey. Cytological confirmation of such a triploid taxon would provide important support for the specific status of *I. appalachiana.* The relationship of this species with other elements of the *I. engelmannii* complex may be clarified further by molecular genetic investigations.

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PROPAGATION AND REINTRODUCTION OF THE ENDANGERED HEMIPARASITE *SCHWALBEA AMERICANA* (SCROPHULARIACEAE)

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ABSTRACT. Propagation of the endangered hemiparasite *Schwalbea americana* was conducted in the presence of several species of potential host plants. Seeds were germinated and the seedlings transferred to pots containing potential host plants. Potted seedlings and potential hosts then were transplanted to field sites adjacent to a population of *S. americana* from which the seed had been collected. Germination of seedlings was >90% after a wet-cold treatment; a dry-cold treatment resulted in low germination. Seedlings grown in association with seedlings of the grass *Schizachyrium scoparium* did not differ in size or longevity from seedlings grown alone. Growth of seedlings was slightly greater in the presence of host plants than without, but seedlings still achieved only limited size in greenhouse conditions before transplantation (2 to 4 mm in width and height). After transplantation to the field the majority of seedlings died rapidly, but several persisted for over 45 days without showing appreciable growth. Poor seedling establishment and survival are believed to contribute to the rarity of this species. The development of improved methods for the propagation and transplantation of *S. americana,* and the greater understanding of the causes for the rarity of this endangered species, will increase options for recovery strategies.

Key Words: *Schwalbea americana,* hemiparasite, Scrophulariaceae, endangered species, propagation, species reintroduction, New Jersey

Schwalbea americana L. is a hemiparasitic, herbaceous perennial which was Federally listed as endangered in 1992 (U.S. Fish and Wildlife Service 1992). *Schwalbea americana* is a showy flowering plant with purplish yellow, bee pollinated, tubular flowers on an unbranched, pubescent, spike-like raceme (Sandhills Field Office 1993; Gleason and Cronquist 1991). As a hemiparasite, it attaches to the roots of a host plant through haustoria which allow the extraction of water, organic substances, and inorganic nutrients (Matthies 1995).

Schwalbea americana is thought to be one of the few species of an ancient Miocene flora to have survived the Pleistocene glaciation (Pennell 1935). It is monotypic, the most primitive member of the tribe Euphrasieae in the Scrophulariaceae, and always has been considered rare (Pennell 1935). Pennell (1935) originally separated the northern and southern populations of *Schwalbea* into two species, *S. americana* in the north and *S. australis* Pennell in the south. Fernald (1937) found instead that morphological variation between the two species had wide overlap and therefore they were combined into one species.

Habitat loss through development and fire suppression is thought to be responsible for the decline of this species (U.S. Fish and Wildlife Service 1994). The one population remaining in New Jersey, out of 18 historical occurrences, represents the current northernmost limit of the species' range. The species once extended into southern New England, but has not been found even where suitable habitat persists (Sorrie 1987). Other surviving locations are on the southeastern Coastal Plain, where the species occurs in longleaf pine (*Pinus palustris* Miller) savannas, flatwoods, and ecotonal areas between pine uplands and wetland depressions (Sandhills Field Office 1993; U.S. Fish and Wildlife Service 1992). It occurs in sandy, acidic soils and high light where frequent fire is often a factor in maintaining an open canopy and sparse vegetation (U.S. Fish and Wildlife Service 1992). Decreased fire frequency and suppression of the natural fire regime is considered a factor which has reduced the amount of available habitat for the species and resulted in the extirpation of some known populations of *Schwalbea americana* (U.S. Fish and Wildlife Service 1992).

The habitat requirements for this species include a fluctuating water table and open, early successional pine lowland habitat (U.S. Fish and Wildlife Service 1992). For a species to persist, it must either have the ability to track the shifting mosaic of available habitat through dispersal and re-establishment, or good conditions must be maintained locally (Thomas 1994). For *Schwalbea americana,* the persistence of locally favorable conditions would require the long-term maintenance of early successional habitat. As locations of *S. americana* are eliminated due to succession or anthropogenic habitat destruction and fire suppression, the species has not been observed in locally good habitat near historical locations (U.S. Fish and Wildlife Service 1992). The anthropogenic impacts on *S. americana* correspond with the predictions of Fiedler and Ahouse (1992), who indicated that long persisting but narrowly distributed species would be especially susceptible to human impact. *Schwalbea americana* would be considered to be in this category due to its Miocene origin (Pennell 1935) and rigid ecotonal habitat requirements.

There are many common hemiparasitic species, so the hemiparasitic nature of the species' biology is not necessarily a factor contributing to the rarity of *Schwalbea americana.* Hemiparasites are believed to have low resource-use efficiency and are often restricted to nutrient-poor habitats (Matthies 1995). The propagation of hemiparasitic plants generally is considered difficult, and past attempts to grow *S. americana* in the absence of host plants have resulted in the eventual death of all seedlings (Brumback 1989). Musselman and Mann (1977) grew seedlings of *S. americana* in association with several host species and concluded that it was a non-host-specific, obligate root parasite. In this study, the propagation of the species was initiated in order to provide plants for reintroduction to and expansion of the New Jersey population. A seed collection strategy was devised to maximize the sampling of genetic variability in the population, while minimizing the amount of seed taken from the population (Obee 1993).

MATERIALS AND METHODS

Seed germination and growth trials alone and with *Schizachyrium scoparium.* Seeds were collected on August 23, 1993, from 12 genets of *Schwalbea americana* at the one remaining population in New Jersey. Seeds were collected from no more than one capsule per ramet and no more than two capsules per genet. Genets producing less than five flowers were excluded from collection. Seeds were stored at room temperature after collection and a wet-cold treatment was initiated after approximately 3.5 mo. For the wet-cold treatment, seeds were placed on moist, absorbent germination paper in plastic sandwich boxes in a cold room at Nelson Hall, Rutgers University, and maintained in the dark at a temperature of 4°C. Light levels and temperature in this cold treatment fluctuated on occasion due to several temporary power losses and the sporadic turning on of lights in the room.

Germination commenced after approximately 4 mo., after which seedlings were transplanted into 25 cm^2 black plastic flats with various soil mixtures. Using tweezers, seedlings were placed into small soil depressions and gently covered with grains of sand. Different combinations of a coarse builder's sand, New Jersey Piedmont loam topsoil, vermiculite, Pro Mix BX (Premiere Brands, Inc., Stamford, CT), or a standard soil mix were used to create soil mixtures varying in texture and drainage capacity. The standard soil mix consisted of, by volume, 12 parts New Jersey Piedmont loam soil, 8 parts sand, 6 parts Canadian sphagnum peat, and 0.125 parts lime. The five additional soil combination ratios used were: (1) 2 sand : 1 vermiculite : 1 standard soil mix; (2) 1 sand : 1 Pro Mix BX: 1 topsoil; (3) 1 sand : 1 vermiculite; (4) 1 sand : 1 standard soil mix; (5) 2 sand : 1 Pro Mix BX: 1 topsoil.

Each of the soil mixtures had three replicate flats planted with *Schwalbea americana* in concentrations from 45 to 120 seedlings from up to six genotypes. Two flats of each soil combination (only 1 for soil mixture #4) also were sowed with approximately 100 seeds of a southern New Jersey population of *Schizachyrium scoparium* (Michx.) Nash (little bluestem) to serve as a potential host species for the *Schwalbea* seedlings. One of the flats of soil mixture #4 without *Schizachyrium* varied in transplantation technique. Strips of germination paper containing approximately 175 germinated seedlings of *Schwalbea* were placed upon the soil surface instead of having individual seedlings transplanted into soil depressions. Flats were maintained in a greenhouse low-light mist room, which kept the soil surface constantly moist.

Several trials were made in pots containing adult plants of *Schizachyrium scoparium* rather than seedlings. Each of two adult plants of *Schizachyrium* were planted with 15 seedlings of *Schwalbea americana* growing in 15 cm clay pots in the standard soil mix. Several hundred seeds of *Schwalbea* were added to the upper 1 cm of soil surface with two additional adult *Schizachyrium* plants. The *Schizachyrium* had been overwintered outside in 15 cm clay pots inserted in soil to the rim of the pots.

Seed germination and growth trials with Pine Barrens species. Pots containing potential host plants of New Jersey Pine

Barrens species were established on July 28, 1994. Host plants from the roadside and along a path near the present *Schwalbea americana* population were located. Roots were severed in a 15 cm diameter around the stem and transplanted with surrounding soil into 15 cm round black plastic pots. These plants, initially containing only limited root systems, were fertilized with NPK 20-20-20 and maintained in the greenhouse. Several Pine Barrens species were collected, some of which were identified as suitable host species for *S. americana* by Musselman and Mann (1977). The species were collected and labeled as follows: *Pinus rigida* Miller (pitch pine; Pot #1), *Vaccinium corymbosum* L. (high bush blueberry; Pots #2 and 4), *Gaultheria procumbens* L. (teaberry; Pot #3), *Ilex glabra* (L.) A. Gray (inkberry; Pots #5 and 6), *Quercus marilandica* Muenchh. (blackjack oak; Pot #7), *Prunus serotina* Ehrh. (black cherry; Pot #8), and *Gaylussacia dumosa* (Andr.) T. & G. (black huckleberry; Pot #9).

Seeds of *Schwalbea americana* were collected again on October 2, 1994, and the seeds were placed on germination paper under the same conditions as the previous year. Seeds were stored under one of two conditions: wet-cold using the same methods as described previously, or dry-cold. Wet-cold germinated seedlings were maintained moist at room temperature in indirect light for 7 days and then transplanted into the nine pots containing host plants maintained in the greenhouse. Pots containing host plants and wet-cold seedling transplants were maintained initially in the greenhouse mist room in approximately 15% of full sunlight. Then, 14–21 days later, 7 of the 9 pots were moved into 80% of full sunlight where they were bottom-watered from trays beneath the pots. After 1 mo., pots were moved back into the mist room to minimize chances of desiccation of seedlings.

Several germination trials were completed with seeds stored dry-cold. After approximately 5 mo., water was added to 30 seeds, half of which were placed in the laboratory at room temperature and half placed back into the previous cold treatment. After approximately 7 mo. of dry-cold storage, 80 seeds were placed in a germinator at a temperature of 30°C (day)/20°C (night) for 14 days and then switched to 20°C (day)/10°C (night) for 14 days.

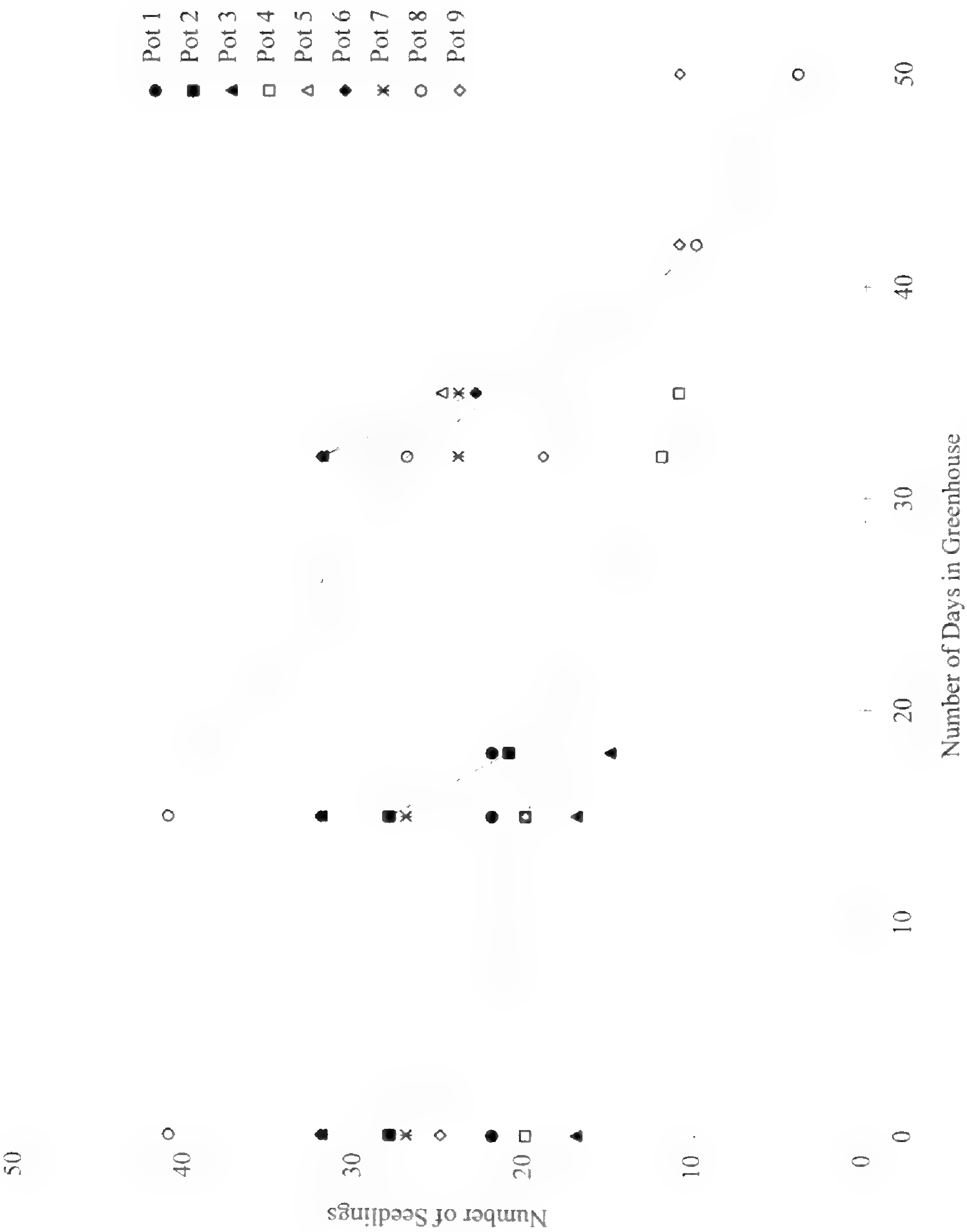
Reintroduction of seedlings. Seedlings were transplanted adjacent to the present population on three occasions. On April

21, 1995, seedlings with hosts in Pots 1–3 were transplanted to locations of similar habitat adjacent to the New Jersey population. These transplants were watered with 2 liters of water each, 1–2 times a week as needed, for 3–4 weeks after transplantation. Pots were cut away from soil clumps which were placed whole, without disturbing seedlings, into carefully cut holes in the ground and watered directly. Two of the transplants had two layers of white cheesecloth placed on wood stakes 1 ft. above the transplants, each covering an area of 1 m^2. The third transplant had no cheesecloth but was placed in a shady area near the forest edge. Cheesecloth was removed from the transplants after one week. On May 8, Pots 4–7 were transplanted adjacent to the existing natural population. These plants were shaded with cheesecloth; remaining seedlings from the previous transplant were shaded again with cheesecloth. On May 23, the remaining greenhouse seedlings in Pots 8 and 9 were transplanted adjacent to the existing population and shaded with cheesecloth.

RESULTS

Seedlings with and without *Schizachyrium scoparium*. Seeds were observed to have germinated in the wet-cold treatment on April 6, 1994, approximately 4 mo. after the initiation of the treatment. Seeds from 10 of the 12 genets germinated at >90%. Seeds from the remaining 2 genets did not germinate due to fungal contamination during the cold treatment. Germinated seedlings were yellowish-green in color with rigid radicles 1–3 mm in length.

Seedlings persisted after transplantation to flats for up to 2 mo. with slow mortality. No differences in vigor or survival were observed between soil treatments, with or without potential host plant *Schizachyrium scoparium,* or based upon genet. Seedlings growing on germination paper placed on the soil surface persisted for 2–5 weeks but failed to develop an extended root system. Seedlings generally did not grow any larger than when planted, i.e., only 2–4 mm in width and height with a single set of cotyledons. However, approximately 10% of seedlings exhibited slight growth and developed a second set of leaves. Seedlings planted with adult *Schizachyrium* did not differ in vigor or survival from other treatments without hosts or with seedling *Schizachyrium*, and died within 2 mo. No germination of *Schwalbea*



Pot 1
Pot 2
Pot 3
Pot 4
Pot 5
Pot 6
Pot 7
Pot 8
Pot 9
Number of Seedlings
0
10
20
30
40
50
Number of Days in Greenhouse
0
10
20
30
40
50

americana was observed from seed overwintered with adult *Schizachyrium.*

Seedlings with Pine Barrens plants. The wet-cold treated seedlings of *Schwalbea americana* were observed to have germinated on February 21, 1995, and transplantation after 7 days resulted in 200–300 established seedlings. By March 23, several plants were observed developing a set of leaves past the initial cotyledons. Seedlings persisted in the pots at a steady state, with negligible growth or mortality. Numbers of seedlings in each pot were recorded beginning April 3 (Figure 1). The rate of mortality remained low over the next 2.5 weeks. As the rate of mortality started to increase, transplantation from pots to the field was initiated. No differences in seedling mortality or growth based upon host plants in the pots were apparent (Figure 1). A firm association could not be made between host species and seedling survival due to insufficient replication and high mortality of seedlings.

No germination was observed from seeds stored dry-cold after the addition of water at room temperature or in a 4°C cold treatment. Of seeds stored dry-cold and incubated in fluctuating temperatures, only 2 of 80 seeds germinated 1 mo. later.

Reintroduction of seedlings. The number of seedlings remaining in each transplant to the field decreased to 0 in most cases from 18–45 days after time of transplantation (Figure 2). By 70 days only 5 seedlings remained viable. No specific host plant produced longer persistence of seedlings or greater growth (Figure 2). Most seedlings from the first reintroduction (Pots 1–3) died within 18 days but some in Pot 2 persisted as long as the

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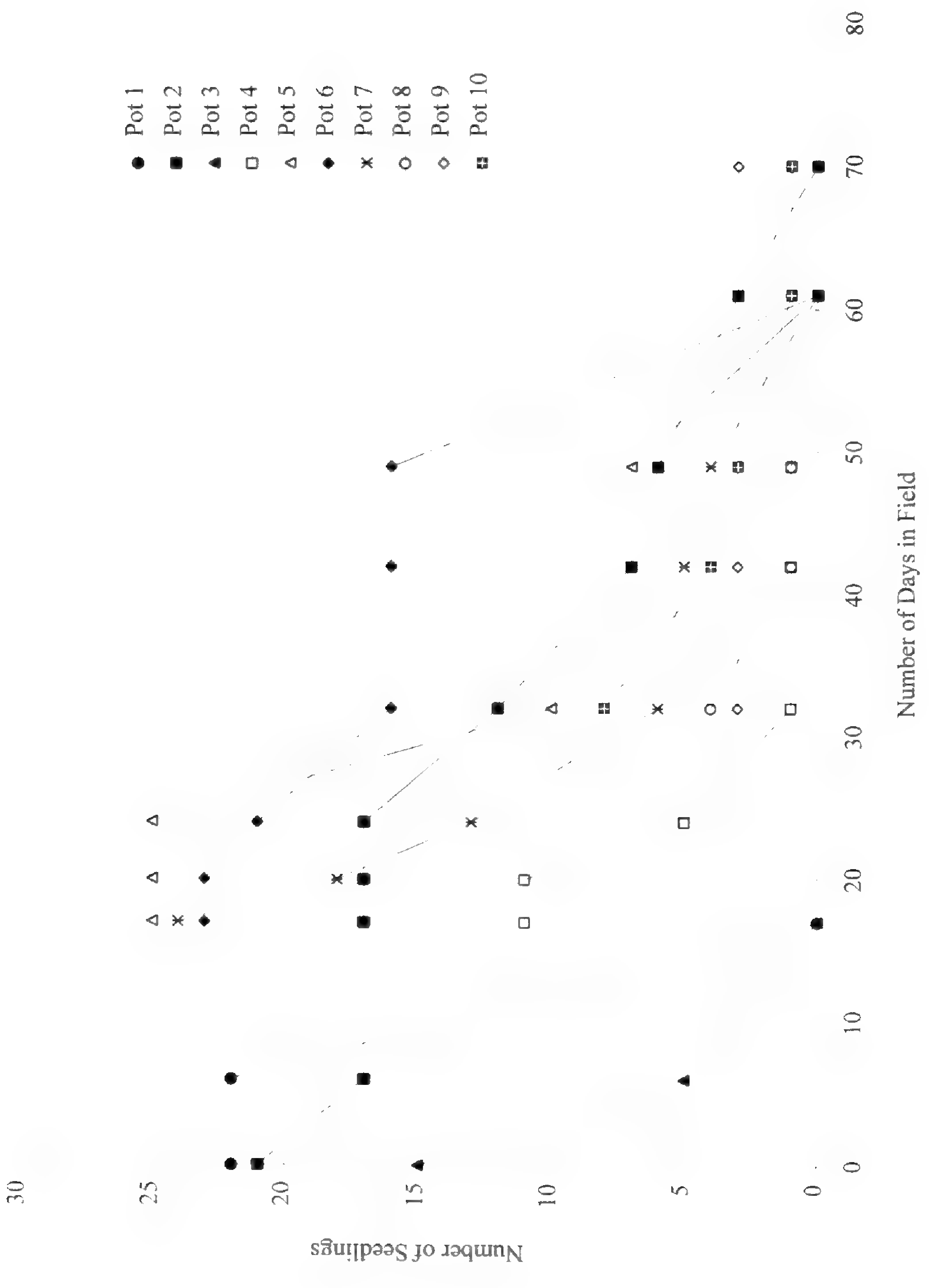
Figure 1. Number of seedlings over time in each of nine pots located in a greenhouse. The last data point for each pot indicates the time at which seedlings were transplanted to field conditions. Day 0 indicates the time at which the collection of mortality data was initiated, on April 3. Species in each pot were as follows: *Pinus rigida* (pitch pine; Pot #1), *Vaccinium corymbosum* (high bush blueberry; Pots #2, 4), *Gaultheria procumbens* (teaberry; Pot #3), *Ilex glabra* (inkberry; Pots #5, 6), *Quercus marilandica* (blackjack oak; Pot #7), *Prunus serotina* (black cherry; Pot #8), and *Gaylussacia dumosa* (black huckleberry; Pot #9).


Number of Seedlings
0
5
10
15
20
25
30
Number of Days in Field
0
10
20
30
40
50
60
70
80
● Pot 1
■ Pot 2
▲ Pot 3
□ Pot 4
△ Pot 5
◆ Pot 6
× Pot 7
○ Pot 8
◇ Pot 9
⊞ Pot 10

seedlings from the second reintroduction (Figure 2). Time of reintroduction affected the initial size of seedlings, with later reintroductions composed of larger seedlings. Only the third reintroduction (Pots 8–10) produced seedlings which persisted until the end of the growing season (Figure 2). Most of these seedlings were initially larger in size when transplanted than previous seedlings, and included four seedlings with leaf spans of 1.2–1.7 cm and heights of 1.0–1.4 cm. Other seedlings were usually less than 1 cm in height and width at time of reintroduction.

DISCUSSION

The greater germination of cold-stratified seeds found for *Schwalbea americana* is common among temperate species and has been found for other hemiparasitic species (Baskin et al. 1991; Masselink 1980). The low germination of dry-cold treated seed is presumed to be due to lack of sufficient conditions to break physiological dormancy. Dormant seeds would have the ability to form a long-term seed bank for *S. americana.* However, the firm but small and fragile seeds are easily damaged, which may limit long-term seed banking ability. The small seed size of many obligate root parasites has been suggested by Musselman and Mann (1977) to be an adaptation for filtering through vegetation and litter to germinate as close as possible to a host plant. Seeds in this study were germinated in the absence of root exudates from potential host plants. Root exudates have been found necessary for germination of some hemiparasites such as *Striga* spp. and *Orobanche minor* J.E. Smith (Sunderland 1960; Vallance 1950). Numerous other hemiparasites, however, are able to germinate without chemical interactions with host roots (Baskin et

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Figure 2. Number of seedlings over time in ten seedling and host plant transplants to field conditions. Transplants occurred at three time points, Days 0, 17, and 32. Pot transplants 9 and 10 each originate from greenhouse Pot 9, which was divided into two sections at the time of transplant. Species in each greenhouse pot were as follows: *Pinus rigida* (pitch pine; Pot #1), *Vaccinium corymbosum* (high bush blueberry; Pots #2, 4), *Gaultheria procumbens* (teaberry; Pot #3), *Ilex glabra* (inkberry; Pots #5, 6), *Quercus marilandica* (blackjack oak; Pot #7), *Prunus serotina* (black cherry; Pot #8), and *Gaylussacia dumosa* (black huckleberry; Pot #9).

al. 1991; King 1989; Masselink 1980; Sahai and Shivanna 1985; Vallance 1951, 1952).

The effect of hemiparasitism on seedling establishment of *Schwalbea americana* is not known. The presence of haustorial connections between *S. americana* seedlings and potential host plants was not investigated due to the limited number of seedlings and host plants. The seedlings of *S. americana* in this study may or may not have established haustorial connections with host plants. Differences in survival or growth of seedlings could not be attributed to specific host plants (Figures 1 and 2). The presence of young seedlings of *Schizachyrium scoparium* also was not successful in stimulating growth of *Schwalbea.* Seedlings growing with woody Pine Barrens species achieved slightly greater size than those growing with *Schizachyrium.* However, this may be due to the use of natural soil instead of artificial soil mixtures rather than to differences among the host species. The general lack of growth of seedlings of *Schwalbea* implies that haustorial connections may be necessary at an early developmental stage. For some other hemiparasitic species, fertilization has been known to replace the necessity for a host species (Lackney 1981; Mann and Musselman 1981). Connections to host plants were observed in the successful cultivation of another rare hemiparasite, the annual *Agalinis auriculata* (Michx.) S. F. Blake [as *Tomanthera auriculata* (Michx.) Raf.], which was grown with host plants in greenhouse studies (Cunningham and Parr 1990). However, preliminary efforts to grow *T. auriculata* resulted in small seedlings which eventually withered and died, similar to many seedlings of *Schwalbea* in this study (Cunningham and Parr 1990).

Seedling establishment of *Schwalbea americana* is believed to take place in early spring when late frosts may have a negative effect on survival. The ability of seeds to germinate at low temperatures in this study indicates that early seedlings may be produced, which then would be susceptible to temperature related mortality. Transplanted seedlings were observed to turn a reddish color after being put into the field and exposed to temperatures ranging down to 5°C. Leaves of adult *S. americana* plants are purple tinged early in the spring and turn greener as the season progresses and temperatures rise.

The increased greenhouse cultivation period required to produce larger seedlings resulted in greater growth but high mortality

(Figure 1). However, these larger seedlings were more successful in becoming established in the field and long-term survival is more likely for these seedlings (Figure 2). The success of future transplants will be dependent upon the development of improved greenhouse techniques. The primary difficulty in growing plants in the greenhouse to a size which would be likely to survive transplantation to the field may lie in re-creating fluctuating moisture conditions common in ecotonal areas. The seedlings in this study were maintained in continuously moist rather than fluctuating conditions, and were maintained in low light to prevent desiccation. Continued experimentation with artificial growing conditions for *Schwalbea americana* seedlings should concentrate upon growing larger plants in a greenhouse or a growth chamber, in higher light, in natural soils with fluctuating moisture levels, and in the presence of host plants.

The results of this study support the hypothesis that poor seedling establishment and survival contribute to the rarity of this species. After very high germination of seed, survival was poor both in artificial greenhouse conditions and after transplantation to suitable habitat (Figures 1 and 2). This corresponds with the lack of observation of seedlings in the field and the poor colonization of new habitat by *Schwalbea americana.* As habitat destruction continues through fire suppression, succession, or outright destruction, this species is likely to continue to decline (U.S. Fish and Wildlife Service 1992). The development of improved methods for the propagation and transplantation of *S. americana* may be critical to the persistence of the species, and will increase options for recovery through population expansion and reintroduction.

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CHROMOSOME NUMBERS OF NEW *ULMUS* (ELM) TAXA INTRODUCED FROM CHINA

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ABSTRACT. Diploid chromosome counts ($2x = 2n = 28$) are reported for the first time in 12 elm taxa newly introduced into the United States from China. These are *Ulmus bergmanniana, U. bergmanniana* var. *lasiophylla, U. castaneifolia, U. changii, U. chenmoui, U. elongata, U. gaussenii, U. glaucescens, U. lamellosa, U. lanceaefolia, U. szechuanica,* and *U. taihangshanensis.*

Key Words: cytology, cytotaxonomy

The most recent account of chromosome numbers in *Ulmus* (Santamour 1993) showed that 24 taxa were diploid ($2x = 2n = 28$) and that only *U. americana* L. (American elm) was a tetraploid ($4x = 2n = 56$). The tetraploid nature of *U. americana* may be a barrier to interspecific hybridization with diploid species but Santamour (1970) reported on a natural triploid hybrid between *U. americana* and *U. pumila* L. A natural triploid involving and resembling *U. americana* was given the cultivar name 'Jefferson' by Sherald et al. (1994) and another similar natural triploid (called "Washington") was reported by Santamour and Bentz (1995). Although Santamour (1972) was unsuccessful in crossing the diploid, fall-flowering Chinese elm (*U. parvifolia* Jacq.) with *U. americana,* Smalley et al. (1993) reported the creation of numerous hybrids between these two taxa, but no chromosome counts on these progenies have been made. Thus, while it may not be impossible to utilize diploid taxa in hybridization programs with the tetraploid American elm, some difficulties may be encountered and these may be related to chromosome numbers.

In recent years, a number of "new" elm taxa have been introduced into the United States from China, and the junior author has been most active in this introduction program. Fu (1980) listed 24 species and four varieties of *Ulmus* growing in China, of which 24 taxa were native to that country. Of these taxa, diploid chromosome counts have been reported for *U. davidiana* Planch., *U. glaucescens* var. *lasiocarpa* Rehd., *U. laciniata* (Trautv.) Mayr, *U. macrocarpa* Hance, *U. parvifolia* and *U. pumila.* Fu (1980) did not recognize *U. japonica* (Rehd.) Sarg. or *U. wilsoniana* Schneid., but placed both in the synonymy of *U. davidiana* var. *japonica* (Rehd.) Nakai, along with *U. propinqua* Koidz. Thus, it is likely that any taxon in the *U. davidiana* complex would be diploid. Still, there remained a rather large number of Chinese taxa that were virtually unknown in the United States.

Some of these taxa may have traits that could be important in breeding programs and *Ulmus szechuanica* has already been shown to be highly resistant to feeding by the elm leaf beetle (Miller and Ware 1994). Resistance of several other taxa to insects and diseases is suspected but many accessions have not been widely tested because they are still relatively young. Likewise, most introductions have not yet reached sexual maturity and thus have not been available for experiments in interspecific hybridization.

Preliminary to such experimentation, it would be desirable to know the chromosome numbers of these taxa. If any of these new Chinese introductions proved to be tetraploid, they might be more crossable with American elm. Therefore, we have made chromosome counts on all of these taxa, none of which, to our knowledge, have been reported previously.

All of the taxa except *Ulmus taihangshanensis* are listed in Fu (1980). In his 1980 paper, Fu recognized ca. 40 species of *Ulmus* and outlined a new infrageneric classification for the genus. The subgeneric category was indicated only for eight of the species, however. For instance, The Chinese *U. elongata* was placed in series *Mexicanae* L. G. Fu with two North American species, but Fu failed to identify those additional species. *Ulmus lanceaefolia,* the only other species treated here, was considered the sole taxon in series *Lanceaefoliae* Schneid. Such classification may have little bearing on sexual compatibilities however, since numerous hybrids have been made between diploid species classified in different sections and series (Santamour 1972).

MATERIALS AND METHODS

All seed collections were accessioned and germinated at the Morton Arboretum. Potted seedlings were grown at the U.S. National Arboretum and chromosome numbers determined at mitotic metaphase in root tips prepared according to the protocols of Snow (1955). At least three unambiguous counts were made on each of two seedlings of each taxon. Herbarium specimens showing vegetative, flowering, and fruiting characteristics will be made as the trees mature at the Morton Arboretum and will be deposited at NA and MOR.

RESULTS

Diploid ($2x = 2n = 28$) chromosome counts were made for each of the following taxa, listed in alphabetical order, with available information on origin. All of the accession numbers are those used at the Morton Arboretum: *Ulmus bergmanniana* Schneid. (R 94-59) Yunnan Province; *U. bergmanniana* var. *lasiophylla* Schneid. (R 94-22) no source data; *U. castaneifolia* Hemsl. (R 94-11) no source data; *U. changii* Cheng (R 94-23) no source data; *U. chenmoui* Cheng (R 93-117) Anhui Province; *U. elongata* L. G. Fu & C. S. Ding (R 94-6) Zhejiang Province; *U. gaussenii* Cheng (R 94-8) Anhui Province; *U. glaucescens* Franch. (R 93-123) Shanxi Province; *U. lamellosa* C. Wang & S. L. Chang ex L. G. Fu (R 93-128) Hebei Province; *U. lanceaefolia* Roxb. ex Wall. (R 95-22) Yunnan Province; *U. szechuanica* Fang (R 94-2) no source data; *U. taihangshanensis* S. Y. Wang (R 95-21) Hainan Province.

DISCUSSION

These 12 new diploid chromosome counts indicate that the tetraploid American elm may be truly unique in the genus *Ulmus.* As far as we know, there are probably only five or six Chinese taxa that have not been studied cytologically. Although it is unlikely that any of these taxa would be tetraploid, and perhaps be more crossable with American elm, we will endeavor to obtain seed of these taxa in the near future.

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NATURAL HYBRIDIZATION IN THE GENUS *CIRSIUM*: *C. ALTISSIMUM* × *C. DISCOLOR*—CYTOLOGICAL AND MORPHOLOGICAL EVIDENCE

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ABSTRACT. Cytological and morphological evidence indicates natural hybridization between *Cirsium altissimum* and *C. discolor.* It is postulated that the high degree of hybrid sterility is correlated with meiotic abnormalities.

Key Words: *Cirsium altissimum, Cirsium discolor,* hybridization, hybrid sterility, Nebraska.

In the genus *Cirsium* (family Asteraceae, tribe Cardueae), variability and intergradation of diagnostic characters make morphological circumscription of many species challenging and difficult. The difficulty is partly explained by the occasional breakdown of sterility barriers between closely related species, thus permitting interspecific hybridization (Ownbey 1951, 1964; Davidson 1963; Bloom 1977; Dabydeen 1987).

Cirsium altissimum (L.) Spreng. and *C. discolor* (Muhl.) Spreng. are two biennial, sympatric species sharing similar mesophytic habitats within an extensive eastern North American range. Both species have a similar extended flowering phenology; thus reproductive structures at all stages of development ranging from immature floral buds to mature capitula are usually observed simultaneously on the same plant. It is generally believed that members of the genus *Cirsium* employ both autogamous and allogamous reproductive strategies.

Petrak (1917) placed *Cirsium altissimum* and *C. discolor* in his series *Altissima* to reflect close affinity. A closer relationship is seen in Gray's (1884) treatment of *discolor* as a variety of *C. altissimum* (as *Cnicus altissimum*).

Phenotypically, *Cirsium altissimum* and *C. discolor* are easily distinguishable and are separated primarily by the degree of lobing or indentation of the leaves. According to Frankton and Moore (1963), in *C. discolor* the "cauline leaves are deeply pinnatifid into narrow linear-lanceolate lobes," and in *C. altissimum* the "cauline leaves are entire or subentire with shallowly sinuate lobes."

Cytologically, in *Cirsium altissimum* and *C. discolor* chromosome numbers have become extremely reliable in the determination of the species, even though supernumerary chromosomes have been observed infrequently in *C. discolor* (Frankton and Moore 1963; Ownbey and Hsi 1963; Bloom 1977).

Frankton and Moore (1963) measured somatic chromosome lengths of *Cirsium discolor* ($2n = 20$) and *C. altissimum* ($2n = 18$) and found no significant differences between the total chromatin lengths of these taxa nor in the size ranges of the individual chromosomes. Apparently, both genotypes contain the same amount of material. They argued that the reduction in the chromosome number of *C. altissimum* may have been accomplished by translocation of portions of two chromosomes to the eighteen surviving chromosomes.

Bloom (1977) mentioned that his results of initial studies (unpublished) of *Cirsium altissimum* and *C. discolor* hybrids showed that chromosomal arrangement of these two species differ by a minimum of four reciprocal translocations and one paracentric inversion.

Observation of a *Cirsium* plant with an unusual leaf lobing pattern (in Nebraska just across the Missouri River from a mixed population of *C. altissimum* and *C. discolor* plants in Iowa) prompted this investigation. The mixed population was growing in an area approximately thirty by ten feet on top of the Missouri River bank. The area was lightly vegetated, mostly with small shrubs and herbs. Beyond the riverbank patches of tall shrubs and a few small trees dominated in what appeared to be abandoned pasture lands.

In *Cirsium altissimum* and *C. discolor,* reports based on analyses of morphological variation have revealed evidence of natural hybridization (Davidson 1963; Ownbey 1964). To this author's knowledge, no cytological evidence supporting spontaneous hybridization between *C. altissimum* and *C. discolor* exists in the literature. Thus, this paper is the first report of chromosomal evidence of natural hybridization between these two taxa.

MATERIALS AND METHODS

In July 1990, a plant with features similar to *Cirsium altissimum* and *C. discolor,* yet phenotypically different from both taxa, was observed growing in a depression on the roadside riverbank. This site was located at Nebraska City, Otoe County, Nebraska, seventy-five yards west of the Missouri River interstate bridge linking Iowa.

This plant was one of a few plants left intact after a recent brush-cut. It was observed that dried-up remnants of additional *Cirsium* plants formed part of the debris, but no other live *Cirsium* plants were observed in the vicinity of the putative hybrid site. However, on the Iowa side of the riverbank about thirty yards across the river obliquely opposite the hybrid site, a mixed population of nine *C. altissimum* and seven *C. discolor* plants grew. No plants phenotypically different from the two species were found at this site. The occurrence of a mixed *C. altissimum* and *C. discolor* population in such close proximity to the putative hybrid site led to speculation that the brush-cut *Cirsium* plants could have been members of either or both of these taxa and/or their derivatives.

The putative hybrid specimen was sampled in addition to specimens of the Iowa *Cirsium altissimum* and *C. discolor* mixed population. Two immature capitula and twenty-seven cypselae were collected from among aborted ovaries of mature capitula of the suspected hybrid plant. Seven immature capitula and fifty-six cypselae from three mature capitula were sampled from *C. altissimum,* and five immature capitula and thirty-three cypselae from two mature capitula were harvested from *C. discolor.* Capitula were bisected and fixed in a mixture of 100% ethyl alcohol and glacial acetic acid (3:1, V/V). Cypselae were germinated in a growth chamber to obtain root tips for chromosome counts.

Microsporocytes were stained according to the method of Feulgen-Rossenbach (1924), and root tips according to the method of Snow (1963). Chromosome spread was achieved by the application of a gentle but firm pressure on the stained specimens by rolling the thumb once over the coverslip. Chromosomes were photographed using an American Optical microscope-camera system with 5 × 97 ocular-objective combination.

Data for morphological comparison were obtained from measurements of nineteen characters (Table 1). The mean values of 10 measurements for each character of each plant were used. Voucher specimens (branches) of *Cirsium discolor, C. altissimum* and their putative hybrid are deposited at NEB.

Cirsium discolor: IOWA, Freemont Co., riverbank, 50 yards west of the Missouri River interstate bridge linking Nebraska City, 27 Jul 1990, *Dabydeen 9001, 9002, 9003* (NEB).

Cirsium altissimum: IOWA, Freemont Co., riverbank, 50 yards west of the Missouri River interstate bridge linking Nebraska City, 27 Jul 1990, *Dabydeen 9004, 9005, 9006* (NEB).

Cirsium altissimum × *Cirsium discolor:* NEBRASKA, Otoe Co., roadside riverbank, 75 yards west of the Missouri River interstate bridge linking Iowa, 27 Jul 1990, *Dabydeen 9007* (NEB).

RESULTS

Cirsium altissimum has a chromosome number of $2n = 18$ (Figures 1a and 1f). In *C. discolor,* the chromosome complement is $2n = 20$ (Figures 1b and 1c). The suspected hybrid individual has a complement of 19 chromosomes (Figure 1d). All chromosome complements observed at mitotic metaphase are composed of metacentric to submetacentric chromosomes.

In most florets of the two immature capitula of the suspected hybrid, microsporogenesis had been completed already, and only a few anthers with microsporocytes at two stages of meiosis were found. Meiotic analysis of the putative hybrid specimens revealed that some of the bivalents were closely associated on an end-to-end basis and illustrated chain formation. In Figure 2g, a chain of six chromosomes, six bivalents, and one univalent (arrow) are shown. Microsporogenesis was not normal; at least one of the four microspore nuclei appeared relatively small (Figure 1e). Only three of twenty-seven (11%) cypselae of suspected hybrid origin germinated; cypselae of both *Cirsium altissimum* and *C. discolor* had 100% germination.

Measurements of nineteen characters (Table 1) of the suspected hybrid individual showed that fourteen were intermediate compared to the parental types. Three characters were approximately the same as either parental type, one character was larger, and one smaller than either of the parental types.

DISCUSSION

In interspecific hybridization events, hybrid phenotypes often express morphological intermediacy of many parental characters. In the suspected *Cirsium* hybrid specimen, fourteen characters, including four leaf features, were intermediate between those of

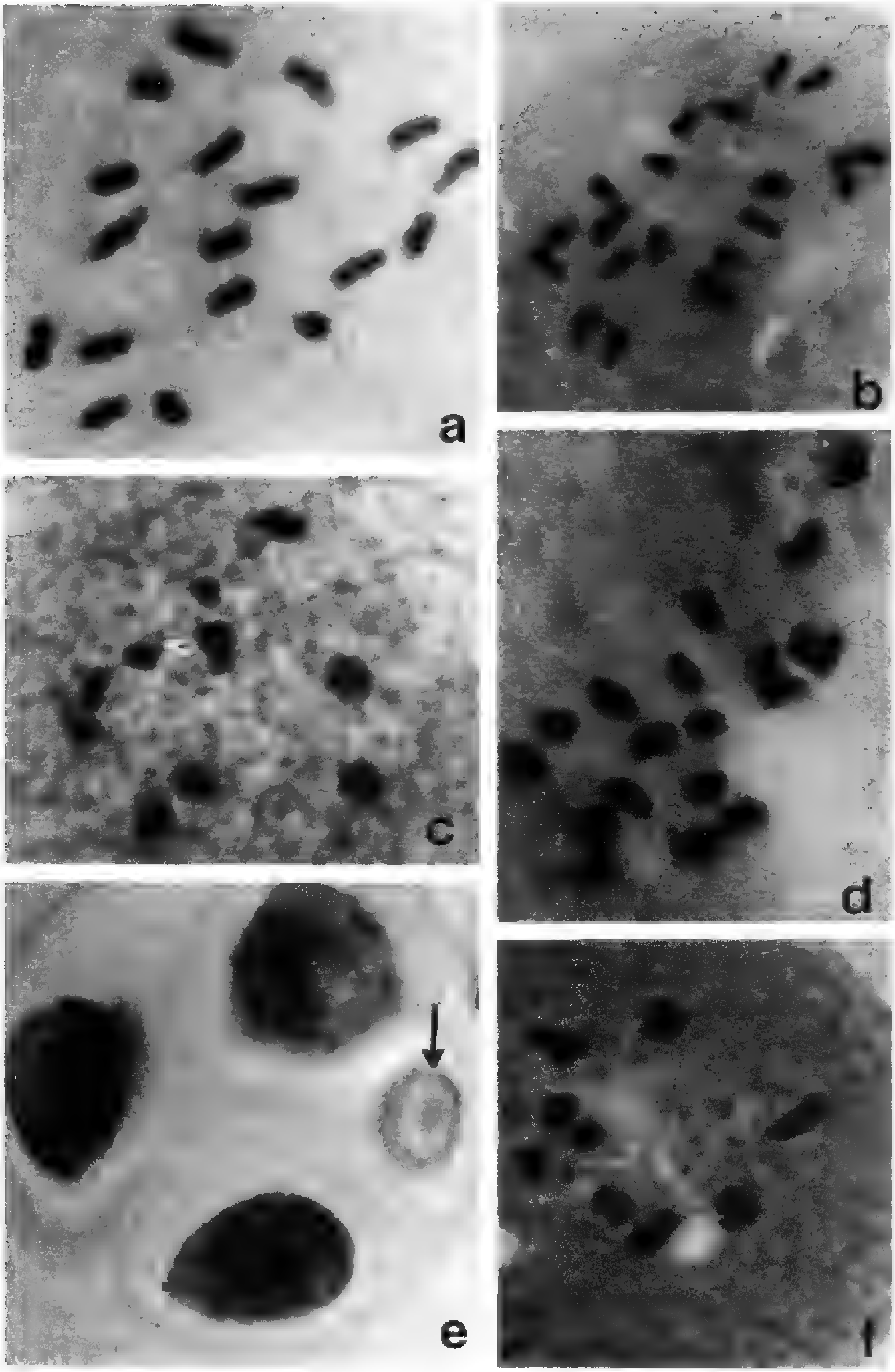

Figure 1. Photomicrographs of mitotic and meiotic chromosome complements of the genus *Cirsium*, X 800 unless otherwise stated. a. *C. altissimum*: mitotic metaphase, $2n = 18$. b. *C. discolor*: mitotic metaphase, $2n = 20$. c. *C. discolor* microsporocyte: metaphase I, 10 bivalents. d. *C. altissimum* × *C. discolor*: mitotic metaphase, $2n = 19$. e. *C. altissimum* × *C. discolor*: abnormal microsporogenesis and micronucleus (arrow) X 300. f. *C. altissimum* microsporocyte: metaphase I, 9 bivalents.

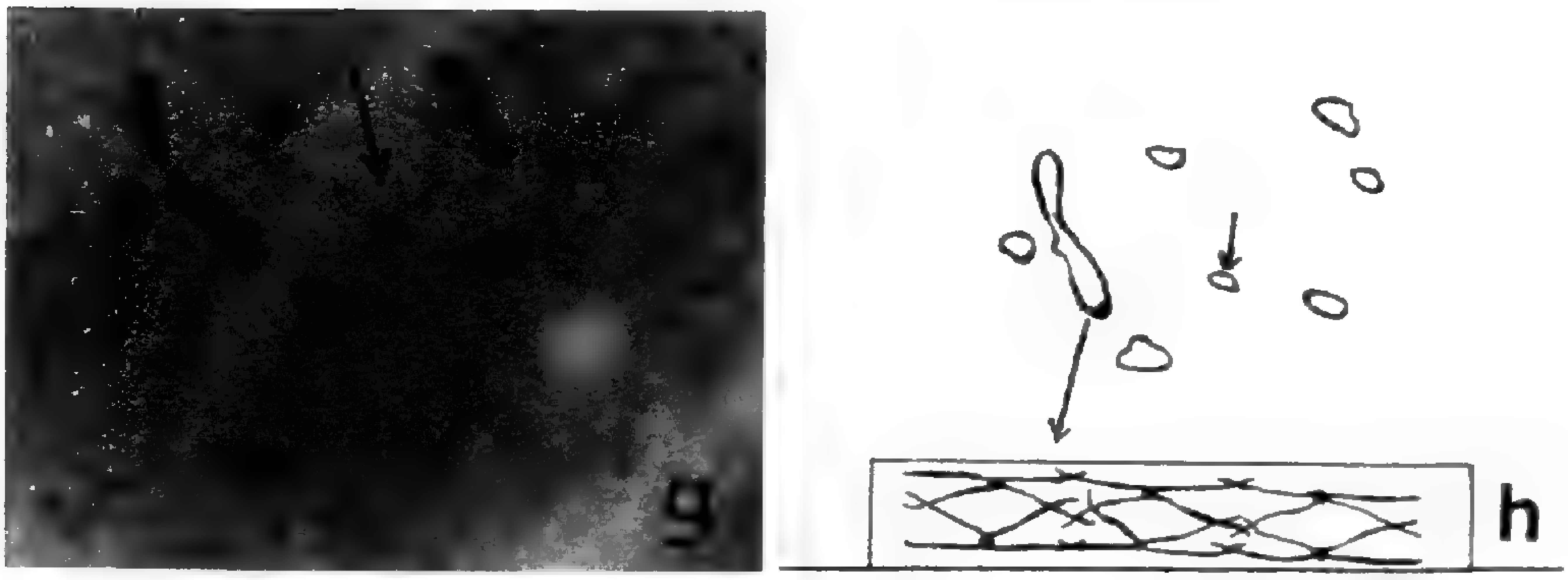

Figure 2. A photomicrograph (×800) and an interpretive drawing of the meiotic chromosome complement of the genus *Cirsium*. g. *C. altissimum* × *C. discolor* microsporocyte: metaphase I showing 1 chain of 3 bivalents, 6 bivalents, 1 univalent (arrow). h. A drawing of the photomicrograph highlighting the chain to illustrate its formation through reciprocal translocations among the 3 bivalents (long arrow).

Table 1. Comparison of character measurements of *Cirsium altissimum*, *C. discolor*, and their hybrid derivative (all measurements in millimeters).

	C. altissimum		*C. altissimum* × *C. discolor*		*C. discolor*	
Characters	Mean	S.E.	Mean	S.E.	Mean	S.E.
Involucre: length	29.7	0.48	28.2	0.85	26.8	1.01
width	21.6	0.85	22.3	0.85	23.7	1.03
Phyllaries: no. of rows	12.3	0.15	11.5	0.25	11.2	0.33
spine length	3.7	0.15	3.7	0.15	4.0	0.26
inner: length	26.1	0.53	24.3	0.47	22.4	0.70
inner: width	1.7	0.09	1.5	0.13	1.5	0.17
Pappus length	26.1	0.44	25.1	0.50	24.7	0.75
Corolla: lobe length	8.6	0.22	8.0	0.26	8.0	0.33
tube length	9.1	0.18	8.2	0.20	6.0	0.26
Stamen length	17.5	0.36	16.4	0.40	13.3	0.34
Stigma length	6.1	0.14	6.1	0.23	5.0	0.29
Style length	32.9	0.78	32.3	0.54	31.8	1.33
Leaf: length	100.8	3.78	103.4	1.96	112.5	3.57
width	18.4	1.30	16.4	0.62	15.4	0.62
lobe length	18.5	1.04	20.2	0.90	22.0	0.77
lobe base width	11.3	0.82	9.3	0.42	10.2	0.49
spine length	4.4	0.18	5.0	0.26	4.8	0.29
Internode length	22.3	1.27	21.1	1.20	20.6	1.11
Flower length	39.0	0.84	39.0	1.62	36.0	1.33

C. altissimum and *C. discolor* (Table 1). Ownbey (1951) investigated *C. discolor, C. altissimum,* and their putative hybrid derivatives and determined that plants with intermediate leaf types were hybrids.

The diploid chromosome complement of $2n = 18$ in *Cirsium altissimum* has been reported previously and the number is regarded as stable (Frankton and Moore 1963; Ownbey and Hsi 1963; Johnson 1974). In *C. discolor,* a diploid chromosome number of $2n = 20$ has been determined (Frankton and Moore 1963; Ownbey and Hsi 1963; Bloom 1977). In this taxon, accessory chromosomes have been occasionally observed, but in a closely related congener, *C. muticum,* frequent observations of extra chromosomes have been reported (Frankton and Moore 1963).

Accessory chromosomes usually do not exert phenotypic influence. Thus, based on morphological data (Table 1) and also cytological features (Figures 1d and 2g), it seems very likely that the nineteen chromosomes observed in the putative hybrid specimen are products of interspecific hybridization between *Cirsium altissimum* and *C. discolor.* These nineteen chromosomes, therefore, likely do not constitute a genotype of a *C. discolor* specimen with a supernumerary chromosome. It is probable that 10 chromosomes must have come from *C. discolor* and 9 chromosomes from *C. altissimum.*

The observation of a chain of six chromosomes, six bivalents, and one univalent (Figure 2g) during meiosis of suspected hybrid microsporocytes suggested that 9 chromosomes of *Cirsium altissimum* and 9 chromosomes of *C. discolor* are homologous or homeologous, and that reciprocal translocation is involved in the formation of the meiotic configuration. The univalent must have come from *C. discolor.* Similar cytological features (e.g., chain formation) were observed in microsporogenesis of interspecific hybrids of other *Cirsium* taxa (Dabydeen 1987; Bloom 1977).

The formation of micronuclei during microsporogenesis was probably due to chromosomal deficiency arising from meiotic aberration. Similar micronuclei formation observed in microsporogenesis of *Cirsium flodmanii* × *C. undulatum* hybrids was attributed to lagging chromosomal materials (Dabydeen 1987).

The failure of many ovaries of the suspected hybrid plant to mature may be due to a lack of fertilization or some genetic aberration attributable to hybridity. There was no insect damage or any other external evidence of damage that would prevent fruit formation. Many of the aborted ovaries were shriveled or extremely flattened. The extremely low rate of viability of cypselae may be due to hybridity. A high degree of sterility of *Cirsium* hybrids has been reported (Ownbey 1951, 1964; Bloom 1977; Dabydeen 1987). Bloom (1977) attributed the high degree of sterility of *Cirsium* hybrids to meiotic irregularities arising from chromosomal rearrangements.

The absence of hybrids at the site of the mixed population of *Cirsium discolor* and *C. altissimum* is not expected. Hybridization events have occurred in many instances where these two taxa grew in close proximity to one another (Ownbey 1964). Apparently, at this site, unknown factors operated to prevent hybridization and/or the establishment of hybrid progenies.

It is suggested that the rather small size and possible recent establishment of the mixed population may have contributed to the absence of hybrids. At the Nebraska site, it is highly possible that the brush-cut may have destroyed a well-established mixed population, including additional hybrids.

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TALL WHEATGRASS, *ELYMUS ELONGATUS* SUBSP. *PONTICUS*, IN NOVA SCOTIA

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ABSTRACT. The distribution of Tall Wheatgrass (*Elymus elongatus* subsp. *ponticus*) in Nova Scotia is summarized and a planted population along a roadside in Quebec is reported.

Key Words: Tall Wheatgrass, *Agropyron elongatum*, *Elymus elongatus* subsp. *ponticus*, Nova Scotia, Quebec

Tall Wheatgrass is a name applied to a decaploid ($2n = 70$) grass (Asay and Jensen 1996) introduced to North America from Turkey in about 1909 (Weintraub 1953). About half a dozen registered cultivars have been developed from Asia Minor and southwest Asian sources (Asay 1995). Several cultivars are popular in western North America as forage for use on saline and alkaline soils (Asay 1995). Its tolerance of high soil salinity is a characteristic which also has led to its specialized use in soil conservation and revegetation projects where less tolerant species fare poorly. The species has become naturalized in Ontario where it is spreading along highways which receive applications of deicing salt during the winter months (Webber et al. 1985; Oldham et al. 1996). It also has been observed along highways in Quebec as a roadside planting in areas receiving large amounts of deicing salt.

The grass tribe to which Tall Wheatgrass belongs, the Triticeae, is the subject of much taxonomic debate, especially at the generic level (cf. Tucker 1996). The taxonomy and nomenclature within the *Elymus elongatus* complex is also controversial. Several species segregates have been proposed in combination with various generic segregates. Tall Wheatgrass cultivars ($2n = 70$) were released initially under the name *Agropyron elongatum.* The genus *Agropyron* is now generally restricted in application to a small group of Asian taxa related to Crested Wheatgrass (*Agropyron cristatum* L.). The epithet *elongatum* is attached by some workers to diploid (and tetraploid) populations, while decaploid (and oc-

Table 1. Names applied to Tall Wheatgrass ($2n = 70$), with references.

Agropyron elongatum (Host) P. Beauv.	Cronquist et al. 1977
Elymus elongatus (Host) Runemark subsp. *ponticus* (Podp.) Melderis	Melderis 1980
Elytrigia elongata (Host) Nevski	Gleason and Cronquist 1991; Kartesz 1994
Elytrigia pontica (Podp.) Holub	Jarvie 1992
Lophopyrum elongatum (Host) Á. Löve	Weber 1990
Lophopyrum ponticum (Podp.) Á. Löve	Löve 1984
Thinopyrum ponticum (Podp.) Barkworth & D. R. Dewey (invalid combination)	Barkworth and Dewey 1985

toploid) races are sometimes connected with the epithet *ponticum* (e.g., Dewey 1984; Löve 1984), either at specific or subspecific rank. Some authors, however, do not consider the various cytological races and slight morphological differences worthy of taxonomic recognition (e.g., Tsvelev 1984). Dvořák (1981) has shown that the decaploid plant contains an additional genome to that of the diploid form and recommended distinguishing it at the rank of species. Table 1 shows a list of some names that have been applied to Tall Wheatgrass, with selected references.

Oldham et al. (1996) first reported Tall Wheatgrass from Nova Scotia based on a collection from Hants County, where a single plant was detected in 1991. The earliest known herbarium specimen of Tall Wheatgrass, however, appears to be one taken along tidal reaches of the Hebert River, Cumberland County, in 1967. This latter specimen may be the basis for the comment by Roland and Smith (1969) that "other species [of *Agropyron*/*Elymus*] from western Canada have been planted on the running dykes and may possibly persist."

In October 1996 two additional populations of Tall Wheatgrass were detected in Hants County. One of these populations was found along a dyke and adjoining salt marsh near the mouth of the Kennetcook River. The other was found about 10 kilometers away at the site of a highway bridge over the St. Croix River and situated in an elevated position just above the reach of high tides. Presence of Tall Wheatgrass at these two sites may well represent persistence from old plantings designed to stabilize disturbed soils along dykes. These two populations are large, occurring along the river dykes and in adjoining salt marsh, old

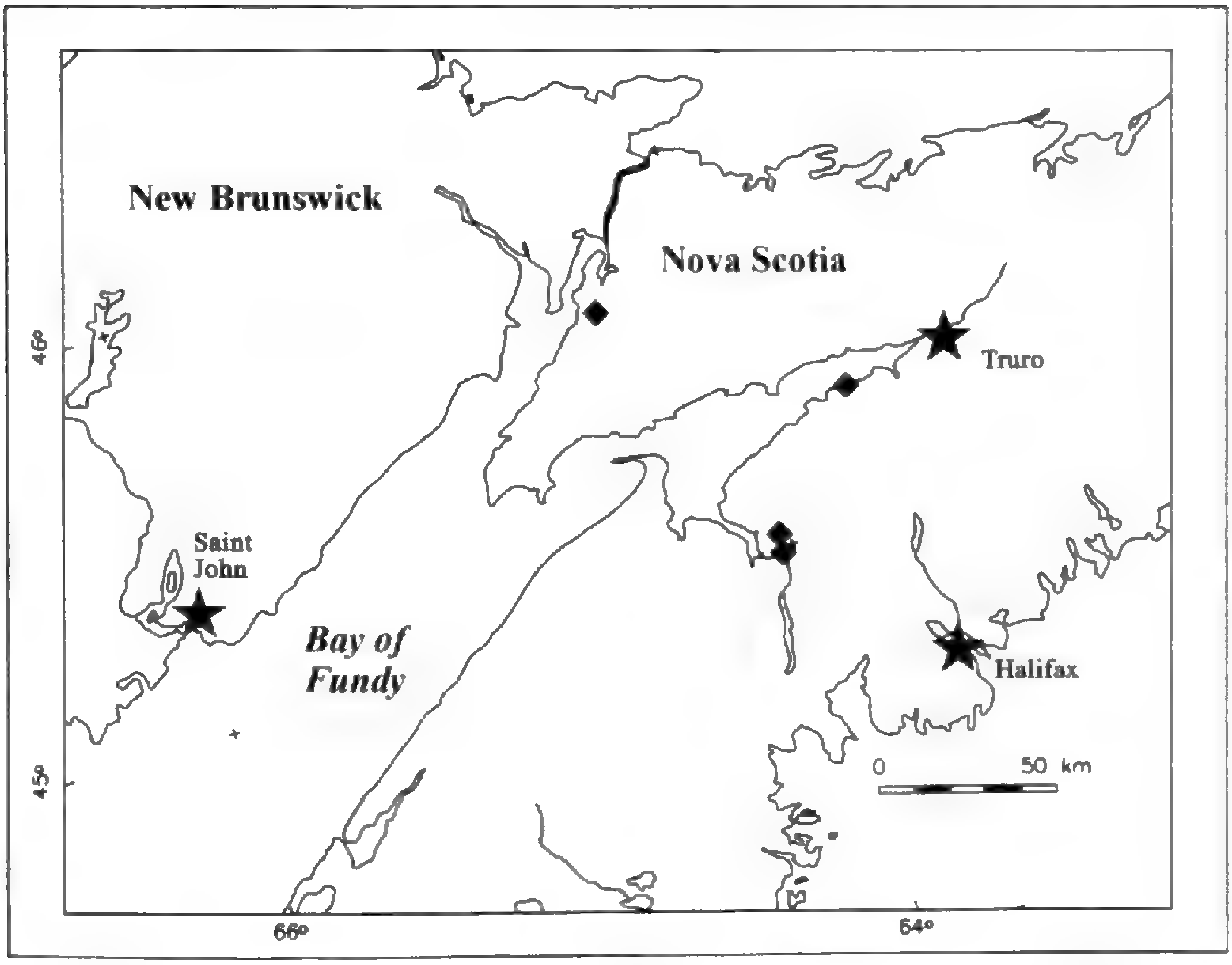

Figure 1. Distribution of Tall Wheatgrass in Nova Scotia, Canada. All known records for the map area are plotted as diamond symbols.

field and roadside habitats where it is unlikely to have been deliberately planted. Neither the provincial Department of Agriculture and Marketing (involved with dyke maintenance) nor the provincial Department of Transportation (involved with road maintenance) utilizes Tall Wheatgrass in revegetation seedings at this time.

All sites are in saline habitats, either on an upper beach or along the lower reaches of rivers within the influence of tides. Population size and the habitats occupied suggest that Tall Wheatgrass is persisting and spreading in saline soils of Nova Scotia. The distribution as known from herbarium specimens is mapped in Figure 1.

Morphological features distinguishing Tall Wheatgrass from other members of the Triticeae in eastern North America include: caespitose habit; glumes stiff, bluntly obtuse to truncate, about half as long as the spikelet; lemmas obtuse, glabrous, awnless (sometimes mucronate); and anthers 4–7 mm long. Keys to the genera and species of Triticeae, including Tall Wheatgrass, in the northeastern United States and southeastern Canada can be found in Gleason and Cronquist (1991). Excellent illustrations of Tall Wheatgrass, as well as other native and introduced relatives, can be found in Cronquist et al. (1977).

SPECIMEN CITATION. **Canada.** NOVA SCOTIA: Cumberland Co., River Hebert, waste ground along shore of tidal Hebert River, 30 Jul 1967, *Dore and Marchant 23079* (DAO); Hants Co., Andrews Public Beach and Picnic Area, Noel Shore, on S side of Cobequid Bay, dry open rocky ground W of boardwalk entrance to beach platform, one large clump with ca. 15 fruiting culms, 23 Aug 1991, *McLeod 91146* (DAO); Kennetcook River, 45°02′N, 64°02′W, along dyke and salt marsh near high tide level, large population along dyke and raised portions of marsh, 2 Oct 1996, *Darbyshire et al. 4695* (DAO, UTC); St. Croix River at Highway 14, 44°59′17″N, 64°02′30″W, large population along riverbank above high tide with *Spartina pectinata, Festuca rubra, Daucus carota,* 3 Oct 1996, *Darbyshire 4696* (DAO, UTC); QUEBEC: Gatineau Co., Masham Tp., Hwy 105 north of Rivière Lapêche, west of Wakefield, 45°38′N, 75°56′30″W, planted after construction along highway shoulder and ditch, large colony established about 4 years ago, 25 Aug 1996, *Darbyshire 4681* (DAO, UTC).

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RECOLLECTIONS[1]

RECOLLECTIONS OF BOTANIST GEORGE JONES GOODMAN[2]

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The recollections of botanists who experience the tenth decade of their lives in the twenty-first century will surely be different from those of George J. Goodman. His life began near the beginning of the twentieth century. He has witnessed immense changes: transportation from horse and buggy on dirt roads to luxury automobiles along interstate highways and from trains to supersonic jets and space shuttles; communication from operator-assisted telephones and telegraphs to E-mail on the Internet; information found in bound volumes of encyclopedias to that on compact discs; photography from box cameras to spy satellites; and meal preparation on wood-burning stoves to microwaves, to name but a few.

So when Janet Sullivan, the editor of *Rhodora,* contacted me about helping George Goodman compile his recollections, I decided it would be best for him to tell his own stories. What follows are the ones he shared with me.

I was born in Evanston, Wyoming, on November 5, 1904, and until I was five years old we lived on a ranch some twenty-five miles south of Evanston. This was a ranch that my Grandfather Goodman had acquired by homesteading in 1883.

My mother's arrival in Wyoming and in this country, for that matter, did not occur until 1886. Her father's aunt had come west and liked it so much that she wrote to her favorite nephew, my Grandfather Jones, to come to Utah. Grandfather Jones did not have enough money to bring his family from Wales, but he came

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[1] This is one in a series of articles appearing occasionally in *Rhodora.* Contributions will be invited by the Editor-in-Chief, and suggestions are welcome.

[2] Currently, George J. Goodman is Curator and Regents Professor Emeritus in the Department of Botany and Microbiology at the University of Oklahoma in Norman.

out to Salt Lake City, a city that was developing rapidly. His elderly aunt had bought considerable real estate there, and she would leave this property to my grandfather if he would join the Mormon Church. He refused, so, as a Mormon convert, she left all her holdings to the Church. My Grandfather Jones did like the West well enough to stay.

At the age of seven, following the death of his father, a coal miner in Wales, this boy, my grandfather, became the wage earner for his mother and sister. He went to work in the coal mines cleaning and filling miners' lamps. As a young man he was a member of the Royal Guard at Carnarvon Castle in Wales. In later years he would become the sheriff of Uinta County, Wyoming, a county which then extended from the state's southern boundary north to Yellowstone Park. This Charlemagne of a man handled these slightly over 200 miles on saddle horse. He was a Welsh giant, 6′2″, which in those days was pretty large. His friends would all greet him with their hands behind them to avoid his handshake.

In 1886 he had enough money to bring his family over from Wales. My Grandmother Jones and their four children—a son and three daughters, one of whom would become my mother—arrived in New York Harbor where the Statue of Liberty was not yet completed. So, as you can see, half of me is a first-generation American. Coincidentally, I went to the New York Botanical Garden in 1986 to do some research, and that summer the 100th anniversary of the Statue of Liberty was celebrated.

Soon after my parents, Arthur and Elizabeth, were married and living on the ranch a survey was being done in the area. The surveyors stayed for a while at the ranch before heading south to the Uintah Mountains, where the sextant they were using was accidentally knocked over and broken. One of the surveyors recalled that the hair of "that young Mrs. Goodman" was the color and texture they would need to replace the crosshairs in the sextant. He rode back nearly a day's ride to the ranch where he asked my mother if he could have a couple of strands of hair to repair the sextant. As the story goes, she laughed and just reached up and pulled out a few strands and rolled them up and gave them to him. He took them back and fixed the sextant. When the survey was completed, one of the mountains had been named Elizabeth Mountain! It bears her name to this day.

My parents sold the first ranch and moved to Buhl, Idaho, a new, tiny, little town not far from Twin Falls. We lived there for two years. That's where I attended the first and second grades in 1910 and 1911. Then we came back to Evanston in 1912 where I finished my public school education. I graduated from high school in 1922. At that time few people from Evanston went on to college. Only the men who planned to be doctors, lawyers, engineers, or ministers went. I had no plans to be any of these, so I got a job. In fact, I tried several jobs.

The first summer out of high school I worked at the Guild Ranch which was about thirty miles east of Evanston. I knew a little about ranching as I had worked on Mr. Newton's ranch out of Ft. Bridger one summer during high school. Then I returned to Evanston, and my next job was on a ranch half way to Ogden near Castle Rock, Utah. I worked there for just a few months and came back to Evanston where I worked next at the Wright Drug Store. I had worked at the Evanston Drug Store during my high school years. The next summer I worked with a small outfit drilling oil wells.

Then there was a job with the Uinta Mill and Elevator Company where I filled sacks with grain. I guess it was about that time that Uncle Lyman roomed at our house. He was a railroad engineer whose run was between Evanston and Green River. On his days off he would ride the train back to Ogden where he and my Aunt Jack lived with my Grandfather and Grandmother Jones. My grandparents were going to California to visit relatives, and this would leave Aunt Jack frequently alone in Ogden, so I agreed to go down and shovel the snow and take care of the furnace for my room and board. I shortly got a job. I had two or three jobs. I sold pianos and phonographs. I learned I could sell, and people would buy, and they shouldn't have. It's late 1923. There was a depression coming on. I felt guilty for selling things to people when they didn't need them, so I quit.

Next I sold printing on a commission-only basis at the Dee Printing Company. We printed menus or tickets for church socials or any little thing like that. One day I was working the restaurants down on 25th Street to see if menus or meal tickets were needed. I was near the U.S. Forest Service Building. The manager there, Mr. Morris, who was my grandparents' neighbor, was just coming out of the building. He said, "Oh, George, you're the man I need to see. Can you drive a Ford truck?" I said I could drive anything. "Oh good," he said. I had never driven a Ford, only three-speed cars. He said, "Can you leave in the morning to take a loaded truck to the Kaibab in Arizona?" It's 5 o'clock on an April afternoon in 1924. I remember wondering what to do. I'm in the vested choir at the church. Easter is coming up the very next week. I had plans for the summer; there were things the family was going to do. What do I do? Grandfather Jones, who was then Chief of Police of Ogden, said, "Take it, boy!" I knew he was right, so I phoned Mr. Dee at the print shop and quit my job. I phoned Evanston and told my parents what I was going to do. I asked mother if father could, at 4 a.m., put some quilts for a bedroll on the train that Uncle Lyman would be coming on from Green River. All father would have to do was be there and throw the bedroll on the cowcatcher and wave to Uncle Lyman. This accomplished, at 8 o'clock the next morning I went down to get the Ford and find I'm riding with the boss to the Kaibab camp. We got down to the camp with no problem whatsoever, but a few days later I'm driving with another man as carefully as I can in a truck taking this new boss down to Kanab, Utah, to the hospital. He had appendicitis. He was operated on and got over that, but I never saw him again.

I drove back to the camp. There was no trucking to be done at that time. There were a couple of young foresters there, and they were the ones who were doing the timber cruising to locate the stands of trees infected by insects, a bug-control operation. These foresters mapped the location of each tree and estimated the amount of board feet in it. They needed someone to do this job. The snow was still about two feet deep on the Kaibab. The foresters said they needed a compass man. They asked me what education I had had. I said none, thinking they meant college education. I said I had been through high school. They said, "Down here that's just like going to college. We think you'll do. In the morning we'll go out and show you how to run a compass." They showed me how you paced the distance. I got good enough that I could hit it right on the head. I would map the location of the trees and tack a card on each one that was infected. I learned how to detect the infection. I could give the map to the timber crew, and they could find the tree. They said it was the first time they had had anyone who could tell them where to go. This was because I would indicate the topography. I had a fine time with that. It was a highlight of my life. The Kaibab is about two or three hundred miles south of Ogden on the Arizona line.

We were over the line into Arizona. I loved the whole episode; it was marvelous! When the summer was over I went back to Ogden.

Jerry's Grocery, on Jefferson Avenue, had a sign up advertising for a delivery boy, so I applied, and Jerry said he would give me a try. It was fun but hard. We opened before 7:30 every morning, and we didn't close until about 6:30 each night. It was a rushing, busy place. I would shelve stock, handle customers, and deliver groceries in a little truck. I just ran all the time. I worked a year and a half for Jerry. It's now about 1925, and father bought the second ranch, which was located due south out of Evanston and a mile over the Utah line. I knew that father and mother probably wouldn't have purchased this ranch had they thought that I wouldn't also be a rancher the rest of my life.

In April or May of 1926 I went to the ranch. I put all the money I had into buying equipment—harnesses, etc. I was loving it. June came and my brother Lloyd, a dentist, phoned one evening. He said there were a couple of people here (in Evanston) from the university who wanted to collect plants. They wanted to know if I could come down and get them. I said I couldn't tomorrow because father and I were riding Whitney Ridge for cattle, but I told Lloyd I'd be down the next day. Whitney Ridge was in Utah due west from the ranch. There was the canyon of Bear River, and then the rise on the west side of the canyon was this north–south ridge.

When I got back from riding for cattle the next afternoon, the Paysons, Dr. Edwin Payson[3] and his wife Lois, were at the ranch. Mr. Williams, the father of Auril Williams, had brought them out. Auril had been a classmate in high school, and she had gone to college in Laramie and had taken botany. When the Paysons arrived by train in Evanston, they called the Williams's. They asked Mr. Williams whom should they get to take them up into the Uintah Mountains. Mr. Williams said, "Oh, there's only one person to get, and that's the local historian." That was the first time that this term had been applied to me. So there they are at the ranch. They asked if they could stay there in the yard (of three or four acres) for a while. They camped there for a week or two,

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[3] Payson (1893–1927) did his graduate work on the Cruciferae at the Missouri Botanical Garden under J. M. Greenman. Payson became a botany professor at the University of Wyoming.

and then I took them on up to Stillwater Fork and Hayden's Peak where Sereno Watson had collected in 1869 on the King Expedition.

One time when I was helping the Paysons change felt driers in their plant presses (I had no idea what any plant was, but I could see what they were doing, so I just sat down and started doing the same thing), they said I was the sort who should go to college. "Oh, no, I said. Not only do I have no money, but I feel an obligation to be here on the ranch with the folks." The Paysons told me to think it over, and if I decided to go, they would give me my room for the year. So I talked it over with the folks, and they finally decided it was easier to get someone to help father with the ranch in the winter than any time. It is not complex; it's chiefly feeding the cattle every day. They decided a year of college really couldn't hurt anybody, so I agreed to go.

No one could have been greener. I didn't know that you went for four years. I didn't know you took required courses. I thought you took what you wanted—as many as you wanted or as few as you wanted. You're grown up, so you didn't need anyone to tell you what to do. I got hooked on college—I loved it. The folks saw it coming. They took it very well although they were worried about it financially. When I decided to go into botany I wanted to be sure I was doing the right thing so that I wouldn't kick myself later. I knew what salaries were for professors. They were low. Very few professors got as much as $3000.00 a year; very few people in Evanston earned $3000.00 either. If you are going to take time off to study and not have a very big payoff, you better get it justified in your mind some other way.

When the Paysons were still at the ranch, they told me they would see if they could find me a job to make enough money to get by on. They wrote to Dr. Aven Nelson and told him they had someone they thought would make a good person to work in the herbarium mounting plants. So one time I went down to the mailbox, which was six miles from the ranch (I went a little more often because I knew they needed the mail), and there was a letter from Dr. Nelson. They opened it and said, "Well, you've got the job in the herbarium." I remember that I had no idea what an herbarium was, but I'll be darned if I was going to ask. I learned.

Dr. Payson died the end of my freshman year in May of 1927. When I left for the summer I asked Lois to come to the ranch, so she came out that August with her sister-in-law-to-be Lillian Borton and Dr. Nelson's daughter Neva. Lillian later married Francis Butler, Lois's brother. Lois went to library school at the University of Illinois at Urbana that fall. She just had to get away from Laramie. She was offered various jobs on the campus to tide her by. She could have taught English, Spanish, or botany, but she decided to become a librarian and did. She fussed about it; she would write back and say there were no mountains to climb—just staircases. She went to Montana after she got her degree and then to the USDA Library in Washington, and then they wanted her back in Montana. That's where she lived the rest of her life. She was a remarkable person.

I lived at the Stevens's after that. He was on the faculty of the speech department. He was married to Alice Hardy, and they had a little girl named Jean. I had a basement room for $3.00/month.

I worked in the herbarium during my years in Laramie. I also worked for two years from 7 to 9 p.m. at the Carnegie Public Library in Laramie and took care of two furnaces. One time Dr. Nelson said that I was doing so well that I should stay for summer school and graduate in three years. I said, "Oh, no, that's a little too much." He thought I should. I said, "Let me see how I do next year. If I can keep my grade point average up and carry twenty-two or twenty-four hours and make it in a summer to graduation, then I'll stay." That's what I did. In order to take over eighteen hours you couldn't get anything but straight A's. With three jobs, I graduated with honors in three years and a summer.

I told Dr. Nelson that I thought I would go to the University of Colorado for my master's degree. He said, "Oh, no, there are other places you ought to go." I told him I would get busy and write letters to as many places as I could think of. He said, "No, there are just two places you ought to go—either to the Missouri Botanical Garden or Harvard." This was before the Botanical Society of America meetings in August of 1929. In longhand Nelson wrote to Dr. Jesse M. Greenman and Dr. B. L. Robinson. I had heard of Dr. Greenman because Dr. Payson had gotten his degree under Greenman at the Garden. I remember seeing the letter he wrote to Dr. Robinson. He said, "This young man is full of promise. He hasn't done anything yet, but he's promised." The response from Dr. Robinson was in longhand; the one from Greenman was typed. They happened to come within a day of each other, and I had been accepted by both. The decision of which to take was done largely by the finances and by the high regard the Paysons held for Dr. Greenman. At Harvard the stipend was very good at first glance, but you had to pay your tuition, and it was high. At the Garden the tuition was free, and I had a Lackland Research Fellowship which paid $50.00 per month for ten months. I sent money home every month. I was just rolling in the stuff.

I stayed in summer school at the University of Wyoming Camp, and then I went back in August to the ranch. I stayed until September and got the hay put up. I bought a jitney for $50.00. I drove it to St. Louis and sold it when I got there. I went up to the herbarium the next morning. I had met Dr. Greenman at the Botanical Society of America meetings which were held at the University of Wyoming Camp that summer and were attended by botanists from all over the world. That was quite an episode. Dr. William Solheim had just been hired at Wyoming, and he came to the meetings to meet Dr. Nelson. They didn't interview people ahead of time. There was no money for that. Dr. Greenman came to the meetings and Milton, his son, came too. I have that picture (Figure 1). When I met Dr. Greenman, I "fell for" him. I think he liked me, and he was impressed by my knowing so many plants. There weren't many of the plants around the camp that I didn't know except for the grasses. Hitchcock's *Manual* wasn't out then. It was slightly unethical to collect a grass. You only collected one if there were room in the press, and you broke every record trying to see that there was no room.

I remember one time Mrs. Greenman, who was much more Bostonian than she was St. Louisan, was asked where she and Dr. Greenman were going that summer. She replied, "Oh, goodness, we used to always go to Europe, but now Jesse has to go out to that Goodman Ranch every summer." It was just incomprehensible to her that anyone would go out to a western ranch when you could go to Europe.

I went up the stairs to Dr. Greenman's office. I, of course, feel perfectly confident with him. I've had a week or so with him at the camp at the University of Wyoming. He was such a handsome man. There was a fellow standing there scowling, beautifully dressed in a nice herringbone suit. Greenman said, "Oh, by the way, Mr. Goodman, this is Mr. Hitchcock from California, you

know." I knew about him because Hitchy[4] (C. L. Hitchcock) had written me. Mildred Mathias[5] had gone west looking for umbellifers that summer. She was Dr. Greenman's assistant. She took over in a helpful way on everything. When she met Hitchy that summer at Pomona, she told him that there were only two students coming to the Garden that fall who were from the West. All the others were from the East. She gave Hitchy my name. Hitchy didn't think he was going to get along very well with an easterner, so he wrote to me and asked, "How about our rooming together?" I was shocked; I never thought of rooming with anybody. Well, why not? It sounded kinda fun; yeah, let's do it. So we met. I saw that he looked a bit crestfallen when Dr. Greenman introduced me. Hitchy was cordial enough, but my utter self-confidence must have bothered him, for he, underneath it all, was very shy. Here I come in, never been together before, ready to take over, and utterly at ease with Dr. Greenman. Hitchy had been nervous the whole time—afraid he'd say the wrong thing. Later on Hitchy and I would be bantering with each other, and he would say something real mean to me in his ever-loving way, and the other students (Figure 2) at the Garden would say, "Isn't it wonderful that the two of you get along so well." "What do you mean," said Hitchy. "The day that I met him I went home and

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Figure 1. Botanical Society of America meetings, August, 1929, University of Wyoming Camp, near Centennial, Medicine Bow Mts. Kneeling, front row, left, is George J. Goodman. Eighth from far right, first row, is Jesse M. Greenman. To his left is Aven Nelson, then J. C. Gilman and J. P. Anderson. On the far right of front row is John Martin. Between and behind Gilman and Anderson is Walter Loomis. Fred Seavers is behind and between Greenman and Nelson. Above and directly behind Greenman is Ada Hayden. The girl, with wavy hair, above and to J. P. Anderson's left is Alice Ellen Ford Cherbeneau, granddaughter of Aven Nelson. William Solheim is on far right of picture. Next to him and directly behind Martin is T. D. A. Cockerell. To Cockerell's right and above is Milton Greenman, son of J. M. Greenman. Photograph by Paul F. Shope, courtesy William A. Weber, Boulder, Colorado.

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[4] Hitchy (1902–1986) would become professor of botany and the curator of the herbarium at the University of Washington, Seattle, where he was a major contributor to the *Flora of the Pacific Northwest.*

[5] Mildred Mathias Hassler (1906–1995) became professor of botany at the University of California, Los Angeles. She was a specialist in the Umbelliferae.

wrote my parents and told them that I had met all the people around here now, and the one I like the least is my new roommate." He was telling me this within a week. I'll never know if it were true, but I think it was. He could be mean as could be but in a way that was just marvelous.

In the summer of 1930 Hitchy and I decided to make a collecting trip. We bought a second-hand panel truck and painted it aluminum so it wouldn't be too hot. We put "Goodman and Hitchcock" on the side. It didn't say what Goodman and Hitchcock did. It happened that I was already working on *Eriogonum*, and Hitchy was working on *Lycium*. We each knew we ought to see the plants in the field, and the Southwest was the place to go for them. Both genera were down there—not exclusively, but some of both. We made collections primarily in New Mexico, Arizona, Nevada, California, and Utah, with a few from Oregon. The trip was a wonderful opportunity to see so many species, and most of them new to us. At the end of the trip Hitchy telegraphed our landlady telling her we would arrive in St. Louis the next day and requesting her to "kill the fatted calf—spare no expense!"

We wrote quite a few people and herbaria to see if they would be interested in purchasing a set of plants, subject to their approval, at 10¢ a sheet. I don't think anybody turned us down. We wrote mostly to the larger institutions. Dr. Greenman had the Garden give us $100.00 in advance on our plants; that was so typical of him. The Garden bought Set #1 after we got back and all the tag-end sets that were left. They could be used for foreign exchange. We wrote to Mr. George E. Osterhout, a lumberman who lived in Windsor, Colorado. I knew about him from the Paysons, who liked him very much. He had been up to Laramie once or twice, and they had been to Windsor. He was a charming person. One time they told him about me. He said he would like to exchange plants with me, so I sent him a couple of hundred specimens, and he sent a couple of hundred back. In the OKL

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Figure 2. Left to right: C. L. Hitchcock, Carolyn Allen, Julian Steyermark, Jo Darlington, Mildred Mathias, Dorothy Francis, and George Goodman along the Mississippi River, near Jefferson Barracks and St. Louis, 1929 or 1930.

herbarium there are some George E. Osterhout specimens. Those are the ones he exchanged with me. We thought he might want some of our southwest plants, so we wrote to him. He wrote right back and said that he was delighted we were making the trip and that he wanted a set. He enclosed a check for $110.00 as advance payment without ever knowing how many plants he would get. The plants weren't even out of the ground yet! When we got our plants identified and labeled that fall, we sent Mr. Osterhout Set #2. He had overpaid us by $28.00, and we told him as soon as the checks came in from the other sets we would send him the money. He wrote back and said, "The plants are wonderful. You fellows deserve a lot of credit. Don't worry about the change. Keep it!" That's like $280.00 now. And then at the end of the letter Mr. Osterhout wrote, "I'm eager to open your package; I've just been so busy; I haven't had time." He was talking about how wonderful they were, and he hadn't even seen them!

When Osterhout died, his herbarium went to the University of Wyoming. So Set #2 of the Goodman-Hitchcock collecting trip is at Wyoming. We didn't send a set there ourselves. Nelson was very frugal about such things. You don't spend public money unnecessarily. He got his specimens on an exchange basis. Places like Harvard, New York, and the University of California bought sets.

The depression had come on by the time I got my doctor's degree in 1933. I was the only one of the ten of us who got our doctor's degrees that year to get a job in a university. I came to the University of Oklahoma. My nine-month's salary, $1600.00, with a Ph.D. at a university was the same as my eleven-month's salary had been as a delivery boy just out of high school. That's why the folks saw me as the failure of the family. I remember when I was forty years old, my mother saying, "Don't tease him about his salary. He's able to pay his bills, he hasn't had to borrow money, and he's enjoying what he's doing." I enjoyed being teased about it. I would get some little honor at the university, be involved in professional societies, and then I'd go home, and there I'm a failure. I'd become a full professor—so what.

I stayed at the University of Oklahoma as an assistant professor and curator of the herbarium from 1933 to 1936. During the summer of 1935 I went to Iowa State College at Ames to teach summer school. In September 1935 I received an offer from Ames from Dr. Melhus, the department head. The offer was for $200.00 more than I was making at the University of Oklahoma, but I turned it down, not wishing to leave Dr. Paul Sears, the department head in Oklahoma, so abruptly. Later, another offer would come from Ames that I couldn't turn down, so in the fall of 1936 I went to Ames where I stayed until 1945.

Dr. Milton Hopkins, who had taken my place as curator at the University of Oklahoma, resigned to take over his family's publishing business. A call came from the president of the University, Dr. George L. Cross. Dr. Cross, a plant morphologist, had come to the University of Oklahoma in 1934, so for two years we worked in the same department. He became president of the University in 1944. Dr. Cross wanted me to come back to the University of Oklahoma. While I liked Ames very much, and my cheerful daughter Sula Grace was born there, I never felt completely at home the way I did in Oklahoma. I told Dr. Cross I wasn't sure since I had been at Ames for nine years and knew the faculty very well. Dr. Cross replied, "Well, this is your home." I realized he was right, so I said, "Okay, I'll come." Dr. Cross exclaimed, "Wait, we haven't discussed salary!" I remarked that that was his problem and hung up the telephone. In 1945 I returned to Oklahoma at a salary of $4000.00 a year, and I remain "at home" still. When Marcia, my wonderful wife of forty-eight years, and I were married in December, 1948, Dr. Cross was best man at the wedding.

The banter between Dr. Cross and me has continued throughout these years. Once I phoned the president's office and asked his secretary, Ada Arnold, if the president were busy. Dr. Cross took the call, and I invited him to the herbarium for coffee. "Well," Dr. Cross inquired, "is it ready?" I assured him it would be by the time he arrived. Dr. Cross asked, "Do you have any doughnuts?" "Yes," I replied. "How many?" asked Dr. Cross. Carelessly, I answered, "eight." "Eight!" he exclaimed. "Why not a dozen? Doughnuts don't cost much!" In just minutes Dr. Cross arrived at the herbarium where I gave him a doughnut and coffee. There were several people who came that morning for coffee. Soon the pot was getting low, so I filled everyone's cup as well as I could. Dr. Cross remarked, "That's not very much coffee." To which I replied, "It's pretty good considering what you paid for it!" One of the coffee drinkers, shocked by my remark, said, "Dr. Goodman, you wouldn't say that to the president if you didn't have tenure." To that Dr. Cross responded, "In Goodman's case, tenure doesn't mean a damn thing!" When Dr. Cross retired

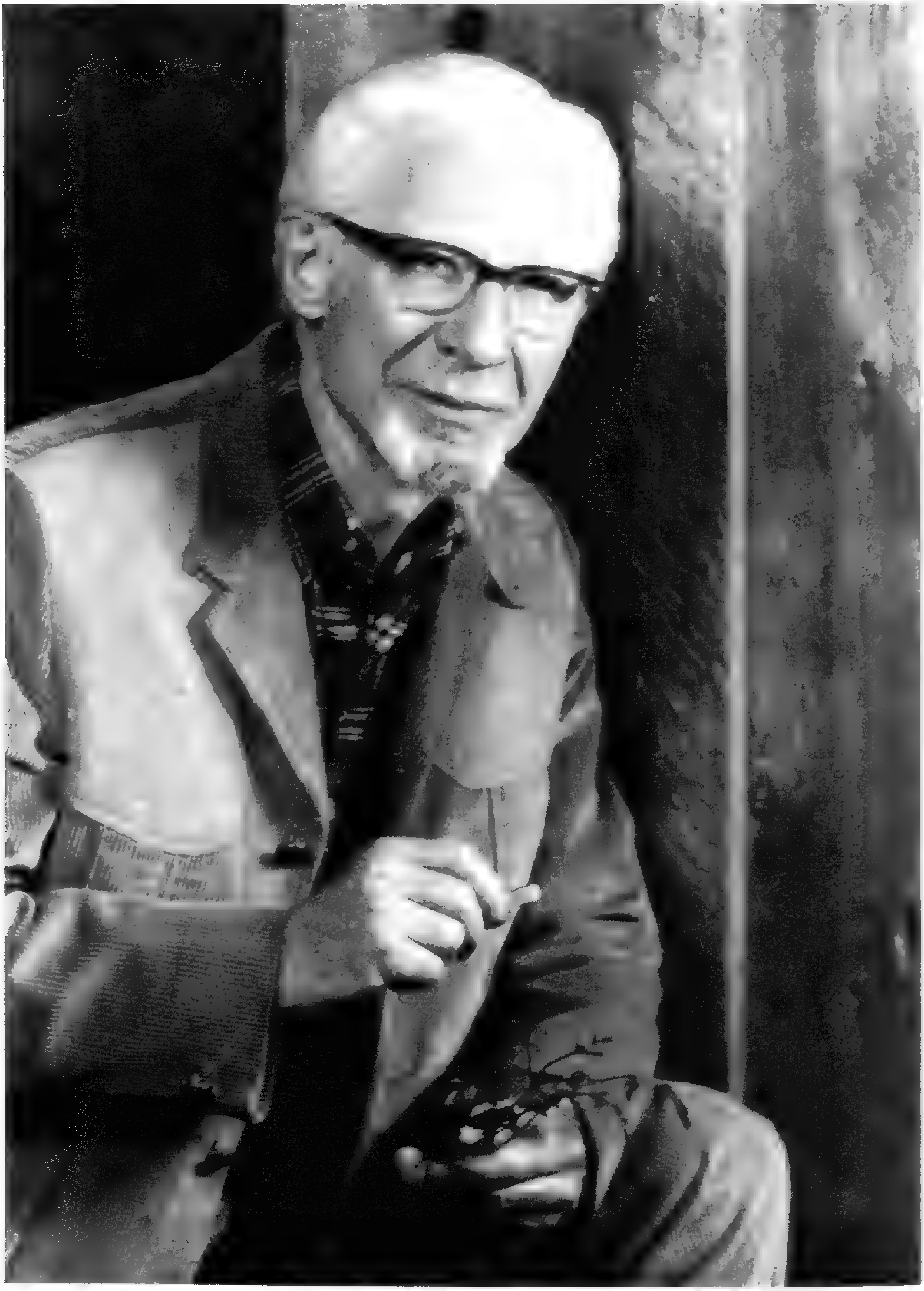

Figure 3. George Jones Goodman, spring 1975.

after nearly twenty-five years as president of the University, I presented him, at a dinner in his and his wife Cleo's honor, with a sack of doughnuts and assured him that there was a full dozen inside. What happy years those were!

My years at the University of Oklahoma have been so wonderful. The students have always been so enthusiastic, never complaining, and so considerate. We've had great classes, great field trips, and, traditionally, great "coffee hours" in the herbarium.

I retired as curator of the herbarium in 1975 (Figure 3), but I've continued to work on taxonomic and botanical problems for the last twenty-two years. Many of those years were spent with Dr. Cheryl Lawson, my last graduate student, collaborating on the botany and itinerary of the Long Expedition of 1820. As with my trip with Hitchy, our trips in the West following the route of this expedition were full of episodes which are recounted in our book, *Retracing Major Stephen H. Long's 1820 Expedition: The Itinerary and Botany,* which was published shortly after my ninetieth birthday.

Life has been such fun!

RHODORA, Vol. 99, No. 898, pp. 182–184, 1997

BOOK REVIEW

Catkin-Bearing Plants of British Columbia by T. Christopher Brayshaw. 1996. 213 pp. illus. ISBN 0-7718-9458-9 $24.95 Canadian (paper). British Columbia Provincial Museum, Victoria, BC, Canada. (Available from the Royal Museum Gift Shop, 675 Belleville Street, Victoria, BC, V8V 1X4.)

The author of this attractive handbook to the catkin-bearing plants in British Columbia has long been interested in the taxonomy of woody plants. He has a great depth of knowledge about woody plants in British Columbia; in his studies of the Salicaceae he has paid particular attention to hybridization and variation. His experience as a forester has helped him to write about these plants in a manner that makes the identification of difficult groups, such as the willows and birches, accessible to the serious amateur, ecologist, forester, wildlife manager, and conservationist.

Catkin-Bearing Plants was originally published in 1976. When it became time for the book to be reprinted it wisely was decided to make extensive revisions. The book is now close to field handbook size (6 × 9″); the maps were moved to the end, and the size of the illustrations reduced, making for a more compact format. The nomenclature was revised to correspond to that used in *The Vascular Plants of British Columbia* (Douglas et al. 1989–1994) and the range maps were extensively updated. The author's illustrations are well done and, although somewhat diagrammatic, are accurate and useful. I was able to recognize almost all of the willows from the illustrations alone. Evidently, the author is able to convey the essence of the species by pen as well as words.

There are five families of woody, flowering plants in British Columbia that have their flowers borne in catkins; they are the Salicaceae, Myricaceae, Juglandaceae, Betulaceae, and Fagaceae. These families once constituted the Amentiferae. The author points out that this is not a natural group but he treats them together because of their similarities including their habit, inflorescence a catkin, flowers unisexual and highly reduced, and perhaps just for "old time's sake." Among these five families only the Salicaceae and Betulaceae have significant numbers of species in the province, with 48 and 12 species, respectively.

This book has the format of a conventional flora. The introduction includes a brief review of the environmental diversity of the province and simplified discussions of classification, nomenclature, and hybridization with examples drawn from the catkin-bearing families. A map of the intensity of botanical collecting in the province reveals that less than half the province is well collected, and the mountainous regions of the interior and the coastal mainland are poorly botanized. The main body of the book includes keys to genera and species, descriptions, comments on variation and hybridization, distribution maps, and illustrations.

The information in this book complements recent publications on the flora of British Columbia (Douglas et al. 1989–1994; Brayshaw 1996; MacKinnon et al. 1992). The updated maps are particularly useful, not only because of the detail they give but because they are the only published maps of the British Columbia distribution of many of these species. The comments on variation, based on the author's field experience, provide useful supplementary information. The author's taxonomy, however, recognizes more infraspecific taxa than is usually done today. Some of these variants are very trivial, such as Andersson's leaf shape variants in *Salix barclayi* and *S. barrattiana,* capsule indumentum variants in *S. polaris* and *S. hookeriana,* and the use of the varietal name *S. pedicellaris* var. *hypoglauca,* which has long been known to be an artifact of drying. To include them, however, does call attention to the variability that exists within these taxa and to that extent it is useful.

Better taxonomic editing could have prevented the occasional misspelling of authority and scientific names. For the new combinations proposed in the first edition (Brayshaw 1976), the words "comb. et stat. nov." were removed from the text but not replaced by the author's name. Two of these new combinations proposed in 1976, namely *Salix alaxensis* f. *obovalifolia* and *Corylus cornuta* f. *glandulosa,* were not validly published (Argus 1977) because a complete citation of the original name was not included. This omission could have been corrected in the present edition.

These criticisms aside, Dr. Brayshaw has done an excellent job of providing an alternative view of the taxonomy of these plants. His work will stand as a useful reference for anyone working with the flora of British Columbia.

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—GEORGE W. ARGUS, 310 Haskins Rd., Merrickville R3, Ontario, K0G 1N0, Canada.

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BOOK REVIEW

Wild Orchids of the Northeastern United States: A Field Guide by Paul Martin Brown. 1997. x + 236 pp. 94 line drawings, 71 maps, and 192 color photographs. ISBN 0-8014-8341-7 $17.95 (paper). Cornell University Press, Ithaca, NY.

The past few years have seen a number of state and regional treatments of orchids. Broad treatments covering large portions of North America exist, but as new knowledge is accumulated it is useful to update available treatments. Given the fact that many local treatments now exist, how can we judge and compare them? I believe that the following questions are relevant when considering a regional orchid volume: Does it cover a previously untreated area? Does it provide a needed synthesis and incorporate new information? Does it make an original contribution? Does it provide improved aids for identification and is it a well-designed book?

The present book is an attractively bound handbook suitable for field use. Introductory sections give information on northeastern conservation organizations and focus on specific regions where native orchids can be seen, in sufficient detail that it would be possible to plan orchid excursions in any of the seven areas covered. The majority of the book comprises species treatments for all taxa known to occur in the coverage area—New England, New York, and adjacent Pennsylvania and New Jersey. The species treatments give range information, flowering period in the area, a minor amount of descriptive information about the plant, additional comments, a drawing of the plant, and color photographs of each species and many varieties and forms. Checklists are provided for the entire region as well as for each of the states included in their entirety (checklists for Pennsylvania and New Jersey are not included). A short bibliography and list of selected synonyms round out the volume.

As if to answer the first of the questions posed above, the first line of the preface states that in the century since 1894, "no other work has been devoted solely to the orchids of the Northeast," and further, of other works, "none is useful as a field guide." A quick look at the bibliography surprisingly finds a reference to *Chapman's Orchids of the Northeast: a field guide,* published in 1996 by Syracuse University Press. Beyond these two books, there has been no modern volume that focuses on the northeast—broader works of Morris and Eames, Correll, and Luer covered the taxa in their time—so indeed there was a need for a field guide to the orchids of this heavily populated region.

One reason that an updated volume is useful is that new taxa may have been recognized in an area, and that is the case in the northeast. There are relatively recently segregated taxa (or old names that have been taken up once again), such as *Malaxis bayardii* and various species of *Spiranthes,* and their inclusion will be helpful to those attempting to sort out variation in these groups. There has also been a recent proliferation of *forma* names and these are included; for some (three-leaved forms of *Listera,* for example) it is not clear whether they have any real genetic component or perhaps are simply developmental anomalies.

Given that there have been a number of recent regional treatments that share a large proportion of species coverage, the problem with a project such as this becomes the difficulty of saying anything that is new. Perhaps the best opportunity for original contribution lies in insightful descriptions of the species' ecology and habitat, necessarily derived from extensive field experience. Such information is very useful to one with little experience who seeks to find these species, and is a distinguishing feature of such books as Case's *Orchids of the Western Great Lakes Region.* Unfortunately, the habitat descriptions in the present work are restricted to a few words or a sentence at best. The distribution maps focus on the coverage area, providing more precise information than may be available in more general references, although it is not clear on what sources of information they are based (i.e., herbarium specimens, literature reports, or personal observations).

With respect to identification, the keys seem workable in general, although there are some rough spots—such contrasts as leaves smooth vs. wrinkled (p. 30), or flowers in a dense spike vs. a lax spike (p. 85), are too relative to be of much use (you essentially have to know the range of variation before using the key). Evidently, *Corallorhiza trifida* would not come out at all in the generic key, since it has a green stem, but *Corallorhiza* is reached by making the choice "stems not green." It is not clear what "petals and sepals indistinct" or "lip undeveloped" would refer to in the key to *Corallorhiza.*

As further identification aids I question whether both extensive habit photographs and habit drawings are necessary; in this case the photographs are superior. Although they vary in quality from very good (e.g., those of *Calopogon, Calypso, Spiranthes cernua*) to essentially out-of-focus (e.g., *Goodyera oblongifolia* rosette, one of *Liparis liliifolia*), they are more useful than the drawings. It would have been better if the drawings had provided critical identification details (occasionally they do, as in the case of a welcome comparison of lips of species of *Listera*). Many of the drawings are rather crudely executed, especially in comparison to excellent illustrations such as those in Smith's *Orchids of Minnesota.* Using coarse parallel lines for shading is particularly dangerous with monocots, because it is not clear whether they are being used just as shading or to represent actual parallel venation. This unusual effect is particularly noticeable in the drawings of *Cypripedium parviflorum* var. *makasin* (p. 71) and *Liparis loeselii* (p. 109).

It seems that a number of new common names have been coined in the volume (or perhaps in previous related publications). The use of the term "orchis" in such names is unfortunate. It is true that this term has long been used for some groups, such as some *Platanthera* species. However, since there is a genus named *Orchis,* to which none of our native species currently belong, it seems that avoiding the term might help avoid confusion. The common name for *Corallorhiza maculata* var. *occidentalis* ("Western spotted coral-root") was clearly derived from the epithet *occidentalis*—but the variety is not particularly western in distribution. Latin names are often inaccurately descriptive, but common names do not have to be.

All in all, the volume provides a workable handbook for the region. It is not a showpiece as regional orchid floras go, but neither is it particularly expensive. Further volumes in the series are planned to focus on other regions in the U.S.

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NEBC MEETING NEWS

May 1997. Dr. Keith Killingbeck of the University of Rhode Island spoke on "The ecology of desert shrubs: Encounters with paradox and dogma in the arid Southwest."

As demonstrated by his spectacular photographs, the deserts are places of vast open spaces, intricate details, and varied cultural history, made unique by the vivid contrasts of light and shadow, desolation and profusion.

Initially intrigued by the physiology of nutrient resorption, Keith investigated the nutrient dynamics of ocotillo, one of the Sonoran Desert's most spectacular flowering plants. Ocotillo is drought-deciduous, forming leaves up to 6 times a year in response to rainfall. He hypothesized that, with this large investment of nutrients and energy in a nutrient-poor environment, the plant should have extraordinary means of reabsorbing nutrients. Through innovative research techniques, the initial research found that researchers who purchase large quantities of pantyhose, twine, and fingernail polish attract attention in the small towns of the Southwest. The research showed that ocotillo has very low nutrient resorption rates (lower than calculated for northeastern deciduous forests) but nutrient concentrations equivalent to those of more mesic plants, and that these rates were controlled by zinc—the critical metal cofactor for the enzymes that break down proteins and release nitrogen for resorption. Nutrient dynamics are controlled, not by adaptation to soil nutrient concentrations, but by soil metal concentrations.

Keith provided a visual tour of the two most interesting North American desert ecosystems. The Chihuahuan desert of Mexico and Texas is characterized by agaves, yuccas, barrel cactus, spectacular perennials such as bluebonnets and bladderpods, and by the ubiquitous creosote bush. Creosote bush is the dominant shrub in both deserts, and is actively invading desert grassland following overgrazing. Clones of this species have been shown to be the oldest known living plant, with documented ages of up to 10,000 years. The Sonoran desert of western Mexico, Arizona, New Mexico, and California has a somewhat different and more diverse flora, whose star players include Saguaro, organ pipe cactus, ocotillo, the fabulous boojum, teddy bear cholla, and palo verde.

Field Trip (June 6, 1997). Twenty-three Club members and guests met at The Holyoke Range State Park Notch Visitors Center in Hadley, MA, for a visit to the balds and barrens of Bare Mountain. The trip was led by Dr. Karen Searcy of the University of Massachusetts, who is conducting research on the flora and ecology of the barrens areas of the Holyoke Range. The group climbed the south face of Bare Mountain, up the weathered surface of the Triassic lava flow known as the Holyoke Diabase by geologists and locally as "traprock." Notable species in the open oak-hickory woods included *Oxalis violacea* (abundant and in full bloom), *Scirpus verecundus, Conopholis americana, Orobanche uniflora, Eupatorium purpureum, Anemonella thalictroides, Vaccinium stamineum, Asclepias quadrifolia, Viola triloba, Thalictrum revolutum,* and *Sanicula marilandica.* The open balds included "grassy balds" on weathered broken rock, dominated by *Schizachyrium scoparium* and *Danthonia spicata,* and "rock balds" on more solid rock. Notable species of the balds and their edges included *Asplenium platyneuron, Woodsia ilvensis, Krigia virginica, Arabis missouriensis, Corydalis sempervirens, Polygonum tenue, Carex umbellata, Pycnanthemum incanum, Celtis occidentalis, Cardamine parviflora* var. *arenicola, Panicum depauperatum, Carex glaucodea, Potentilla arguta,* and *Senecio pauperculus.*

Field Trip (June 7, 1997). Hidden Valley Memorial Forest, Wendell, MA. Club members joined the Mount Grace Land Conservation Trust and Mrs. Mabel Cronquist for the dedication of the Hidden Valley Memorial Forest, an approximately 80-acre property owned by Arthur and Mabel Cronquist. Les Mehrhoff provided a summary and reminiscence of Art Cronquist's life and accomplishments, and Mrs. Cronquist described how they enjoyed camping on the site and exploring its forests and streams and the adjacent Wendell State Forest lands. Following the ceremony, a group of seven Club members, led by Matt Hickler and Karen Searcy, explored the property and initiated a floristic inventory. Although no rarities were encountered, over 100 species were recorded in the rich hemlock-northern hardwoods vegetation, along the rocky brooks, and in the drier oak-hemlock woods along the higher slopes. *Viola macloskeyi, V. rotundifolia, Panax trifolius, Trillium undulatum,* and numerous *Carex* species were noted.

June 1997. Dr. Karen Searcy of the University of Massachusetts spoke on the "Balds on Bare Mountain," her work with Paul Godfrey on the ecology and flora of the balds or barrens of the Holyoke Range. The Holyoke Range is a series of Triassic basalt flows known as the Holyoke Diabase, formed during rifting associated with the opening of the Atlantic. When Dr. Searcy started her research, she found that although the flora of the range had been well documented in the 1860–1880 period, there was a poor inventory and understanding of its grassland or bald sites, and no information on the status or persistence of rare species that had been documented from the area over 100 years previously.

Two types of balds occur on the south-facing slope of the range. Rock balds form where basalt is little weathered, with exposed outcrops of solid rock. These have a relatively low diversity, with an average of 15 species. Grassy balds form where the basalt is more weathered and broken into "clinkers," and are dominated by *Danthonia spicata* and *Schizachyrium.* The grassy balds have a higher diversity, with an average of 42 species. The total flora of the balds includes 124 species, with an exceptionally low contribution (2%) of non-native taxa. Lichens, not yet inventoried, form a major part of the plant community. Rare species, notably *Ranunculus fascicularis, Arabis missouriensis, Asclepias verticillata, Polygonum tenue, Verbena simplex,* and *Carex bicknellii*, frequently occur in the openings.

Knowledge of the successional status and vegetation dynamics of the balds is important for the protection of rare species populations. Dr. Searcy's research suggests that the balds are maintained by severe climate, particularly the much hotter surface temperatures, lower soil moisture, and higher winds than in the adjacent forests, which appear to inhibit the growth of woody plants and maintain the openings. Further research will focus on understanding the factors that preserve these balds and on understanding the population biology of the rare species that occur on these habitat "islands."

—Lisa A. Standley, Recording Secretary.

RHODORA, Vol. 99, No. 898, p. 191, 1997

ANNOUNCEMENTS

THE 1997 JESSE M. GREENMAN AWARD

The 1997 Jesse M. Greenman Award has been won by Elena Conti for the publication "Circumscription of Myrtales and their relationships to other rosids: Evidence from *rbc*L sequence data," coauthored by E. Conti, A. Litt, and K. J. Sytsma, and published in *American Journal of Botany* 83(2): 221–233 (1996). This study is based on a Ph.D. dissertation from the University of Wisconsin under the direction of Dr. Kenneth J. Sytsma.

The Greenman Award, a certificate and a cash prize of $1,000, is presented each year by the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year. Papers published during 1997 are now being accepted for the 30th annual award, which will be presented in the summer of 1998. Reprints of such papers should be sent to Dr. P. Mick Richardson, Greenman Award Committee, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. In order to be considered for the 1998 award, reprints must be received by 1 June 1998.

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GENERAL: Manuscripts should be submitted in triplicate. The text must be double-spaced throughout, including tables, figure legends, and literature citations. Use a non-proportional font throughout and do not justify the right margin. Do not indicate the style of type through the use of capitals, underscoring, or bold, except for names of genera and species which should be in italics or underscored throughout. Do not underline punctuation. All pages should be numbered in the upper right-hand corner. For guidance in matters not addressed here, consult the editorial office by phone at (603) 862-3205, FAX (603) 862-4757, or e-mail: janets@christa.unh.edu. Brevity is urged for all submissions.

TITLE, AUTHOR(S), AND ADDRESS(ES): Center title, in capital letters. Omit authors of scientific names. Below title, include author(s) name(s), affiliation(s), and address(es). If "current address" is different, it should follow immediately below, not as a footnote.

ABSTRACT: An abstract and a list of key words should be included with each paper, except for shorter papers submitted as Notes. An abstract must be one paragraph, and should not include literature citations or taxonomic authorities. Please be concise, while including information about the paper's intent, materials and methods, results, and significance of findings.

TEXT: Main headings are all capital letters and centered on one line. Examples are: MATERIALS AND METHODS, RESULTS, and DISCUSSION. Do not title the Introduction. Do not combine sections of the paper (such as Results and Discussion), or use Conclusions or Summary. Second level headings should be indented, bold, upper and lower case, and end with a period. Taxonomic authorities should be cited for all species names at their first usage in the text, or in a referenced table. Cite each figure and table in the text in numerical order. Each reference cited in the text must be in the Literature Cited. Cross-check spelling of author(s) name(s) and dates of publication. Literature citations in the text should be as follows: Hill (1982) or (Hill 1982). For two or more authors, cite as follows: Angelo and Boufford (1996) or (Angelo and Boufford 1996). Within parentheses, use a semicolon to separate different types of citations (Hill 1982; Angelo and Boufford 1996) or (Figure 4; Table 2).

FLORAS AND TAXONOMIC TREATMENTS: Specimen citation should be selected critically, especially for common species of broad distribution. Keys and synonymy for systematic revisions should be prepared in the style of "A Monograph of the Genus *Malvastrum*,"

S. R. Hill, RHODORA 84: 159–264, 1982. Designation of a new taxon should carry a Latin diagnosis (rather than a full Latin description), which sets forth succinctly how the new taxon differs from its congeners.

LITERATURE CITED: All bibliographic entries must be cited in the paper, unless a special exception has been made by the Editor (such papers will be allowed a REFERENCES section). Verify all entries against original sources, paying special attention to spelling and details of publication. Cite references in strict alphabetical order by first author's surname. Do not write authors' names in all capital letters. References by a single author precede multi-authored works of same senior author, regardless of date. Use a long dash when the author(s) are the same as in the entry immediately preceding (see recent issues). Refer to Botanico-Periodicum-Huntianum (B-P-H 1968) and B-P-H/Supplement (1991) for standardized abbreviations for journals.

TABLES: Tables must be double-spaced. Tables may be continued on an extra page, if necessary. As much as possible, the title should be self-explanatory. Do not use footnotes; instead, add notes after the end of the table title. Broadside tables should be avoided, if possible. Each table should be cited in the text in numerical order.

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THE NEW ENGLAND BOTANICAL CLUB

22 Divinity Avenue
Cambridge, MA 02138

The New England Botanical Club is a nonprofit organization that promotes the study of plants of North America, especially the flora of New England and adjacent areas. The Club holds regular meetings, and has a large herbarium of New England plants and a library. It publishes a quarterly journal, RHODORA, which is now in its 99th year and contains about 400 pages per volume. Visit our web site at http://www.herbaria.harvard.edu/nebc/

Membership is open to all persons interested in systematics and field botany. Annual dues are $35.00, including a subscription to RHODORA. Members living within about 200 miles of Boston receive notices of the Club meetings.

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ADDRESS CHANGES: In order to receive the next number of RHODORA, changes must be received by the business office prior to the first day of January, April, July, or October.

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THE BRYOPHYTE AND VASCULAR FLORA OF LITTLE DOLLAR LAKE PEATLAND, MACKINAC COUNTY, MICHIGAN

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ABSTRACT. Little Dollar Lake peatland is a 14 ha, lake-fill, poor fen peatland complex on Michigan's Upper Peninsula. Field studies over three years revealed the peatland to be composed of seven contiguous mats characterized by several habitats. These habitats included narrow floating mats; extensive grounded mats with hummock-hollow zonation dominated by *Sphagnum* spp., *Chamaedaphne calyculata,* and *Carex oligosperma*; and a lagg adjacent to the upland. Lagg habitats were dominated by *Carex* spp. and *Calamagrostis canadensis.* The bryophyte flora of the peatland was characterized by eleven species of *Sphagnum* that dominated the floating and grounded mats surrounding Little Dollar Lake. The total bryophyte flora (liverworts, peat mosses, and mosses) consisted of 36 species while the vascular flora (pteridophytes, gymnosperms, and angiosperms) consisted of 93 species.

Key Words: peatland, *Sphagnum,* bryophyte flora, vascular flora, Michigan

Due to their confined topography, daunting physical conditions, limited mineral availability, relatively conservative flora, and readily apparent vegetation patterns, peatlands have been examined by a wealth of floristic and ecological studies throughout North America. Since the early 1900s, peatlands of eastern upper Michigan have been the topic of numerous ecological investigations (Woollett et al. 1926; Sigler and Woollett 1927; Dean and Coburn 1928; Coburn et al. 1933; Gates 1942; Bevis 1960).

In the 1970s, Vitt and Slack (1975) discussed the environmental factors influencing plant distribution in kettle-hole peatlands dominated by *Sphagnum.* Vitt et al. (1975) examined the zonation of *Sphagnum* species along the hummock-hollow gradient in northern Michigan peatlands. Schwintzer and Williams (1974) summarized the changes in vegetation zonation through time in a small lake-fill peatland. Schwintzer (1978, 1981) and Schwintzer and Tomberlin (1982) investigated ground water and nutrient dynamics of northern Michigan peatlands and similar wetlands. In the 1980s, research shifted to the postglacial development of northern Michigan peatlands (Futyma 1982; Futyma and Miller 1986; Miller and Futyma 1987; Madsen 1989).

Discussions of vegetation have relied mostly on vegetation sampling or rough species lists, not on a complete inventory of the bryophyte and vascular species inhabiting the study sites. This study, and a companion paper (Hellquist and Crow, ms. in prep.), will detail the species composition and associations of bryophytes and vascular plants at Little Dollar Lake peatland.

SITE DESCRIPTION

Site characteristics. Little Dollar Lake (46°11′05″ N, 85°18′20″ W) is in Lake Superior State Forest in Michigan's eastern Upper Peninsula in west-central Mackinac County (T44N, R8W, NE1/4 Sec. 28, Hudson Township), approximately seven miles north of Lake Michigan. The peatland basin is approximately 14 hectares (34 acres) in area, with the surface of Little Dollar Lake comprising 5.6 hectares (14 acres) of the basin surface area (Humphrys and Greene 1965; Figure 1). Little Dollar Lake is shallow (1.3 m–2.0 m; Futyma, field notes of July 24, 1979), and over half of the original expanse of open water has been covered by peatland vegetation (Futyma 1982). The lake is acidic with a mean pH of 4.5 (n = 40, range 4.2–4.8; August 20, 1995) along the shoreline. The peatland basin is shallow, with depths to nonpeat substrates one to almost four meters (Hellquist 1996).

Although the basin shows no active surficial outflow, it does have a relict stream channel on the southern mat colonized largely by *Carex lasiocarpa* and a stagnant outlet/beaver channel at the north end of the basin. Futyma (1982) concluded that any drainage out of the basin was presumably through seepage. Beaver activity in the lake basin was apparent to Futyma in the late 1970s and early 1980s, yet no damming was observed. No beavers or beaver dams were observed during the summers of 1994 through 1996, although three beaver lodges, in various states of maintenance, were found along the lake margin. Trees recently felled by beavers were observed in the surrounding uplands during 1995.

The adjacent upland. The Little Dollar Lake peatland basin is surrounded by gently undulating glacial topography. This land-

Figure 1. Oblique aerial view of Little Dollar Lake peatland. Photograph by Lauren C. Wemmer: 24 July 1995.

scape supports northern hardwood forests with a mixture of conifers and deciduous hardwoods of the "hemlock-white pine-northern hardwoods region" of Braun (1950). Hardwood species include *Acer pensylvanicum* L., *A. rubrum, A. saccharum, A. spicatum* Lam., *Betula alleghaniensis, B. papyrifera,* and *Fagus grandifolia* Ehrh. Conifers are represented by *Abies balsamea, Picea glauca* (Moench) Voss, *Pinus strobus,* and *Tsuga canadensis* (L.) Carrière. This forest also has a rich understory of herbaceous vegetation including *Pteridium aquilinum* (L.) Kuhn, *Huperzia lucidula* (Michx.) Trevisan, *Lycopodium clavatum* L., *Allium tricoccum* Aiton, *Clintonia borealis* (Aiton) Raf., *Cornus canadensis* L., *Cypripedium acaule* Aiton, *Gaultheria procumbens* L., *Maianthemum canadense* Desf., *Medeola virginiana* L., and *Trientalis borealis* Raf.

As part of Lake Superior State Forest, the forests surrounding Little Dollar Lake are periodically logged. The most valuable timber is in stands of northern hardwoods classified as fully stocked with predominately log-sized timber (Area Forest Manager D. I. Reid 1996, pers. comm.). Clear-cutting occurred to the north-northeast of the lake in 1990. In 1994, selective timber harvests occurred to the south-southwest of the lake (Figure 2). The northern hardwood stands to the south-southwest of the lake and bordering the southwestern peatland mat are scheduled to be selectively harvested again in fifteen years. Northern hardwood stands to the west and north are scheduled to be logged within five years, whereas the stands of *Betula papyrifera* to the east and southeast of the peatland will remain as buffers between logged acreage and the peatland basin (D. I. Reid 1996, pers. comm.).

Although large, charred stumps were observed on the upland ridge to the east of the peatland basin, the peatland has not been seriously affected by any recent fire events based on the absence of charcoal fragments in sediment cores and pollen diagrams (Futyma 1982). Area Forest Manager D. I. Reid (1996 pers. comm.) had no records available relating to the fire history of the area, but asserted that there has been no burning in that area since at least 1977.

Soils of the upland and peatland basin. The upland substrates immediately surrounding Little Dollar Lake are coarse tills and undifferentiated glacial deposits dominated by sand, clay, and

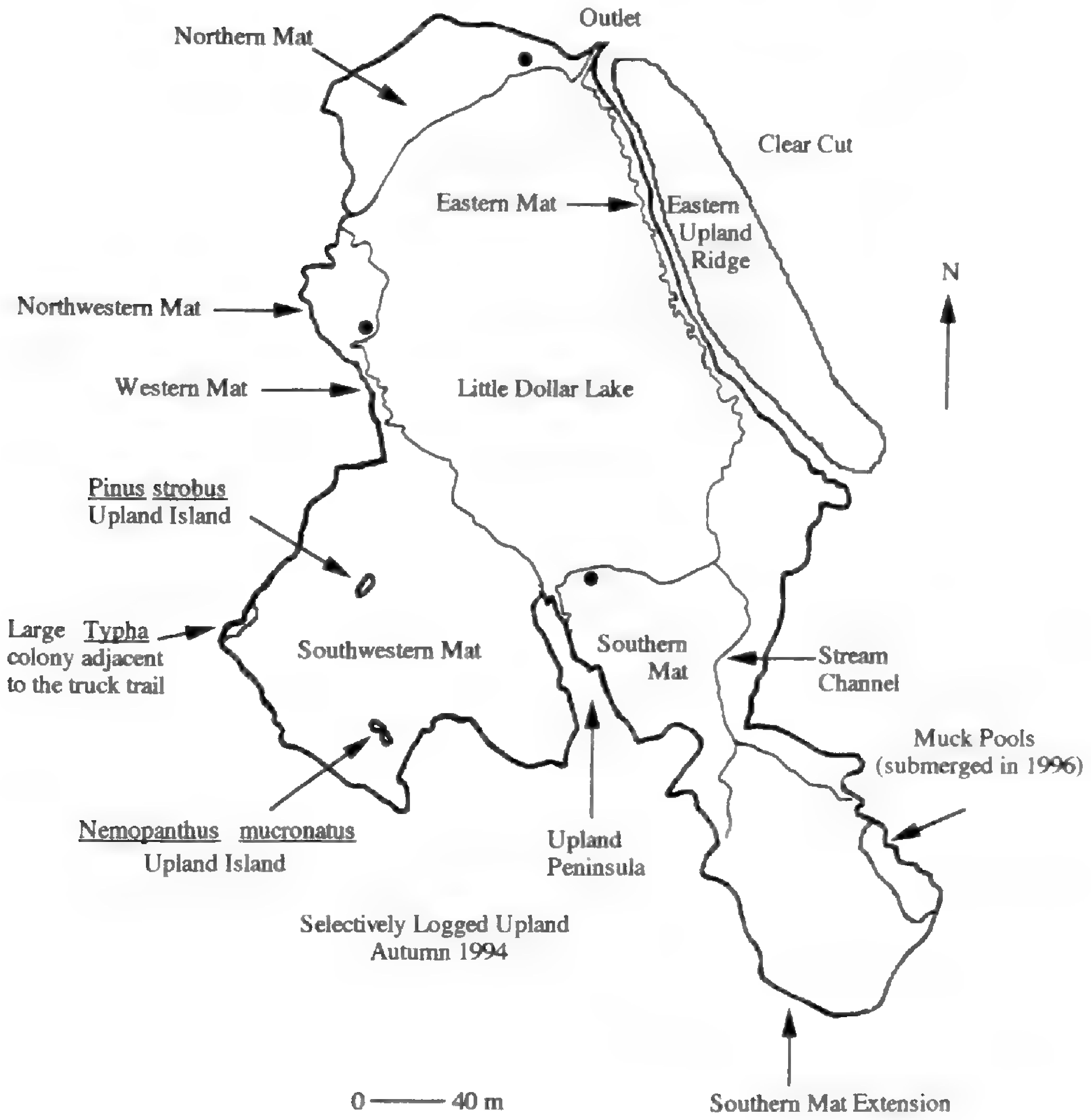

Figure 2. Map of Little Dollar Lake peatland illustrating selected features of local geography around and in the peatland basin. Solid dots indicate the positions of old beaver lodges. Scale is approximate.

loam in various proportions (Farrand 1982). These sandy upland soils include Wallace sand (6–15% slopes), Springlake loamy coarse sand (6–15% slopes), and Paquin-Finch sands (0–6% slopes; Anonymous 1995). Wallace and Springlake sands characterize gently rolling dunes, outwash plains, and lake plains; Paquin sands level or undulating topography; and Finch sands level areas on lake and outwash plains (Anonymous 1995).

The organic soils within the peatland basin are classified as Dawson and Loxley soils (Anonymous 1995). These soils have a high water capacity, are characteristically deep and very poorly drained, and develop in depressed areas on moraines as well as lake and outwash plains. Horizons in Dawson soil profiles usually contain layers of yellowish brown peat, followed by black muck, and grayish brown to yellowish brown sand. Loxley soils tend to be more uniform in composition with a shallow upper layer of dark yellowish brown peat followed by a more extensive zone of black and dark reddish brown muck. Ponded histosols and aquents, characteristic of depressions, beaver dam areas, and marshes, are also present at the north end of the lake near the outlet/beaver channel (Anonymous 1995).

Climate. The local climate of the Little Dollar Lake vicinity is strongly influenced by its proximity to both Lake Michigan, approximately 11 km (7 mi.) to the south, and Lake Superior, approximately 58 km (36 mi.) to the north and 48 km (30 mi.) to the northeast. The Great Lakes have a moderating effect on local weather conditions, with their water remaining cool in the summer and freezing slowly in winter months, creating cloudy, wet conditions (NOAA 1995). Due to the low elevation of eastern upper Michigan (ca. 700–800 ft.), and a lack of physical relief, topography has virtually no influence on the local climate (NOAA 1995).

The closest full scale climatological station operated by the National Oceanic and Atmospheric Administration (NOAA) is located approximately 72 km (45 mi.) to the northeast of Little Dollar Lake at Sault Ste. Marie, Michigan. The average date of the first frost is September 27 and the average date of the last frost is May 26. On average, snow remains on the ground from mid-November to the first week in April. Snowfall totals in Sault Ste. Marie range from approximately 30″ to over 175″. Total snowfall for the winter of 1994–1995 was 93.7″ (NOAA 1995).

At Sault Ste. Marie the mean monthly temperatures for June, July, and August are 58.0°F, 63.8°F, and 62.6°F, respectively (NOAA 1995). In 1995, the average temperatures for the months of June, July, and August were 63.4°F, 63.7°F, and 66.1°F, respectively (NOAA 1995). The normal yearly precipitation (water equivalent) at Sault Ste. Marie is 34.23″ (NOAA 1995). Total precipitation for 1995 was 45.84″ (NOAA 1995). Normal monthly precipitation for June, July, and August at Sault Ste. Marie is 3.14″, 2.71″, and 3.61″, respectively. The monthly precipitation for June, July, and August of 1995 was 2.17″, 3.54″, and 6.52″, respectively (NOAA 1995).

Postglacial history of Little Dollar Lake peatland. Futyma (1982) outlined events surrounding the postglacial revegetation of eastern upper Michigan through the analysis of lake sediments and pollen, some of which were extracted from Little Dollar Lake. During the hypsithermal period following the retreat of the Valders or Greatlakean ice sheet, between 8000 and 5000 years before present (B.P.), the upper Great Lakes region was experiencing the warmest and driest climate of the postglacial epoch. Despite these dry conditions, sediment stratigraphy indicated that the Little Dollar Lake basin was intermittently flooded. Pollen analysis of the sediments of Little Dollar Lake revealed the presence of *Nymphaea* sp., *Nuphar* sp., and *Brasenia schreberi* J. F. Gmelin in the basin at more than 6000 years B.P. (Futyma 1982). The presence of these floating-leaved aquatic species indicates that an extensive expanse of shallow water was present within the basin at this time. Prior to this interval, the lake was either smaller in extent or dry. Following its peak pollen abundance (just prior to 6000 years B.P.), *B. schreberi* pollen levels declined in the next two to three thousand years (Futyma 1982). Today *B. schreberi,* a species of quiet, acidic waters (Voss 1985), does not inhabit Little Dollar Lake.

At approximately 4500 years B.P., a climate shift occurred that resulted in a one to two meter increase in regional water tables. By 3500 years B.P., this gradual increase of the regional water table had inundated the Little Dollar Lake basin creating the lake ancestral to contemporary Little Dollar Lake (Futyma 1982). Further increases in water levels and subsequent flooding began to erode the surrounding upland causing the deposition of a sand layer that was apparent 133–137 cm below the present day lake bottom. Once shore stabilization was established, sand deposition subsided and organic sedimentation occurred. Presumably, this increase in organic material marked the genesis of the contemporary peatland that surrounds Little Dollar Lake (Futyma 1982).

Vegetation of the constituent peatland mats. Based on the bryophyte and vascular species associations within the basin, three major vegetation community types were delineated. Each community consisted of two phases or subtypes (Hellquist 1996; Hellquist and Crow, ms. in prep.). The outermost community of the peatland was a graminoid lagg (moat) characterized by *Cal-*

amagrostis canadensis and *Carex lasiocarpa,* as well as *Iris versicolor, Lysimachia thyrsiflora,* and *Triadenum fraseri.*

The second major community type was an ericaceous scrub, concentrated on the grounded mat. The ericaceous scrub was dominated by *Sphagnum* spp., *Chamaedaphne calyculata, Kalmia polifolia, Andromeda glaucophylla,* and *Carex oligosperma.* The grounded mat blended into a narrow floating *Sphagnum* lawn at the lake margin where species such as *Scheuchzeria palustris, Sarracenia purpurea,* and *Eriophorum virginicum* grew in abundance.

The third major peatland community consisted of an association characteristic of a stream channel area (Figure 2). This channel apparently was open water based on a 1978 infrared aerial photograph of the peatland (Hellquist 1996). Although flooded in years when the water table is high, this channel is now almost entirely colonized by an unstable, floating network of *Carex lasiocarpa, Menyanthes trifoliata, Potentilla palustris,* and *Triadenum fraseri.*

The peatland surrounding Little Dollar Lake consisted of seven spatially distinct mats (Figure 2). Since Little Dollar Lake is situated in an approximately north-south lengthwise orientation, the mats were identified based upon their relative compass-point around the lake perimeter. The northern mat was abutted by a lagg community dominated by *Calamagrostis canadensis.* The majority of the mat was covered by an ericaceous scrub that subsequently merged into a narrow band of *Sphagnum* lawn along the lake shore.

The eastern shore of Little Dollar Lake was fringed by an irregular, narrow (ca. 5.0–10.0 m wide) floating mat similar in appearance and species composition to the western mat (Figure 2). The dominant bryophytes were *Sphagnum majus* and *S. recurvum.* The ericaceous scrub of the eastern mat was distinguished by its high hummocks colonized by robust individuals of *Chamaedaphne calyculata, Kalmia polifolia,* and *Vaccinium macrocarpon.*

The southern mat was very similar in physiognomy to the southwestern mat, having a *Calamagrostis canadensis*-dominated graminoid lagg community, ericaceous scrub community, and a narrow *Sphagnum* lawn along the lake margin. At its southern limits this mat gradually narrowed into a constriction, then flared out into a long, narrow mat named the "southern mat extension" (Figure 2).

The southern mat extension was characterized by an ericaceous scrub community and a diverse *Calamagrostis canadensis* lagg community. The southern mat and its extension were distinctive due to the presence of a meandering stream channel and the nearby "muck pools." The stream channel originated in an open area of peaty muck in the eastern lagg of the southern mat extension, and wound through the southern mat extension and the southern mat, eventually reaching the lake (Figure 2). A second muck pool was located near the southeastern corner of the eastern lagg of the southern mat extension. During the summer of 1994 and 1995 these areas were composed of a soupy peat, but during the summer of 1996 they were flooded by over 0.25 m of water.

The southwestern mat possessed a floating *Sphagnum* lawn community along the margin of the lake, although the physiognomy of this mat was distinguished by an extensive ericaceous scrub that was bordered along the upland by a *Calamagrostis canadensis* lagg association. In the southwestern mat's basin there are two small, upland, mineral soil communities with a suite of species different from those of the ericaceous scrub (Figure 2). The larger island is topped with mature individuals of *Acer rubrum* (15 cm diameter at breast height [dbh]), *Betula papyrifera, Pinus strobus* (28 cm dbh), and an understory of *Chamaedaphne calyculata, Gaylussacia baccata* (Wangenh.) K. Koch, *Vaccinium angustifolium,* and *Pteridium aquilinum.* The smaller of the two islands on the southwestern mat is dominated by one large *Pinus strobus* (30.7 cm dbh) and eight clumps of *Nemopanthus mucronatus.* The southwestern mat and the southern mat are separated by an elevated, finger-like projection of upland that protrudes northward to the open water of Little Dollar Lake (Figure 2).

Like the northern mat, the northwestern mat was relatively narrow with an extensive ericaceous scrub that blended into a narrow *Sphagnum* lawn at the lake margin (Figure 2). The periphery of this mat was composed of a *Calamagrostis canadensis*-dominated lagg community or a *Chamaedaphne calyculata* community that directly abutted the upland. Near Little Dollar Lake, this mat was perforated with holes that apparently have been accentuated by beaver activity.

The northwestern mat and the southwestern mat were joined by the narrow western mat. Like the narrow eastern mat, the western mat was situated along a steep-sloped upland and was characterized by an ericaceous scrub with high hummocks and wet hollows. At its broadest, the western mat was approximately 11.0 meters wide (Figure 2).

MATERIALS AND METHODS

The floristic survey began during July and August of 1994. During the summer of 1995, Little Dollar Lake peatland was visited a minimum of two times a week to inventory the flora and conduct a vegetation analysis (Hellquist 1996). The peatland was visited during the summer of 1996 also. Throughout the summer of 1995, all habitats were thoroughly explored in the peatland basin.

Species found colonizing old beaver lodges were included in the flora since these plants were growing on peat excavated from the peatland mat by beaver to cover the branches and debris on the lodges. Species that occurred only on the small islands of upland mineral soil stranded in the southwestern peatland mat, such as *Pteridium aquilinum* and *Gaylussacia baccata,* were not included in the flora. These species were excluded due to their establishment on upland mineral soils that were not influenced by the unique physical conditions characteristic of peat substrates.

Taxonomy of the bryophyte classes follows a summary presented in Crum (1991). Bryophyte nomenclature at the family, generic, and species levels follows Stotler and Crandall-Stotler (1977) for the liverworts, Anderson (1990) for the peat mosses, and Anderson et al. (1990) for the mosses. Bryophyte species were identified using Crum and Anderson (1981), Ireland (1982), Crum (1983, 1991), and Smith (1990).

Taxonomy and nomenclature for ferns, fern allies, and gymnosperms follows *Flora of North America* (Flora of North America Editorial Committee 1993). Angiosperm taxonomy follows Cronquist (1981) as well as *Flora of North America* for the Magnoliidae and the Hamamelidae (Flora of North America Editorial Committee 1997). With a few exceptions, nomenclature follows Gleason and Cronquist (1991). Angiosperm species were identified using Gleason (1952), Voss (1972, 1985), and Gleason and Cronquist (1991).

Voucher specimens of the bryophyte and vascular species are deposited in the Hodgdon Herbarium of the University of New

Table 1. Total species and percent composition of higher taxonomic levels of bryophytes and vascular plants at Little Dollar Lake peatland.

	Number of Species	Percent of Flora
BRYOPHYTES	36 Total	
HEPATICOPSIDA (Liverworts)	6	16.7
SPHAGNOPSIDA (Peat Mosses)	11	30.6
BRYOPSIDA (Mosses)	19	52.8
VASCULAR PLANTS	93 Total	
PTERIDOPHYTES (Ferns & Allies)	5	5.4
GYMNOSPERMS (Conifers)	5	5.4
ANGIOSPERMS (Flowering Plants)	83	89.2

Hampshire (NHA) and the University of Michigan Biological Station Herbarium (UMBS).

RESULTS

The bryophytes of Little Dollar Lake peatland were represented by 14 families, 20 genera and 36 species of liverworts, peat mosses, and true mosses (Table 1). The liverworts consisted of six "leafy" taxa making up 16.7% of the total bryophyte flora. *Sphagnum* (peat moss; Sphagnaceae) was the most abundant bryophyte genus in the peatland. Eleven *Sphagnum* species accounted for 30.6% of the total bryophyte species diversity. The most diverse group of bryophytes present in the peatland was the mosses (Bryopsida), consisting of 19 species that composed 52.8% of the total bryophyte species richness. The most diverse family of the mosses was the Amblystegiaceae, represented by four genera and six species, a total of 17% of the bryophytes.

Crum (1983) cites the presence of six species of Bryopsida at Little Dollar Lake that were not located during this inventory: *Dicranum scoparium* Hedw. (Dicranaceae), *Mnium spinulosum* Bruch & Schimp. in B. S. G. (Mniaceae), *Brachythecium populeum* (Hedw.) Schimp. in B. S. G. and *B. reflexum* (Starke in Web. & Mohr) Schimp. in B. S. G. (Brachytheciaceae), *Herzogiella turfacea* (Lindb.) Iwats. (Hypnaceae), and *Polytrichum formosum* Hedw. (Polytrichaceae). These collections are cited as "Mackinac County: Little Dollar Lake." Until the herbarium

Table 2. Visual abundance index employed in the bryophyte and vascular species inventory.

Abundant: Dominant or codominant in at least one cover type.
Frequent: Easily recognizable in one or more cover types, but not the most dominant in any single community.
Occasional: Widely distributed throughout the peatland, can be located relatively easily.
Infrequent: Difficult to find due to scant populations limited to several localities.
Rare: Very difficult to find, limited to two or fewer distinct localities in the peatland.

vouchers are examined, it will remain unclear whether these species were collected within the peatland basin or in the upland habitats within the surrounding forests. Based on their characteristic habitats, it is probable that these species were collected in the vicinity of Little Dollar Lake, but not within the peatland itself.

The vascular flora of Little Dollar Lake peatland was composed of 93 species representing 38 families and 62 genera (Table 1). Due to recent annotations during the summer of 1997, the following species list differs slightly from the inventory presented in Hellquist (1996). The two best-represented families in the peatland flora were the Cyperaceae and the Ericaceae. The Cyperaceae (18 species) accounted for 20% of the total flora, while the Ericaceae (8 species) accounted for 9% of the total flora. *Hieracium piloselloides* and *Rumex obtusifolius* were the only nonnative species present. One species, *Potamogeton confervoides,* is protected under the Endangered Species Act of the State of Michigan (Public Act 203 of 1974, as amended) with "Threatened" status (Beaman et al. 1985; Anonymous 1994).

In the following checklist, overall abundance of the species growing in the peatland was estimated visually using an abundance index (Table 2) modified from a similar index of Palmer et al. (1995). The checklist designates mat areas with the following acronyms: EM = Eastern Mat, NM = Northern Mat, NWM = Northwestern Mat, SM = Southern Mat, SME = Southern Mat Extension, SWM = Southwestern Mat, and WM = Western Mat.

THE BRYOPHYTE AND VASCULAR FLORA OF LITTLE DOLLAR LAKE PEATLAND

BRYOPHYTA (Bryophytes)

HEPATICOPSIDA (Liverworts)

CEPHALOZIACEAE

Cladopodiella fluitans (Nees) Joerg. Occasional; throughout the ericaceous scrub of the peatland, especially in moist areas among *Sphagnum majus*; also on exposed peat along the lake margin, deer trails, or on hummocks.

Cephalozia connivens (Dicks.) Lindb. Rare; SWM southern lagg, on rotting wood.

CEPHALOZIELLACEAE

Cephaloziella elachista (Jack) Schiffn. Rare; SWM, leaf litter in the ericaceous scrub.

Cephaloziella hampeana (Nees) Schiffn. Rare; SME, in moist, decaying leaf litter in the ericaceous scrub.

LOPHOCOLEACEAE

Lophocolea heterophylla (Schrad.) Dum. Rare; SWM southern lagg, on rotting wood.

Chiloscyphus polyanthos (L.) Corda. Rare; SWM southern lagg, on rotting wood.

SPHAGNOPSIDA (Peat Mosses)

SPHAGNACEAE

Section *Sphagnum*

Sphagnum magellanicum Brid. Abundant; throughout the peatland, a dominant species of the ericaceous scrub and floating *Sphagnum* lawn; often initiates hummock topography and forms the basal areas of hummocks.

Sphagnum papillosum Lindb. Abundant; the primary pioneer *Sphagnum* species forming a lush fringe that extends into the open water of the lake from the floating mat; also forms undulating patches on the *Sphagnum* lawn and in low-lying areas of the ericaceous scrub.

Section *Squarrosa*

Sphagnum squarrosum Crome. Rare; SWM, SME lagg, in leaf litter or on decorticated logs.

Section *Cuspidata*

Sphagnum cuspidatum Ehrh. ex Hoffm. Infrequent; most prominent in the southeastern lagg of the SME, often intermixed with *S. majus* in areas subject to periodic inundation; occasionally found along the lake margin with *S. papillosum.*

Sphagnum majus (Russ.) C. Jens. Frequent; throughout the peatland in damp hollows and low troughs in wet saturated areas of the mat; especially prominent on the EM and WM.

Sphagnum recurvum P. Beauv., *sensu lato.* Abundant; the most prominent bryophyte in the peatland, exhibiting the widest ecological amplitude of all the *Sphagnum* species present; throughout the peatland along the upper edges of shallow, damp hollows of the ericaceous scrub; occasionally among *S. papillosum* at the lake margin.

Section *Subsecunda*

Sphagnum subsecundum Nees in Sturm, *sensu lato.* Infrequent; among *Carex lasiocarpa* in the eastern lagg of the southern mat extension, and at the bases of the taller hummocks at the constriction of the SM and SME, also on the EM and WM.

Section *Acutifolia*

Sphagnum capillifolium (Ehrh.) Hedw. Frequent; scattered throughout the peatland, usually at intermediate levels of hummocks; also forms extensive, flat lawns on or near the *Sphagnum* lawns within ten meters of the lake.

Sphagnum fimbriatum Wils. in Wils. & J. D. Hook. Rare; limited to large hummocks along the upland on the eastern and western mats.

Sphagnum fuscum (Schimp.) Klinggr. Infrequent; Widely scattered populations on hummock tops within the ericaceous scrub; occasionally on the *Sphagnum* lawn of the SM.

Sphagnum russowii Warnst. Rare; a single population located on hummocks >1.0 m at the edge of the *Calamagrostis canadensis* lagg where the lagg merges into the ericaceous scrub on the northern edge of the NM.

BRYOPSIDA (Mosses)

AMBLYSTEGIACEAE

Calliergon cordifolium (Hedw.) Kindb. Frequent; forms lush carpets in densely shaded areas of graminoid lagg.

Calliergon stramineum (Brid.) Kindb. Infrequent; Widely scattered, typically on top of drier hummocks in the ericaceous scrub.

Campylium chrysophyllum (Brid.) J. Lange. Rare; SWM southwestern lagg, adjacent to the truck trail, intermixed with *Brachythecium rutabulum* on decorticated wood.

Sanionia uncinata (Hedw.) Loeske [*Drepanocladus uncinatus* (Hedw.) Warnst.]. Rare; a single population on a decorticated *Betula papyrifera* trunk fallen into the southwestern lagg of the SME.

Warnstorfia exannulata (Schimp. in B. S. G.) Loeske [*Drepanocladus exannulatus* (Schimp. in B. S. G.) Warnst.]. Infrequent; SME eastern lagg, carpeting exposed muck pools; during wet years, it grows submerged here.

Warnstorfia fluitans (Hedw.) Loeske [*Drepanocladus fluitans* (Hedw.) Warnst.]. Infrequent; usually in saturated hollows among *Sphagnum majus*; also in the stream channel at the constriction of the SM and SME.

AULACOMNIACEAE

Aulacomnium palustre (Hedw.) Schwaegr. Occasional; on hummocks or along deer trails.

BRACHYTHECIACEAE

Brachythecium rutabulum (Hedw.) Schimp. in B. S. G. Rare; SWM southwestern lagg adjacent to the truck trail, with *Campylium chrysophyllum* on decorticated wood.

BRYACEAE

Bryum capillare Hedw. Occasional; sporadic on hummocks throughout the ericaceous scrub.

Pohlia nutans (Hedw.) Lindb. Infrequent; scattered in open lagg habitats and in the ericaceous scrub.

CLIMACIACEAE

Climacium dendroides (Hedw.) Web. & Mohr. Rare; in rich muck and on decorticated logs in the eastern lagg of the SME.

DICRANACEAE

Dicranum flagellare Hedw. Infrequent; dry hummock tops among leaf litter of the ericaceous scrub.

Dicranum montanum Hedw. Rare; among *Chamaedaphne calyculata* branches in the ericaceous scrub of the SWM.

Dicranum undulatum Brid. Infrequent; on the sides or on top of *Sphagnum* hummocks in the ericaceous scrub.

HYPNACEAE

Callicladium haldanianum (Grev.) Crum. Infrequent; on dry hummocks or on decorticated wood.

HYLOCOMIACEAE

Pleurozium schreberi (Brid.) Mitt. Infrequent; on dry hummocks; occasionally in the lagg on decorticated wood.

PLAGIOTHECIACEAE

Plagiothecium denticulatum (Hedw.) Schimp. in B. S. G. Rare; SWM southern lagg, in leaf litter and on decorticated logs.

POLYTRICHACEAE

Polytrichum commune Hedw. Occasional; on old beaver lodges.

Polytrichum strictum Brid. Occasional; usually on relatively dry, open hummocks in the ericaceous scrub, also on old beaver lodges.

LYCOPODIOPHYTA (Lycopods)

ISOËTACEAE

Isoëtes echinospora Durieu, Quillwort. Infrequent; submerged in the lake, especially along the eastern shore.

LYCOPODIACEAE

Lycopodiella inundata (L.) Holub [*Lycopodium inundatum* L.], Bog-clubmoss. Rare; NWM, *Sphagnum* lawn.

EQUISETOPHYTA (Horsetails)

EQUISETACEAE

Equisetum fluviatile L., Water-horsetail. Infrequent; SME, mucky lagg.

POLYPODIOPHYTA (Ferns)

DRYOPTERIDACEAE

Dryopteris intermedia (Muhl. ex Willd.) A. Gray, Fancy wood-fern. Rare; SME, SWM, on rotting nurse logs in the lagg.

OSMUNDACEAE

Osmunda cinnamomea L., Cinnamon fern. Rare; SWM, on rotting nurse log in the lagg.

PINOPHYTA (Conifers)

PINACEAE

Abies balsamea (L.) Miller, Balsam fir. Infrequent; NWM, SWM, sporadic along the interface of the *Sphagnum* lawn and ericaceous scrub.

Larix laricina (Duroi) K. Koch, Tamarack. Occasional; NWM, SM, open areas of the *Sphagnum* lawn along the interface of the ericaceous scrub.

Picea mariana (Miller) BSP., Black spruce. Occasional; throughout the peatland especially on the *Sphagnum* lawn or in the ericaceous scrub near the *Sphagnum* lawn.

Pinus resinosa Aiton, Red pine. Rare; SM, a single juvenile, approximately 1.0 m tall, on the *Sphagnum* lawn.

Pinus strobus L., White pine. Occasional; the most abundant conifer, found on all mats, typically in the ericaceous scrub or along its interface with the lagg.

MAGNOLIOPHYTA (Flowering Plants)

MAGNOLIOPSIDA (Dicotyledons)

ACERACEAE

Acer rubrum L., Red maple. Occasional; seedlings and saplings scattered throughout the bog mat, established in the lagg or on hummocks of the ericaceous scrub.

Acer saccharum Marshall, Sugar maple. Rare; SWM, extremely sporadic seedlings found in the ericaceous scrub.

AQUIFOLIACEAE

Ilex verticillata (L.) A. Gray, Winterberry. Occasional; sporadic individuals in the ericaceous scrub near the lagg as well as within the lagg itself.

Nemopanthus mucronatus (L.) Loes., Mountain holly. Occasional; sporadic individuals in the lagg.

ASTERACEAE

Bidens cernua L., Nodding beggar-ticks. Occasional; NM, SME, primarily in shaded lagg areas in wet, mucky leaf litter.

Bidens connata Muhl., Purplestem beggar-ticks. Occasional; NM, SME, primarily in shaded lagg areas in wet, mucky leaf litter.

Hieracium piloselloides Villars, Yellow hawkweed. Rare; a single individual located on the beaver lodge on the NWM, apparently dispersed from plants growing along the shoulder of the truck trail; introduced from Europe (Gleason and Cronquist 1991).

BALSAMINACEAE

Impatiens capensis Meerb., Spotted touch-me-not. Infrequent; SWM lagg, adjacent to the truck trail.

BETULACEAE

Betula alleghaniensis Britton, Yellow birch. Rare; NM, saplings in the lagg.

Betula papyrifera Marshall, White birch. Occasional; scattered saplings on all peatland mats, often on old beaver lodges.

CAPRIFOLIACEAE

Viburnum nudum L. var. *cassinoides* (L.) T. & G., Wild-raisin. Occasional; in lagg areas, especially on the NM.

CLUSIACEAE

Hypericum boreale (Britton) E. Bickn., St. John's wort. Infrequent; EM, NM, NWM, beaver lodges and rotting nurse logs; in 1996, *H. boreale* forma *callitrichoides* Fassett, a partially submerged aquatic form, was frequent along the lake shore, especially along the EM.

Hypericum majus (A. Gray) Britton, St. John's wort. Infrequent; EM, NWM, beaver lodges and rotting nurse logs.

Triadenum fraseri (Spach) Gleason, Marsh St. John's wort. Frequent; throughout the peatland in wet areas along the lake margin, stream channel, and in mucky lagg areas.

DROSERACEAE

Drosera intermedia Hayne, Sundew. Rare; NWM *Sphagnum* lawn on exposed peat.

Drosera rotundifolia L., Sundew. Frequent; inconspicuous, on the *Sphagnum* lawn or in damp, sheltered microhabitats on hummocks.

ERICACEAE

Andromeda glaucophylla Link, Bog-rosemary. Frequent; widely scattered throughout, especially in the ericaceous scrub.

Chamaedaphne calyculata (L.) Moench, Leatherleaf. Abundant; the most dominant species of the peatland; invades open water, stunted sprigs on the *Sphagnum* lawn, ubiquitous in the ericaceous scrub, especially robust individuals inhabit areas where the graminoid lagg association was absent.

Kalmia polifolia Wangenh., Bog-laurel. Frequent; throughout all peatland mats, especially prominent in the ericaceous scrub.

Ledum groenlandicum Oeder, Labrador-tea. Occasional; SM, SWM, dry hummocks of the ericaceous scrub.

Vaccinium angustifolium Aiton, Low sweet blueberry. Occasional; on well-elevated, dry hummocks in the ericaceous scrub.

Vaccinium macrocarpon Aiton, Large cranberry. Frequent; among ericaceous shrubs growing into the lake and along the stream channel, also conspicuous on the EM and WM.

Vaccinium myrtilloides Michx., Velvetleaf blueberry. Infrequent; SME lagg, on rotting nurse logs, rarely in the ericaceous scrub.

Vaccinium oxycoccos L., Small cranberry. Frequent; on dry, open hummocks in the ericaceous scrub; also on the *Sphagnum* lawn.

LAMIACEAE

Lycopus uniflorus Michx., Bugleweed. Frequent; SM, SWM, SME, graminoid lagg.

Scutellaria galericulata L., Marsh skullcap. Frequent; lagg habitats, especially the SWM lagg adjacent to the truck trail.

Scutellaria lateriflora L., Mad-dog skullcap. Rare; SWM lagg, adjacent to the truck trail.

LENTIBULARIACEAE

Utricularia geminiscapa Benj., Mixed bladderwort. Frequent; free-floating in the lake along the peatland mat.

Utricularia intermedia Hayne, Northern bladderwort. Infrequent; limited to the periodically inundated muck pools of the southeastern lagg of the SME.

MENYANTHACEAE

Menyanthes trifoliata L., Buckbean. Occasional; prefers saturated habitats such as exposed peat along the lake margin or stream channel.

NYMPHAEACEAE

Nuphar variegata Durand, Yellow pond-lily. Rare; two sites, one aquatic and one semiterrestrial; the single aquatic population off the NWM; a cluster of stranded individuals among *Sphagnum majus, Carex lasiocarpa,* and *Potentilla palustris* in the lagg of the SME near the stream channel.

Nymphaea odorata Aiton, Fragrant water-lily. Rare; SM, SWM, isolated individuals among *Chamaedaphne calyculata* branches and *Sphagnum* encroaching into the lake.

ONAGRACEAE

Epilobium ciliatum Raf., American willow-herb. Rare; SWM lagg, a single localized population adjacent to the truck trail.

Epilobium leptophyllum Raf., American marsh willow-herb. Rare; NM, on the beaver lodge.

POLYGONACEAE

Polygonum amphibium L., Water smartweed. Infrequent; in lagg communities or in wet hollows of the ericaceous scrub.

Polygonum cilinode Michx., Fringed bindweed. Rare; SWM lagg, adjacent to the truck trail.

Rumex obtusifolius L., Bitter dock. Rare; SWM lagg, adjacent to the truck trail; introduced from Europe (Gleason and Cronquist 1991).

PRIMULACEAE

Lysimachia terrestris (L.) BSP., Swamp-candles. Frequent; SWM lagg, adjacent to the truck trail.

Lysimachia thyrsiflora L., Tufted-loosestrife. Frequent; SWM, SME in partially shaded lagg habitats.

ROSACEAE

Aronia prunifolia (Marshall) Rehder, Chokeberry. Infrequent; NM, NWM mats, widely scattered in the ericaceous scrub adjacent to the lagg.

Potentilla palustris (L.) Scop., Marsh cinquefoil. Frequent; in low, wet, mucky habitats along the stream channel or in the lagg.

Rubus canadensis L., *sensu lato,* Blackberry. Rare; NWM, SWM lagg, adjacent to the truck trail.

Spiraea alba Duroi, Meadowsweet. Infrequent; SME lagg, often on decorticated nurse logs.

RUBIACEAE

Galium tinctorium L., Southern three-lobed bedstraw. Frequent; SM, SWM, SME lagg.

SALICACEAE

Salix pedicellaris Pursh, Bog willow. Infrequent; SME lagg, scattered in wet, mucky habitats.

Salix petiolaris J.E. Smith, Meadow willow. Rare; SM lagg, isolated populations near the constriction joining the SM and the SME.

SARRACENIACEAE

Sarracenia purpurea L., Pitcher plant. Frequent; throughout the *Sphagnum* lawn, usually within a few meters of the lake margin, also in hollows of the ericaceous scrub.

VIOLACEAE

Viola macloskeyi F. Lloyd, Smooth white violet. Infrequent; SWM, SME lagg, in partially shaded habitats, on decorticated nurse logs or among leaf litter.

LILIOPSIDA (Monocotyledons)

ARACEAE

Calla palustris L., Wild calla. Occasional; in wet, mucky habitats along the lake margin, stream channel, and lagg.

CYPERACEAE

Carex brunnescens (Pers.) Poiret, Sedge. Rare; SWM lagg, on decorticated nurse logs.

Carex canescens L., Sedge. Abundant; sunken, wet habitats, prominent along the lake margin, also in the graminoid lagg and in the mucky periphery of the stream channel.

Carex chordorrhiza L.f., Sedge. Rare; SME, a single population along the muck pools.

Carex echinata Murray, Star-sedge. Infrequent; NWM, SWM, in the lagg or on beaver lodges.

Carex lasiocarpa Ehrh., Sedge. Abundant; one of the dominant species of the graminoid lagg, also in hollows of the ericaceous scrub adjacent to lagg areas; a major pioneer instrumental in the terrestrialization of the stream channel.

Carex limosa L., Sedge. Occasional; wet microhabitats along the lake margin, *Sphagnum* lawn, or graminoid lagg.

Carex oligosperma Michx., Sedge. Abundant; throughout the peatland, in hollows between hummocks; the dominant sedge species of the open ericaceous scrub.

Carex retrorsa Schweinitz, Sedge. Infrequent; SWM graminoid lagg, in mucky leaf litter.

Carex stipata Muhl., Sedge. Rare; SWM, a single population in the graminoid lagg.

Carex utriculata F. Boott, Sedge. Occasional; SM, in wet areas along the stream channel, also in deer trails.

Carex vesicaria L., Sedge. Rare; SME, shaded lagg habitats.

Dulichium arundinaceum (L.) Britton, Three-way sedge. Occasional; SM, SME, scattered in and along the muck pools, also in exposed peat along the stream channel.

Eleocharis intermedia (Muhl.) Schultes, Spike-rush. Infrequent; NW, SM, isolated individuals in exposed peat along the lake margin.

Eriophorum gracile Koch, Slender cotton-grass. Rare; SWM, a single locality in the graminoid lagg near the junction of the WM.

Eriophorum vaginatum L. [*E. spissum* Fern.], Tussock cotton-grass. Infrequent; isolated localities primarily on the *Sphagnum* lawn of the SWM.

Eriophorum virginicum L., Tawny cotton-grass. Frequent; in hollows throughout the ericaceous scrub and *Sphagnum* lawn.

Rhynchospora alba (L.) Vahl, Beak-rush. Frequent; in saturated microhabitats along the lake margin and stream channel.

Scirpus cyperinus (L.) Kunth, Wool-grass. Occasional; SM, SWM, SME, sporadic in the lagg.

ERIOCAULACEAE

Eriocaulon aquaticum (Hill) Druce [*E. septangulare* With.], Pipewort. Frequent; colonizes exposed peat along the lake margin, also submerged in the lake.

IRIDACEAE

Iris versicolor L., Wild blue flag. Frequent; throughout graminoid lagg areas, especially in the SWM.

JUNCACEAE

Juncus alpinus Vill., Rush. Infrequent; SME, mucky lagg.

Juncus brevicaudatus (Engelm.) Fern., Rush. Rare; EM, a single locality on a decorticated nurse log.

Juncus effusus L., Soft rush. Occasional; widely scattered, usually in hummocky lagg habitats.

ORCHIDACEAE

Calopogon tuberosus (L.) BSP., Grass-pink. Rare; *Sphagnum* lawn of the SM and the NWM in open areas near the lake margin.

Pogonia ophioglossoides (L.) Ker Gawler, Rose pogonia. Rare; NWM, *Sphagnum* lawn in open areas near the lake margin.

POACEAE

Calamagrostis canadensis (Michx.) P. Beauv., Blue-joint. Abundant; the dominant species in the open, graminoid lagg that fringes areas of the NM, NWM, SWM, SM and SME.

Glyceria borealis (Nash) Batchelder, Northern mannagrass. Infrequent; SME, in mucky lagg areas.

Glyceria canadensis (Michx.) Trin., Rattlesnake grass. Occasional; in wet habitats along the stream channel, the northern outlet channel, and in the lagg.

Puccinellia pallida (Torr.) R. T. Clausen. Infrequent; SWM, SME, mucky graminoid lagg habitats.

POTAMOGETONACEAE

Potamogeton confervoides Reichb., Alga-pondweed. Abundant; Submersed in open water and among the branches, roots, and rhizomes of ericaceous shrubs along the lake margin; State status—Threatened.

Potamogeton oakesianus Robbins, Oakes' pondweed. Rare; SME lagg, a single population restricted to the muck pools.

SCHEUCHZERIACEAE

Scheuchzeria palustris L., Pod-grass. Occasional; SM, SWM, on the *Sphagnum* lawn or along the lake margin, inhabiting hollows and saturated level areas, usually among *Sphagnum majus.*

SPARGANIACEAE

Sparganium minimum (Hartman) Fries, Bur–reed. Rare; SME, restricted to the periodically inundated muck pools of the southeastern lagg.

TYPHACEAE

Typha latifolia L., Common cat-tail. Infrequent; two small, widely separated populations in the basin; the largest locality in the lagg of the SWM where runoff from the truck trail drains into the peatland basin; the smaller locality, isolated in the SME near the stream channel.

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OPUNTIA PINKAVAE (CACTACEAE), A NEW SPECIES FROM ARIZONA AND UTAH

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ABSTRACT. A new species of octoploid, dry-fruited prickly-pear (*Opuntia* subgenus *Opuntia*), *O. pinkavae*, is described from the Arizona–Utah boundary region. *Opuntia pinkavae* is most closely allied with *O. aurea*, a dry-fruited endemic, although its gross morphology resembles that of *O. macrorhiza*, a fleshy-fruited species.

Key Words: Cactaceae, *Opuntia* subgenus *Opuntia*, *Opuntia pinkavae*, prickly-pear, dry-fruited prickly-pear, polyploidy, pollen

Study of the *Opuntia polyacantha* complex (Parfitt unpubl.) revealed an undescribed species from northwestern Arizona and southwestern Utah. The name honors Dr. Donald J. Pinkava of Arizona State University, who brought modern biosystematic methods to the study of species-level relationships in the taxonomically challenging genus *Opuntia.*

Opuntia pinkavae Parfitt, *sp. nov.* (Figure 1). HOLOTYPE: USA, Arizona: Mohave Co., northwest of Bulrush Canyon south of Pipe Spring, 1400 m, *n* = 44, 30 May 1980, *B. D. Parfitt 2874* (ASU 111287!).

A *Opuntia macrorhiza* fructis siccis, perianthio magenteo-roseo, cladodiis interdum minute pappillatis, et chromosomatum numero octoploideo differt. A *O. aurea* spinis 1–4 per areolam in 20–50% distale areolarum, perianthio magenteo-roseo, chromosomatum numero octoploideo, et habitatione graminosa differt. A *Opuntia erinacea* (var. *erinacea* et var. *hystricina*) spinis tantum 1–4 solum in areolis distalibus caulis, spinis fructorum plerumque absentibus, cladodiis interdum papillatis, et chromosomatum numero octoploideo differt.

Low shrub with ascending to prostrate branches, 10–25 cm tall. Stem segments narrowly to broadly obovate, flat, glabrous or sometimes very minutely pubescent with erect papilla-shaped trichomes; terminal segments not readily detached, 6.5–15 cm long, 3–11 cm wide, thickness generally much less than half the width; areoles about 15–20 mm distant; rows of areoles transversing

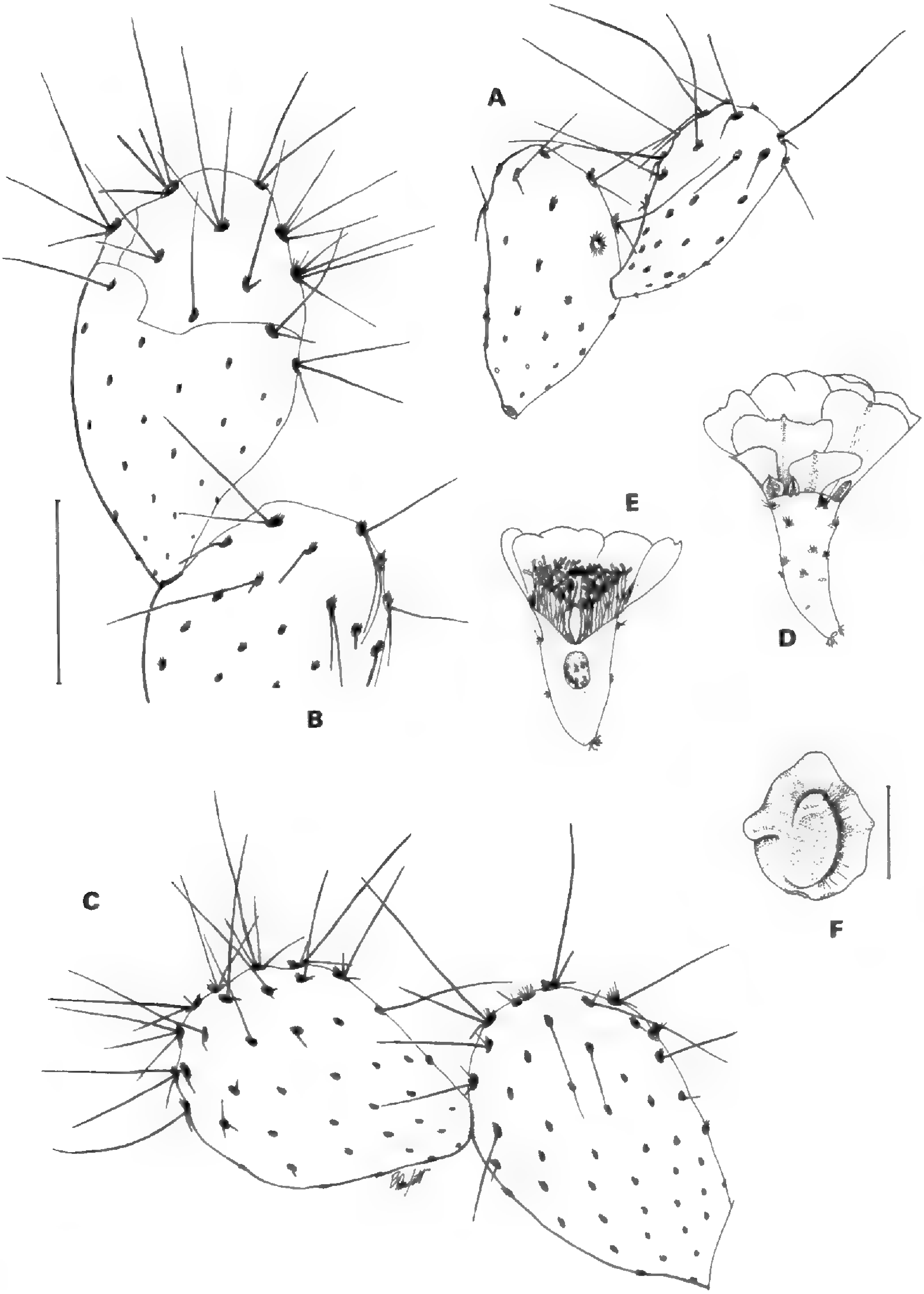

Figure 1. *Opuntia pinkavae:* A–C, stem segments; D, flower; E, flower, longitudinal section; F, seed. Scale bars: A–E, 5 cm; F, 5 mm. (A and D from *Brown 851 & Parfitt*; B and F from *Parfitt 2874* (holotype); C from *Brown 657 & Parfitt*; E from *Parfitt 3958 & Roberts.*)

stem segments (4–) 7–8. Spines occurring in upper 20–50 (–70)% of the areoles; major spines 1–3 (–4) per areole, the longest (3.5–) 5–7 cm long, 0.7–0.8 (–1) mm in basal diameter, descending to porrect, yellow-gray to white-gray, occasionally brown in basal half; minor spines (spines less than one-fourth the length of the longest spine in the same areole) 0–1, present in areoles with fewer than 3 major spines, 2–16 mm long. Glochids conspicuous, protruding 2–4 mm, forming a very dense crescent at apex of the areole, the sides of the crescent sometimes closing in and almost forming a column. Flowers 4.5–7.5 cm long; perianth magenta-pink, 2.5–3.5 cm long; filaments yellow to magenta; style white; stigma lobes green. Pollen dodecaporate, apertures smooth, margos semi-tectate, finely reticulate or nearly punctate with baculate lumina and columellate muri; tectum of the tetragonal, non-apertural faces punctate. Fruit 2–2.5 cm, dry; areoles (8–) 12–17; spines 1–4 per areole, 4–15 mm long, occurring mostly in upper areoles. Seeds 6.5–8 mm in maximum diameter; raphe 1.5–2 mm wide from embryo chamber to margin of seed. Chromosome number $2n = 8x = 88$ (Pinkava and Parfitt 1982, as *O. erinacea* var. *utahensis*; Parfitt unpubl.).

PARATYPES: **United States.** ARIZONA: Coconino Co., House Rock Valley, N of Rock Canyon, *Parfitt 2859* (ASU!); 1 mi N of Fredonia, *Brown 651 & Parfitt* (ASU!); Mohave Co., 1.2 mi N of hwy 389 on road to Moccasin, *Brown 657 & Parfitt* (ASU!); W of Kaibab Indian Reservation, *Parfitt 3958 & Roberts* (ASU!); Main Street Valley, W of Hurricane Cliffs, *Palmer & Hodgson 4620* (ASU!, DES); Navaho Trail near Hurricane Rim, *Gierisch 5132* (ASU!); 4.2 mi SW of Wolf Hole, *Brown 851 & Parfitt* (ASU!). UTAH: Washington Co., Warner Valley [SE of St. George], T43S R14W S7, *Gierisch 5049* (BRY!); 16 mi SSW of Hurricane on Fort Pierce Wash, *Earle s.n.* (ASU 108725!).

DISTRIBUTION, HABITAT, AND PHENOLOGY. *Opuntia pinkavae* is not uncommon in northwestern Arizona and extreme southwestern Utah at elevations of 1370–1560 m. The species occurs from the arid grasslands to the margins of pinyon-juniper woodlands. It is also found to persist in grasslands that have been damaged by excessive grazing and subsequent erosion. The substrate is usually fine, red sand; much less often it is limestone-derived loam. Flowering occurs in May and early June; fruits ripen in July.

TAXONOMIC RELATIONSHIPS. *Opuntia pinkavae* has long been overlooked as one of the many morphotypes included in Benson's (1969, 1982) concept of *O. erinacea* Engelmann & J. Bigelow var. *utahensis* (Engelmann) L. Benson. Any dry-fruited prickly-pear with few, flattened spines on the stem segments, and few to none on the ovaries, was referred to *O. erinacea* var. *utahensis* by Benson (1982). The polyphyletic *O. erinacea* var. *utahensis sensu* Benson includes *O. pinkavae* and few-spined ecotypes of *O. erinacea* var. *erinacea* and var. *hystricina* (Engelmann & J. Bigelow) L. Benson. The type of *O. erinacea* var. *utahensis* represents a few-spined individual from within the range of *O. erinacea* var. *hystricina.*

Opuntia pinkavae is most closely allied with the yellow-flowered *O. aurea* McCabe ex Baxter, a species of deep sand in pinyon-juniper woodlands along a small portion of the Arizona–Utah boundary. The similarities of pubescence, pollen ultrastructure, and seed morphology indicate a close relationship between the two species. *Opuntia aurea* differs in having the perianth yellow (without red or pink), stem segments spineless (rarely with a single short spine in one or two areoles), and hexaploid chromosome number ($2n = 6x = 66$; Pinkava et al. 1973; Pinkava and Parfitt 1982; Pinkava et al. 1992; Parfitt unpubl.). Stem segments of *O. aurea* are very minutely papillate, the trichomes visible at magnification of 25× or greater. In about two thirds of the known populations of *O. pinkavae* some individuals have similar papilliform trichomes. One population of *O. pinkavae* east of the Kaibab Plateau has many individuals almost spineless (e.g., only 3 spines on one segment), further suggesting relationship with *O. aurea.* Benson's (1982) remarks on hybridization between *O. aurea* and *O. erinacea* var. *utahensis* apply to *O. aurea* × *O. pinkavae.* Hybrids and backcrosses between the two species are known (Parfitt unpubl.) at the interface between their respective pinyon-juniper and arid grassland habitats.

Opuntia pinkavae resembles *O. macrorhiza* Engelmann in habit and gross morphology of the stem and spines. However, *O. macrorhiza* has fruits fleshy, perianth yellow with a red base, stem segments always glabrous, tetraploid chromosome number ($2n = 4x = 44$; Pinkava et al. 1992; Parfitt unpubl.), and pollen with foveolate or large-pitted non-apertural faces, and margines with broad, strongly baculate lumina. The tuberous roots for which *O. macrorhiza* was named have not been observed in *O. pinkavae.*

Opuntia erinacea var. *erinacea* and var. *hystricina* occasionally occur within a few kilometers of *O. pinkavae.* They are, however, very spiny tetraploids (Pinkava et al. 1973; Pinkava and Parfitt 1982; Pinkava et al. 1985; Pinkava et al. 1992; Parfitt unpubl.) with very spiny fruits, and bear little resemblance to *O. pinkavae*. On the eastern side of House Rock Valley, Coconino County, Arizona, the geographic distributions of *O. pinkavae* and *O. nicholii* L. Benson overlap by about 0.5 km. Specimens from throughout the range of either species are distinctive and not at all likely to be confused. Although some individuals of *O. nicholii* are heptaploid and some octoploid at a site about 27 km east of the geographic range of *O. pinkavae* (Parfitt unpubl.), *O. nicholii* is hexaploid throughout most of its geographic range (Pinkava et al. 1977; Parfitt unpubl.), including the area of sympatry. There is no evidence of interbreeding between the two taxa. *Opuntia phaeacantha* Engelmann, a fleshy-fruited hexaploid, is the only other *Opuntia* species occasionally occurring with *O. pinkavae*.

Plants of *Opuntia pinkavae* in the Warner Valley of Washington County, southwestern Utah, are often spineless or nearly so and pink-flowered, and have been treated as a variety of *O. basilaris* Engelmann & J. Bigelow—var. *woodburyi* W. Earle (1980). Plants in that population share a greater number of morphological characters with *O. pinkavae* than with *O. basilaris*. Furthermore, *O. basilaris* is diploid (Pinkava and McLeod 1971; Pinkava et al. 1973; Pinkava et al. 1977; Parfitt 1978; Takagi 1938; Sato 1958; Yuasa et al. 1973) and Warner Valley plants are octoploid ($2n$ = 88; Pinkava and Parfitt 1982, as *O. basilaris* var. *woodburyi*; Parfitt unpubl.). The name, *O. basilaris* var. *woodburyi,* was published for the Warner Valley plants without the required, specific indication of a holotype. It is, therefore, invalid (see Art. 37.1, 37.3 of Greuter et al. 1994). The Warner Valley plants are a robust, somewhat tuberculate-stemmed form of *O. pinkavae*.

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INTERSPECIFIC RELATIONSHIPS AND GENETIC DIVERGENCE OF THE DISJUNCT GENUS *LIQUIDAMBAR* (HAMAMELIDACEAE) INFERRED FROM DNA SEQUENCES OF PLASTID GENE *MAT*K

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ABSTRACT. Sequence data of the chloroplast *mat*K gene generated a phylogeny of *Liquidambar* containing two robust clades. One clade consisted of the Chinese species *L. acalycina* and *L. formosana,* while the other was composed of *L. orientalis* from Turkey and the North American *L. styraciflua.* The data support a close relationship between the western Asian and North American species, but not the division of *Liquidambar* into section *Cathayambar* (*L. formosana*) and section *Euliquidambar* (*L. acalycina, L. orientalis* and *L. styraciflua*). Sequence divergence of the *mat*K gene ranged from 0.1 to 1.0% among *Liquidambar* species and the estimated divergence times of the disjunct species in the genus were 45–90 mya, which agrees with the fossil record.

Key Words: phylogeny, *Liquidambar, mat*K, divergence

Liquidambar L. is the only genus in the Hamamelidaceae that has a disjunct distribution with species occurring in western Asia, eastern Asia, and North America. Four species are currently recognized in the genus. *Liquidambar formosana* Hance is widespread in eastern Asia (Chang 1979; Li 1977). *Liquidambar acalycina* Chang is found in at least nine provinces in mainland China (Chang 1979). *Liquidambar orientalis* Mill. occurs in Turkey and some nearby islands such as Rhodes (Rechinger 1943) and Cyprus (Holmboe 1914). *Liquidambar styraciflua* L. is widely distributed in eastern and southeastern North America and southward at high elevations in the mountains of Mexico and Central America to Honduras (Bogle 1986).

In *Liquidambar, L. acalycina* and *L. formosana* differ from *L. orientalis* and *L. styraciflua* in having 3-lobed instead of 5 (–7)-lobed leaves. The leaf lobes of *L. orientalis* are further subdivided, but they can intergrade with those of *L. styraciflua* (Bogle 1986). The presence of "setae" (Harms 1930), the carpel-like organs in pistillate flowers of *L. formosana,* has been used to distinguish *L. formosana* as section *Cathayambar* Harms from the other *Liquidambar* species as section *Euliquidambar* Harms (Harms 1930; Chang 1979).

Disjunct distribution of closely related plant species has long attracted the attention of both plant systematists and biogeographers (see review in Boufford and Spongberg 1983; Crawford and Lee 1992; Lee and Crawford 1991; Lee et al. 1996; Tiffney 1985a, b; Wen et al. 1996; Wen and Zimmer 1996). For *Liquidambar,* Hoey and Parks (1991, 1994) studied genetic divergence of the four species using allozymes and found that *L. orientalis* was more closely related to *L. styraciflua* than to either of the two eastern Asian species. Their study provided support for the existence of Atlantic land bridges between eastern North America and western Europe in the upper Cretaceous and Tertiary periods.

Crawford et al. (1992) pointed out that DNA sequence data may provide a more precise estimate of divergence than secondary chemicals or allozymes. Recent studies support that suggestion, and have shown that both nuclear and chloroplast DNA sequence data are informative in resolving phylogenetic relationships of disjunct taxa, even though resolution is variable for different taxa at different levels (Kim and Jansen 1994; Suh et al. 1993; Xiang et al. 1994). Undoubtedly, a high resolution of phylogeny provides a foundation for understanding phytogeography of disjuncts (Wen and Zimmer 1996).

The objective of this study is to use DNA sequences of the chloroplast *mat*K gene to investigate genetic divergence of the species of *Liquidambar* at the nucleotide level and to evaluate the phylogenetic and biogeographic relationships among the four *Liquidambar* species.

MATERIALS AND METHODS

Fresh leaves were collected from small trees of *Liquidambar styraciflua, L. acalycina,* and *L. formosana* cultivated in the greenhouse of the University of New Hampshire. Leaf buds of *L. orientalis* were provided by Tracy Omar at the University of Washington Arboretum, Seattle. Leaves of *Mytilaria laosensis*

Table 1. Locations and base compositions of amplification and sequencing primers used in this study. * this primer was synthesized with equal parts of "C" and "T" at base position 6.

Primer	5′ sequence 3′	Designed by
Forward		
*mat*KF1	ACT GTA TCG CAC TAT GTA TCA	Tao Sang
*mat*KF2	GTT CAC TAA TTG TGA AAC GT	Tao Sang
*mat*KF4	ACC CCA CCC CAT CCA TCT	Jianhua Li
*mat*KF5	TGG AGY CCT TCT TGA GCG A*	Jianhua Li
*mat*KF6	TCA GTG GTA CGG AAT CAA ATG C	Jianhua Li
Reverse		
*mat*KR1	GAA CTA GTC GGA TGG AGT AG	Tao Sang
*mat*KR2	TTC ATG ATT GGC CAG ATC A	Tao Sang
*mat*KR2-2	ACG GGG CCA TAA GAA AGT CG	Jianhua Li
*mat*KR3	GAT CCG CTG TGA TAA TGA GA	Tao Sang

Lec. were provided by Zhong-chun Luo at the Forest Bureau of Xinning, Hunan, China.

Total genomic DNAs were extracted from fresh leaves or buds following the protocol of Doyle and Doyle (1987). Polymerase Chain Reaction™ (PCR) was conducted in 0.2 ml thin-walled microcentrifuge tubes. Each 50 μl reaction included 5 μl of 10× *Taq* extender buffer (Stratagene, CA), 4 μl of 2.5 μm dNTP, 4 units (0.8 μl) of *Taq* extender (Stratagene, CA) and *Taq* polymerase (Promega, WI), 1 μl 20 μm primers, 2–3 μl genomic DNA solution (50–100 ng DNA), and an appropriate amount of UV-treated distilled water. The PCR thermocycler program followed Johnson and Soltis (1995) and the primers were *mat*KF1 and *mat*KR1. The PCR products were loaded on 0.8% LMP (Low Melting Point) agarose gel along with lambda *Hind*III DNA size markers and run for 2–3 hours at 40 volts in 0.5× TBE buffer. The band identified by comparison to the markers was then excised from the gel, liquefied at 65°C, and treated with agarase for 30 minutes at 37°C. This gel-purified PCR product was used directly as a sequencing template.

Sequencing reactions were carried out using the Cycle Sequencing Kit and following the manufacturer's protocols (Applied Biosystems, CA). The primers for sequencing were *mat*KF1, *mat*KF2, *mat*KF4, *mat*KF5, *mat*KF6, *mat*KR1, *mat*KR2, *mat*KR2-2 and *mat*KR3 (Table 1). The approximate locations and exact base compositions of the *mat*K primers are shown in Figure

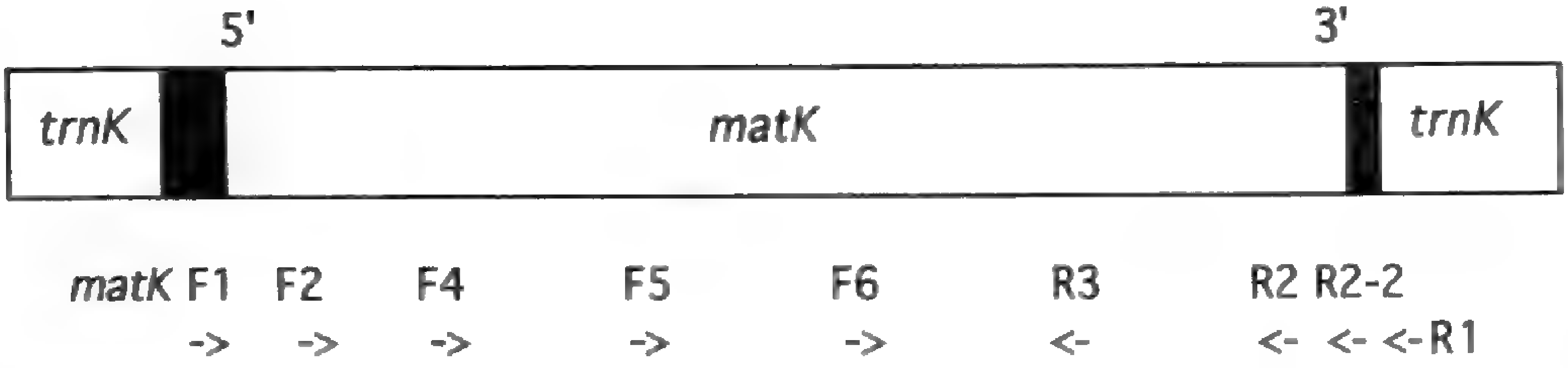

Figure 1. Approximate relative locations of *mat*K primers (base compositions are listed in Table 1, shaded areas are introns).

1 and Table 1. The cycle sequencing products then were separated on 6% polyacrylamide gel using an Automated Sequencer 373A (Applied Biosystems, CA) in the Sequencing Facility Center at the University of New Hampshire. The sequence chromatograms were analyzed using the SEQED program (Applied Biosystems, CA). Also, in order to assure correct basecalling, we overlapped sequences generated from adjacent primers of either the same or opposite directions. The complete *mat*K sequences of *Saxifraga integrifolia* (GenBank accession number L20131) and *Sullivantia sullivantii* (GenBank accession number L20130) were used to determine the limits of *mat*K sequences in *Liquidambar.*

The sequences were readily aligned using the MEGALIGN program of DNA* software packages (DNA* Inc., WI) and by sight. The aligned sequences were imported into the PAUP (Phylogenetic Analysis Using Parsimony) computer program (Swofford 1993) to search for the shortest trees, using the exhaustive search option. Our analysis of intergeneric relationships of the Hamamelidaceae using sequences of internal transcribed spacers (ITS) of nrDNA has shown that *Mytilaria laosensis* is the sister taxon to *Liquidambar* (Li et al., unpubl.). Thus, *M. laosensis* was used as the outgroup in this analysis. All characters and their states were treated equally. The pairwise distances were exported from PAUP and were used for the analysis of divergence. To test the level of clade support, we conducted 500 replicates of bootstrapping (Felsenstein 1985) and decay analysis (Bremer 1988; Donoghue et al. 1992) using the PAUP program. The aligned sequence matrices are available from the first author. The *mat*K sequences of the four species of *Liquidambar* have been submitted to the GenBank and their accession numbers are AF015649 through AF015652.

Studies have not been done previously to estimate substitution rates in the *mat*K gene. Therefore, we estimated a hypothetical

Table 2. *Liquidambar matK* gene sequence divergence (%).

Species	1	2	3	4
L. acalycina	—	0.1	0.5	0.9
L. formosana		—	0.7	1.0
L. orientalis			—	0.5
L. styraciflua				—

rate by using our unpublished data on the divergence between two closely related genera of the Hamamelidaceae—*Dicoryphe* Du Petit-Thours (endemic to Madagascar) and *Trichocladus* Pers. (endemic to eastern and southern Africa; Endress 1989)—and an estimated time of 100 mya, after which Africa and Madagascar were geologically stabilized and direct migration between them was probably not possible (Harland et al. 1990; Raven and Axelrod 1974; Schuster 1976). The resulting estimated substitution rate is 5.5×10^{-11} base per site per year for the *mat*K gene (assuming a constant substitution rate).

RESULTS

Sequence length and divergence. Sequences of the *mat*K gene in *Liquidambar* species were consistently 1512 bases long. Sequence divergences ranged from 0.1 to 1.0% (Table 2). In the aligned sequences there were 90 variable sites, seven of which were found to be phylogenetically informative.

Phylogenetic relationships. A single shortest phylogenetic tree of 92 steps was generated and the consistency index was 1.0 (Figure 2). The tree consisted of two clades, one of which included the east Asian species *Liquidambar acalycina* and *L. formosana,* while the other clade contained *L. orientalis* of western Asia and *L. styraciflua* of North America. Bootstrap percentages and decay indices were 99%/5 and 86%/2 for the two clades, respectively.

Time of divergence. Based on the substitution rate of *mat*K, 5.5×10^{-11} base per site per year (see above), the divergence times for *Liquidambar* species were 9 mya for *L. acalycina* and *L. formosana,* 45 mya for *L. acalycina* and *L. orientalis,* 81 mya for *L. acalycina* and *L. styraciflua,* 90 mya for *L. formosana* and

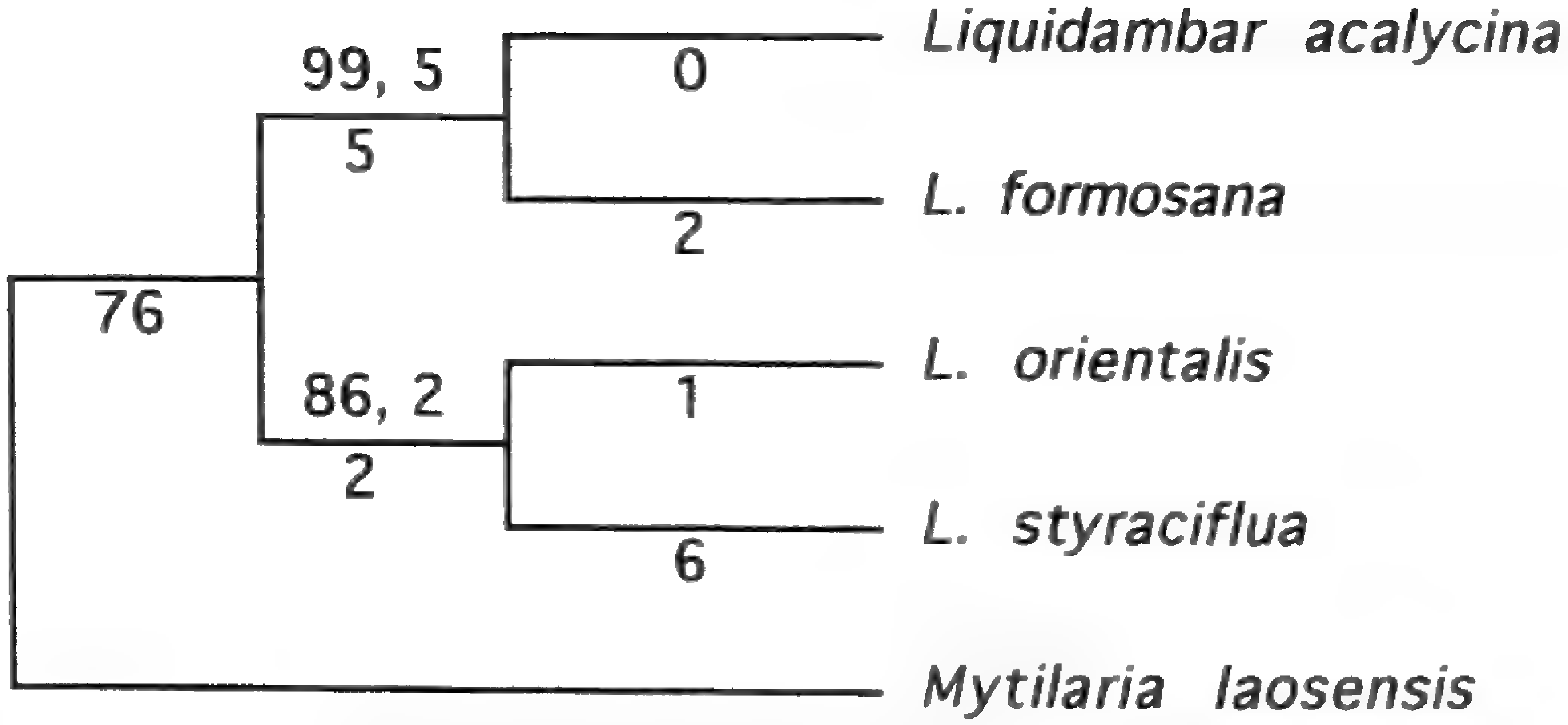

Figure 2. A single shortest phylogenetic tree of 92 steps of *Liquidambar.* Numbers above branches are bootstrap percentages and decay indices, and below branches are branch lengths. Consistency index is 1.0.

L. styraciflua, 63 mya for *L. formosana* and *L. orientalis,* and 45 mya for *L. orientalis* and *L. styraciflua.*

DISCUSSION

How to estimate genetic differences among taxa has long been one of the critical questions about disjuncts in general. Unfortunately, it is very difficult to use morphological, phenological, or even cytological characters to quantitatively assess genetic difference among the disjunct taxa (Lee et al. 1996; Oginuma and Tobe 1991). In contrast, molecular data, especially DNA sequences, have evident advantages over morphological characters in this respect (Crawford et al. 1992). Active research has been carried out in the last several years, using different sources of molecular data to quantify genetic divergence for a variety of disjunct taxa (Hoey and Parks 1991, 1994; Lee et al. 1996; Parks and Wendel 1990; Sang et al. 1994, 1995; Wen and Zimmer 1996; Xiang et al. 1994).

Recent discoveries of fossil flowers attributable to the subtribe Loropetalinae (Hamamelidoideae) have extended the fossil record of the Hamamelidaceae back to the Campanian (~70–75 mya) of the Late Cretaceous (Magallon-Puebla et al. 1996), while flowers of hamamelidaceous affinity extend back to the Santonian (~80 mya; Endress and Friis 1991) and the Turonian (~90 mya; Crepet et al. 1992).

The fossil record of *Liquidambar* and other altingioid plant remains is abundant in the Tertiary, dating back to at least the Tertiary–Late Cretaceous, and possibly to the mid-Cretaceous. Fossil altingioid fruiting inflorescences of the extinct genus *Steinhauera* Presl. are known from the Late Cretaceous–Tertiary boundary (Maastrichtian/Danian) to the Eocene of Europe (Friis and Crane 1989; Mai 1968) and have been considered close to either *Liquidambar* or *Altingia* (Ferguson 1989; Mai 1968; Tiffney 1986). *Liquidambar* pollen was present in the Paleocene (~55–65 mya) of North America and northeastern China (Li et al. 1995; Muller 1981; Taylor 1990; Tiffney 1986; Wang 1992), and Late Cretaceous to Paleocene of China (Sun 1979). Hedlund (1966) reports, with reservation, the possible occurrence of *Liquidambarpollenites* in the Cenomanian of Oklahoma (~95–100 mya).

By comparison, the estimated divergence times (~45–90 mya) for *Liquidambar* species from *mat*K data, using the hypothetical substitution rate described above, were fairly close to the fossil record, indicating an ancient origin and separation of *Liquidambar* populations in disjunct areas of eastern and western Asia, and North America.

As noted in the phylogenetic tree (Figure 2), the two clades are well supported by bootstrap percentages (99% and 86%, respectively). One clade consists of the two east Asian species, *Liquidambar acalycina* and *L. formosana,* and the other includes *L. orientalis* of Turkey and *L. styraciflua* from North America. Thus, the *mat*K phylogeny does not support the recognition of the two sections proposed by Harms (1930) and Chang (1979) based on the presence or absence of setae, and suggests that the presence of setae is an autapomorphy. This pattern, especially the close relationship of the west Asian species *L. orientalis* and North American *L. styraciflua,* has been suggested by an allozyme study (Hoey and Parks 1991). This relationship is also supported by leaf morphology (Bogle 1986).

The divergence times estimated from allozyme data by Hoey and Parks (1991), when Nei's (1987) formula was used, were 7 and 10 mya for *Liquidambar styraciflua–L. orientalis,* and *L. styraciflua–L. formosana,* respectively. However, when Sarich's (1977) and Thorpe's (1982) formulas were adopted, the times for *L. styraciflua–L. orientalis* were 13 and 16 mya, respectively. The estimated divergence times using allozyme data are rather recent compared to those from *mat*K data and the fossil record (~45–100 mya). Although calibrating the substitution rates is still not certain for either allozyme or *mat*K data sources, allozyme analysis tends to underestimate divergences, especially when amino acid substitutions not affecting electrophoretic mobility go undetected (Crawford et al. 1992). We believe that a comprehensive study of pairs of disjunct taxa whose times of separation have been known more or less precisely, using both nuclear and chloroplast DNA sequences, will provide an invaluable basis for evaluating substitution rates and divergence times of many other taxa.

The *mat*K gene has been widely used in resolving relationships of angiosperms at generic or higher levels (Johnson and Soltis 1995; Soltis et al. 1996; Steele and Vilgalys 1994), but this study suggests that it may be informative also in studying long separated species within a genus even though the substitution rate is low. Nonetheless, due to the low number of informative sites in the *mat*K gene, it seems to be important and interesting to further pursue the phylogenetic relationships of *Liquidambar* species using a fast evolving region such as the internal transcribed spacers of nuclear ribosomal DNA.

In summary, the *mat*K phylogeny supports the close relationship of west Asian *Liquidambar orientalis* and North American *L. styraciflua,* but does not agree with the division of the genus into two sections. The divergence of disjunct *Liquidambar* species was probably at least as early as 45 mya.

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NESTED TAXA-AREA CURVES FOR EASTERN UNITED STATES FLORAS

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ABSTRACT. The slopes of log-log species-area curves have been studied extensively and found to be influenced by the range of areas under study. Two such studies of eastern United States floras have yielded species-area curve slopes which differ by more than 100%: 0.251 and 0.113. The first slope may be too steep because the flora of the world was included, and both may be too steep because noncontiguous areas were used. These two hypotheses were tested using a set of nested floras centered in Ohio and continuing up to the flora of the world. The results suggest that this set of eastern United States floras produces a log-log species-area curve with a slope of approximately 0.20 with the flora of the world excluded, and regardless of whether or not the floras are from nested areas. Genera- and family-area curves are less steep than species-area curves and show similar patterns. Taxa ratio curves also increase with area, with the species/family ratio showing the steepest slope.

Key Words: species-area curves, flora, taxonomic ranks

The slopes of log-log species-area curves have been studied extensively because of their theoretical importance in biogeography and practical importance in biological conservation. The slope basically portrays the rate at which the number of species increases with an increase in geographic area. Slopes vary from about 0.1 to 1.0 and are influenced by the range of areas under study. A two-fold difference in slopes is biologically significant because it may indicate real differences in biota or problems in underlying methods. Log-log species-area curves for floras of the eastern United States have been studied by Monk (1971) and Wade and Thompson (1991). Both studies used floras from noncontiguous areas, and found slopes of 0.251 and 0.113, respectively. Monk pointed out that there was an absence of floras of areas between 0.25 and 100 km^2, and Wade and Thompson added some floras in this area range, calling them regional floras. The use of non-nested floras, however, may inflate the steepness of the species-area slope because the floras will be from areas that contain species not in the contiguous areas (Rosenzweig 1995).

Wade and Thompson pointed out that their slope was much less than Monk's for two reasons: in addition to using small floras, Monk used floras of larger areas and from different regions, and also did not have floras in the 0.25 to 100 km^2 range. It appears, therefore, that although Wade and Thompson filled in the gaps in the middle area range, they failed to use nested floras, thereby leading to an inflated slope estimate for the species-area curve for this region. In this study, I have used a recent flora from south-central Ohio (Bennett and Course 1996) to determine whether data from nested floras produce species-area curves with lower slopes than data from non-nested floras.

Species-area curves spanning at least a dozen orders of magnitude on a log area axis, i.e., up to about 10^9 km^2, follow a reverse S-shaped pattern (Williams 1964; Rosenzweig 1995). The slope is steep initially due to sampling effects, then becomes more gradual, and then increases again due to increasing diversity caused by continental-scale biota differences brought about by evolutionary changes in time. The interprovincial variation at larger geographic scales produces species-area curves with the steepest slopes because the biotic provinces rarely exchange species and are thus evolutionarily independent (Rosenzweig 1995). Thus, the use of larger sample areas in the data set may influence the regression slope by making it steeper than it is in the region under study. Monk added the flora of the world to his data set while Wade and Thompson did not, which may partially explain the steeper slope in Monk's study. Here I have studied this effect by comparing regressions with and without the flora of the world.

Taxa of higher ranks than species, e.g., genera and families, represent aggregations of species, so a tabulation of increasing numbers of genera and families is also a tabulation of more species. Even though there are smaller numbers of genera and families than species of plants, it is possible that the numbers of genera and families should increase with area as well, although no data could be found on this in the literature. In addition, the ratios of taxa, which represent taxonomic diversity, have not been examined in relationship to area. The ratios of species to genus, genera to family, and species to family also should increase with area, with the ratio that spans the greatest hierarchical range (species to family) showing the steepest slope. The relationships between taxonomic ratios and area were explored in this study using the floristic data mentioned above, as well as a larger set of 26 other floras.

MATERIALS AND METHODS

The initial data set was composed of eight floras that were completely nested within one another and spanned nine orders of magnitude in area (Table 1). This set centered on a Midwestern national park in south-central Ohio, Hopewell Culture National Historical Park (Figure 1). Floras of 26 other areas were analyzed to expand the sample set. Counts of taxa included species, genera, and families of vascular plants, including the pteridophytes, gymnosperms, and angiosperms. Infraspecific taxa were not included. For some floras, only data on angiosperms were available, and estimates of the numbers of gymnosperms and pteridophytes were made using other references. The totals for the world were calculated by combining the angiosperm numbers of Thorne (1992) with the gymnosperm and pteridophyte numbers of Mabberley (1987). Areas for the floras were obtained directly from the flora publications, atlases, and/or estimated by planimetry from maps. Some counts of taxa were available from the publications directly, while others had to be computed by hand. Ratios of taxa were computed by dividing total numbers of each taxon by the other appropriate taxon. Count and area data then were analyzed by log-log regression using Microsoft Excel. Analyses of covariance using a nested model were performed with Minitab in order to test for significant differences between regression slopes.

RESULTS

The log-log taxa-area curves for species, genera, and families of eight nested floras centered in south-central Ohio and the 26 other floras are shown in Figure 2. The set of all 24 regression slopes (6 taxa and ratios × nested or large data set × with or without the flora of the world = 24) is listed in Table 2. In general, the slopes decrease with an increase in taxonomic level, with the largest decrease in slopes occurring in the nested set of floras with the flora of the world included. Removing the flora of the world, however, decreases the slope as much as adding more floras, an unexpected result. There is virtually no difference in slope between the nested set and large set of floras with the flora of

Table 1. Areas, numbers of plant species, genera and families, and taxonomic ratios for 34 locations. The nested set locations (Figure 1) are indicated in bold print.

Location	Area (km^2)	Species	Genera	Families	S/G	G/F	S/F	Source
High Banks Unit	0.0324	174	135	57	1.29	2.37	3.05	Bennett & Course 1996
Seip Unit	0.2146	220	166	65	1.33	2.55	3.38	Bennett & Course 1996
Mound City Unit	0.4858	271	200	80	1.36	2.50	3.39	Bennett & Course 1996
Hopeton Unit	0.6275	238	172	67	1.38	2.57	3.55	Bennett & Course 1996
Hopewell Unit	1	348	229	86	1.52	2.66	4.05	Bennett & Course 1996
Hopewell Park	2.36	442	283	94	1.56	3.01	4.70	Bennett & Course 1996
Ft. Hill Memorial, Highland Co., OH	4.86	650	352	103	1.85	3.42	6.31	Braun 1969
Short Mtn., TN	12	477	262	92	1.82	2.85	5.18	McKinney 1986
Obed Wild & Scenic River, TN	40	733	392	122	1.87	3.21	6.01	Schmalzer et al. 1985
Bernheim Forest, KY	41	859	426	115	2.02	3.70	7.47	Gunn 1959
Savage Gulf, TN	44	677	360	111	1.88	3.24	6.10	Wofford et al. 1979
Mammoth Cave Nat. Park, KY	202	668	415	105	1.61	3.95	6.36	Davies 1955
Wirt Co., WV	609	673	360	106	1.87	3.40	6.35	Bartholomew 1948
Land Between the Lakes, KY-TN	688	789	427	116	1.85	3.68	6.80	Ellis et al. 1971
Giles Co., VA	923	1,026	482	124	2.13	3.89	8.27	Cooperrider & Thorne 1964
Calloway Co., KY	995	1,000	462	129	2.16	3.58	7.75	Woods & Fuller 1988
Ross Co., OH	1,792	1,104	495	122	2.23	4.06	9.05	Cusick & Silberhorn 1977
Monongahela Nat. Forest	6,568	1,353	535	129	2.53	4.15	10.49	Clarkson 1966
Delaware	15,688	2,111	721	142	2.93	5.08	14.87	Tatnall 1946

Table 1. Continued.

Location	Area (km²)	Species	Genera	Families	S/G	G/F	S/F	Source
Chicago region	28,490	2,530	793	143	3.19	5.55	17.69	Swink & Wilhelm 1994
Southeast Ohio	34,548	2,071	701	141	2.95	4.97	14.69	Cusick & Silberhorn 1977
Ohio	115,996	2,587	820	166	3.15	4.94	15.58	Braun 1989, 1967; Cooperrider 1995; Fisher 1988; J. Furlow, Unpubl. data
Pennsylvania	119,262	3,319	982	179	3.38	5.49	18.54	Rhoads & Klein 1993
Iowa	145,791	1,958	673	141	2.91	4.77	13.89	Eilers & Roosa 1994
Illinois	145,933	2,853	898	172	3.18	5.22	16.59	Mohlenbrock 1986
New England	172,678	2,882	790	151	3.65	5.23	19.09	Seymour 1982
Missouri	178,568	2,438	799	144	3.05	5.55	16.93	Steyermark 1963
Great Plains	1,564,995	2,909	850	161	3.42	5.28	18.07	Great Plains Flora Association 1986
Northeast U.S. & Canada	2,362,836	4,285	1,091	191	3.93	5.71	22.43	Gleason & Cronquist 1991
Northeast & north central U.S. & Canada	2,900,000	5,523	1,133	168	4.87	6.74	32.88	Fernald 1950
Canada	9,970,656	4,102	934	154	4.39	6.06	26.64	Scoggan 1978
North America north of Mexico	21,479,211	21,757	3,164	290	6.88	10.91	75.02	Kartesz 1994
Former Soviet Union	22,101,001	22,270	1,945	216	11.45	9.00	103.10	Czerepanov 1995
World	149,702,000	243,893	13,087	488	18.64	26.82	499.78	Mabberley 1987; Thorne 1992

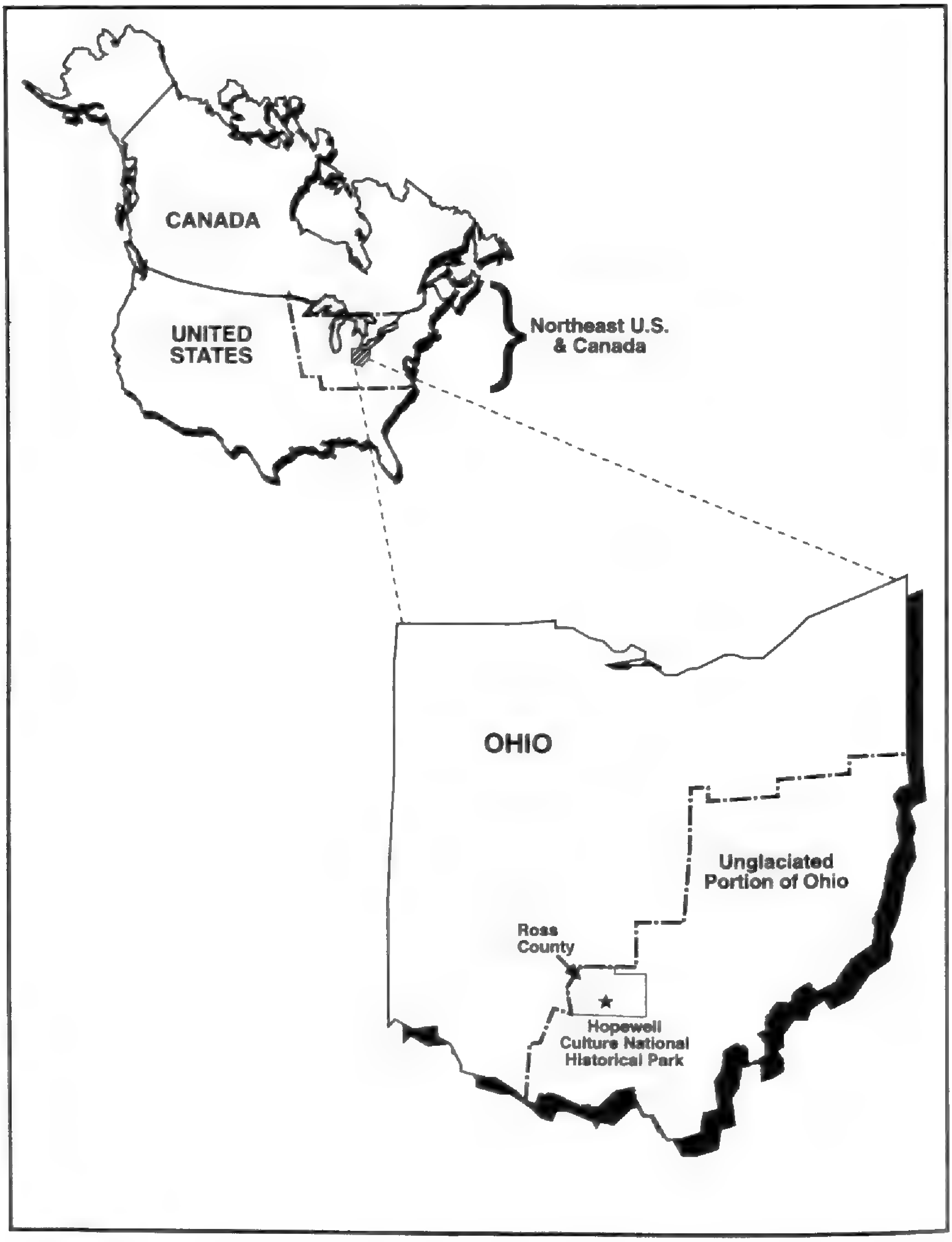

Figure 1. Map of six of the eight nested areas for which floras were used in this study. Missing are the Hopewell Unit of Hopewell Culture National Historical Park because it is too small to show, and the world.

the world removed. The set with the lowest slope for species was for the large set of 34 floras with the flora of the world omitted. The differences between slopes for genera and families followed similar patterns, although to a lesser degree.

The slopes of the taxa-area curves of species, genera, and fam-

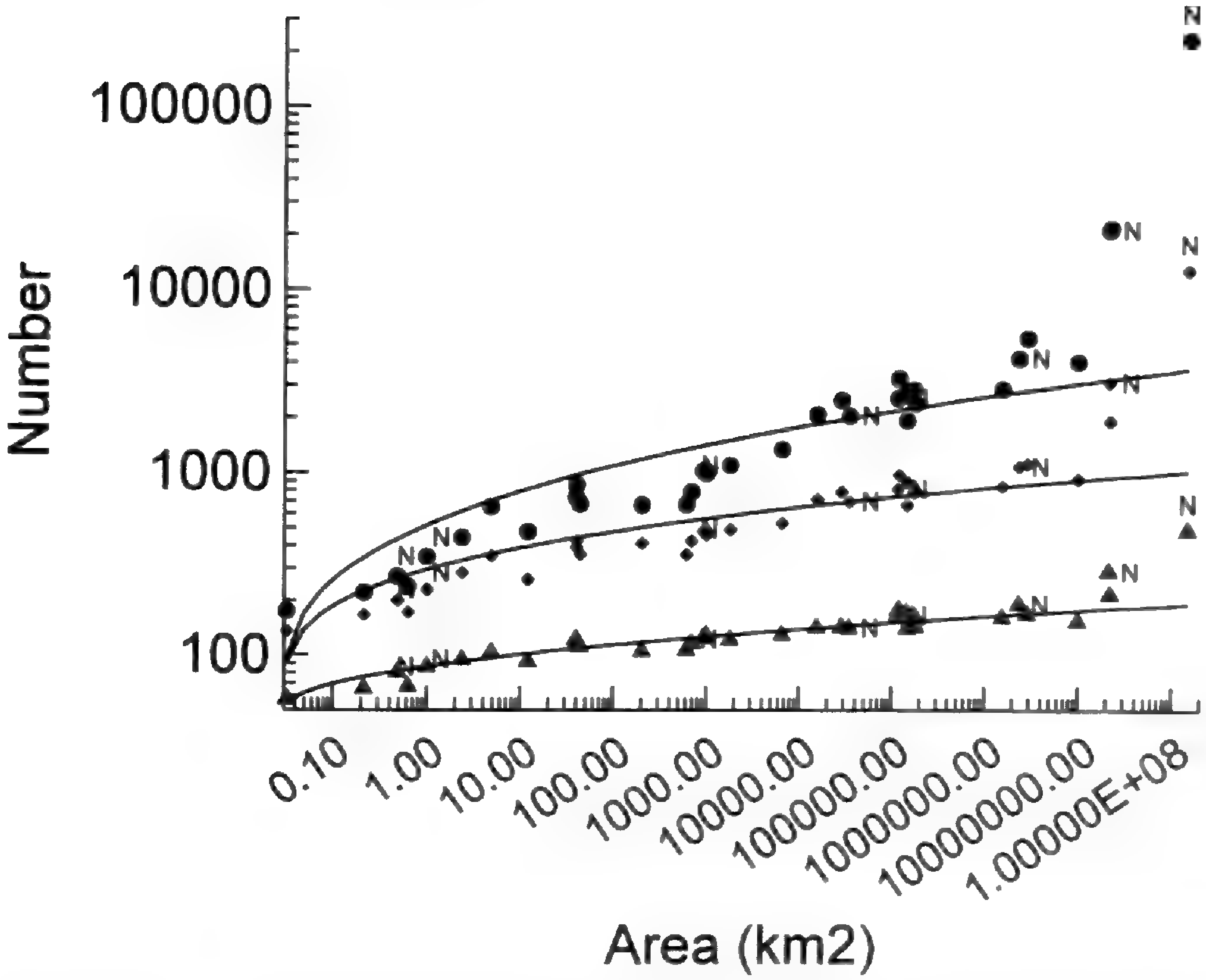

Figure 2. Taxa-area curves for 34 floras of the eastern United States, the former Soviet Union, and the world. Lines through points represent fitted log-log (power) regression equations for species (circles), genera (diamonds), and families (triangles). The subset of eight nested floras in the eastern United States is marked with an N. The three regression equations are: species = 264 $\text{area}^{0.22}$ ($r^2 = 0.83$), genera = 200 $\text{area}^{0.13}$ ($r^2 = 0.83$), and families = 79 $\text{area}^{0.06}$ ($r^2 = 0.84$).

Table 2. Log-log regression slopes of species, genera, families, and their ratios against area for four data sets. Each set of three regression slopes is significantly different ($P < 0.000$).

	Nested Set		Large Set	
Taxon or Ratio	+ World Flora	− World Flora	+ World Flora	− World Flora
Species	0.2800	0.2085	0.2216	0.1942
Genera	0.1724	0.1295	0.1332	0.1159
Families	0.0779	0.0626	0.0629	0.0563
Species/genus	0.1075	0.0790	0.0884	0.0783
Genera/family	0.0945	0.0669	0.0703	0.0597
Species/family	0.2020	0.1459	0.1587	0.1380

ilies within each set (Table 2) were significantly different ($P < 0.000$) in the analyses of covariance, indicating that they are separate regressions. All regression models accounted for 81 to 89% of the variation in taxa numbers (coefficients of determination).

Counts of taxa are measures of floristic richness. Another view of richness is that of taxonomic diversity, which is measured as the ratios of taxa, e.g., species/genus. The taxa-area slopes decline in the order species/family > genera/family = species/genus. Species/family increases with area about twice as much as the other two ratios. Omitting the flora of the world had the same effect on the slope as with the taxa-area curves, and the large set of floras had slopes that were less than those for the nested set.

DISCUSSION

The steepest slope in this study was for the species-area curve in the nested set of floras with the flora of the world included. The slope for the species-area curve for the complete set was somewhat lower, perhaps because many floras were added from smaller areas rather than larger, provincial areas. Regression models for the taxa-area curves explained 82% or more of the variation in numbers of taxa, as found by others (Monk 1971; Wade and Thompson 1991). Regression slopes and coefficients of determination of the taxa ratio curves were slightly lower overall than the taxa-area curves.

The eight-flora data set is highly nested from 1 km^2 to 1.49×10^8 km^2, so none of the increase in slope with increase in area is due to the study areas being noncontiguous. However, it appears that a large part of the increase in slope may be due to including the flora of the world, as Monk did. Without this flora the slopes for the nested set of floras and the larger set of 34 floras are practically the same, and average about 0.20. Adding more noncontiguous floras did not make the slope steeper as expected, probably because many of the floras that were added were for small areas. This data set, then, does not support the hypothesis that including noncontiguous areas will increase the slope of the species-area curve.

The 0.20 value of the slope for floras of the eastern United States is greater than the 0.15 for within-province variation, but less than variation between islands (0.25–0.45) and considerably less than variation between provinces (0.90; Rosenzweig 1995).

This suggests that this collection of floras of the eastern United States is related to area within a slightly larger province than Rosenzweig envisioned, and is not as different as islands would be in the same area range. Therefore, the slope appears more reasonable than the Monk or Wade and Thompson slopes.

The slopes for plant genera and families are all progressively less steep than the species slopes, which is explained by the fact that there are fewer genera and families to begin with, so the curves can't be as steep. Sixty percent of all the families in the world and 24% of all the genera are found in North America.

The taxa ratio curves increase with area much like the taxa-area curves, although only the species/family ratio curve is comparable. This ratio spans two levels of the hierarchy (species, genus, family), while the other two ratios span one level each. This is merely a reflection of the previous observations that the slope for the species-area curve is steeper than the family-area curve, so the ratio of the two must increase as well. Some authors, however, might question the usefulness of this because it is known that taxonomic ratios are manmade entities, and have been subject to arbitrary limits by some taxonomists (Stevens 1997).

To conclude, this set of eastern United States floras produces a log-log species-area curve with a slope of approximately 0.20, regardless of whether the floras are from nested areas or not, and with the flora of the world excluded. Genera- and family-area curves are less steep than species-area curves and follow a similar pattern. Taxa ratio curves also increase with area, with the species/family ratio showing the steepest slope.

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A SYNOPSIS OF THE GENUS *MACROPHARYNX* (APOCYNACEAE)

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ABSTRACT. A synopsis of the genus *Macropharynx* is provided. *Macropharynx renteriae* is reported for the first time from Mesoamerica. A new combination, *M. steyermarkii* is proposed here.

Key Words: Apocynaceae, Apocynoideae, *Macropharynx*

Macropharynx is a neotropical genus of lianas with 5 species ranging from Costa Rica to northern Argentina. The genus was described by Rusby (1927), with a single species, *M. fistulosa.* Some years later Woodson (1931) found an older basionym for the same species and proposed a new combination, *M. spectabilis.*

Macropharynx is characterized by having eglandular leaves, subumbelliform to somewhat short-racemose, unbranched inflorescences, sepals with a solitary colleter, corolla tubes exappendiculate within and without a faucal annulus, nectaries longer than the ovary and as numerous as the sepals, and anther apices with attenuate to acute and indistinct auricles. According to Rusby (1927), Woodson (1933, 1936), and Pichón (1950), the most striking characteristic of *Macropharynx* is the presence of 7–13 sepals, an unusual condition in Apocynaceae. However, the eventual description of more species within the genus shows that this condition is restricted to *M. spectabilis* and occasionally to *M. renteriae,* which sometimes has flowers with six sepals. The variability of the number of sepals was pointed out by Woodson (1936) when he described *M. anomala,* a species which was included within *Macropharynx* in spite of the presence of only five sepals. In addition, Markgraf (1932) remarked that there is no clear demarcation between the sepals and the several bracts just below them in some species and he found that there is even a gradation in the presence of the characteristic episepalous colleter at the base of the bracts or sepals (e.g., *M. spectabilis*).

Recently, Morillo (1995) characterized *Macropharynx* as having an indefinite number of glands (nectaries) distributed within the calyx, as opposed to *Asketanthera steyermarkii* Markgraf (here included in *Macropharynx*), which has only a solitary, episepalous gland per colleter. However, this characterization is erroneous because *Macropharynx* always has only one episepalous gland per colleter. In species such as *M. spectabilis* all the sepals share one colleter, but when lacerated, the colleter may be mistaken for many separate colleters. This is obvious in some genera such as *Prestonia* (Morales 1997), in which at anthesis, the colleters are generally entire or scarcely lacerate, but later exhibit many different kinds of laceration.

Macropharynx and *Asketanthera* Woodson are closely related within the Echiteae. These two genera can be distinguished using the following key:

1. Inflorescence bracts broadly ovate to broadly lanceolate-ovate, 1–2.5 cm long, 0.7–1.3 cm wide; anther auricles usually somewhat rounded or nearly so; nectaries shorter than the ovary; West Indies .... *Asketanthera*
1. Inflorescence bracts linear, narrowly elliptic, elliptic to lanceolate, 0.5–1.6 cm long, 0.2–0.5 cm wide; anther auricles acute to short-acuminate; nectaries equalling or longer than the ovary; Costa Rica to Argentina .... *Macropharynx*

Since the last treatment of *Macropharynx* (Woodson 1936), additional field and herbarium studies have increased the number of recognized species and altered our concept of the genus. In addition, while preparing the treatment of Apocynaceae for *Flora Mesoamericana,* the genus *Macropharynx* was reported for the first time from this area, increasing the range of distribution of the genus. This unacceptable situation seemed to warrant the synopsis presented here, which provides an up-to-date account of the genus.

A diagnostic key to the recognized species is presented here. In common species, only selected specimens are cited.

TAXONOMIC TREATMENT

Macropharynx Rusby, Mem. New York Bot. Gard. 7: 327, pl. 6. 1927. TYPE: *M. spectabilis* (Stadelmeyer) Woodson.

Suffruticose lianas. Stems usually terete to somewhat flattened, minutely ferrugineous-tomentulose, hispid to glabrate, inconspicuously to somewhat lenticellate, with milky sap or clear latex (even in the same species). Leaves opposite, membranaceous to firmly membranaceous, blade minutely puberulent, rarely sparsely strigillose or hispid, eglandular, petiole minutely appendiculate, slightly fused at the base, mostly glandular in the axils. Inflorescence a subumbellate cincinnus cyme, axillary, variously puberulent, (1) 3–16-flowered, short-pedunculate, bracts foliaceous to somewhat foliaceous, rarely scarious. Flowers: sepals 5–13, imbricate at the base, bearing a solitary episepalous colleter within, entire or minutely erose or denticulate; corolla infundibuliform or salverform, hispid, minutely puberulent to glabrous or glabrate without, tube exappendiculate within, the limb 5-parted, actinomorphic, dextrorsely convolute; stamens 5, included to somewhat exserted, infrastaminal indument within, anthers connivent and agglutinated to the pistil head, consisting of 2 parallel, uniformly fertile thecae borne adaxially near the apex of an enlarged, sagittate, 2-auriculate, peltate connective, auricles short, acute to short-acuminate, filaments short, puberulent to pilose; carpels 2, united at the apex by a common stylar shaft surmounted by the fusiform pistil head, ovules numerous, multiseriate; nectaries 5, distinct. Follicles 2, apocarpous, smooth, terete to subterete, thick or thin, dehiscing along the ventral suture, seeds numerous, dry, rostrate, comose, usually rugose.

Macropharynx comprises 5 species, ranging disjunctly from Costa Rica and Colombia to Bolivia and northern Argentina.

KEY TO THE SPECIES OF *MACROPHARYNX*

1. Sepals 7–13, linear to very narrowly elliptic . . 1. *M. spectabilis*
1. Sepals 5, rarely 6, narrowly lanceolate or elliptic to narrowly to broadly ovate . . . . (2)
    2. Sepals broadly ovate; inflorescence racemose and somewhat elongate; Northern Argentina . . . . 2. *M. meyeri*
    2. Sepals narrowly lanceolate, narrowly elliptic to narrowly ovate; inflorescence subumbelliform, fasciculate or cymose, reduced and congested; Venezuela, Ecuador, Colombia, and Costa Rica . . . . (3)
        3. Stems and leaf blades densely to sparsely hispid, indument yellowish . . . . 3. *M. steyermarkii*
        3. Stems and leaf blades minutely ferrugineous-tomentulose to glabrate . . . . (4)

4. Corolla salverform; tube 1.4–1.6 cm; lobes 0.9–1.2 cm . . . . 4. *M. anomala*
4. Corolla subsalverform to very narrowly infundibuliform; tube 2.3–3 cm; lobes 2–2.4 cm . . 5. *M. renteriae*

1. **Macropharynx spectabilis** (Stadelmeyer) Woodson, Ann. Missouri Bot. Gard. 18: 552. 1931.

Echites spectabilis Stadelmeyer, Flora 24 (1), Beibl. 1 (3): 44. 1841. TYPE: BRAZIL. Amazonas: Río Negro et Río Solimoes in regione Japurensi, *Martius s.n.* (HOLOTYPE: M; ISOTYPE: B, destroyed; photographs, F, INB, MO, NY, US ex M).

Elytropus spectabilis (Stadelmeyer) Miers, Apoc. South Am. 116. 1878.

Macropharynx fistulosa Rusby, Mem. New York Bot. Gard. 7: 329. fig. 6. 1927. TYPE: BOLIVIA. Rurrenabaque, 30 Jan 1922, *White 3260* (HOLOTYPE: NY; ISOTYPE: MO).

Macropharynx strigillosa Woodson, Fieldiana, Bot. 28: 499. 1953. TYPE: BRAZIL. Pará: Belem, northeast woods of the I.A.N., 20 Oct 1942, *Archer 7770* (HOLOTYPE: MO; ISOTYPE: US).

Stem terete to subterete, densely hispid to minutely and densely ferrugineous-tomentulose, eventually becoming glabrate. Leaves: blade 8–33.5 cm long × 4.5–21 cm wide, membranaceous to subchartaceous, broadly ovate, elliptic-ovate to ovate, apex shortly and abruptly acuminate, base obtuse, rounded to somewhat cordate, the upper surface minutely ferrugineous-puberulent, becoming glabrate, lower surface minutely ferrugineous-pilosulous to glabrate (sometimes sparsely hispid on both surfaces), petiole 2.5–9 cm long, hispid, ferrugineous-tomentulose to glabrate. Inflorescence axillary, subumbellate to subumbellate-fasciculate, (1) 2–7 (10)-flowered, peduncle 0.3–0.7 (1.5) cm, pedicels 0.7–1.5 (2) cm, bracts 0.5–0.6 cm long, linear to very narrowly elliptic, conspicuous, scarious to somewhat foliaceous. Flowers: sepals 7–13, linear to very narrowly lanceolate to very narrowly elliptic, 0.8–1.4 cm, minutely puberulent to glabrate, slightly foliaceous, bearing 1 colleter within, minutely denticulate; corolla infundibuliform to subsalverform, greenish-white, glabrous to glabrate without, tube 2–5 cm, sometimes inflated at the insertion of the stamens, lobes 1.2–2.3 cm long, obliquely obovate; stamens inserted approximately in the middle of the corolla tube, anthers 9–10 mm, included, glabrous; ovary ca. 3 mm long, glabrous to glabrate, pistil head 1.5–2 mm long; nectaries 3–3.5 mm long, separate. Follicles 14–25 cm long × 1.3–1.8 cm wide, somewhat falcate, ferrugineous-hispidulous to glabrous or glabrate, seeds 1.2–1.5 cm long, the coma 4.4–5 cm long, tannish-cream.

Macropharynx spectabilis occurs in wet forests of Colombia, Ecuador, Venezuela, Guyanas, Peru, Bolivia, and Brazil, from 50–1000 m, and is the most widely distributed species in the genus.

A good character to identify this species is the 7 to 13 linear sepals of the calyx. The only other species of *Macropharynx* with more than five sepals (occasionally) is *M. renteriae,* but it differs greatly in having wider sepals and bracts. The consistent presence of 7 to 13 sepals is an unusual condition in Apocynaceae. Among all the neotropical genera known to me, this characteristic is otherwise found in only one species of *Aspidosperma, A. darienensis* Woodson ex Dwyer, which has 6 to 7 sepals.

Macropharynx spectabilis exhibits great variation in the density of indument on the inflorescence and stems, and in the length and shape of the corolla, as was pointed out by Xifreda (1984). These characters are variable in other genera of Apocynaceae (e.g., *Prestonia, Mandevilla, Odontadenia*) and cannot be used to separate species (Morales 1996, 1997, 1998).

Only a selection of specimens examined is cited for each country, but a list of all the specimens examined is available on request.

REPRESENTATIVE SPECIMENS. **Colombia.** CAQUETÁ: Río Orteguaza, 25 Jan 1969, *Plowman et al. 2279* (MO, NY). VAUPÉS: Sorotama, Río Apaporis, entre el Río Pacoa y el Río Kananari, 15 Sep 1951, *Schultes et al. 13991* (COL [2 sheets], F, MO); above mouth of Río Kananari, Jan 1952, *Schultes et al. 19592* (COL, F, MO).

Ecuador. NAPO: near Lago Agrio, road to Baeza, 5 Aug 1974, *Plowman et al. 4086* (COL, UC).

Venezuela. BOLÍVAR: Caño Pablo, tributary of Río Caura, 10 May 1982, *Liesner et al. 14002* (MO); forested middle slopes near Río Tirica, 5 Mar 1955, *Steyermark et al. 1254* (NY); along Río Karuai of Sororopán Tepui, W of La Laja, 29 Nov 1944, *Steyermark 6077* (NY, MO).

Bolivia. BENI: Rurrenabaque, 1 Dec 1921, *Cárdenas 1894* (K, NY, US); Moxos, San Ignacio de Moxo, 12 Apr 1979, *Krapovickas et al. 34954* (CTES, MO, SI); Ballivian Province, road Caranavi-San Borja, Serranía del Pilón Lajas, 16 Feb 1990, *Smith et al. 13939* (INB, LPB, MO). LA PAZ: San Carlos, 21 Dec 1926, *Buchtien 1743* (NY); Larecaja, 24 Jan 1988, *Solomon 17688* (LPB, MO). SANTA CRUZ: Ichilo Province, 15 km SSE of Buena Vista, San Rafael de Amboro, 19 May 1991, *Gentry 74127* (INB, MO); Ichilo, Parque Nacional Amboro, 12 Dec 1989, *Nee 38099* (MO, NY); Lara, Río Surutu, 27 Dec 1924, *Steinbach 6813* (B, BA, K, MO); Buenavista, 23 Dec 1916, *Steinbach 3200* (MO, SI).

Peru. LORETO: Iquitos, 3–11 Aug 1929, *Killip & Smith 27102, 27493* (both MO, NY, US); Mishuyacu, near Iquitos, Oct 1929, *Klug 541* (NY, US); Río Nanay, 25 Feb 1976, *Revilla 237* (F, MO); Maynas, Río Ampiyacu, 19 Jul 1976, *Revilla 918* (F, MO); Maynas, Río Nanay, near Iquitos, 12 Apr 1978, *Rimachi 3545* (MO). SAN MARTÍN: Province Mariscal Cáceres, Río Sión, 2 Oct 1969, *Schunke 3457* (COL [2 sheets], F, MO, NY); Mariscal Cáceres, Tocache Nuevo, 20 Apr 1970, *Schunke 3950* (COL, F, MO); Tocache Nuevo, road to Pushurumbo, 2 Mar 1978, *Schunke 9969* (COL, F, MO, NY).

Brazil. AMAZONAS: Estrada de Petrobas, 17 Jun 1958, *Coelho 10* (MO); Manaus, Reserva Experimental do INPA, 3 Aug 1973, *Prance et al. 18724* (INPA, NY). PARÁ: Belem, 1 Jan 1926, *Ducke 21586* (B, RB, US); Santarem, km 70 da estrada do palhao, arredores do Acampamento do Igarape Guarana, 8 Nov 1969, *Silvia et al. 2517* (MG, NY).

2. **Macropharynx meyeri** (C. Ezcurra) Xifreda, Kurtziana 17: 164. 1984. *Temnademia meyeri* C. Ezcurra, Hickenia 1: 241. 1981. TYPE: ARGENTINA. Jujuy: Santa Bárbara, Sierra de Santa Bárbara, 1300 m, 15 Dec 1962, *de la Sota 2967* (HOLOTYPE: LP; photograph, INB ex LP).

Stem terete to subterete, minutely tomentulose to glabrate. Leaves: blade 7–15 (17.5) cm long × 5–11 (14.5) cm wide, membranaceous, ovate, apex acute, obtuse to short-acuminate, base broadly obtuse to rounded, the upper surface puberulent, lower surface densely and minutely tomentulose to puberulent, petiole 1.4–3.2 (3.6) cm long, puberulent. Inflorescence axillary, racemose, 6–11-flowered, peduncle 2.5–4 cm, pedicels 1.4–2.2 cm, bracts 0.8–1.3 cm long, lanceolate to narrowly elliptic, relatively conspicuous, somewhat foliaceous. Flowers: sepals 5, broadly ovate, 0.8–1.2 cm, foliaceous, minutely puberulent, bearing 1 colleter within, minutely lacerate; corolla salverform, reddish or yellowish to lilac, minutely puberulent without, tube 0.8–1 cm, 0.2–0.3 cm in diameter, not inflated at point of stamen insertion, lobes 0.5–0.6 cm long, narrowly obliquely ovate; stamens inserted near the mouth of the corolla tube, anthers 5–6 mm, somewhat exserted, glabrous to glabrate; ovary ca. 2 mm long, glabrous, pistil head ca. 2 mm long; nectaries ca. 2.5 mm long, separate. Follicles and seeds unknown.

This species occurs in northern Argentina, where it grows in premontane wet forests from 1300 to 1600 m, but probably will be found in Bolivia as well.

Macropharynx meyeri could be confused with *M. anomala,* which is endemic to western Ecuador, but the latter species has a subumbelliform, somewhat congested inflorescence, and a longer corolla tube. Vegetatively this species is similar to *Prestonia riedelii* (Müller Argoviensis) Markgraf, but is easily distinguished by the exappendiculate corolla tube (without callus ridges) and the absence of a faucal annulus.

REPRESENTATIVE SPECIMENS. **Argentina.** JUJUY: Valle Grande, road Valle Grande to San Francisco, *Villa et al. 758* (LIL); Santa Bárbara, Sierra de Santa Bárbara, El Tipal, *Fabris 8077* (LP). SALTA: Santa Victoria, road to Los Toldos, ca. 12 km N of Lipeo, *Legname et al. 10030* (LIL, xerox INB ex LIL).

3. **Macropharynx steyermarkii** (Markgraf) J. F. Morales, *comb. nov.* Basionym: *Asketanthera steyermarkii* Markgraf, Acta. Bot. Venez. 5: 65–66. 1975. TYPE: VENEZUELA. Falcón: Sierra de San Luis, montaña de Paraguariba, 1400 m, 23 May 1979, *Steyermark 99348* (HOLOTYPE: Z; ISOTYPES: MO, VEN; photograph, INB ex MO).

Stem terete, densely to sparsely hispid. Leaves: blade 9.5–14 cm long × 5–8.5 cm wide, coriaceous, ovate, apex acuminate to acute, base rounded to somewhat cordate, the upper surface strigillose, lower surface hispid, petiole 0.9–1.4 cm long, hirsute. Inflorescence axillary, subumbellate-fasciculate, 3–7-flowered, peduncle 0.1–0.2 cm, pedicels 0.7–1.1 cm, bracts 0.6–0.7 cm long, narrowly elliptic, slightly subfoliaceous to scarious, inconspicuous. Flowers: sepals 5, narrowly lanceolate-ovate to narrowly elliptic, 1.1–1.3 cm, somewhat foliaceous, hispid, bearing 1 colleter within, minutely denticulate; corolla salverform to subsalverform, olive-green to yellowish-green, hispid, tube 1.8–2.2 cm, ca. 0.3 cm in diameter, lobes 0.9–1.2 cm long, obliquely ovate; stamens inserted near the base of the corolla tube, included, anthers 7–8 mm, included, glabrous; ovary 1–1.5 mm long, glabrous, pistil head 1.5–2 mm long; nectaries 1–1.5 mm long, separate. Follicles 15–18 cm long × 1.5–2 cm wide, somewhat falcate, hispid, seeds unknown.

Macropharynx steyermarkii occurs in premontane wet forests from 1000 to 1600 m in Venezuela, in the Falcón and Yaracuy states. It is known only from a few collections.

This species was originally described within *Asketanthera,* but following Pichón (1950), it must be transferred to *Macropharynx.* Characters suggesting its inclusion in *Macropharynx* are disk glands longer than the ovary, anther apices with attenuate to acute auricles and the ovules in series of 10 in each carpel. In *Asketanthera* the disk glands are shorter than the ovary, anther auricles are somewhat rounded and the bracts of the inflorescence are foliaceous and well developed. In addition, *Asketanthera* is restricted to the West Indies.

Despite the fact that Woodson (1936) and Pichón (1950) characterized *Macropharynx* as having more than six sepals, five sepals occur in other species of the genus (*M. anomala, M. meyeri*).

REPRESENTATIVE SPECIMENS. **Venezuela.** FALCÓN: Sierra de San Luis, montaña de Paraguaribo, 23 May 1979, *F. Falcón 675* (MO, VEN); Cerro Socopo, 29 Jun 1979, *Liesner et al. 8411* (MO, U). YARACUY: Sierra de Aroa, Cerro Tigre, 3 Apr 1980, *Liesner et al. 9983* (MO).

4. **Macropharynx anomala** Woodson, Ann. Missouri Bot. Gard. 21: 614. 1934. TYPE: ECUADOR. Pilatón, Oct 1902, *Sodiro 107/16* (HOLOTYPE: B, destroyed; photographs, INB, MO ex B); *Dodson & Gentry 9704* (NEOTYPE: designated here, MO!; ISONEOTYPE: SEL!).

Stem subterete, minutely and densely ferrugineous-tomentulose to glabrate. Leaves: blade 9.5–21 cm long × 4.5–10 cm wide, membranaceous, broadly ovate to ovate, apex short-acuminate, base broadly obtuse to rounded, sometimes somewhat cordate, the upper surface ferrugineous-puberulent, lower surface densely and minutely ferrugineous-tomentulose, petiole 2–3.2 cm long, ferrugineous-tomentulose. Inflorescence axillary, subumbellate-fasciculate to subumbellate, 3–7-flowered, peduncle 1.5–2.9 cm, pedicels 1.3–2 cm, bracts 1–1.6 cm long, linear to very narrowly elliptic, relatively conspicuous, somewhat foliaceous. Flowers: sepals 5, narrowly lanceolate to narrowly elliptic, 1.6–1.9 cm, somewhat foliaceous, minutely puberulent, bearing 1 colleter within, entire to minutely denticulate; corolla salverform, white-cream, minutely puberulent without, tube 1.3–1.7 cm, ca. 0.2 cm in diameter, somewhat inflated at the insertion of the stamens, lobes 0.9–1.2 cm long, narrowly ovate; stamens inserted near the base of the corolla tube, anthers 7–8 mm, included, glabrous to glabrate; ovary 1.5–2 mm long, glabrous, pistil head 1.5–2 mm long; nectaries 1.5–2.5 mm long, somewhat separate. Follicles 32–36 cm long × 0.8–1.3 cm wide, linear, finely and glabrescently rufous-tomentose, seeds unknown.

This species occurs in western Ecuador, where it grows in wet forests from 1000 to 1400 m. Until recent collections, it was known only from the type at the Berlin Herbarium (B), which was destroyed during World War II.

The diagnostic characteristics of this species are the small, salverform corolla, the narrowly elliptic to narrowly lanceolate sepals, and the subumbelliform inflorescence. It resembles *Macropharynx meyeri,* from northern Argentina, but the latter species is easily distinguished by its racemose inflorescences.

I chose *Dodson & Gentry 9704* as the neotype because, of the two collections known to me of this species, it represents the most complete specimen, with both flowers and fruits.

REPRESENTATIVE SPECIMEN. **Ecuador.** PASTAZA: road between Baños and Mera, 8 Mar 1985, *Neill et al. 6164* (MO, USF).

5. **Macropharynx renteriae** A. H. Gentry, Phytologia 47: 99. 1980. TYPE: COLOMBIA. Chocó: ca. 37 km W of Las Animas on new Panamerican Highway, 180 m, 10 Jan 1979, *Gentry & Rentería 23955* (HOLOTYPE: COL; ISOTYPES: HUA, INB, MO, NY; photograph, INB ex MO).

Stem terete to subterete, minutely and densely ferrugineous-tomentulose to glabrate. Leaves: blade 11–30 cm long × 6–22.5 cm wide, membranaceous, broadly elliptic, ovate-elliptic to ovate, apex acute to acuminate, base obtuse, rounded to somewhat cordate, the upper surface glabrous to glabrate, lower surface sparsely to moderately and minutely ferrugineous-tomentulose, petiole 3–8.5 cm long, ferrugineous-tomentulose. Inflorescence axillary, subumbellate to subumbellate-fasciculate, (1)2–8 (16)-flowered, peduncle 0.3–0.7 cm, pedicels 0.9–2 cm, bracts 1–1.6 cm long, elliptic to narrowly elliptic, relatively conspicuous, somewhat foliaceous. Flowers: sepals 5–6, narrowly lanceolate to narrowly elliptic, 1.1–2.1 cm, somewhat foliaceous, minutely puberulent to glabrate, bearing 1 colleter within, minutely denticulate; corolla subsalverform to very narrowly infundibuliform, white to white-cream, the tube yellow within, minutely puberulent to glabrate without, tube 2.3–3 cm, 0.3–0.4 cm in diameter, inflated at the insertion of the stamens, lobes 2–2.4 cm long, obliquely obovate; stamens inserted approximately in the middle of the corolla tube, anthers 7–8 mm, included, pubescent dorsally to glabrate; ovary ca. 2 mm long, glabrous, pistil head 1.5–2 mm long; nectaries 2–

3 mm long, separate. Follicles 40–46 cm long × 0.7–1 cm wide, linear, densely and minutely ferrugineous-tomentulose, seeds 0.7–0.9 cm long, the coma 3.3–4.8 cm long, tannish to tannish-cream.

This species is known from wet forests and premontane forests in Costa Rica, Colombia, and Ecuador at 300 to 1000 m. Until recent collections from Costa Rica and Ecuador, *Macropharynx renteriae* was known only by the Colombian type collection. This is the first species of *Macropharynx* reported from Mesoamerica. Despite its disjunct status and the few collections available, in Costa Rica *M. renteriae* is a common liana in some parts of the Cordillera de Guanacaste and the Cordillera de Tilarán. The fruits and seeds are described here for the first time.

REPRESENTATIVE SPECIMENS. **Costa Rica.** ALAJUELA: Reserva Biológica Alberto Manuel Brenes, 24 Apr 1993, *Gómez-L. et al. 12422* (USJ); Reserva San Ramón, 1 Apr 1994, *Gómez-L. et al. 12638* (USJ); Upala, Bijagua, 15 Nov 1987, *Herrera 1288* (F, INB, MO). GUANACASTE: Parque Nacional Guanacaste, Pitilla, 15 Jun 1989, *Hammel et al. 17476* (INB, MO); Santa Cecilia, 20 Aug 1993, *Ramírez 58* (INB, MO); Parque Nacional Guanacaste, Fila Orosilito, 2 Mar 1991, *Ríos 326* (CR, INB, MO). LIMÓN: Parque Nacional Braulio Carrillo, Estación Carrillo, 25 Apr 1986, *Chacón 1847* (CR, INB).

Ecuador. ESMERALDAS: Quinindé, NE of Las Golondrinas, La Bella Jungla, Cooperativa La Bella Jungla, 10 Oct 1993, *Palacios 11514* (INB, MO, QCNE).

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POLLEN ABORTION IN THE *RANUNCULUS GMELINII–HYPERBOREUS* GROUP (RANUNCULACEAE, SECTION *HECATONIA*) AND ITS TAXONOMIC IMPLICATIONS

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ABSTRACT. In order to determine the likelihood of hybridization involving *Ranunculus gmelinii* and *R. hyperboreus,* petal length, presence or absence of receptacle pubescence, pollen stainability, and maximum leaf lobe number were recorded in 60 plants from throughout boreal and arctic North America. Within a group of 37 plants with pubescent receptacles, and thus referable to *R. gmelinii,* a subgroup of 16 with aborted pollen had significantly fewer leaf lobes based on the Kruskal-Wallis test, suggesting that they were hybrids of *R. gmelinii* and *R. hyperboreus.* The type specimens of *R. hyperboreus* var. *turquetilianus* and *R. yukonensis* have high percentages of aborted pollen and both are referred to *R. gmelinii* × *R. hyperboreus.* Past emphasis on phenotypic plasticity and a lack of understanding of the potential importance of hybridization may be limiting to necessary improvements in classification.

Key Words: *Ranunculus gmelinii, Ranunculus hyperboreus,* Ranunculaceae, hybridization, taxonomy, Canada, Arctic

Hybridization has been implicated in the taxonomic complexity of the North American buttercups (Whittemore 1997) and is documented in some of the aquatic species (Les and Philbrick 1993), but has not been associated with the yellow-flowered aquatic or semi-aquatic species in section *Hecatonia* DC. This section includes *Ranunculus gmelinii* DC. (including *R. purshii* Richards.) and *R. hyperboreus* Rottb. The former is represented by poorly defined geographic races throughout Canada and the northern

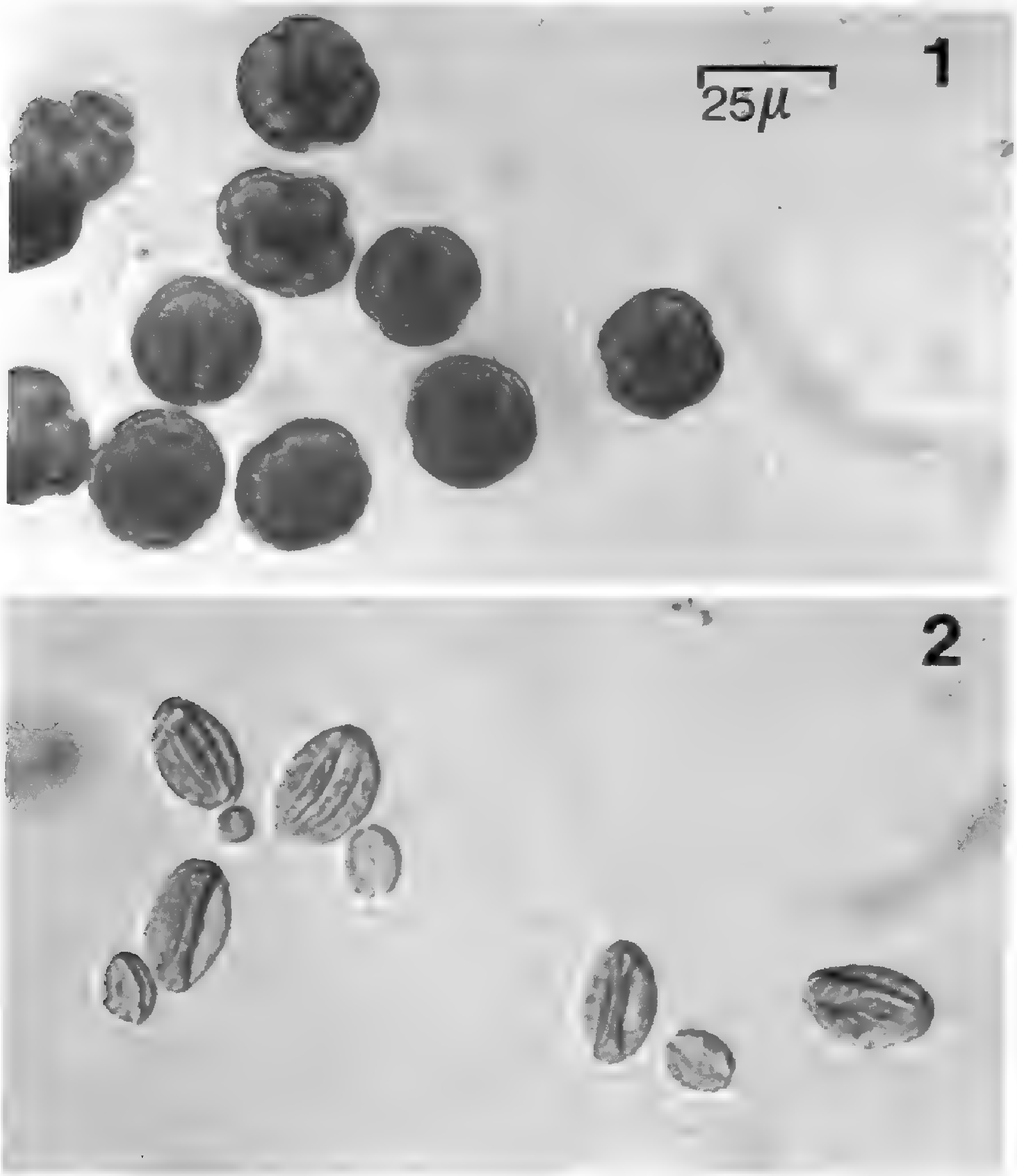
United States while the latter is less variable and occurs primarily in arctic regions of North America (Cody 1996; Hultén 1968; Welsh 1974; Whittemore 1997).

Plants from northern Quebec with relatively few leaf lobes and relatively small flowers, but otherwise referable to *Ranunculus gmelinii sensu lato,* were found to have aborted pollen, suggesting that they were hybrids of *R. gmelinii* and *R. hyperboreus.* At least one of these putative parents occurred intermixed with the putative hybrids while the other putative parent was found in the vicinity. This observation is important because taxonomists have disagreed over the assignment and rank of taxa described in the *R. hyperboreus* complex, while believing that hybridization was not relevant (e.g., Scott 1974). In particular, *R. hyperboreus* var. *turquetilianus* Polunin and *R. yukonensis* Britt. have been classified differently (e.g., Benson 1948, 1954; Scott 1974).

If plants with pubescent receptacles and aborted pollen are of hybrid origin they may be expected to differ from other plants with pubescent receptacles in having fewer leaf lobes and smaller flowers, features possessed by *Ranunculus hyperboreus,* the putative parent. The purpose of this study was to determine (1) whether a hybridization hypothesis could be supported by morphological data, (2) the geographic extent and frequency of hybridization, and (3) the taxonomic implications of hybridization.

MATERIALS AND METHODS

Plants for analysis (Appendix) were selected from CAN, DAO, NY, and QFA on the basis of adequacy of flowering material. An attempt was made to utilize material collected from throughout northern Canada and Alaska (Appendix), and no more than two samples (sheets) were used from a single locality. Type material [*Ranunculus hyperboreus* var. *turquetilianus*: Northwest Territories: Chesterfield, 19–20 Aug 1936, *N. Polunin 2234* (ISOTYPE: CAN!); 6 Aug 1936, *A. Dutilly 346* (TOPOTYPE: CAN!); *R. yukonensis:* Yukon: near mouth of Bonanza, 18 Jun 1899, *R. S. Williams* (HOLOTYPE: NY!)], hybrids suspected on the basis of circumstantial evidence (*Blondeau Tq92397, 96PX-145; Garneau 91-581-M*), and associated putative parents (*Blondeau Tq92409, Tq92411, 96PX-111; Garneau 91-616-M*) were included. Within the context of geographic selection, two thirds of the sample were ran-



Figures 1 and 2. Pollen of aquatic *Ranunculus* stained according to Owczarzak (1952). 1. *R. hyperboreus*, Igloolik, *Manning s.n.* (DAO); 2. Putative *R. gmelinii* × *R. hyperboreus*, Pastolik, *Porsild & Porsild 997* (CAN).

dom. The nonrandom selection involved putative hybrids selected at CAN from material labelled as *R. gmelinii* or *R. hyperboreus*.

Morphological characters scored were maximum petal length, presence or absence of pubescence on the receptacle, and maximum leaf lobe number from the same stem that the flower data were obtained. Presence of fertile pollen was evaluated following staining with the technique described by Owczarzak (1952). Pollen grains were recorded as "fertile" if they were essentially circular, uniform in size, and took up stain readily (Figure 1). Pollen grains were recorded as "aborted" if they were less than ½ or over 1 ½ times average diameter, and/or if they took up stain slowly and/or poorly, and/or were elliptic with prominent longitudinal grooves, or collapsed (Figure 2). The percentage of fertile pollen grains was calculated based on a sample of the first 100 grains seen on the slide. Plants with <30% fertile pollen were distinguished as an aborted pollen group.

Because of the small sample size the nonparametric Kruskal-Wallis test was used to evaluate morphological differences between groups of plants with pubescent receptacles and either aborted or normal pollen. Maps were produced with Quikmap version 2.51 (ESL Environmental Sciences Ltd., Sidney, British Columbia).

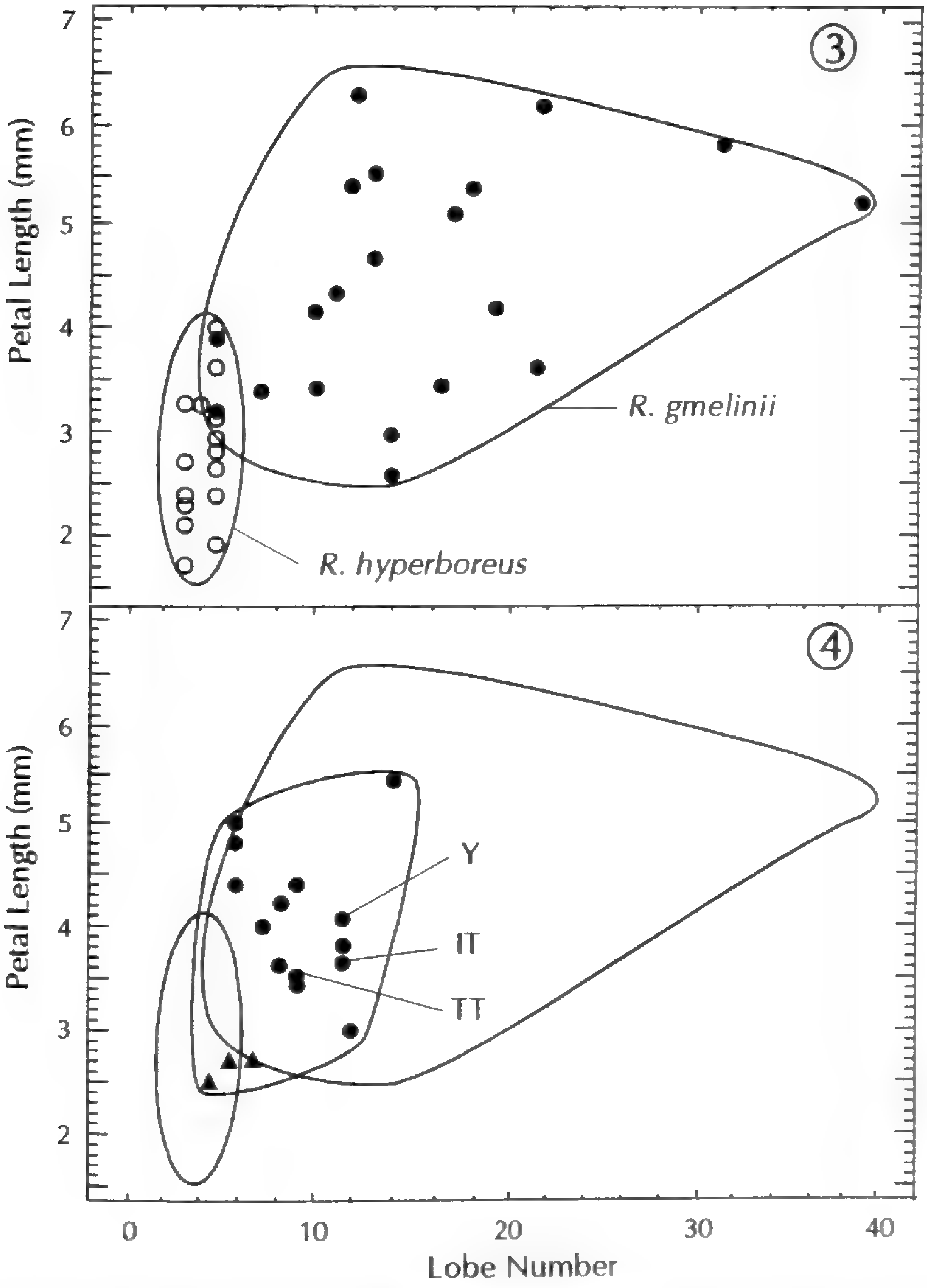
RESULTS AND DISCUSSION

Support for hybridization hypothesis. With one exception (*Ranunculus yukonensis*—see below), plants had either >70% fertile pollen or <30% fertile pollen; thus, two separate pollen groups could be identified readily. Within a group of 37 plants with pubescent receptacles referable to *R. gmelinii* (e.g., Scott 1974), a subgroup of 16 with aborted pollen had significantly fewer leaf lobes (P = 0.001) in the Kruskal-Wallis test. Petal length did not differ significantly between these two subgroups (P = 0.254). The combination of fewer leaf lobes and aborted pollen suggested that the 16 plants were hybrids of *R. gmelinii* and *R. hyperboreus.*

Three plants with glabrous receptacles and aborted pollen are considered referable to the same hybrid, but a comparison within the group of plants with glabrous receptacles is unwarranted due to the small sample size. Although a discrete morphological hybrid zone cannot be identified due to parental overlap, the group of putative hybrids with aborted pollen is morphologically intermediate between the putative parental groups (Figures 3 and 4).

At four sites where plants with aborted pollen occurred, *Ranunculus gmelinii* was found once with the suspected hybrid population (Tasiujaq), and *R. hyperboreus* was found twice (Aupaluk, rivière Boniface). The other putative parent was seen within 2 km from the hybrid site where only *R. hyperboreus* was sympatric with the putative hybrid. At the fourth site (Puvirnituk), the putative parents were seen within 1.25 km of the suspected hybrid population.

Extent of hybridization. With the exception of types and



Figures 3 and 4. Plots of maximum leaf lobe number versus maximum petal length for plants in the *Ranunculus hyperboreus* complex. 3. Dispersion of plants with more than 70% normal pollen, including plants with glabrous receptacles (circles) referable to *R. hyperboreus*, and plants with pubescent receptacles (dots) referable to *R. gmelinii*. 4. Dispersion of plants comprising a putative hybrid group with less than 30% normal pollen, and either glabrous (triangles) or pubescent (dots) receptacles. IT = Isotype of *R. hyperboreus* var. *turquetilianus* Polunin, *Polunin 2234* (CAN); TT = Topotype of *R. hyperboreus* var. *turquetilianus* Polunin, *Dutilly 346* (CAN); Y = Holotype of *R. yukonensis* Britt., *Williams s.n.* 18 Jun 1899 (NY).

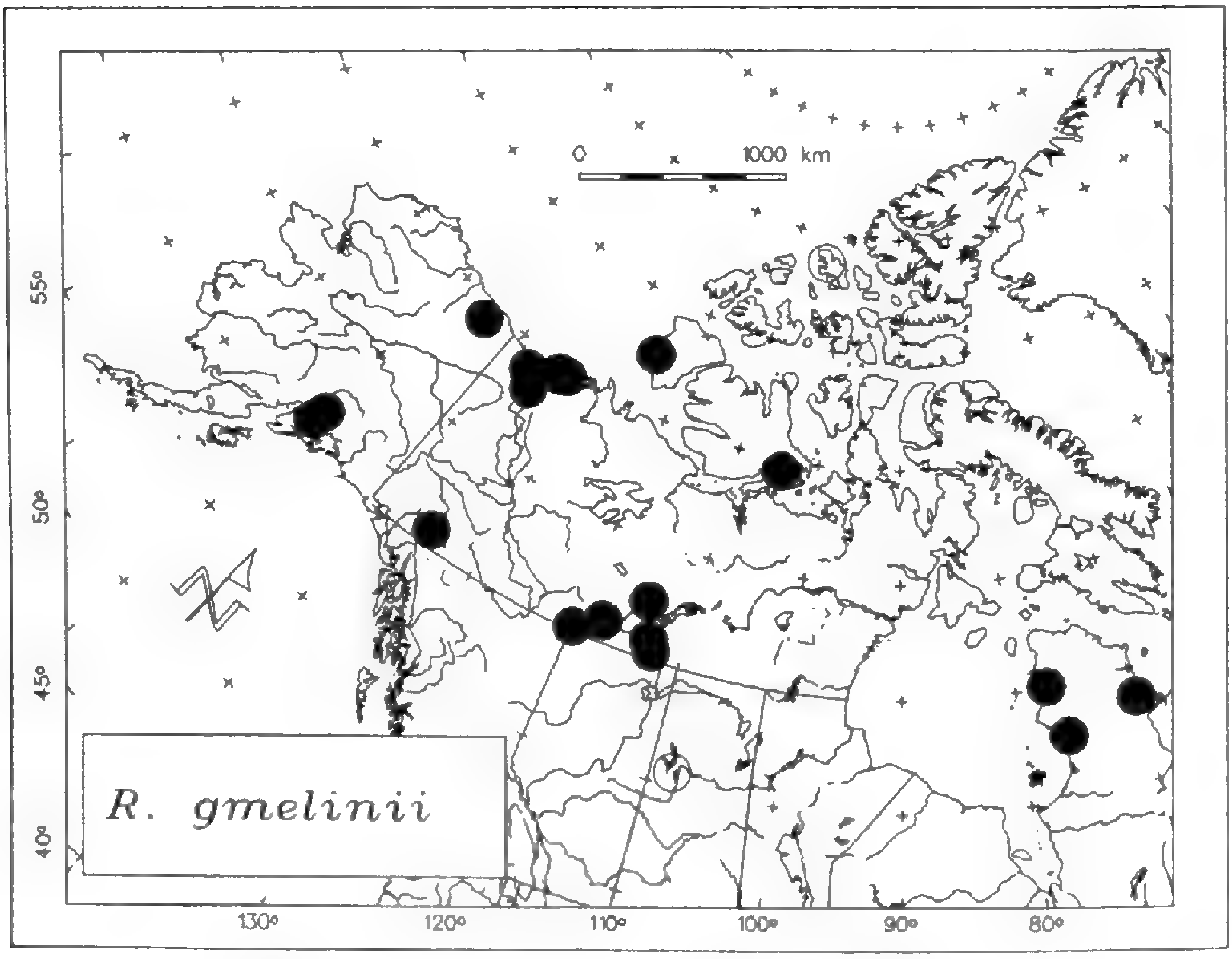


Figure 5. Origin of specimens with pubescent receptacles and more than 70% normal pollen, referable to *Ranunculus gmelinii.*

specimens selected on the basis of circumstantial field evidence, the geographically widespread sample of 55 specimens (Figures 5, 6, and 7) contained 18 (32.7%) with aborted pollen. Not only are the putative hybrids frequent, but they are widespread throughout the North American arctic from 60° to 78° N and 70° to 165° W (Figure 7).

Key to the *Ranunculus gmelinii* group. The putative hybrids reported here and their parents are a distinctive group of aquatic or semi-aquatic buttercups with prostrate stems rooting at the nodes, leaves lobed or filiform and dissected, and flowers with 3–4 yellow petals less than 7 mm long. The following key will separate the two species and the putative hybrids.

1. Pollen mostly (>70%) aborted, variable in size and elliptic (Figure 2); leaves with 5–14 lobes . . *R. gmelinii* × *R. hyperboreus*
1. Pollen mostly (>70%) normal, uniform in size and circular (Figure 1); leaves with 3–38 lobes . . . . (2)

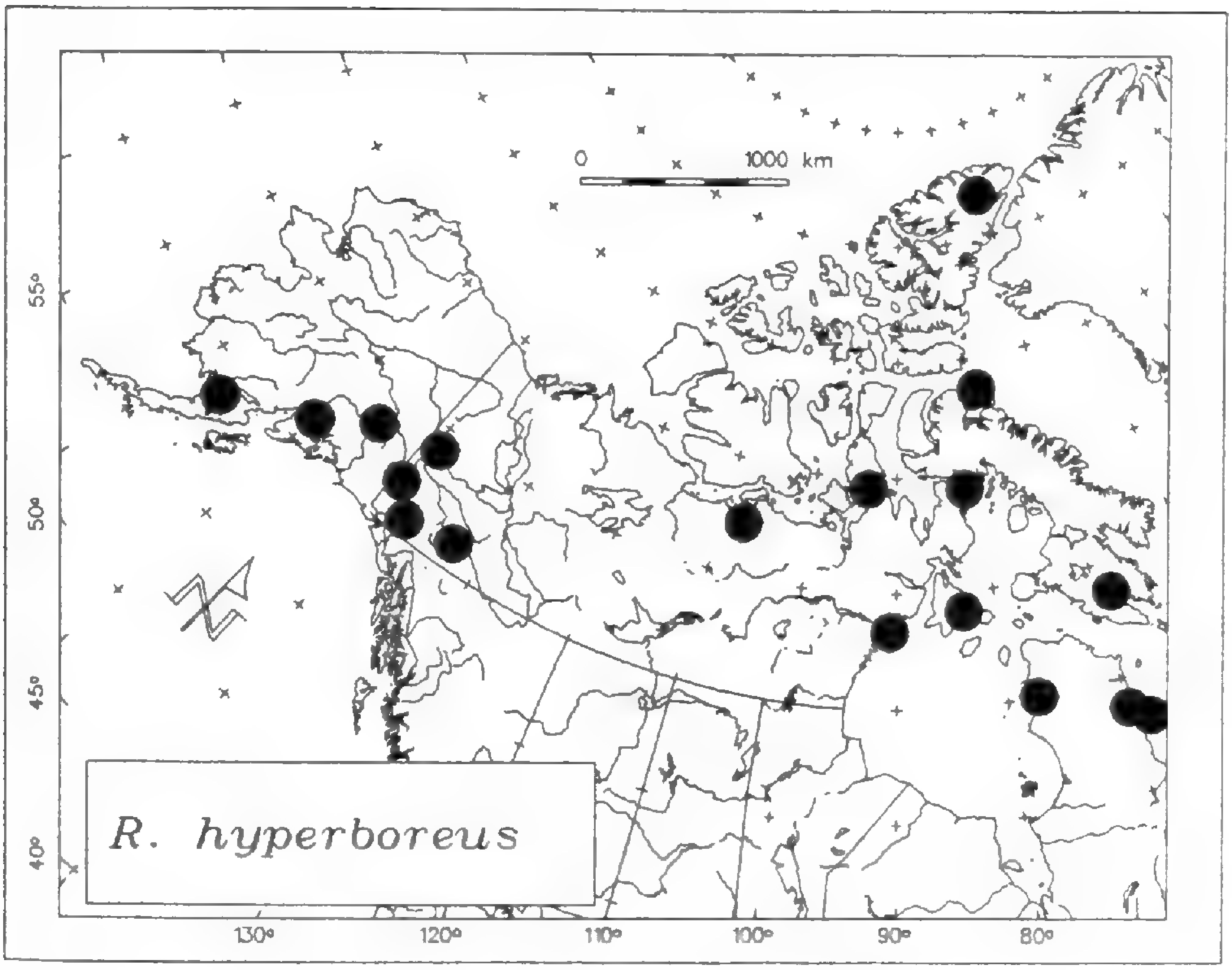


Figure 6. Origin of specimens with glabrous receptacles and more than 70% normal pollen referable to *Ranunculus hyperboreus.*

2. Receptacle glabrous; leaf lobes 3–5 ..... *R. hyperboreus*
2. Receptacle pubescent; leaf lobes 5–38 ...... *R. gmelinii*

Taxonomic implications. *Ranunculus hyperboreus* var. *turquetilianus* was described by Polunin in 1940 from Chesterfield Inlet, the name honoring A. Turquetil, then the Roman Catholic Bishop of Hudson Bay. Benson (1948, 1954) made it a synonym of *R. hyperboreus.* Later, Savile and Calder (1952) pointed out that the distinctive characteristics of *R. turquetilianus* may have an ecological basis and they treated it as a form of *R. hyperboreus.* Scott (1974), however, treated it as a synonym of *R. gmelinii,* based partly on the pubescent receptacle, that of *R. hyperboreus* being glabrous. Scott (1974) attributed much of the complex variation in the group to phenotypic plasticity. Tolmatchev (1961) noted the earlier suggestion of Savile and Calder (1952), but astutely commented that *R. turquetilianus* may be related to *R. gmelinii.* He pointed out that hybrids of *R. hyperboreus* and *R. gmelinii* may also be relevant to the problem, although no such

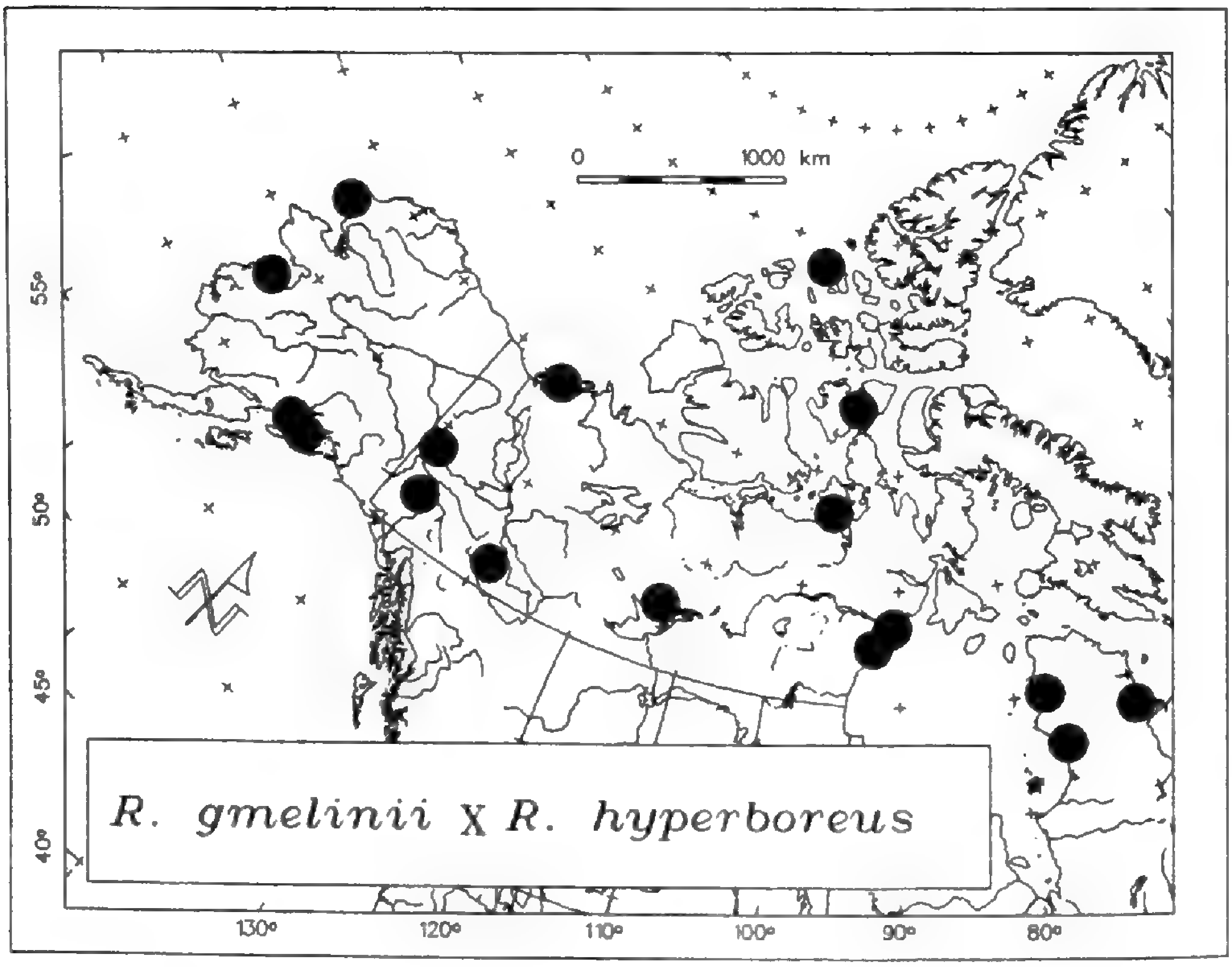


Figure 7. Origin of putative *Ranunculus gmelinii* × *R. hyperboreus*, all specimens with less than 30% normal pollen.

hybrids had been encountered over a large portion of Siberia where *R. hyperboreus* and *R. gmelinii* were sympatric.

Although the holotype of *Ranunculus hyperboreus* var. *turquetilianus* could not be found at BM or OXF, an isotype and topotype (cited above) had less than 30% fertile pollen, were positioned within the morphological limits of the putative hybrid group (Figure 4), and occurred with both putative parents at the type locality. Consequently, the type collections of *R. hyperboreus* var. *turquetilianus* are probably hybrids of *R. gmelinii* × *R. hyperboreus*. These type specimens possess characteristics of the two different parental species, thus making their assignment difficult.

Ranunculus yukonensis was described from the mouth of Bonanza Creek in the Yukon Territory by Britton (Britton and Rydberg 1901). It was treated as a subspecies of *R. purshii* by Porsild (1939). Benson (1942) treated it as a variety of *R. gmelinii*, and later (1948) as a synonym of *R. gmelinii*. Cody (1996), Hultén (1968), Porsild and Cody (1980), Scott (1974), and Welsh (1974) also treated it as a synonym of *R. gmelinii*, based partly on the pubescent receptacle. The type collection of *R. yukonensis* had 25–40% aborted pollen and was positioned within the putative hybrid group in morphology (Figure 4). Again the differing opinions of taxonomists were likely a result of cryptic hybridization, the plants in question possessing features of both putative parents. Thus, placement depended on the taxonomists' concepts of the limits of the parental taxa, which did not take potential hybridization and introgression into account.

Pending experimental work aimed at further supporting hybridization, the hybrids recognized in this paper must be considered putative and may be designated with the combinational name, *Ranunculus gmelinii* DC. × *R. hyperboreus* Rottb. A future revision will require consideration of more than 10 North American names placed in synonymy of *R. gmelinii* by Scott (1974), as well as Eurasian names published before 1901.

Hybridization in aquatic and semi-aquatic *Ranunculus* is likely to be cryptic as a result of overlapping morphological characters making intermediacy difficult to evaluate. Past emphasis on phenotypic plasticity and a lack of understanding of the potential importance of hybridization in this genus may have hindered improvements in classification. Moreover, several other factors have contributed to the difficulty of studying hybridization in aquatic plants in general. These include the rarity of flower production, difficulties in documenting sterility, and predominant asexual rather than sexual reproduction (Les and Philbrick 1993).

Previous documentation of aquatic *Ranunculus* hybrids was summarized in Les and Philbrick (1993), but it included only species in subgenus *Batrachium* (DC.) A. Gray. Few cases of hybridization are known within aquatic or semi-aquatic species of subgenus *Ranunculus*: the example reported here and another involving the arctic-boreal species *R. pallasii* Schlecht. of section *Pallasiantha* (L. Benson) Tutin and *R. lapponicus* L. of section *Coptidium* (Prantl) Tutin (Cody et al. 1988). The evidence of hybridization in arctic buttercups, as shown in the last two examples, is also important as part of an emerging concept of increased significance of hybridization in the glaciated portion of northern North America (Cayouette and Catling 1992; Cayouette et al. 1992; Cayouette and Darbyshire 1993).

ACKNOWLEDGMENTS. The authors wish to thank S. Porebski (DAO) for the preparation of the maps, M. Garneau (QFA) for the loan of her collections and data from Northern Québec, R. Vickery (BM) and S. Marner (OXF) for their help in searching Polunin type material, and W. J. Cody and E. Small for their comments on an earlier version of the manuscript.

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APPENDIX. LIST OF THE SPECIMENS USED IN THIS STUDY. TYPE MATERIAL USED IS CITED UNDER "MATERIALS AND METHODS."

R. gmelinii

Canada, N.W.T.: Egg River, *MacInnes 535836* (CAN); Ferguson Lake, *Edlund & Argus 12776* (CAN); Kakisa Lake, *Thieret & Reich 4681* (DAO); Kidluit Bay, *Cody & Ferguson 9979* (DAO); Le Grand Detour, *Cody 13965* (DAO); Mackenzie River-Yellowknife Highway, *Thieret & Reich 6728* (DAO); Richards Island, *Cody 13028* (DAO), *Scotter 10259* (DAO); Richardson Mountains, 22 Aug 1965, *Lambert s.n.* (DAO); Toker Pt., *Cody & Ferguson 10311* (DAO); Wynn's Mill, *Cody & Loan 3996* (DAO); Yellowknife, *Cody & McCanse 2310* (DAO); QUÉBEC: Rivière Boniface, *Garneau 91-616-M* (QFA); Puvirnituk, *Blondeau 96PX-111* (DAO); Tasiujaq, *Blondeau Tq92409* (QFA); SASKATCHEWAN: N of Buffalo Narrows Village, *Harms & Skoglund 19607* (DAO); YUKON TERRITORY: McIntyre Creek, *Cody et al. 35397* (DAO); N of Watson Lake, *Harms 17159* (DAO); Shingle Point, *Parmelee 2763* (DAO); **U.S.A.,** ALASKA: Hope, *Calder 5211* (DAO); Lake Peters, *Batten 492* (DAO); Wasilla Creek, *Lepage 23502* (QFA).

R. hyperboreus

Canada, N.W.T.: Bathurst Inlet, *Scotter & Zoltai 31820* (DAO); Bylot Island, *Scotter & Zoltai 67037* (DAO); Chesterfield Inlet, *Savile & Watts 1030* (DAO), *Savile & Watts 1566* (DAO); Coral Harbor, *Cody 1236* (DAO); Frobisher Bay, *Senn & Calder 3857* (DAO); Hazen Camp, *Savile 4584* (DAO); Igloolik, 25 Jul 1983, *Manning s.n.* (DAO); Spence Bay, *Chillcott 59* (DAO); QUÉBEC: Fort Chimo, *Calder 2545* (DAO); Tasiujaq, *Blondeau Tq92411* (QFA); YUKON TERRITORY: Bonanza Creek, *Cody & Ginns 34030* (DAO); Canol Road km 96, *Cody & Ginns 28806* (DAO); Mile 1158 Alaska Highway, *Douglas & Tait 10402* (DAO); SW Haines Junction, *Pearson 141* (CAN); **U.S.A.,** ALASKA: Anchorage, *Dutilly et al. 20310* (DAO); King Salmon, *Schofield 2031* (DAO); Mile 188 Richardson Highway, *Webster 17* (DAO).

R. gmelinii × *R. hyperboreus*

Canada, N.W.T.: Adelaide Peninsula, *Macpherson 123* (CAN); Chesterfield Inlet, *Savile & Watts 1198* (DAO), *Savile & Watts 1329* (DAO); Ellef Ringnes Island, *Savile 4317* (DAO); Rankin Inlet, *Korol 220* (DAO); Somerset Island, *Savile 3707* (DAO); Tuktuk, *Cody & Ferguson 9896* (DAO); QUÉBEC: Rivière Boniface, *Garneau 91-581-M* (QFA); Puvirnituk, *Blondeau 96PX-145* (DAO);

Tasiujaq, *Blondeau Tq92397* (QFA); YUKON TERRITORY: Frances Lake area, *Rosie 1220* (DAO); Nisling River Valley, *Cody & Ginns 28353* (DAO); **U.S.A.,** ALASKA: Cape Thompson, *Wood & Wood 516* (CAN); Kenai Lake, *Calder 6566* (DAO); NW of Kasilof, *Calder 5373* (DAO); Pastolik, *Porsild & Porsild 997* (CAN).

RHODORA, Vol. 99, No. 899, pp. 275–277, 1997

NEBC MEETING NEWS

August Field Trip. On Saturday, August 9, Pam Weatherbee and David Hunt led eight Club members on a scramble up Cedar Mountain in Mount Washington, MA, an 1800 ft. peak on the Massachusetts–New York border. The south-facing slope is remarkably similar to the grassy balds on the traprock slope of Bare Mountain, visited on the June field trip, but with schist providing the substrate. The slopes have an open and diverse oak-hickory canopy and a grassy herbaceous layer dominated by *Carex pensylvanica* and *Deschampsia flexuosa,* with *Viburnum rafinesquianum* in the shrub layer. Some of the more exciting herbaceous species occurred on the rock outcrops, including *Paronychia canadensis, Asplenium platyneuron, Woodsia ilvensis, Galium pilosum, Carex virescens, Pycnanthemum incanum,* and *Viola palmata.* The low scrub oak and pitch-pine community at the summit yielded both *Arctostaphylos uva-ursi* and *Potentilla tridentata,* as well as spectacular views into both states. A return trip in spring was recommended to see the many now-dormant spring ephemerals.

September 1997. The Club met at Lyndon State College in Lyndonville, VT. Arthur Gilman spoke on "The Flora of Caledonia County, Vermont," which he has spent the last five years investigating. Caledonia County has 1185 species and 457 genera (326 indigenous), 60% of the species diversity and 80% of the generic diversity found in the state. Twenty-nine species in the Caledonia County flora are state-listed. Weedy non-native species contribute about 30% of the flora, and many are expanding in their ranges. The flora is still a work in progress; Art added one new species (*Nardus stricta*) only last week.

Caledonia County occupies 619 square miles over 17 townships, including the piedmont and northeast highlands provinces of Vermont. Elevations range from 426 ft. along the Connecticut River to 3364 ft. on Signal Mountain. Tills over calcareous bedrock are the predominant substrate. These calcareous substrates are responsible for the range of interesting and unique habitats, including Peacham Bog, one of the largest Vermont peatlands and the second largest raised bog in the state. Limestone fens and outcrops support unique floras, including *Saxifraga virginiensis, Hepatica acutiloba, Viola canadensis, Parnassia glauca, Lobelia* *kalmii, Carex flava,* and *Scirpus hudsonianus.* The calcareous substrates also result in a high diversity of orchids, including *Cypripedium arietinum, Calypso bulbosa* (Art says he has seen more herbarium specimens than living plants), *Cypripedium reginae, Listera convallarioides, Spiranthes,* and *Orchis spectabilis.* Aquatics are also unusually diverse. Barre Hellquist has said that this is one of the most interesting aquatic floras in New England, due to the many "hard" water ponds, "soft" water ponds, and the Connecticut River. Barre has collected 13 species of pondweeds in a single pond.

Many species reach either the northern or southern limits of their ranges here, including *Epigaea repens,* white spruce, and *Monarda fistulosa.* Several other southern elements reach their limits in the Connecticut River valley a few miles south of the Caledonia County limits, including *Carya cordiformis, Betula lenta, Carex baileyi, Diplazium pycnocarpon,* and *Asplenium platyneuron.* Many northern species occur in the county, including *Saxifraga oppositifolia, Primula mistassinica, Luzula parviflora, Astragalus robbinsii, Carex capillaris, Huperzia selago, Woodsia glabella, Dryopteris fragrans,* and *Solidago macrophylla.* The flora includes some interesting disjunctions. *Rhododendron maximum* occurs around several ponds in the Groton area, more than 100 miles from the nearest populations in southern New Hampshire.

September Field Trips. Arthur Gilman led two botanical explorations in southern Caledonia County on September 19 and 20, 1997. On Friday, 25 Club members and friends ambled along a natural gas pipeline right-of-way in East Burke, VT, in search of calciphiles growing in the calcareous groundwater seeps. Following moose tracks up along the pipeline, we found an exciting flora with large numbers of flowering *Spiranthes cernua.* Highlights included a large range of "fern allies" (*Equisetum variegatum, Lycopodium clavatum, Lycopodiella inundatum, Huperzia selago,* and *Selaginella apoda*), sedges (*Carex baileyi, C. gynandra,* and *C. flava, Scirpus hudsonianus* and *S. microcarpus, Eriophorum viridicarinatum,* and *Eleocharis tenuis*) and other species, including *Parnassia glauca* (still in bloom!). Surprisingly, most of these calciphiles were growing in and among dense mounds of *Sphagnum.* Southern New England Club members were delighted to find *Gaultheria hispidula* and *Linnaea borealis* growing along the edges of the cleared right of way.

On Saturday, 27 Club members, friends, and families met Art at the Pine Grove Picnic Area at the Comerford Reservoir in East Barnet, VT, and explored the nearby lake shore, old field, powerline, swamp, and roadside habitats within the Connecticut River valley. Several plants we encountered, including *Stellaria aquatica* and *Asplenium trichomanes,* are at their only known station in Caledonia County. Other highlights included *Gentiana clausa, Isoetes riparia, Polystichum acrostichoides* f. *multifidum, Fraxinus nigra, Spiranthes ochroleuca* and *S. casei, Botrychium dissectum, Carex muhlenbergii,* and *Panicum xanthophysum,* as well as numerous red efts and unusual caterpillars. The *Botrychium* population was remarkable for its size, and extended over most of a large old field.

—LISA A. STANDLEY, Recording Secretary.

ANNOUNCEMENT

NEW ENGLAND BOTANICAL CLUB GRADUATE STUDENT RESEARCH AWARD

The New England Botanical Club will offer $2,000 in support of botanical research to be conducted by graduate students in 1998. 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.

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. It is anticipated that two awards will be given, although the actual number and amount of awards will depend on the proposals received.

Applicants must submit a proposal of no more than three double-spaced pages, a budget, a curriculum vitae, and two letters in support of the proposed research, one from the student's thesis advisor. Three paper copies of the proposal, budget, and CV must be submitted.

Proposals and supporting letters must be received no later than March 2, 1998. The recipient(s) will be notified by April 30, 1998. Send proposals to: Awards Committee, The New England Botanical Club, 22 Divinity Avenue, Cambridge MA 02138.

Two Graduate Student Research Awards were given in 1997. Tatyana Rand, of Brown University, received support for her study on the processes influencing the distribution and abundance of halophytic forbs in New England salt marshes. Thomas Vining, of the University of Maine in Orono, received support for his study of the phenology and hybridization of two *Picea* species.

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TITLE, AUTHOR(S), AND ADDRESS(ES): Center title, in capital letters. Omit authors of scientific names. Below title, include author(s) name(s), affiliation(s), and address(es). If "current address" is different, it should follow immediately below, not as a footnote.

ABSTRACT: An abstract and a list of key words should be included with each paper, except for shorter papers submitted as Notes. An abstract must be one paragraph, and should not include literature citations or taxonomic authorities. Please be concise, while including information about the paper's intent, materials and methods, results, and significance of findings.

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FLORAS AND TAXONOMIC TREATMENTS: Specimen citation should be selected critically, especially for common species of broad distribution. Keys and synonymy for systematic revisions should be prepared in the style of "A Monograph of the Genus *Malvastrum*," S. R. Hill, RHODORA 84: 159–264, 1982. Designation of a new taxon should carry a Latin diagnosis (rather than a full Latin description), which sets forth succinctly how the new taxon differs from its congeners.

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22 Divinity Avenue
Cambridge, MA 02138

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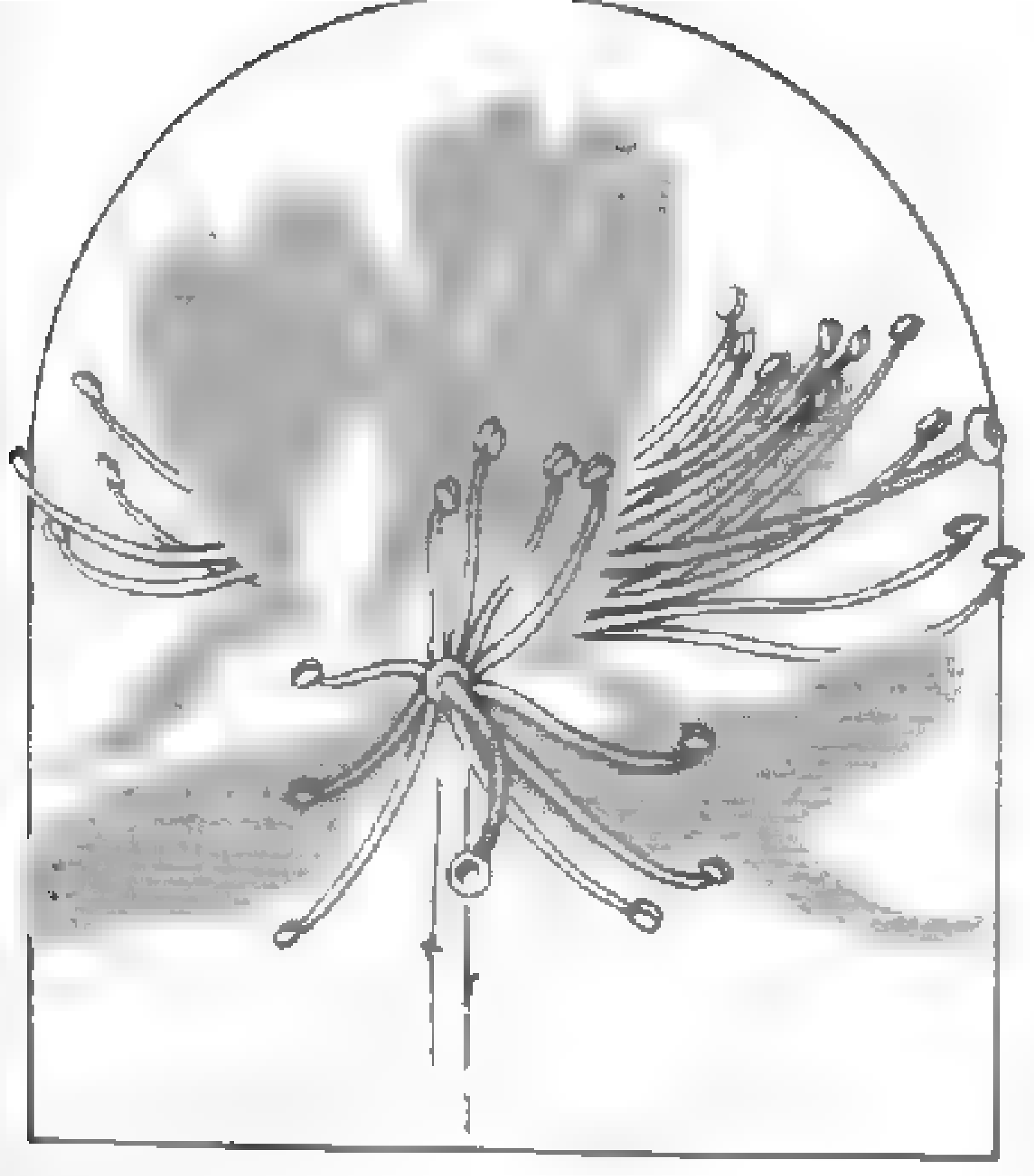

RHODORA

The Journal of the New England Botanical Club

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RHODORA

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RHODORA, Vol. 99, No. 900, pp. 283–286, 1997

A NEW PERUVIAN SPECIES OF *JALTOMATA* (SOLANACEAE) WITH BLOOD-RED FLORAL NECTAR

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ABSTRACT. *Jaltomata paneroi* (Solanaceae) of northern Peru is described and illustrated. This is the only species in the genus that has a green, campanulate-rotate corolla 23–25 mm across and 5–10 mm deep. This species, and at least six others of the genus, provide red floral nectar. This species is self-compatible and its berries are eaten by humans.

Key Words: *Jaltomata,* flora of Peru, Solanaceae

The genus *Jaltomata* Schldl. includes about 35 species of herbs and shrubs and is widely distributed in Latin America. As part of ongoing taxonomic work on this genus (Leiva G. 1995; Mione et al. 1993; Mione and Bye 1996; Mione and Coe 1996), we describe a new species.

Jaltomata paneroi Mione & S. Leiva, *sp. nov.* TYPE: PERU. Dept. Cajamarca: Prov. Cajamarca, carretera Cajamarca-Celendín, approx. 9 km NW de La Encañada, frente al poblado de Quinuamayo, 3324 m, 2 Jul 1987, *José L. Panero, I. Sanchez, S. Leiva G. and C. Sagástegui 854* (HOLOTYPE: CONN; ISOTYPES: CPUN; specimens of plants grown from seeds of the type collection: CONN, MO, NY). Figure 1.

Frutex pilis dendriticis simplicibusque dense vestitus. Folia dense pubescentia. Pedunculi et pedicellique breves. Corolla campanulato-rotata, viridis, 10–lobata, nectar copiosum rubrum ad basim exudans.

Perennial shrub to 1.5 m high with a dense vestiture of short, dendritic and unbranched, uniseriate trichomes. *Leaves* simple, ovate, the apex acute, the margin entire or subentire, to 6 cm long × 4 cm wide, densely pubescent on both surfaces with intermixed unbranched, forked, and dendritic trichomes to 0.5 mm long, the

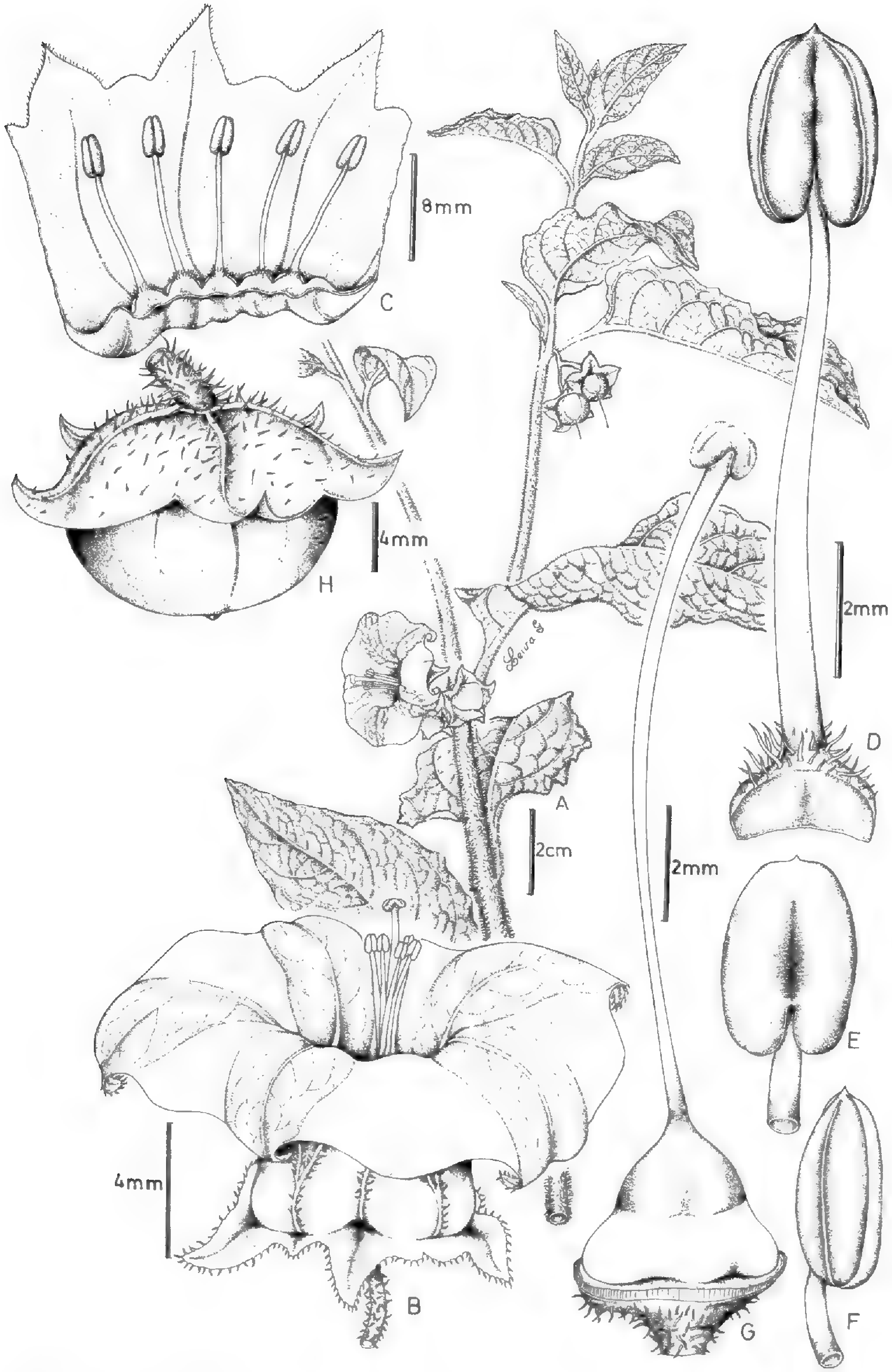

Figure 1. *Jaltomata paneroi,* drawn from *Leiva and Guevara 1130.* (A) Habit. (B) Flower. (C) Corolla expanded. (D, E, F) Stamen in ventral, dorsal, and lateral view, respectively; these share a scale bar. (G) Gynoecium. (H) Berry with calyx.

trichomes never gland-tipped. *Inflorescence* umbelliform, 3–4 (6)-flowered. *Peduncles* axillary, 3–5 mm long; *pedicels* 7–10 mm long, both densely vestitured. *Calyx* 13 mm in diameter during anthesis (flattened against ruler for measuring), abaxially densely pubescent, the lobes acuminate, at fruit maturity to 25 mm diameter. *Corolla* campanulate-rotate, green, 5 lobes alternating with 5 smaller lobules, 23–25 mm in diameter when pressed, 5–10 mm deep; corolla veins with dendritic trichomes abaxially. *Nectar* blood-red, copious, produced in the base of the corolla. *Stamens* 5, elongating during anthesis, ultimately 9–10 mm long; *filaments* pubescent at base, with unbranched or occasionally forked trichomes to 0.6 mm long; *anthers* 2.0–2.9 mm long prior to dehiscing, 1.5–1.6 mm long after dehiscing. *Pollen* grains 61,000–121,000 per flower, 35–40 μm in diameter. *Style* 7.3–10.7 mm long; *stigma* bilobed, 0.84–1.0 mm × 0.78–0.88 mm, exserted beyond anthers 1.5–4.5 mm; *ovules* 110–180 per ovary. *Infructescence* one- or two-fruited. *Berries* 10–11 mm × 14–15 mm, glabrous, orange in greenhouse. *Seeds* 1.52–1.68 mm long × 1.24–1.41 mm wide × 0.44–0.52 mm thick, suborbicular to reniform, alveolate.

Jaltomata paneroi occurs in Peru in the Department of Cajamarca between 3200 and 3550 meters of elevation along roadsides with shrubs. The type was collected on a very steep slope with acidic black soil, in an area that is generally moist but somewhat dry in July and August. Flowering and fruiting occur in June and July. This is the only species in the genus that has a green, campanulate-rotate corolla 23–25 mm across and 5–10 mm deep, producing blood-red nectar in its base. This species is similar only to *Saracha herrerae* C. V. Morton of southern Peru (soon to be transferred to *Jaltomata*), which also produces blood-red nectar in the base of its corolla. The latter species is glabrate and has larger (to 4.5 cm in diameter and to 2 cm deep) cream to white corollas. Although not validly published until now, *J. paneroi* was described by Mione (1992) and Leiva (1995). The specific epithet was chosen to honor José L. Panero, who sent the holotype and seeds to T. M.

Flowers of *Jaltomata paneroi* remain open 3–5 days (n = 5 flowers) in the greenhouse (observations were made at the University of Connecticut, Storrs). Anthers remain undehisced for a few hours after anthesis. Filaments are parallel to the style during the life of the flower, and the corolla remains open at night. In contrast, in many other *Jaltomata* the filaments are oriented such that the dehisced anthers are positioned a few mm away from the stigma, and the corolla closes at night, reopening the next morning. A few fruits were set in a pollinator-free greenhouse (without manual pollination) during the spring of 1992. Thus the species seems to be self-compatible, as are all other *Jaltomata* tested to date (Mione and Coe 1996). This brings the number of species that provide red nectar to seven in the genus (Mione and Anderson 1996). Fruits of *J. paneroi* are eaten and considered tasty (Leiva 1995).

OTHER SPECIMENS EXAMINED: **Peru.** Dept. CAJAMARCA: Prov. Cajamarca, Jalca de Kumulca (ruta a Celendín), 17 Jun 1975, *A. Sagástegui A. et al. 8111* (F, HUT, MO, NY); Quinuamayo, entre La Encañada y jalca de Kumulca, 17 Jun 1975, *Sánchez 1613* (F, CPUN); La Encañada-Kumulca (ruta a Celendín), 28 Jun 1994, *Leiva and Guevara 1130* (F, HAO, HUT).

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THE UNUSUAL DEFLEXED PODETIUM OF THE LICHEN *CLADONIA INCRASSATA*

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ABSTRACT. Lichens in the genus *Cladonia* are characterized by an erect, photosynthetic secondary thallus called a podetium. Growth of the podetium is influenced primarily by a meristem-like bundle of fungal tissue near the apex, which lacks direct contact with the algal host. In most *Cladonia* species the podetium, whether branched or unbranched, grows perpendicular to the growing surface and the habit of the podetium is erect. Apothecia are borne apically and they are generally upward-facing. In *C. incrassata,* vertical growth may be interrupted very early in ontogeny, resulting in mature podetia that are deflexed. In these podetia, the hymenial (spore-bearing) surface of the apothecium faces the growing surface instead of facing upward. In addition to variability of their habit, mature podetia of *C. incrassata* may be branched or unbranched. When branching occurs it is initiated by divisions of the fungal meristem, either early in ontogeny or later, as a by-product of the migration of the meristem during deflexion. Unbranched podetia are narrow, club-like structures with a more or less continuous outer layer, or they may be wide with a flabelliform-hooded habit and a deeply fissured exterior. Branched podetia resemble *C. cristatella,* which has contributed to confusion in the taxonomic literature surrounding this species.

Key Words: Cladoniaceae, growth dynamics, morphogenesis, variability

Cladonia incrassata Flörke is an inconspicuous, relatively uncommon lichen species of New England and the eastern United States. It grows on soil, stumps, and decaying wood in shady or semi-exposed habitats, and it is usually found in damp microenvironments or on substrata where moisture is perennially available. The size and growth habit of this lichen may contribute to its infrequent appearance in herbarium collections. The podetia of *C. incrassata* are generally shorter than 1 cm. The red apothecia that make species such as *C. cristatella* Tuck. conspicuous in the field are often obscured by podetial growth and deflexion in *C. incrassata.* Finally, the damp, shady habitat of this species is somewhat less accessible than that of other Cladonias. Mature specimens of *C. incrassata* are variable, and the development and gross morphology of this species are poorly understood. Mature podetia may be narrow (1–2 mm), club-like structures with an unbroken outer surface. Frequently, mature podetia are broad (≥ 1 cm), deeply fissured, hood-like structures. Instead of an erect habit, the podetium of mature *C. incrassata* is often deflexed and the apothecia face the growing surface. *Cladonia incrassata* is usually distinguished from *C. cristatella* in the laboratory on the basis of its sorediate primary thallus (squamules) and the presence of squamatic acid, rather than by the subtly articulated features of its podetium. This may explain why the deflexed habit has been overlooked in the literature.

While specimens from the eastern United States are conspecific with European material (Ahti, pers. comm.), this species is absent from western North America (Hammer 1995a, 1996a). Thomson (1968) listed three forms for *Cladonia incrassata* in North America but he did not mention its peculiar growth habit. The formae listed by Thomson reflect minor variations in mature thalli, which may be attributable to growing conditions, but which are also the result of varying rates of growth and development. Thomson also provided the synonym *C. cristatella* var. *paludicola* Tuck., which reflects the taxonomic controversy that surrounds this species in North America. The goal of this study is to describe the developmental stages that give rise to the unusual deflexed podetium of mature *C. incrassata.*

MATERIALS AND METHODS

Specimens of *Cladonia incrassata* for dissection were collected from soil and decaying wood in shady or semi-exposed habitats in Barnstable and Plymouth Counties, Massachusetts. Several hundred thalli were examined, including podetia of all developmental stages. These included immature, incipient podetia < 1 mm tall, to mature podetia > 1 cm tall. In addition, preserved specimens from North America and Europe at the Farlow Herbarium (FH) and the Tuckerman Herbarium (FH-TUCK) were examined and annotated (Table 1), and compared with *C. cristatella* (see Hammer 1997b for representative specimens of *C. cristatella*).

Longitudinal sections of freshly collected podetia were prepared for microscopy. Sections were mounted in lactophenol cotton blue (Stevens 1981) with glycerin. Photomicrographs (LM) were prepared under bright field refraction with an Olympus BHS microscope. Scanning electron micrographs (SEM) were prepared

Table 1. Representative specimens of *Cladonia incrassata* from FH and FH-TUCK examined in this study (all with deflexed podetia).

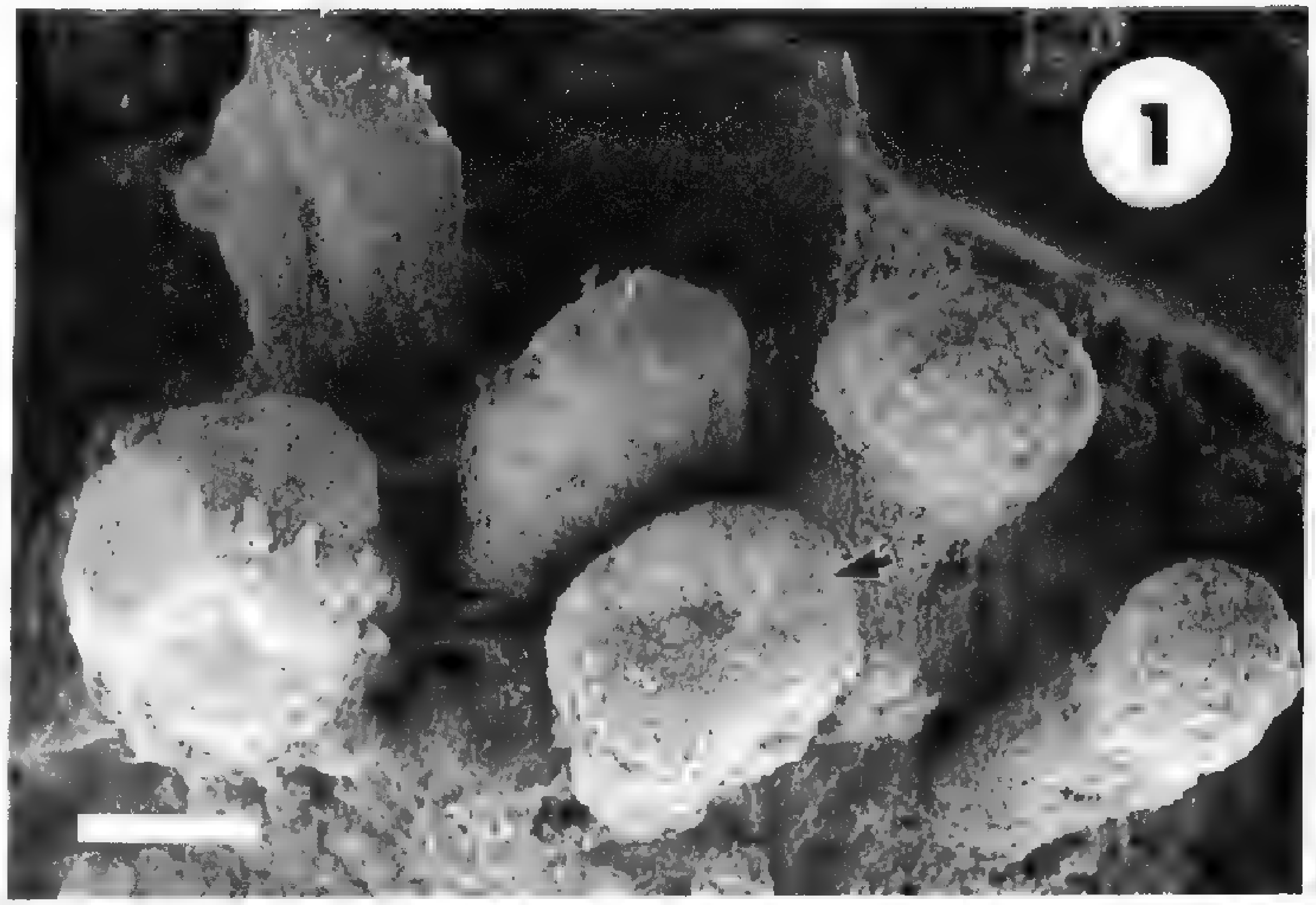
Specimen	Locality
Ahmadjian 491	Massachusetts
Evans 1308	Connecticut
Gray 1308	West Virginia
Hammer 5751	Massachusetts
Hammer 6010	Massachusetts
Luttrell 3032	Virginia
Merrill s.n.	Maine
Merrill 2097	Vermont
Riddle 382	Massachusetts
Riddle 615	Massachusetts
Robbins s.n.	Massachusetts
Tuckerman s.n.	Massachusetts (lectotype, *C. paludicola*)
Sandstede Exs. 1652	Germany
Santesson 14402	Sweden
Savicz 528	Belarus

from approximately 30 freshly collected specimens. See Hammer (1996b) for details on SEM methodology.

The descriptive terminology for lichen morphogenesis is not yet an established convention and here I use certain terminological conventions adopted in previous papers. For example, the cluster of apical cells that comprises meristem-like fungal tissue is called the "meristem" or "meristem bundle." As bundles elongate and begin to form a stipe, they are referred to as "incipient podetia." Bundles split in a characteristic fashion, producing a distinct cluster called the "meristem initial." The meristem initial refers to a developmental unit of up to five bundles that usually gives rise to branches.

RESULTS

The very early ontogeny of *Cladonia incrassata* is similar to that of other species in *Cladonia,* as described in Hammer (1995b, 1996b, c, 1997a, b). The earliest distinguishable podetial structure, which is ca. 100 μm tall, is exclusively fungal (Figure 1). In earliest ontogeny it is a roughly spheroid structure comprised of irregularly arranged meristematic tissue, which gives rise to all of the subsequent fungal tissue of the podetium. The podetium is a solid mass of cells at this early stage, and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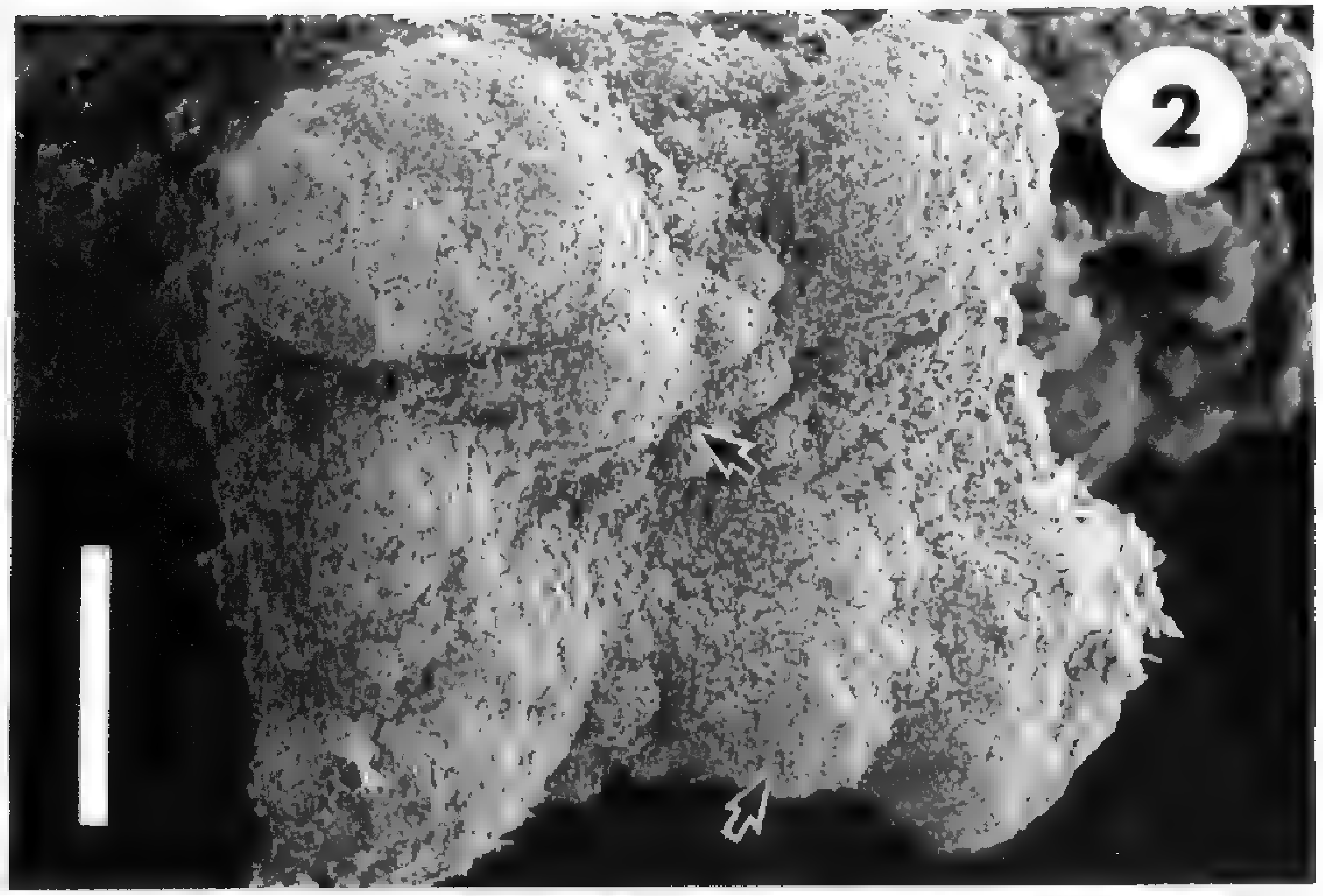
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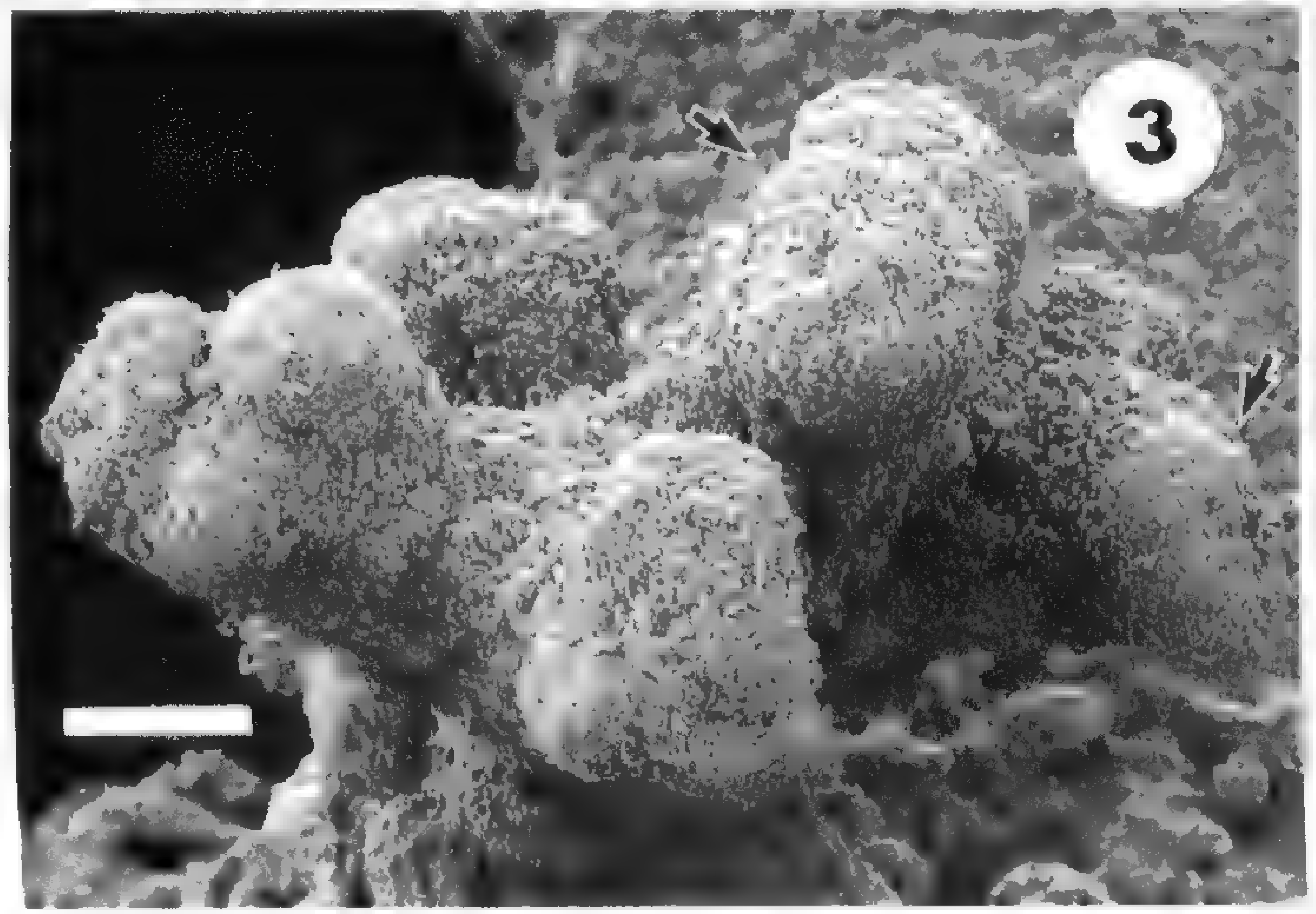
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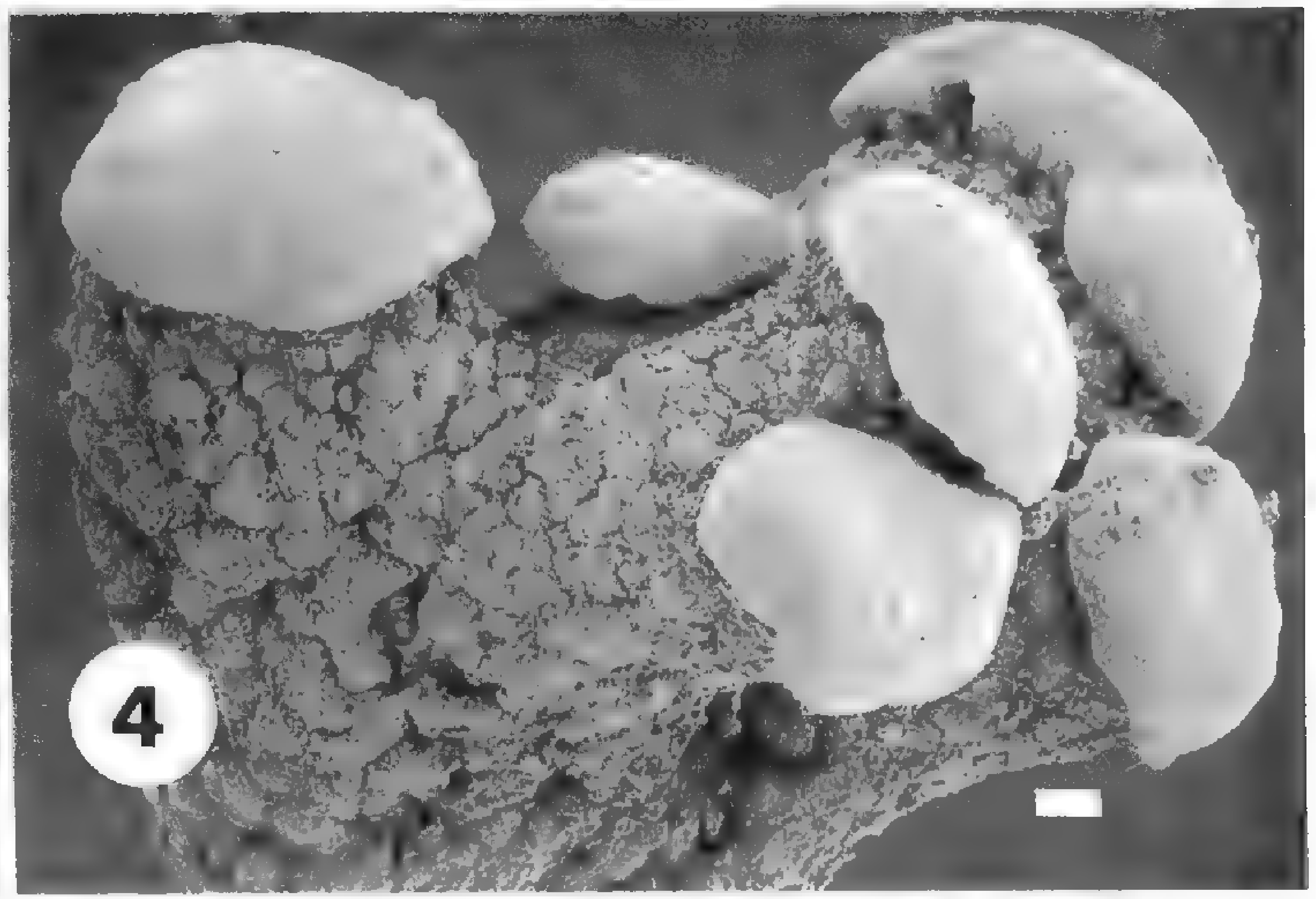
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internal lacunae, which are a by-product of growth and elongation, have not developed. As the structure elongates, the cells of the lower portion assume a vertical orientation, generally growing perpendicular to the substratum. The upper portion of the podetium, which is distal to the substratum, widens, and the cells in the upper ½–⅓ of the podetium are oriented in a radial conformation. As development continues, the upper portion of the podetium remains solid and lacunae develop below. A layer of algal cells develops toward the base of the podetium, which is eventually distinguishable as a stipe. The upper (fungal) portion of the podetium grows wider than the supporting stipe, which is composed of both fungal and algal cells. The upper portion, which remains meristematic at this stage, usually does not exceed 100 μm diam. until it divides. During early ontogeny podetium elongation and meristem widening and division can occur independently of one another (Figures 2 and 3).

The earliest divisions of the meristem follow roughly the pattern described for *Cladina subtenuis* (Abb.) Hale & Culb. (Hammer 1997a) and *Cladonia cristatella* (Hammer 1997b). One difference is that the meristem of *C. incrassata* may divide at the surface of the squamule at a very early stage, before elongation of the podetium, as well as later, on maturing podetia. Division of the meristem can be interrupted at any stage, or it may follow through to the completion of a five-part meristem initial (see Hammer 1996d), which is formed by a series of four divisions

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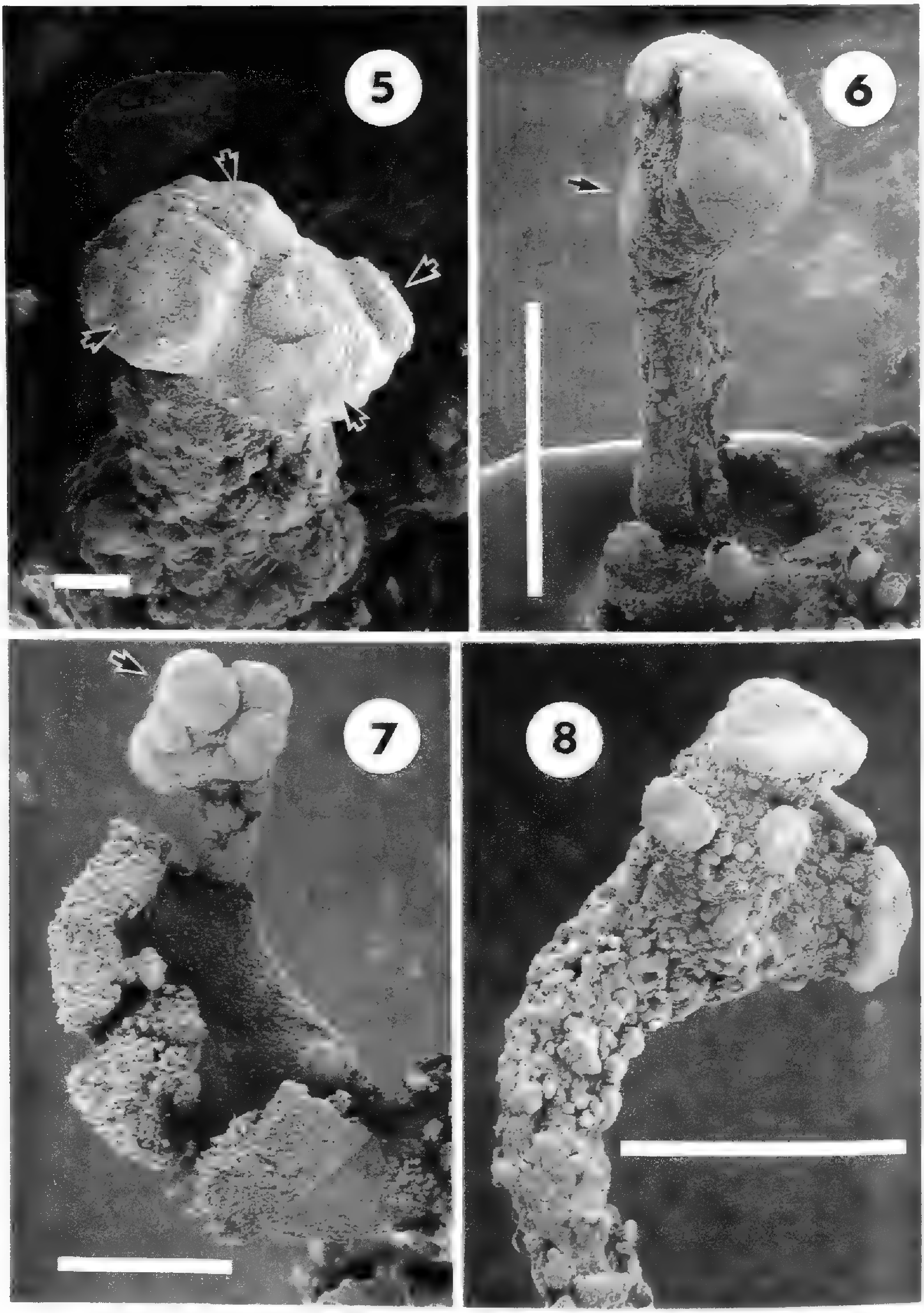
Figures 1–4. Early bending and branching in *Cladonia incrassata* (SEM). 1. Cluster of meristem bundles (incipient podetia) in early stages of ontogeny. Note two right-hand structures, whose apices are bent toward the left. Rim of one bundle has begun to grow differentially (arrow). Differential growth and deformation further advanced in bundle in upper left. Further widening and meristem division (see next figure) could occur in similar bundles. 2. Top view of very early division of meristem, slightly later in ontogeny than previous figure. Bundles are forming a five-part meristem initial, reminiscent of *C. cristatella.* Arrows indicate secondary divisions forming from bundles. 3. Side view of meristem initial derived from a single bundle. Slightly later in ontogeny than previous figure. Bundles face sideways or downward (arrows) and subsequent branching follows this growth pattern. 4. Maturing apex of podetium. Note orientation of four right-hand bundles and incipient branches that bear them. Two left-hand bundles are still vertically oriented. Scale bars = 100 μm.



Figures 5–8. Early ontogeny and podetial elongation of *Cladonia incrassata* (SEM). 5. Fungal apical meristem in early stage of podetial development. The meristem has begun to split into four distinct regions (arrows). 6. Podetium later in ontogeny. Meristem has migrated upward and is positioned obliquely at apex of podetium. Arrow indicates portion of meristem left behind (on future adaxial surface), which will later form a new branch on the podetium. Note pycnidia near base of podetium. 7. Maturing, deflexed podetium growing from end of squamule. Meristem has begun to split. Largest

of the fungal tissue (Figure 2). The tissue beneath any portion of the meristem initial may grow vertically at any stage (Figure 3), independent of the other meristem bundles. Bundles that continue to divide may form separate podetia or irregularly branched podetia. Alternatively, their growth may be synchronized as branches on one podetium (Figure 4), which resembles *C. cristatella* at maturity.

Generally, the podetium of *Cladonia incrassata* elongates in early growth stages (Figures 5 and 6) and the meristem divides as ontogeny progresses (Figure 7). As the podetium elongates, the (usually undivided) fungal meristem grows asymmetrically, appearing to be pushed to one side of the axis of growth by the underlying tissue (Figure 6). As the fungal meristem migrates (or is pushed) upward and sideways, portions of it may split off and remain isolated on the opposite side of the axis of vertical growth. This isolated meristem tissue (Figure 6) can later form branches that arise from the adaxial side of the deflexed podetium. As deflexed growth continues, most of the fungal meristem is borne abaxially, facing the substratum (Figures 7 and 8). The partially divided meristem may split into separate bundles or the meristem may continue to widen, resulting in irregular openings on the abaxial surface near the apothecium. In some cases the meristem divides indefinitely, producing a roughly cerebriform mass of apothecial tissue at maturity.

Mature podetia of *Cladonia incrassata* may be deeply fissured, a characteristic that is partly determined by meristem growth very early in ontogeny (Figures 9 and 10). As the meristem widens and splits (Figures 11 and 12), the cells diverge in a flabellate orientation (Figures 13–15). The fungal meristem tissue determines the first fissures, which continue to form once the algal layer develops. The widening apothecium, which is borne on the abaxial side of the podetium, develops from a band of dark-staining cells that is found directly beneath the hymenium (Figures 14–16). These cells continue to divide, while the

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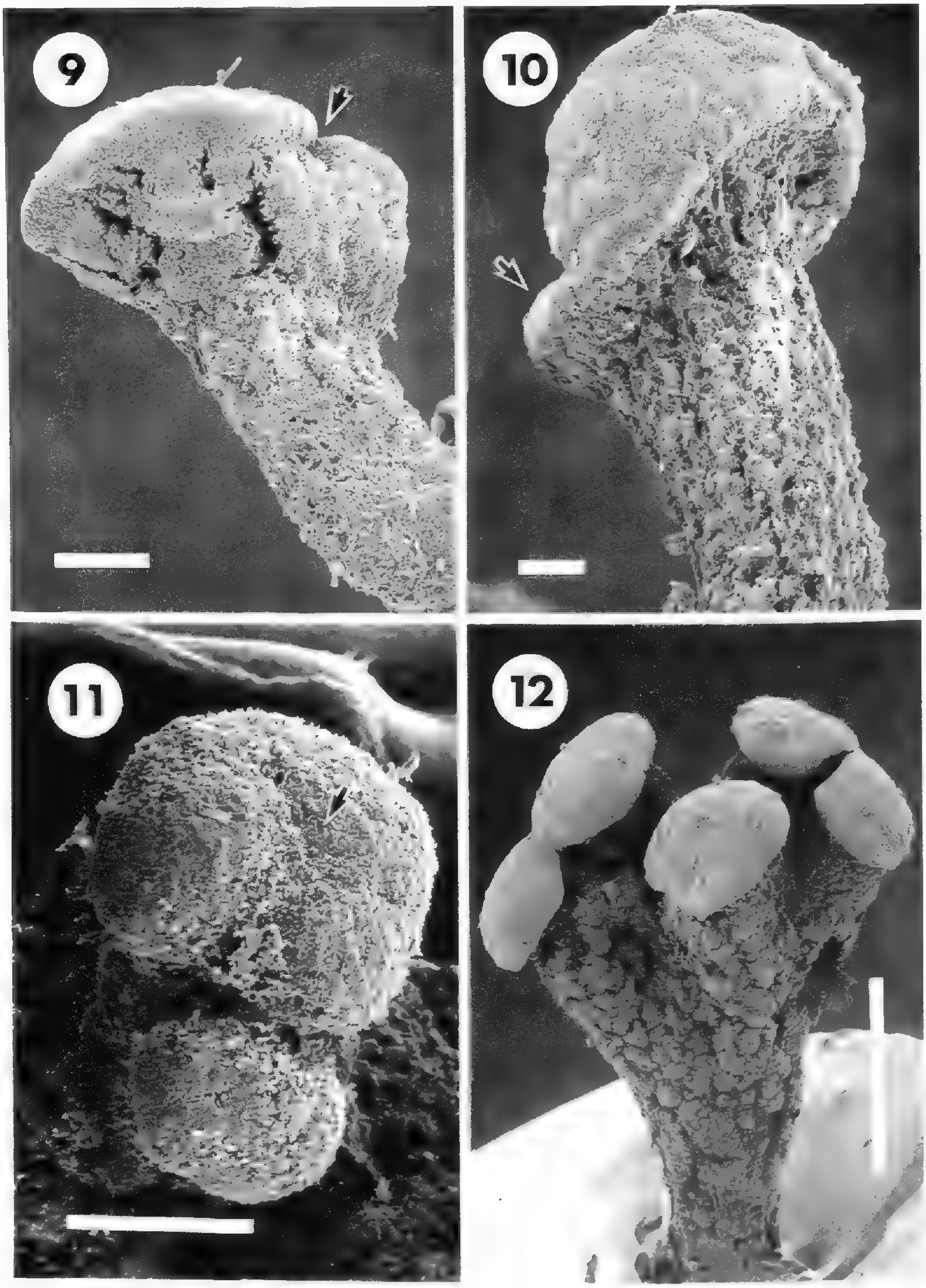
portion of meristem (arrow) is near apex of the podetium. Note soredia on upturned surface of squamule. 8. Branch initiation late in ontogeny. Meristem bundles have split and most face sideways or downward. Subsequent elongation of thallus under meristem tissue will produce branches. Scale bar in Figure 5 = 100 μm; other scale bars = 1 mm.



Figures 9–12. Growth patterns in *Cladonia incrassata* (SEM). 9. Early ontogeny of podetium. Interior of podetium at this stage is solid. Longitudinal fissures have begun to form and apical meristem has begun to divide (arrow). 10. Slightly later ontogeny of podetium, side view. Note large, oblique upper portion of meristem with smaller portion below to the left (arrow). 11. Front view of meristem in previous figure. Note incipient division on upper portion of meristem (arrow). 12. Maturing podetium with side branches slightly deflexed away from camera. Note that the meristem bundles have not completely

cells beneath them apparently do not continue to divide. Once the meristem has moved to the abaxial position all of the cells distal to it, including those on the opposite (adaxial) surface of the podetium, appear to stop dividing. This results in widening and proliferating fissures that make the podetium appear hood-like macroscopically.

DISCUSSION

Many of the features of the mature podetium in *Cladonia incrassata* are laid down early in ontogeny by a meristem-like mass of fungal tissue. As the meristem grows, the orientation of its cells (irregular, parallel, or radial) changes. The conformation of the meristem tissue (divided or undivided) and its position on the podetium (adaxial, apical, or abaxial) also change. The rate of change for all of these conditions differs among podetia and one result is macroscopic variability. Yet the earliest ontogeny of *C. incrassata,* like other Cladonias, follows a distinct pattern. The unusual developmental morphology of *C. incrassata* can be traced to early meristem development, with variability arising throughout ontogeny.

The source of this variability may have a genetic basis. Like the variable *Cladonia cristatella, C. incrassata* is fertile. In both species, the hymenium is well developed and abundant ascospores are common in mature specimens. Thus, the variable growth dynamics of *C. incrassata* may be the result of a heterogeneous gene pool in which recombination is frequent. While sexual processes in *Cladonia* have not been convincingly documented (see Hammer 1993), *C. incrassata* does appear to produce ascogenous cells such as those illustrated by Jahns (1970). We may infer from this that *C. incrassata* undergoes some sort of sexual reproduction, which may be reflected in developmentally based variation. It is, however, important to note that sexuality in lichens, and particularly the Cladoniaceae, is poorly understood. For example, in spite of specialized cells such as asci and ascospores that he observed in lichens, Hale (1974) was cautious

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split. Podetium resembles *C. cristatella.* Scale bar in Figures 9–11 = 100 μm; Figure 12 = 1 mm.

about attributing their presence to full sexual function. Rather, he attributed their presence to what he called "homomictic plasmogamy," a form of self-fertilization. Other authors, for example Henssen (1981), documented ascomycete sexual processes in lichens, including some *Cladonia* species, but acknowledged that those findings were contradictory.

Variability in the deflexed podetium of *Cladonia incrassata* may be attributable to environmental conditions. For example, deflexion could be a phototropic response. It might also be related to moisture availability. The effectiveness of close range spore dispersal may also be affected by downward-facing apothecia. However variable, the deflexed habit seems to be constant in this species. Specimens from eastern North America and Europe (see Table 1), which represent most of the geographical range of this species, show deflexed growth. Whatever its origin, variability is present in *C. incrassata,* and it has led to confusion in the taxonomic literature surrounding this species.

Confusion arose in the nineteenth century when Tuckerman (1882) described a "reduced form" of *Cladonia cristatella* from New England, which he named var. *paludicola.* Tuckerman was aware of *C. incrassata,* to which he also compared the new variety, stating it "corresponds closely." The basis of his statement is unclear, as *C. cristatella* and *C. incrassata* are morphologically distinct. Tuckerman may not have considered the primary squamules an important character, but the squamules of *C. incrassata* are always sorediate while those of *C. cristatella* are esorediate. Tuckerman may have studied only developing specimens that had not become sufficiently deflexed, or he may not have considered this unusual habit as a distinguishing characteristic. He may have

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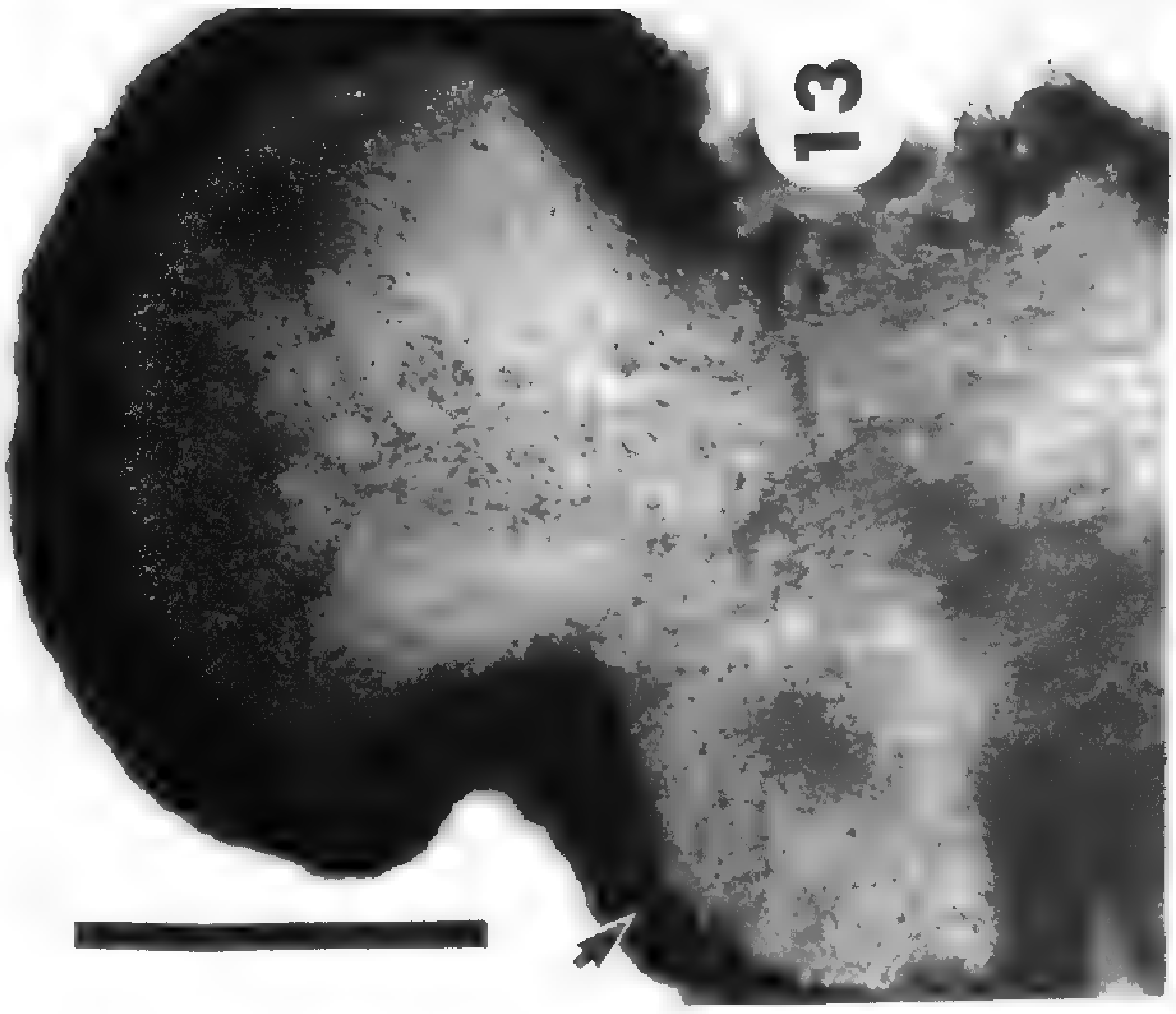
Figures 13–16. Longitudinal sections of podetia of *Cladonia incrassata* (LM). Figures show very early growth with developing hymenium borne apically or laterally. 13. Early ontogeny of podetium. Note two developing apical regions. Smaller region (arrow) will form adaxial branch after larger region grows toward right and downward. Dark band surrounding developing regions is layer of rhodocladonic acid. 14. Early deflexed growth (growing toward left). Hymenium has not formed. Meristematic cells concentrated in band indicated by arrow. Note developing lacunae (l) and algal cells (a). 15. Later deflexed growth (toward left). 16. Developing hymenium with presumed ascogenous cells (arrow). Scale bar in Figures 13–15 = 50 μm; Figure 16 = 10 μm.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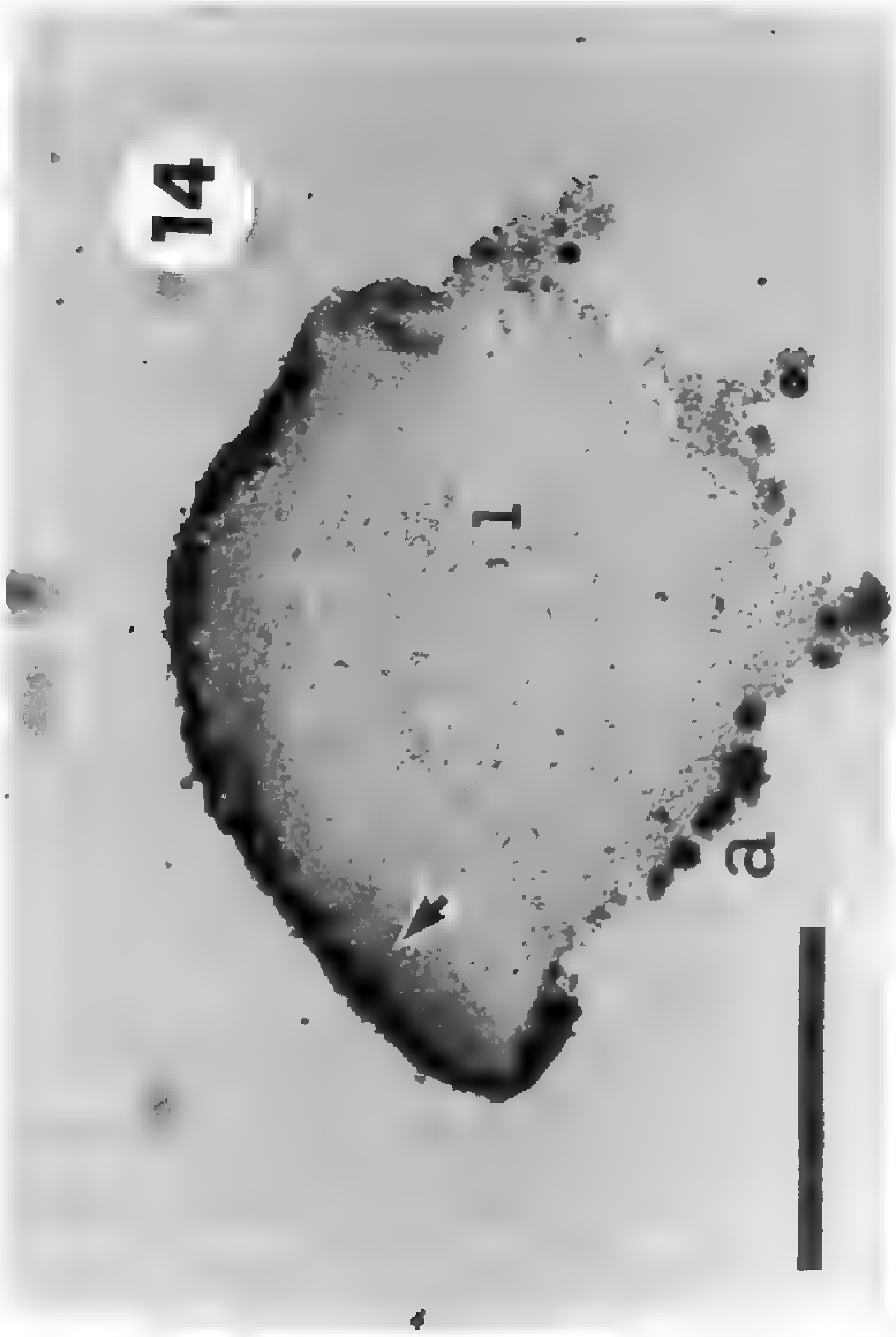
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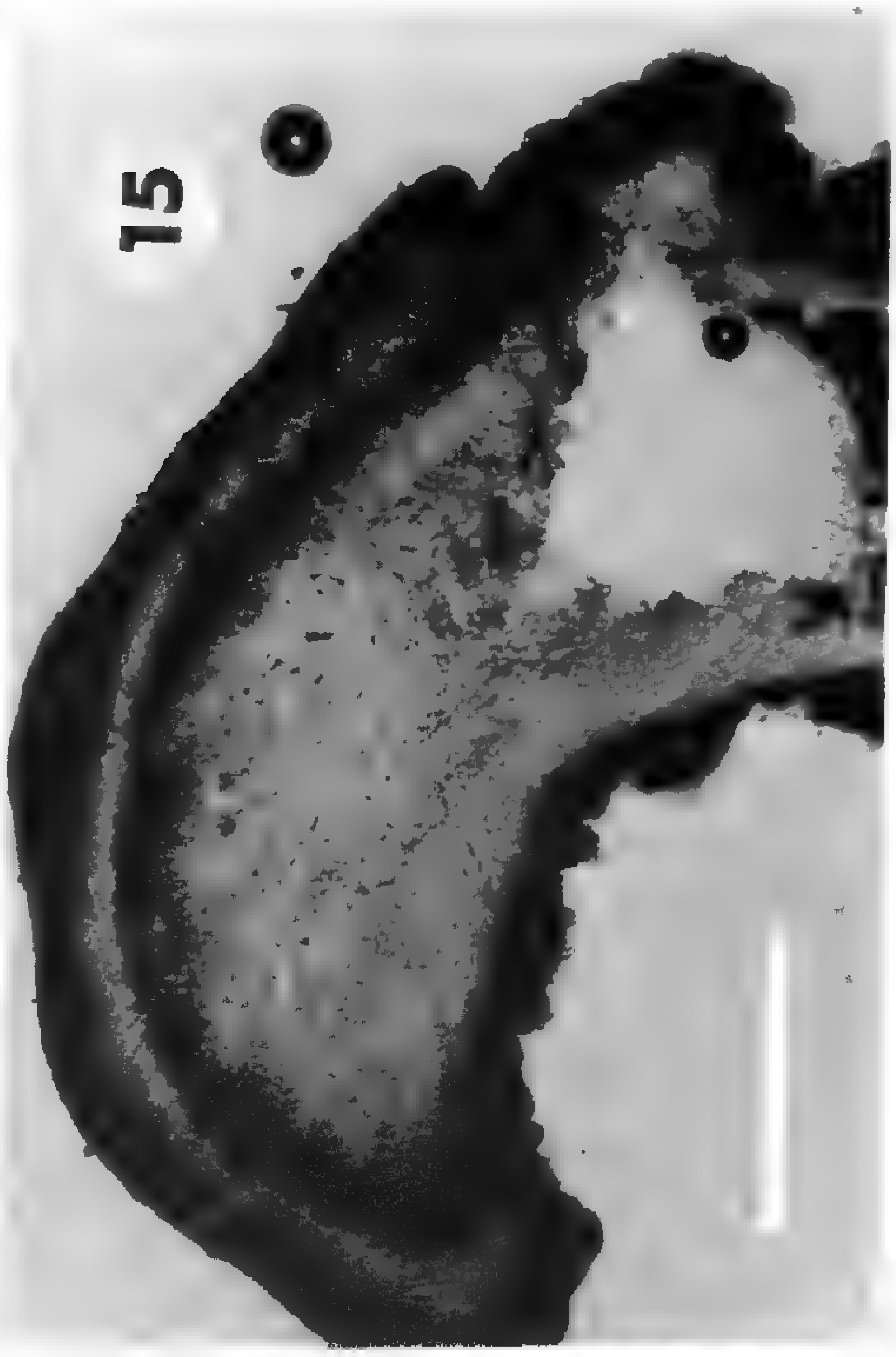
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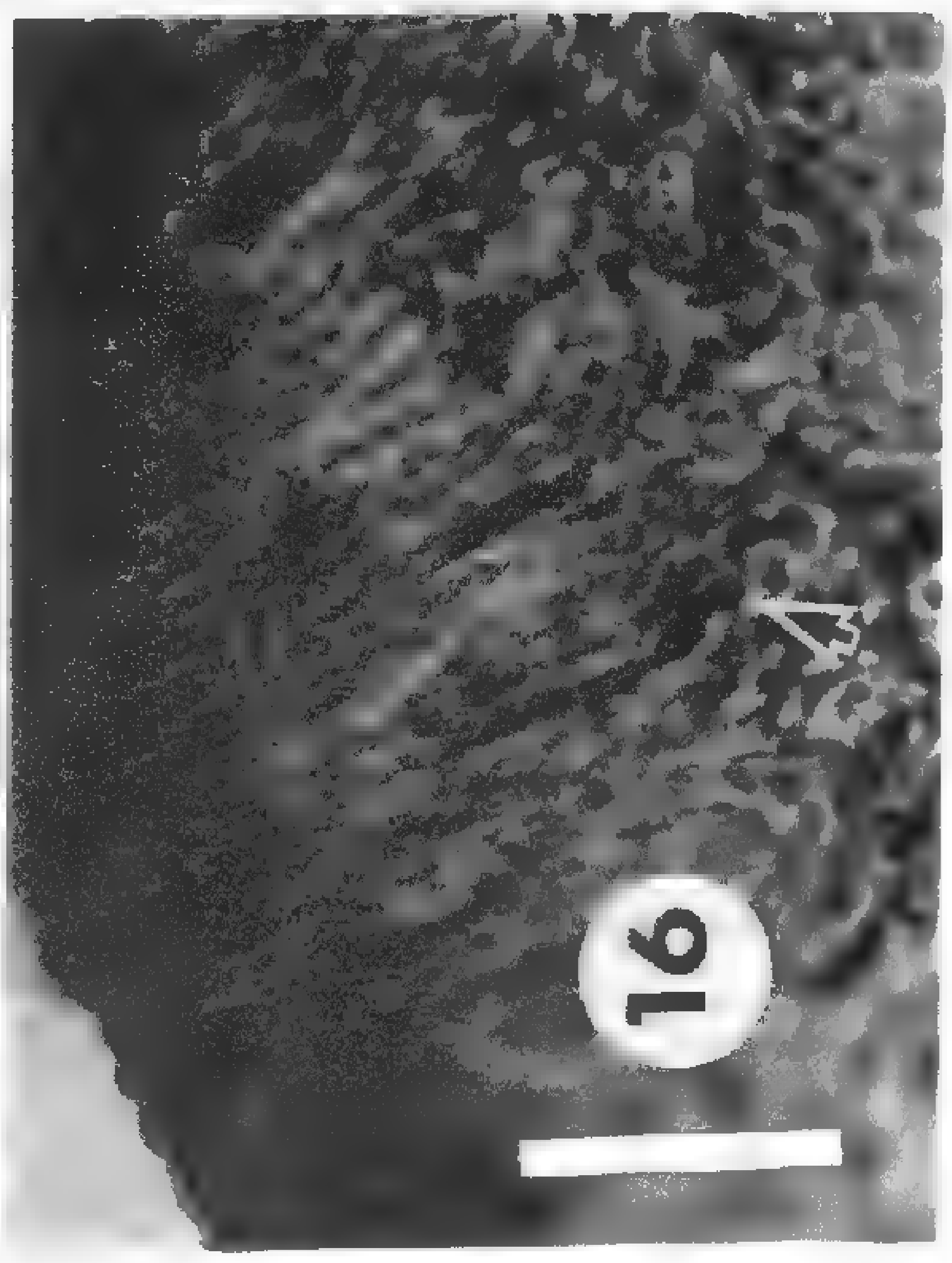
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considered the "reduced" deflexed podetia as somehow atypical of the species. Deflexion in *C. incrassata* is sometimes subtle and it may become apparent late in ontogeny. Podetia at all stages that are not strongly deflexed may be confused for *C. cristatella* in the absence of microchemical tests. The name *paludicola* ("a dweller in marshes," see Stearn 1966) came to be misapplied to North American specimens of *C. incrassata* through the 1930s. Much of the problem during this century can be attributed to Charles A. Robbins, an indefatigable collector and enthusiastic amateur.

In his correspondence with George Knox Merrill, Robbins expressed indignation over what he considered to be the domination of lichenology by Europeans. In a 1923 letter to Merrill (Farlow Reference Library, unpubl.) Robbins mentioned *Cladonia paludicola,* which he considered to be distinct from *C. cristatella.* He apparently did not recognize *C. incrassata* in New England, since he labeled all of his corresponding specimens as *C. paludicola.* Perhaps to shore up his concept of what he considered to be an American endemic species, Robbins began to assign formae to his specimens such as "f. *squamulosa.*" He influenced Merrill, who finally recombined var. *paludicola* and elevated it to the status of species, a decision that was made on the strength of Robbins's protestations that it was distinct (Merrill 1924). Based on Robbins's findings, Merrill reported that there was "little similarity" between the new *C. paludicola* and *C. cristatella* but conceded that "transitional states" between the species could be found in "damp situations." Evans (1930) reasserted the independent status of *C. paludicola,* which he discussed at some length, and which he considered as an endemic species. He later recognized it as a variety of *C. cristatella* (Evans 1938) and finally included it in synonymy (Evans 1944), while maintaining *C. cristatella* and *C. incrassata* as distinct species. There is no record in the literature as to the basis of Evans's decision to finally exclude *C. paludicola,* but it is noteworthy that Sandstede labeled a North American specimen (*Exsiccatum* 1684) as *C. incrassata.* It seems that Sandstede's conservative view was the most appropriate, since mature *C. incrassata* possesses a wide range of morphological variability.

Cladonia incrassata traditionally has been classified within sect. *Cocciferae* (Del.) Matt. on the basis of its red hymenium, which contains the pigment rhodocladonic acid. This convention has been accepted since Vainio (1887, 1894, 1897), but it is based solely on the color and secondary chemistry of the podetium, without considering other characters. Choisy (1928) expressed reservations about the use of rhodocladonic acid in a natural classification of *Cladonia.* He considered developmental morphology when he rejected the monophyly of the *Cocciferae,* which he considered to be a polyphyletic, ancestral group. *Cladonia incrassata* shares certain morphological characteristics with other species in sect. *Cocciferae,* but some of these characteristics are widespread. For example, early branch initiation in this species is similar to that of *C. cristatella* although both are similar to species in sect. *Perviae* (Del.) Matt. and *Cladina* Nyl. (Hammer 1997a, b). The characteristic pattern of branch initiation is thus shared by species in various sections of *Cladonia,* and can be considered as plesiomorphic. Jahns and Beltman (1973) included *C. incrassata* with many taxa outside of sect. *Cocciferae* when they categorized its developmental morphology as "Type II," in which ascogonia are formed at the top of mature podetia. However, they hesitated to use this feature as a tool for classification. Rather, they invoked "variability" to explain how developmental morphology in *Cladonia* crossed taxonomic boundaries, an explanation that recalls Krabbe (1891), who considered *Cladonia* as a "polymorphic" group. Unfortunately, these biases have hindered the development of a natural classification for the Cladoniaceae. Variation in this important lichen group needs to be reconsidered (Hammer 1996b), and we must consequently be prepared to reconsider the established classification system in the family.

The developmental morphology of *Cladonia incrassata* suggests its placement outside of sect. *Cocciferae.* For example, the fissured podetium and indeterminate meristem of *C. incrassata* may link it to species in sect. *Helopodium* (Ach.) Matt. The five-part meristem initial in this species may be homologous to similar structures in sections *Perviae* and *Unciales* (Del.) Ahti, and the genus *Cladina* Nyl. (see Hammer 1996b, 1997a, b). Growth dynamics in *C. incrassata* suggest affinities that lie beyond *Cladonia,* suggesting an outgroup with which to compare the genus. For example the deflexed habit, which is rare or subtly expressed in other *Cladonia* species, characterizes the genus *Thysanothecium* Mont. & Berk., an endemic genus in temperate Australia and New Zealand. An outgroup such as *Thysanothecium* may provide a useful basis for phylogenetic inferences in *Cladonia.* Understanding the evolution of morphological characters in this difficult group will provide the groundwork for a natural classification in the Cladoniaceae.

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PHYLOGENETIC RELATIONSHIPS IN THE *CORYLOPSIS* COMPLEX (HAMAMELIDACEAE): EVIDENCE FROM SEQUENCES OF THE INTERNAL TRANSCRIBED SPACERS OF NUCLEAR RIBOSOMAL DNA AND MORPHOLOGY

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ABSTRACT. Morphological and nuclear ribosomal Internal Transcribed Spacer (ITS) sequence data were used to examine relationships among the genera in the *Corylopsis* complex, comprising *Corylopsis, Distylium, Eustigma, Fortunearia,* and *Sinowilsonia.* The ITS-2 based cladogram had the lowest resolution, whereas the ITS-1 and the pooled data of ITS-1 and ITS-2 produced similar phylogenies with complete resolution of intergeneric relationships within the complex. Both morphological data and ITS DNA sequences support separation of *Corylopsis* from the other genera, and a closer relationship of *Sinowilsonia* to *Fortunearia* than to *Distylium.* The monophyly of *Eustigma-Fortunearia-Sinowilsonia* was supported by the ITS sequence data. This study substantiates Endress's recent interpretation of the intergeneric relationships in the *Corylopsis* complex. The ITS phylogeny also supports the hypothesis that floral structures in members of the *Corylopsis* complex appear to have been modified for wind pollination in the course of evolution.

Key Words: phylogeny, *Corylopsis* complex, Hamamelidaceae, ITS DNA sequences

The Hamamelidaceae, consisting of 31 genera and about 140 species, is widely distributed in subtropical and temperate areas of both the Old and New Worlds (Endress 1993; Zhang and Lu 1995). Morphological diversity in this family, especially of reproductive attributes, has prompted numerous systematic studies (Bogle 1970, 1986, 1987, 1989, 1990; Bogle and Philbrick 1980; Chang 1973, 1979; Endress 1967, 1970, 1976, 1977, 1989a, b, c; Harms 1930; Mione and Bogle 1990; K. Tong 1930; Y. Tong 1943). Although subfamilial classification of the family has been, and is still, controversial, the subfamily Hamamelidoideae has been widely accepted as a monophyletic clade (Bogle and Philbrick 1980; Endress 1989a, b). The most definitive characteristics of this subfamily are uniovulate carpels, 2-carpellate capsules, and a ballistic mechanism for seed dispersal (Endress 1989a). However, the phylogenetic relationships among some members of the Hamamelidoideae remain problematic. One unresolved problem is that of the relationships of the genera that have been considered more or less related to *Corylopsis* Sieb. et Zucc. The *Corylopsis* complex for the purpose of this study encompasses five well-defined genera: *Corylopsis, Distylium* Sieb. et Zucc., *Eustigma* Gardner et Champ., *Fortunearia* Rehd. et Wils., and *Sinowilsonia* Hemsl.

The *Corylopsis* complex shows a high diversity of floral structures and can be considered as an epitome of the family. For example, flowers have conspicuous sepals and petals in *Corylopsis*; petals are rather reduced in *Eustigma, Fortunearia,* and *Sinowilsonia*; there are no sepals or petals in *Distylium.* Therefore, resolution of the intergeneric relationships within the complex may shed light on the evolutionary directionalities of floral characters in the Hamamelidaceae.

Harms (1930) made the first comprehensive taxonomic treatment of the Hamamelidaceae, placing 21 genera in five subfamilies (two additional genera that were little known were not placed). The Hamamelidoideae was the largest subfamily, containing 16 genera in five tribes. The genera of the *Corylopsis* complex fell into three of these tribes: the monogeneric Eustigmateae (*Eustigma*); the Corylopsideae (*Corylopsis* and *Fortunearia*), and the Distylieae (*Distylium, Sinowilsonia,* and *Sycopsis*).

Schulze-Menz (1964) basically adopted Harms's classification, but moved *Sinowilsonia* out of the tribe Distylieae and placed it close to *Fortunearia* of the Corylopsideae. Many botanists have followed Harms's system at the tribal level (e.g., K. Tong 1930; Chang 1973, 1979).

Endress (1989a, b), however, moved both *Fortunearia* and *Sinowilsonia* into the Eustigmateae, thus treating the Corylopsideae as a monogeneric tribe. Nonetheless, as admitted by Endress (1989a), the phylogenetic relationships among the genera were not well resolved.

Sequences of the Internal Transcribed Spacer (ITS) of nuclear ribosomal DNA have been widely and almost routinely used for phylogenetic studies of angiosperms at specific and generic levels

Table 1. Vouchers for the species sampled. AA, the Arnold Arboretum; GUNH, the Greenhouse at the University of New Hampshire; WI, Woodlanders Inc., SC. Each species name is followed by a 3-letter acronym used in other tables and figures.

Species	Voucher	Source	GenBank Accessions
Corylopsis pauciflora (*cpa*)	Li01	AA	U65462
C. sinensis (*csi*)	Li02	AA	U65461
C. spicata (*csp*)	Li03	AA	U65463
Distylium myricoides (*dim*)	Bogle	GUNH, WI	U65464
D. racemosum (*dir*)	Bogle	GUNH, WI	U65465
Eustigma oblongifolia (*eus*)	Chung, N. J.	Taiwan	U65466
Fortunearia sinensis (*for*)	Li04	AA	U65467
Sinowilsonia henryi (*sin*)	Li05	AA	U65468
Mytilaria laosensis (*myt*)	Luo, Y. C.	Xinning, China	U65469

(Baldwin et al. 1995; Campbell et al. 1995; Suh et al. 1993; Wojciechowski et al. 1993). In this study, therefore, we based our analysis of relationships on the evidence from both the ITS and morphological data. The objective of this investigation has been to evaluate the alternative hypotheses concerning the relationships among the genera of the complex, which can be translated into the following questions: 1) Should *Corylopsis* be isolated from the other genera and be treated as a monogeneric tribe? 2) Is it reasonable to put *Eustigma* together with *Fortunearia* and *Sinowilsonia* in the Eustigmateae even though *Eustigma* is somewhat different from the others morphologically and geographically? and 3) Is *Sinowilsonia* more closely related to *Distylium* than to *Fortunearia*?

MATERIALS AND METHODS

The internal transcribed spacers ITS-1 and ITS-2 were sequenced for nine species, representing all five genera of the *Corylopsis* complex and an outgroup, *Mytilaria* Lecomte (Table 1). Three of the six genera sampled are monotypic, including *Fortunearia*, *Mytilaria*, and *Sinowilsonia*. Several to many species have been described in *Corylopsis* (9–20), *Distylium* (10–18), and *Eustigma* (2–4; Zhang and Lu 1995). These three genera, however, have not been monographed in recent years and the number of valid species is debatable. Furthermore, materials of some species were unavailable for this study. Therefore, the representation of these three genera is unavoidably limited to generally accepted, valid species for which samples could be obtained from cultivated plants or from accessible field locations.

The genera of the *Corylopsis* complex represent three of the four tribes in the monophyletic Hamamelidoideae, but the tribal relationships are unresolved (Endress 1989a). Thus, it is uncertain which genera should be used as outgroups from within the Hamamelidoideae. Endress (1989a) used Exbucklandioideae (incl. *Disanthus, Mytilaria,* and *Exbucklandia*) as the outgroup in his phylogenetic evaluation of the Hamamelidoideae based on morphological data. Our preliminary results from sequences of *mat*K gene encoding plastid maturase suggested that the most closely related genera to the Hamamelidoideae were *Mytilaria* and *Disanthus* (unpubl.). Therefore, we chose *Disanthus* and *Mytilaria* as outgroups. Although we obtained the same tree topology when using either or both of these two genera as outgroups, the confidence of the sequence alignment decreased when both *Mytilaria* and *Disanthus* were used. Thus, we included only *Mytilaria* in the parsimony analysis. The DNA sequences obtained in this study have been submitted to the GenBank and their accession numbers are listed in Table 1 (*Disanthus* is not included).

Molecular techniques. Total genomic DNAs were extracted from young leaves using the standard DNA extraction procedures of Doyle and Doyle (1987). The universal primers ITS4 and ITS5 of White et al. (1990) were used to amplify the entire ITS nuclear DNA region using the Polymerase Chain Reaction™ (PCR). Each 50 μl reaction included 4–5 units of *Taq* (Promega, Madison, WI), 4–5 units of *Taq* Extender (Stratagene, La Jolla, CA), 1× *Taq* extender buffer, 2.5 mM dNTPs, 50–100 ng DNA, and 20 μM primers. Amplifications were preceded by a three minute 94°C Hot Start (D'Aquila et al. 1991) and conducted in thin-walled tubes in a MJ-Research thermocycler (Watertown, MA). The PCR program consisted of 30 cycles with 94°C denaturation for 30 seconds, 45°C annealing for 115 seconds, and 72°C extension for 115 seconds. The final cycle was followed by a ten minute extension step at 72°C.

The PCR amplified products were purified on 1.1% low melting point agarose gels in 1× TBE buffer (pH 8.0). The ITS bands of about 740 bp, identified by comparison to ØX174 *Hae*III DNA size markers, were excised and agarase-digested for 30 minutes. Then the purified PCR products were used as templates for direct double-stranded sequencing using cycle sequencing and dye-dideoxynucleotide terminator chemistry reactions, and the products were resolved on an ABI 373A fluorescent sequencer (Applied Biosystems, Foster City, CA). The procedures were carried out according to the manufacturer's instructions at the University of New Hampshire Sequencing Facility Center. Besides ITS4 and ITS5, ITS2 and ITS3 of White et al. (1990) were used as internal sequencing primers.

DNA sequence chromatograms were analyzed using the *Seqed* program (Applied Biosystems) and the sequences were then contigged using the *Seqman* of DNA* software package (Madison, WI). The boundaries of ITS-1 and ITS-2 were determined by comparing the limits of the 3′ end of the 18S, 5.8S, and 5′ end of the 26S rRNA sequences of the ITS region in *Canella winterana* (GenBank accession number: L03844).

Statistical analysis. Chi-square independence tests were applied to test whether the distribution of base compositions was significantly different among the genera. Analysis of variance (ANOVA) was utilized to test the null hypothesis that pairwise divergences among the genera were significantly different between ITS-1 and ITS-2 (Zar 1996).

Morphological data. Twenty-three morphological characters for the *Corylopsis* complex and the outgroup *Mytilaria* were collected based on literature and our own observations (Bogle 1990; Bogle and Philbrick 1980; Chang 1979; Endress 1989b; Li and Bogle 1995; Li et al. 1993; Y. Tong 1943). The characters and their states are described in Table 2. We included one species for each genus in the morphological analysis, since little intrageneric variation in the collected morphological characters resulted in identical scores for species within a genus. As a result, the number of species included in the morphological data set is smaller than the number of species in the ITS data set.

Phylogenetic analyses. The DNA sequences were aligned using the clustal option of the *Megalign* program of DNA*. The aligned sequences are available from the authors. All DNA sequence characters and their states were unweighted, and indels were coded as missing data. Phylogenies were reconstructed using PAUP 3.1.1. (Swofford 1993) with the exhaustive search option.

Table 2. Morphological characters and their states used in the parsimony analysis.

Character	State and Code
1. Seed dispersal	Nonballistic (0), ballistic (1)
2. Venation	Pinnate (0), intermediate (1), palmate (2)
3. Number of ovules per carpel	>3 ovules (0), 3 ovules (1), 1 ovule (2)
4. Nodal anatomy	Trilacunar (0), multilacunar (1)
5. Sexuality	Bisexual (0), andromonoecious (1), monoecious (2)
6. Petals	Distinct (0), reduced (1), absent (2)
7. Pollen apertures	Tricolpate (0), tetracolpate (1)
8. Pollination	Insect (0), wind (1)
9. Pollen surface	Smooth (0), verrucate (1)
10. Ovary position	Semi-inferior (0), superior (1)
11. Stipules	Filamentous (0), leafy (1)
12. Trichome types	Scale (0), stellate (1)
13. Stigma	Unexpanded (0), strongly expanded (1)
14. Habit	Evergreen (0), deciduous (1)
15. Inflorescence	Spike (0), spadix (1)
16. Staminodes	Present (0), absent (1)
17. Anther connective protrusion	Absent (0), present (1)
18. Filament	Longer than or equal to anther (0), shorter than anther (1)
19. Vessel bars	More than 30 (0), 30 or fewer (1)
20. Crystal types	Absent (0), simple (1), cluster (2)
21. Flower parts	Fixed (0), variable (1)
22. Foliar sclereids	Absent (0), fusiform (1), libriform (2)
23. Lenticel on ovary	Absent (0), present (1)

One thousand replicate bootstrap and decay analyses were performed to obtain the indices of relative support for individual clades. The morphological characters were treated as unordered and their states were unweighted to avoid biases in the parsimony analysis. The tree generated based on the combined ITS and morphology data sets was imported into the MacClade 3.03 program (Maddison and Maddison 1992) to analyze the unambiguous changes of the morphological characters along the branches.

RESULTS

Sequence characteristics. Sequence lengths in the *Corylopsis* complex ranged from 236 to 275 bases in ITS-1 and from 224 to

238 bases in ITS-2. ITS-1 was longer than ITS-2 for all taxa sampled except *Eustigma, Fortunearia,* and *Sinowilsonia,* whose two spacers were more or less equal in length. GC contents for ITS-1 and ITS-2 were very similar, 57–64% and 61–67%, respectively (Table 3). An Independence test showed that distribution of base compositions (A, T, G, C, and GC content) was not significantly different for all the genera ($P > 0.8$).

The pairwise divergences among the genera ranged from 3.4% to 17.8% in ITS-1 and from 6% to 14.9% in ITS-2, and divergences between these genera and the outgroup *Mytilaria* varied slightly from 21.6% to 25.8% in the ITS sequences. In *Corylopsis* and *Distylium,* where more than one species was sampled, the divergences within each genus were generally lower than 4% (Table 3). Analysis of variance (ANOVA) demonstrated that pairwise divergences between ITS-1 and ITS-2 were not significantly different ($P = 0.8$), nor were the pairwise divergences among the genera in the combined data of ITS-1 and ITS-2 ($P = 0.1$).

Alignment of the sequences required 14 indels, six of which were two or more bases in length. Table 4 lists the largest six indels in these ITS sequences. Noticeably, deletion 4 occurred only in *Corylopsis,* whereas deletion 2, consisting of 36 bases, was found in *Eustigma, Fortunearia,* and *Sinowilsonia.* These three genera also had deletion 3 in common with *Corylopsis.* Both species of *Distylium* sampled possessed deletion 5, and shared deletion 6 with *Corylopsis pauciflora, Eustigma, Fortunearia,* and *Sinowilsonia.* None of the six indels was found in *Mytilaria.*

Phylogenetic trees. When only ITS-1 sequences were utilized in the parsimony analysis, an exhaustive search found one shortest tree of 131 steps (Figure 1a) in which a clade of *Corylopsis* and a clade of *Distylium-Eustigma-Fortunearia-Sinowilsonia* were well resolved, with bootstrap values and decay indices of 100%, 11 steps, and 98%, six steps, respectively. However, *Eustigma* and *Fortunearia* were grouped within a clade weakly supported by a 60% bootstrap value and one step of decay.

The strict consensus tree of the two shortest trees of 114 steps based on ITS-2 data (Figure 1b) did not resolve the relationships of the three groups, *Corylopsis, Distylium,* and *Eustigma-Fortunearia-Sinowilsonia.* However, the internal relationships of the three clades were basically the same as in the ITS-1 phylogeny,

Table 3. Sequence length, GC content and divergences of ITS-1 and ITS-2 in the sampled species (above diagonal ITS-2, below diagonal ITS-1; Taxon abbreviations as in Table 1).

Species	Length	GC Content	*cpa*	*csi*	*csp*	*dim*	*dir*	*eus*	*for*	*sin*	*myt*	Length	GC Content
cpa	269	59.85	0	3	3.9	11.7	12.6	12	11.2	14.9	22.7	233	63.09
csi	274	57.66	4.1	0	0.9	10.4	10.8	11.2	10.7	12.9	22.6	234	64.95
csp	275	57.45	3.7	2.2	0	11.3	11.7	12	11.6	13.7	22.1	234	64.11
dim	271	62.21	15.8	17.8	17.7	0	1.7	9.9	8.2	12.8	22	235	65.95
dir	271	64.21	15.8	17.8	17.7	1.1	0	9.4	8.5	12.8	21.6	235	66.81
eus	236	59.74	13.5	15.4	15.3	8.5	8.9	0	6	9.4	22.5	235	64.25
for	236	62.71	13.9	16.6	16.5	9.3	9.7	5.1	0	7.6	21.9	236	65.26
sin	236	60.16	11.7	14.5	14.4	8.5	8.9	3.4	3.8	0	25.8	238	65.18
myt	275	63.64	22.7	25	24.5	23.4	23	24	25.2	24.8	0	224	61.34

Table 4. Indels of two or more bases in length of ITS DNA sequences in the sampled species (+ presence; − absence; * deletion number; ** base range; Taxon abbreviations as in Table 1).

	1*	2	3	4	5	6
Species	63–67**	110–145	302–323	334–337	338–339	490–491
cpa	+	−	+	+	−	+
csi	−	−	+	+	−	−
csp	−	−	+	+	−	−
dim	−	−	−	−	+	+
dir	−	−	−	−	+	+
eus	−	+	+	−	−	+
for	−	+	+	−	−	+
myt	−	−	−	−	−	−
sin	−	+	+	−	−	+

with the exception of *Fortunearia* and *Sinowilsonia* forming a clade supported by a bootstrap value of 61% and a decay index of one step.

When ITS-1 and ITS-2 were combined in the analysis, a single shortest tree of 246 steps was generated (Figure 1c), showing relationships similar to those of the ITS-1 tree, but with *Fortunearia* and *Sinowilsonia* forming a clade sister to *Eustigma.* The combination of the two spacers resulted in stronger support for the group of *Eustigma, Fortunearia,* and *Sinowilsonia* relative to either of the separate data sets.

The single shortest phylogenetic tree (34 steps) produced, based on morphological data (Figure 2), contained two clades in the complex: *Corylopsis* and *Eustigma-Distylium-Fortunearia-Sinowilsonia.* Within the second clade, *Eustigma* was the basal genus followed by *Distylium,* and sister to *Distylium* was the clade of *Fortunearia* and *Sinowilsonia.* The bootstrap value and decay index were 75% and two steps for the clade of *Eustigma-Distylium-Fortunearia-Sinowilsonia,* and these supporting values were all small for the internal relationships.

A parsimony analysis using the combined data set of morphology and ITS sequences produced the same cladogram (Figure 3) as the combined ITS phylogeny (Figure 1c).

As shown in Figure 3, mapping unambiguous changes of the morphological characters on the tree that was generated using the combined ITS and morphological data revealed that the clade of *Distylium* and *Eustigma-Fortunearia-Sinowilsonia* was

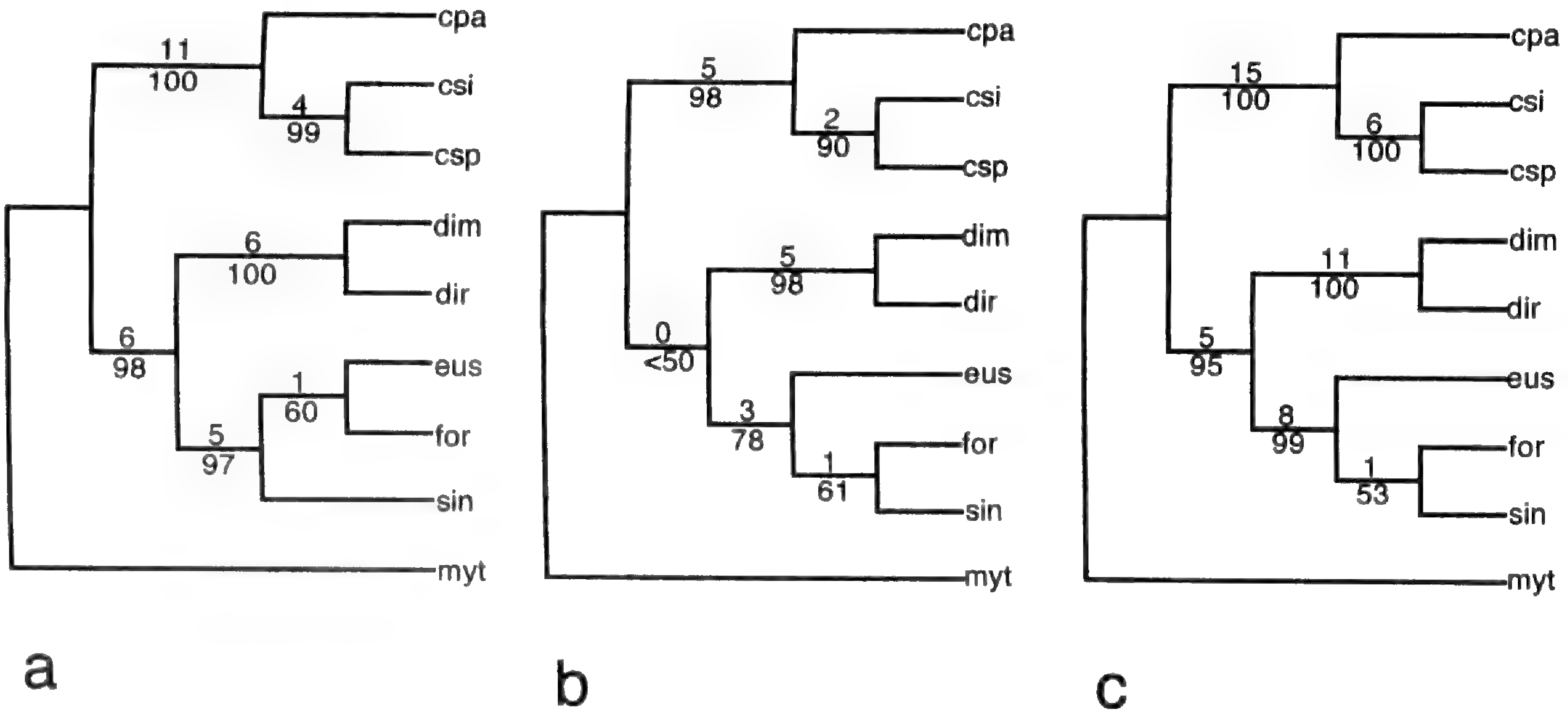

Figure 1. Parsimony analyses of DNA sequences of ITS-1, ITS-2, and the pooled data set of ITS-1 and ITS-2, for eight species of the *Corylopsis* complex using *Mytilaria* as the outgroup. Numbers above branches are decay index values, and numbers below branches indicate bootstrap percentages. Taxon abbreviations as in Table 1. a. The single most parsimonious tree of 131 steps for ITS-1 DNA sequences, CI = 0.916, RI = 0.885. b. One of the two most parsimonious trees of 114 steps based on ITS-2 DNA sequences, CI = 0.868, RI = 0.779. c. The single most parsimonious tree of 246 steps generated from the pooled DNA sequences of ITS-1 and ITS-2, CI = 0.89, RI = 0.835.

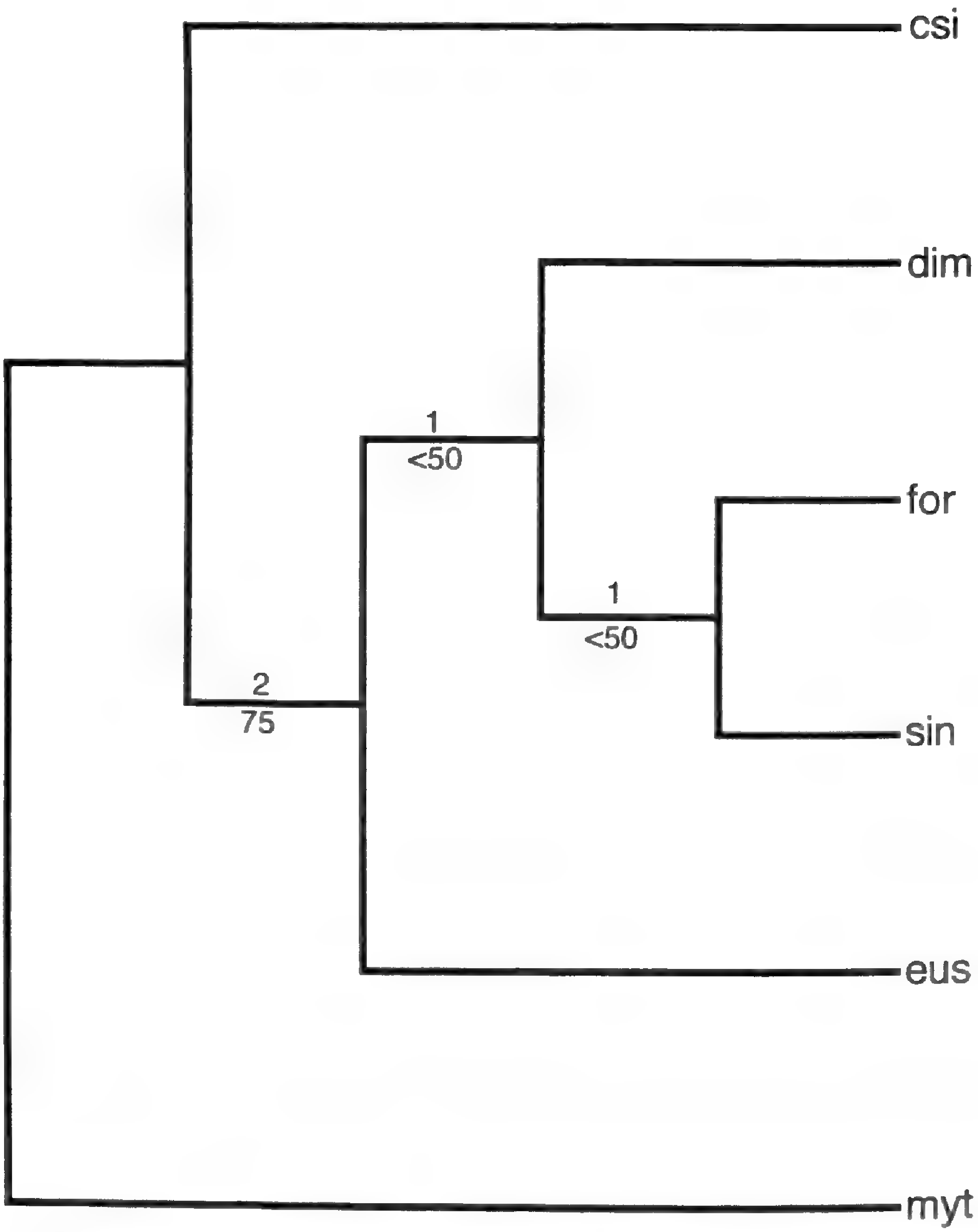

Figure 2. The single shortest tree of 34 steps based on morphology. CI = 0.824, RI = 0.538. Numbers above branches indicate decay index values, and numbers below branches are bootstrap percentages. Taxon abbreviations as in Table 1.

supported by three unambiguous character state changes: pollination from entomophilous to anemophilous, stipules from leafy to filamentous, and staminodes from present to absent. *Fortunearia* and *Sinowilsonia* share deciduousness and absence of foliar crystals.

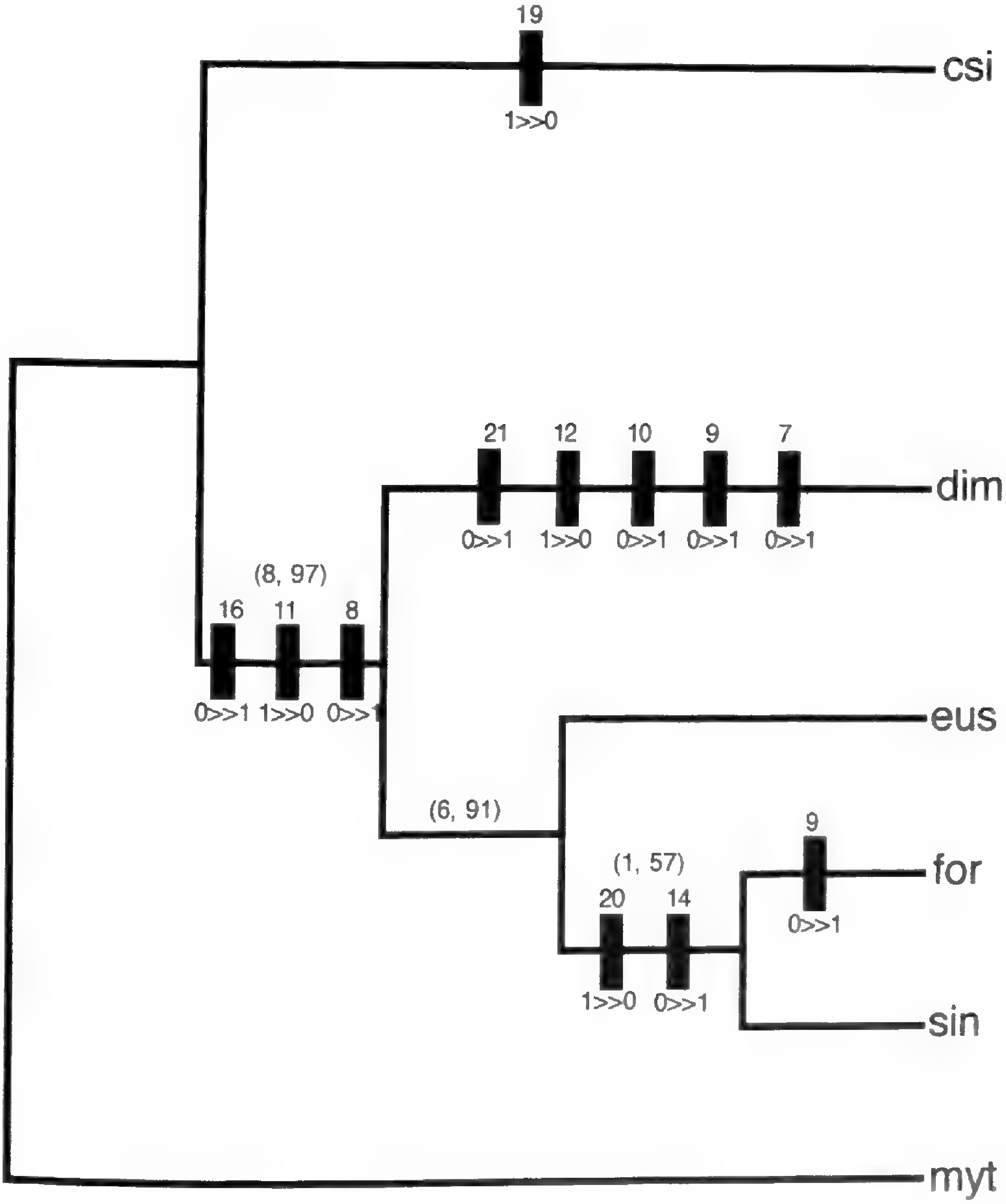

Figure 3. The single most parsimonious tree of 264 steps based on morphology and ITS data. CI = 0.894, RI = 0.52. Taxon abbreviations as in Table 1. Numbers in parentheses are decay index values and bootstrap percentages, respectively. Black rectangles represent the unambiguous changes of morphological characters. Characters and their states are shown in Table 2.

DISCUSSION

Sequence characteristics. The ITS DNA sequences from available angiosperms have shown that ITS-1 and ITS-2 range from 187 to 298 and 187 to 252 bases, respectively, and that ITS-1 is generally larger than ITS-2 (Baldwin et al. 1995). In the

Corylopsis complex, sequence lengths of the ITS region are generally within this range; however, in *Eustigma, Fortunearia,* and *Sinowilsonia,* the sizes of ITS-1 and ITS-2 are nearly equal because these three genera share a 36-base deletion in ITS-1 that shortens this spacer. GC contents for ITS-1 and ITS-2 in subfamily Maloideae (Rosaceae) were found to be toward the high end of the range for angiosperms (Campbell et al. 1995). This is true also for the genera of the *Corylopsis* complex (Table 3). The pairwise sequence divergences of the genera are slightly higher in ITS-1 than in ITS-2, but the statistical analysis shows that the difference is not significant ($P = 0.8$). This result agrees with previous studies (Baldwin et al. 1995; Campbell et al. 1995). As expected from the results found in most angiosperms (Baldwin et al. 1995), ITS-1 is slightly more informative than ITS-2 in the *Corylopsis* complex. The trees generated from the two spacers are mostly congruent (Figure 1a, b); therefore, the pooled data produced a phylogeny with at least the same level of resolution as ITS-1 (Figure 1c).

Phylogenetic relationships. The pooled ITS-based phylogeny (Figure 1c) clearly indicates that the *Corylopsis* complex is composed of two well-differentiated clades. The first clade is of *Corylopsis* and the second clade consists of *Distylium* and *Eustigma-Fortunearia-Sinowilsonia. Corylopsis* is seemingly similar to *Fortunearia* in leaf morphology; therefore, it has been treated, together with *Fortunearia,* as belonging to the tribe Corylopsideae (Chang 1979; Harms 1930; Schulze-Menz 1964). However, *Corylopsis* differs greatly from *Fortunearia* in its semi-evergreen, shrubby habit, bisexuality, and broad, showy petals. Therefore, the phylogeny based on ITS data is consistent with a group of floral characters. The results support the hypothesis that *Corylopsis* is not closely related to any of the other genera in the complex (Endress 1989a, b). Endress (1989a, b) recognized the genus *Corylopsis* as a monogeneric tribe. We believe, however, that this treatment cannot be fully evaluated until a study including a broader range of genera is conducted (Li et al., unpubl. data).

The clade of *Distylium* species is sister to the clade of *Eustigma-Fortunearia-Sinowilsonia* in the trees generated using ITS data (Figure 1a, b, c), but the morphology-based tree (Figure 2) suggests that *Eustigma* is sister to *Distylium-Fortunearia-Sinowilsonia.* However, in the morphology tree, clade support is weak for the relationship. Therefore, the combined analysis using ITS and morphology (Figure 3) seems to be appropriate (de Queiroz 1993). The resulting tree shows the same tree topology as the ITS phylogeny. Thus, as proposed by Schulze-Menz (1964) and supported by Endress (1989a, b), *Sinowilsonia* is not closely related to *Distylium.*

The clade of *Eustigma-Fortunearia-Sinowilsonia* is strongly supported with a bootstrap value of 91% and a decay index of six steps in the phylogeny based on the combined data set of morphology and ITS. Interestingly, these three genera also share a unique long deletion of 36 bases (Table 4). Therefore, the three genera are undoubtedly closely related, not distantly allied as described by Endress (1989b). However, neither the clade of *Eustigma-Fortunearia* nor the clade of *Sinowilsonia-Fortunearia* is very strongly supported by decay indices and bootstrap values (Figure 1a, b, c). Both *Fortunearia* and *Sinowilsonia* are monotypic, and *Eustigma* has debatably only several species; thus, some taxa bridging them are possibly missing. This might contribute to the loose relationships among them. Morphologically, *Eustigma* is characterized by its greatly expanded purple stigma; as a result, it has been recognized as a monotypic tribe (Chang 1979; Harms 1930). Recently, Endress (1989a, b) put this genus into a tribe containing *Fortunearia* and *Sinowilsonia* based on the fact that *Eustigma* shares reduced petals with *Fortunearia* and *Sinowilsonia* and has lenticellate capsules in common with *Fortunearia.* ITS data in this paper offer strong support for this hypothesis.

Bogle and Philbrick (1980) and Endress (1989c) pointed out that floral structures of the *Corylopsis* complex appear to have become reduced for wind pollination in the course of evolution. The phylogenetic tree based on the combined ITS and morphology data sets (Figure 3) shows a similar picture of character evolution when morphological character states are mapped on the tree. That is, flowers evolved from bisexual (*Corylopsis*) to andromonoecious (*Distylium, Fortunearia*) to monoecious (*Sinowilsonia*); petals gradually became reduced from broad and showy in *Corylopsis* to inconspicuous in *Eustigma* and filament-like in *Fortunearia* and *Sinowilsonia,* to completely absent in *Distylium*; pollen grains, however, showed a tendency to increase the number of apertures from three in *Corylopsis* to four in *Distylium*; and flower parts evolved from a fixed number in *Cory-*

lopsis (5), to slightly variable in *Fortunearia* and *Sinowilsonia* (mostly 5 or rarely 6), or to much more variable in *Distylium* (4–8 stamens).

The reconstructed phylogeny of the *Corylopsis* complex based on both morphology and ITS DNA sequences (Figure 3) suggested that: 1) *Corylopsis* should be separated from the other genera; 2) It is justifiable that *Eustigma* be put in the clade of *Fortunearia* and *Sinowilsonia*; and 3) *Sinowilsonia* is more closely related to *Fortunearia* than to *Distylium.*

This study contributes to a better understanding of the intergeneric relationships in the *Corylopsis* complex. However, the tribal relationships in the Hamamelidoideae remain unclear. This is the focus of our ongoing research.

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NOTES ON THE *CYPERUS RETROFLEXUS* COMPLEX (CYPERACEAE) WITH THREE NOMENCLATURAL PROPOSALS

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ABSTRACT. This poorly understood and confusing group is centered around *Cyperus retroflexus,* until recently known as *C. uniflorus.* Typification of *C. uniflorus* var. *pumilus* is discussed, and the following new combination is made: *C. retroflexus* var. *pumilus.* Two varieties of *C. uniflorus* are discussed and elevated to species: *C. floribundus* and *C. pseudothyrsiflorus.* Included is a dichotomous key treating the aforementioned taxa and putative allies of *C. pseudothyrsiflorus: C. hermaphroditus, C. lentiginosus, C. tenuis,* and *C. thyrsiflorus.*

Key Words: Cyperaceae, *Cyperus* section *Umbellati, C. floribundus, C. pseudothyrsiflorus, C. retroflexus* var. *retroflexus, C. retroflexus* var. *pumilus, C. uniflorus*

Revisional studies in *Cyperus* section *Umbellati* (Carter 1984; Carter, in prep.) and preparation of treatments of the genus for *Flora of North America* and *Vascular Plants of Texas* by Jones, Wipff, and Montgomery (1997) have brought to light several taxonomic and nomenclatural problems bearing heavily on the Texas flora. These problems involve the species formerly known as *C. uniflorus* Torr. & Hook., now properly known as *C. retroflexus* Buckley (Tucker 1987, 1994). Fernald and Griscom (1935) wrote that the "supposed new species" *C. uniflorus* was based on an immature specimen of *C. strigosus* L., evidence that the taxon has long been problematic. Although we concur with Fernald and Griscom that type material (*Drummond 287*) of *C. uniflorus* is immature, we disagree, as did Kükenthal (1936) and others (Horvat 1941; O'Neill 1942), that the type belongs in *C. strigosus.* Kükenthal, in a comprehensive monograph of the genus, treated this complex as five taxa shown in Table 1. Horvat subsequently placed all of these names into synonymy under *C. uniflorus,* a view essentially upheld by O'Neill. Tucker (1994) followed Horvat and O'Neill in recognizing but a single taxon, albeit under *C. retroflexus.* Table 1 compares these various taxonomies and ours.

RESULTS AND DISCUSSION

Our field and herbarium studies support Kükenthal's contention that multiple taxa are involved; however, as shown in Table 1, in departure from Kükenthal, we recognize three species and one variety. Our revised taxonomy is based upon combinations of vegetative, spike, spikelet, scale, and achene characters, some previously unused, which are summarized in key form and in Tables 2, 3, and 4. Moreover, discovery that *Cyperus uniflorus* Torr. & Hook. is illegitimate (Tucker 1987, 1994) complicates the problem somewhat, especially since we have determined, as did Horvat (1941), that the type of *C. uniflorus* Torr. & Hook. is not the same as *C. retroflexus,* but instead is an immature specimen of *C. uniflorus* var. *floribundus,* which we treat as a distinct species. All of this necessitates revision of the taxonomy and nomenclature of this complex. Thus, we propose: *C. retroflexus* var. *pumilus* (Britton) R. Carter & S. D. Jones, *comb. nov.*; *C. floribundus* (Kük.) R. Carter & S. D. Jones, *stat. nov.*; and *C. pseudothyrsiflorus* (Kük.) R. Carter & S. D. Jones, *stat. nov.*

Typification of *Cyperus uniflorus* var. *pumilus* Britton. Britton (1884) described *Cyperus uniflorus* var. *pumilus,* based primarily upon an S. B. Buckley collection from the "Valley of the Lower Rio Grande, in Texas and Northern Mexico." Subsequently, Small (1903) elevated this taxon to species rank and, crediting Britton with authorship, called it "*Cyperus subuniflorus* Britton," citing in synonymy "*C. uniformis* [sic] var. *pumilus* Britton, not *C. pumilus* L." Kükenthal (1936), like Small, treated *C. subuniflorus* as a distinct species allied with *C. uniflorus.* Apparently unaware of Britton's 1884 publication of var. *pumilus,* Horvat (1941) and O'Neill (1942) mistook an entry in a list published by Britton two years later (1886) as a *nomen nudum.* In fact, Britton in 1884 had provided a description with the name and thus had validly published it under Articles 32 & 36 of the ICBN (Greuter et al. 1994).

As was usually the case then, Britton (1884) did not explicitly designate in publication a holotype for *Cyperus uniflorus* var.

Table 1. Comparison of taxonomic treatments of the *Cyperus retroflexus* complex.

Present Treatment 4 Taxa	Kükenthal (1936) 5 Taxa	Horvat (1941) O'Neill (1942) 1 Taxon	Tucker (1994) 1 Taxon
C. floribundus	*C. uniflorus* var. *uniflorus*	*C. uniflorus*	*C. retroflexus*
	C. uniflorus var. *floribundus*		
C. pseudothyrsiflorus	*C. uniflorus* var. *pseudothyrsiflorus*		
C. retroflexus var. *retroflexus*	*C. uniflorus* var. *retroflexus*		
C. retroflexus var. *pumilus*	*C. subuniflorus*		

pumilus. However, the title of his article "A list of Cyperaceae collected by the late Mr. S. B. Buckley from 1878 to 1883 in the valley of the lower Rio Grande, in Texas and northern Mexico" obviously indicated that a Buckley collection was the basis for *C. uniflorus* var. *pumilus.* At NY, there are two sheets of Buckley collections from the valley of the Lower Rio Grande, dated 1878–1883. On virtually identical labels, handwritten by N. L. Britton, these specimens are identified as "Cyperus uniflorus, Torr.; var. pumilus, Britton." The only substantive difference between the two labels is that one bears the additional designation "type."

It would seem that the NY specimen marked "type" should be recognized as holotype. However, in addition to his obvious reference to Buckley's collections, Britton (1884) cited another collection as follows: "I refer here also No. 350, Palmer, Indian Territory." Specimens of *Palmer 350* are at NY and US. Although no Buckley collections were cited beyond the title, the new taxa described by Britton, including *Cyperus uniflorus* var. *pumilus,* were obviously based upon collections of S. B. Buckley, and only secondarily were other specimens such as *Palmer 350* cited. Unfortunately, Horvat (1941) and O'Neill (1942) stated "*Palmer 350* from the Indian Territory and Buckley's specimen from the valley of the Lower Rio Grande (1879–1883) are respectively the

Table 2. A comparison of *Cyperus retroflexus* var. *retroflexus* and *C. retroflexus* var. *pumilus*.

	C. retroflexus var. *retroflexus*	*C. retroflexus* var. *pumilus*
Plant height	Except for depauperate specimens, plants usually greater than 25 cm tall	Plants diminutive, 3–35 (–45) cm tall
Length longest peduncle	Longest peduncle (0.5–) 2.4–6.8 cm long	Longest peduncle less than 2.7 (–3.9) cm long
Fertile floral scale length	Fertile floral scales (2.8–) 3.0–3.9 mm long	Fertile floral scales 1.9–3.0 (–3.3) mm long
Terminal floral scale	Terminal sterile floral scale usually not greatly reduced, ⅔ or more the length of fertile scales	Terminal sterile floral scale of spikelet often much reduced, then less than ⅔ the length of fertile scales
Rachilla nerves	Rachilla usually with two conspicuous nerves, one on either side of median	Rachilla usually without conspicuous nerves
Rachilla wing texture	Rachilla wing usually chartaceous beyond clasped achene angle, border membranaceous (rarely wing almost entirely membranous)	Rachilla wing membranaceous throughout (rarely medially chartaceous)
Spikelet length	Longest spikelets 4.9–9.0 (–11.3) mm long	Longest spikelets 2.8–5.8 (–8.0) mm long

Table 3. Comparison of *Cyperus floribundus* and *C. retroflexus* var. *retroflexus*.

	C. floribundus	*C. retroflexus* var. *retroflexus*
Spikelet length	Longest spikelets (9.0–) 9.8–21.25 mm long	Longest spikelets 2.8–9.0 mm long
Spikelet outline	Spikelets strongly flexuous-contorted	Spikelets not strongly contorted, at most flexuous with curved tips
Spikelet base	Spikelet base strongly stipitate, 0.4–1.0 mm long	Spikelet estipitate or only weakly stipitate and stipe 0.1–0.3 (–0.5) mm long
Length longest floral scale	(3.5–) 3.7–4.8 mm	(2.8–) 3.0–3.9 mm
Floral scale color	Sanguineous to reddish brown, rarely brownish or pale whitish	Pale whitish or reddish brown, less commonly sanguineous, usually reddish brown maculate
Floral scale apex	Distal fertile floral scales with prominent mucro 0.6–1.9 mm long	Distal fertile floral scales obtuse to acute or with short mucro 0.1–0.3 (–0.5) mm long
Floral scale keel	Keel of distal fertile floral scales usually scabrid (30× magnification)	Keel of distal fertile floral scales smooth (30× magnification), excluding cluster of small teeth at mucro tip
Anther length	0.5–1.3 mm	0.3–0.5 (–0.6) mm
Achene length : width ratio	Achenes more than 3 times as long as wide	Achenes 2–3 (–3.3) times as long as wide
Distribution	Plants restricted to lower Rio Grande valley and adjacent areas of southern Texas and northeastern Mexico, with outlier in Travis County, Texas	Plants more widely distributed, throughout northern Mexico and Texas westward into New Mexico, northward into Oklahoma and southeastern Missouri, and eastward through Arkansas and northern Louisiana with outliers in western Kentucky, Mississippi, and eastern Alabama

Table 4. Comparison of *Cyperus pseudothyrsiflorus*, *C. thyrsiflorus*, *C. tenuis*, *C. lentiginosus* and *C. hermaphroditus*.

	C. pseudothyrsiflorus	*C. thyrsiflorus*	*C. tenuis*	*C. lentiginosus*	*C. hermaphroditus*
Mid-culm diameter	2.0–2.6 mm	0.5–1.1 mm	1.2–2.2 mm	(0.8–) 1.1–3.0 mm	(1.3–) 2.0–3.6 mm
Mid-peduncle diameter	0.4–0.7 mm	0.2–0.5 (–0.55) mm	0.4–0.8 mm	(0.4) 0.5–0.9 mm	(0.5–) 0.7–1.4 mm
Leaf/bract width	(3.0–) 4.0–5.8 mm	0.8–2.8 (–3.0) mm	1.8–3.1 mm	(2.6–) 3.0–8.0 mm	(3.5–) 5.0–10 mm
Inflorescence	4–12 rays; peduncles usually conspicuous, longest mostly 1–4× as long as spike axis	(2–) 3–6 rays; peduncles conspicuous, longest mostly at least 3× as long as spike axis	Spikes mostly sessile to subsessile, peduncles obscure to 3× (–3.3) as long as spike axis	5–11 rays; peduncles conspicuous, longest mostly at least 3× as long as spike axis	7–12 rays; peduncles conspicuous
Spike shape	Oblong to elliptical (rarely subglobose)	Oblong to subglobose	Oblong to subglobose	Oblong to broadly oblong	Narrowly oblong to oblong
Spike density	Tight; (11–) 14–21 spikelets per 5 mm span upper rachis	Loose; 7–9 spikelets per 5 mm span upper rachis	Tight; 22–45 spikelets per 5 mm span upper rachis	Loose to tight; 8–12 spikelets per 5 mm span upper rachis	Tight; 18–26 spikelets per 5 mm span upper rachis
Lower bracteoles of pedunculate spikes	Narrowly triangular to setaceous, mostly longer than associated prophyll	Triangular to narrowly triangular, mostly no longer than associated prophyll	Narrowly triangular to setaceous, usually longer than associated prophylls	Narrowly triangular to linear-triangular and setaceous, exceeding associated prophylls	Linear triangular to setaceous, exceeding associated prophylls
Spikelet posture	divaricate (to ascending)	Mostly divaricate	Ascending to divaricate	Mostly divaricate	Mostly divaricate

Table 4. Continued.

	C. pseudothyrsiflorus	*C. thyrsiflorus*	*C. tenuis*	*C. lentiginosus*	*C. hermaphroditus*
Spikelet length	(4.0–) 4.8–11.5 mm	3.4–7.4 (–17.0) mm	5.3–8.7 (–14) mm	8.9–11 mm	(2.5–) 4.0–7.2 mm
Spikelet stipe length	Absent or 0.1–0.2 mm	Absent to 0.1 mm	Absent or 0.1–0.2 mm	0.3–0.5 mm	Absent to 0.1 mm
Spikelet, prophyll, bracteole, rachis pigmentation	Usually conspicuously reddish brown maculate or striate	Usually reddish brown striate	If present, then reddish brown specks or streaks tiny and inconspicuous	Conspicuously reddish brown maculate	Pigmented spots or streaks absent, or at least inconspicuous
Scale length	2.4–3.4 mm	2.0–3.0 mm	2.4–2.8 mm	3.3–4.0 mm	2.3–3.0 mm
Apex of distal fertile scales	Short mucronate, mucro 0.1–0.3 mm	Obtuse to acute, or with short mucro to 0.1 mm long	Obtuse to acute, or with short mucro to 0.1 mm long	Mucronate, mucro 0.3–0.5 mm long	Obtuse
Scale color	Usually bilaterally variable, whitish to sanguineous or reddish brown sometimes tinted ferruginеous or yellowish	Whitish nerves and margins, with chocolate to liver brown undercolor	Pale olivaceous to brown, usually with chocolate to liver brown undercolor	Chestnut to cinnamon brown, sometimes yellow tinted	Scales golden yellow to stramineous (to red-brown)
Achene shape; width	Elliptic to narrowly elliptic to narrowly obovate; 0.5–0.75 mm	Narrowly elliptic to oblong; 0.5–0.65 mm	Narrowly oblong; 0.4–0.45 mm	Oblong to elliptic; 0.55–0.6 mm	Elliptic to oblong to narrowly obovate; 0.6–0.8 mm
Scale length : achene length ratio	ca. 1.5 [1.35–1.74 (–1.81)]	ca. 1.5 [1.31–1.75 (–1.88)]	ca. 1.5 [1.53–1.67]	ca. 2 [(1.61–) 1.72–2.55]	(1.3–) 1.5–3.5
Achene color	Light brown, base and apex darker	Dark brown	Brown	Light brown, base and apex darker	Brown

type and cotype . . . ." Furthermore, O'Neill annotated as "TYPE" a duplicate of *Palmer 350* (US). Although *Palmer 350* (US) was annotated by Britton as *C. uniflorus* var. *pumilus,* we think it is significant that Britton in no way indicated it was a type. Duplicates of *Palmer 350* (NY, US) examined by us are very immature, and although the plants are diminutive, as would be expected with *C. uniflorus* var. *pumilus,* their yet immature fertile scales are already 2.9–3.2 mm long, which is at the taxon's upper limit as understood by us. In contrast, the Buckley specimens (NY) are more mature, have shorter [2.4–2.5 (–2.8) mm long] scales, and are generally more representative of the taxon. Thus, we reject the Horvat (1941) and O'Neill (1942) designations of *Palmer 350* as "type" and the *Buckley* specimen as "co-type" and think the Buckley specimen at NY, annotated by Britton as "type," should stand as holotype.

***Cyperus retroflexus* var. *pumilus, comb. nov.* [=*C. uniflorus* var. *pumilus; C. subuniflorus*].** Fernald and Griscom (1935) asserted that this taxon "is merely small individuals of *C. globulosus.*" However, we think this taxon is a distinct variety and find no evidence that it is related to *C. globulosus* auct. non Aubl., now properly known as *C. croceus* Vahl (Carter and Kral 1990). Small (1903) and Kükenthal (1936) recognized this taxon as a distinct species (*C. subuniflorus*) allied with *C. uniflorus.* Horvat (1941) and O'Neill (1942) treated it as a synonym of *C. uniflorus,* commenting that "it is impossible to draw any kind of dividing line between [*C. uniflorus* and *C. subuniflorus*] . . . when a large number of specimens are studied" and further that "[*C. uniflorus* and *C. subuniflorus*] appear to stand at opposite ends of a long series of intergrading forms." We concur with Horvat and O'Neill that these taxa do not merit species rank. As shown in Table 2, there is overlap in virtually every characteristic we examined in *C. retroflexus* var. *retroflexus* [=*C. uniflorus, sensu* Horvat and *sensu* O'Neill] and *C. retroflexus* var. *pumilus* [=*C. subuniflorus*]. Despite this, we find that most specimens may be reliably placed in var. *retroflexus* or var. *pumilus* when combinations of characteristics are used, and given the disparate nature between specimens at opposite extremes of this continuum, we think infraspecific rank is both logical and useful. In the absence of evidence of geographical or habitat isolation, we maintain *C. uniflorus* var. *pumilus* at varietal rank but transfer it to *C. retroflexus.* Differences between *C. retroflexus* var. *retroflexus* and *C. retroflexus* var. *pumilus* are summarized in Table 2 and in the accompanying key.

***Cyperus floribundus, stat. nov.* [=*C. uniflorus* var. *floribundus*].** Kükenthal (1936) described *Cyperus uniflorus* var. *floribundus* based upon its relatively loose spikes, longer 3–5 fruited spikelets, and distal scales with long recurved mucros. Subsequently, the taxon was placed in synonymy under *C. uniflorus* (Horvat 1941; O'Neill 1942) and *C. retroflexus* (Tucker 1994). We concur with Horvat and with O'Neill that *C. uniflorus* var. *floribundus* is the same as *C. uniflorus* Torr. & Hook. and with Tucker (1987, 1994) that *C. uniflorus* Torr. & Hook. 1836 is illegitimate (non *C. uniflorus* Thunb. 1825), requiring use of *C. retroflexus,* the next available name.

We also concur with Horvat and with O'Neill that Kükenthal's brief diagnosis of *Cyperus uniflorus* var. *retroflexus* as having culms 45–75 cm high and terete, reflexed spikelets is insufficient to allow its separation from the rest of the complex. However, we find numerous characteristics to distinguish *C. floribundus* from *C. retroflexus* (summarized in Table 3) and do not agree with Horvat (1941), O'Neill (1942), and Tucker (1994), who have placed *C. uniflorus* var. *floribundus* into synonymy under *C. uniflorus* and *C. retroflexus.* Both *C. floribundus* and *C. retroflexus* var. *retroflexus* exhibit bewildering variation in habit from low slender plants to more robust ones of moderate stature; therefore, in our circumscription we use spikelet, scale, and achene characters almost exclusively. Moreover, although *C. retroflexus* and *C. floribundus* are sympatric, the distribution of *C. floribundus* appears to have integrity as a rather tight cluster of populations in southeastern Texas and adjacent northeastern Mexico, nested entirely within the range of *C. retroflexus.* Thus, we propose recognition of *C. floribundus* as a distinct species.

***Cyperus pseudothyrsiflorus, stat. nov.* [=*C. uniflorus* var. *pseudothyrsiflorus*].** *Cyperus uniflorus* var. *pseudothyrsiflorus* Kük. was treated as a synonym of *C. retroflexus* by Tucker (1994). Horvat (1941) wrote "[o]f doubtful status is *C. uniflorus pseudothyrsiflorus* Kükenth. [=*Mariscus dissitiflorus* C. B. Clarke]" and she further speculated "[t]hese plants may possibly be hybrids of *C. uniflorus* and *C. setigerus.*" These views were echoed by O'Neill (1942). We can find no morphological evidence that *C. pseudothyrsiflorus* is a hybrid between *C. uniflorus* and *C. setigerus* Torr. & Hook., and we think such a hybrid is unlikely given the genetic disparity between the putative parents; *C. setigerus* is a member of section *Rotundi* (with *C. rotundus* L.) and is not even remotely related to *C. uniflorus*. Curiously, despite erroneous speculation with regard to hybrid origin, Horvat (1941) and O'Neill (1942) did observe a relationship between *C. uniflorus* var. *pseudothyrsiflorus* and *Mariscus dissitiflorus* [=*C. thyrsiflorus* Jungh.], with which we concur. Also, in choosing the epithet *pseudothyrsiflorus*, Kükenthal (1936) obviously saw some resemblance, although to him presumably superficial, with *C. thyrsiflorus*.

Although *Cyperus* sections are ill-defined and poorly understood and its sectional taxonomy is sorely in need of revision, we think *C. pseudothyrsiflorus* is more closely allied with *C. thyrsiflorus* [=*Mariscus dissitiflorus*], *C. tenuis* Sw., *C. lentiginosus* Millsp. & Chase, and *C. hermaphroditus* (Jacq.) Standl. than with *C. retroflexus* (*C. uniflorus* as previously treated). Also, Correll and Johnston (1970, p. 298) suggested a relationship between var. *pseudothyrsiflorus* and *C. hermaphroditus*. However, this putative alliance contains members of three sections (see Table 5) as understood by Kükenthal (1936), and additional study is needed before a formal proposal to realign the sections can be made. Herein, we propose species rank for *C. uniflorus* var. *pseudothyrsiflorus* and provide a dichotomous key to allow its separation from *C. retroflexus* and *C. floribundus* and from its putative allies: *C. thyrsiflorus, C. tenuis, C. lentiginosus,* and *C. hermaphroditus*. Species in this putative alliance are further compared in Table 4.

REVISED TAXONOMY

1. **Cyperus retroflexus** Buckley, Proc. Acad. Nat. Sci. Philadelphia. 1862: 9. 1863.

Cyperus uniflorus var. *retroflexus* (Buckley) Kük., Pflanzenreich IV. 20 (101): 521. 1936. TYPE: U.S.A. Texas: northern Texas, *S. B. Buckley s. n.* (LECTOTYPE designated here: PH!).

a. **Cyperus retroflexus var. retroflexus**

b. **Cyperus retroflexus var. pumilus** (Britton) R. Carter & S. D. Jones, *comb. nov.*

Table 5. Sectional classification (*fide* Kükenthal 1936) of *Cyperus retroflexus* and "allies."

Section *Umbellati*	Section *Tetragoni*	Section *Strigosi*
C. retroflexus* var. *retroflexus	***C. thyrsiflorus***	***C. tenuis***
(as *C. uniflorus* var. *uniflorus*)	***C. hermaphroditus***	***C. lentiginosus***
C. retroflexus* var. *pumilus		(as *C. tenuis* var. *lentiginosus*)
(as *C. subuniflorus*)		
C. floribundus		
(as *C. uniflorus* var. *floribundus*)		
C. pseudothyrsiflorus		
(as *C. uniflorus* var. *pseudothyrsiflorus*)		

Cyperus uniflorus var. *pumilus* Britton, Bull. Torrey Bot. Club 11: 87. 1884. *Cyperus subuniflorus* Britton in Small, Fl. S.E.U.S. 173, 1327. 1903. *Mariscus subuniflorus* (Britton) T. Koyama, Phytologia 29: 74. 1974. TYPE: "valley of the Lower Rio Grande, in Texas and Northern Mexico, 1879–1883," *S. B. Buckley s. n.* (HOLOTYPE: NY!; ISOTYPE: NY!).

PARATYPE: U.S.A. Indian Territory, chiefly on the False Washita, between Fort Cobb and Fort Arbuckle, 1868, *Palmer 350* (NY!, US!).

2. **Cyperus floribundus** (Kük.) R. Carter & S. D. Jones, *stat. nov.*

Cyperus uniflorus var. *floribundus* Kük., Pflanzenreich IV. 20 (Heft 101): 521. 1936. TYPE: MEXICO. Tamaulipas: vic. Victoria, 1 May–13 Jun 1907, *Palmer 287* (LECTOTYPE designated by Tucker [1994]: B; ISOLECTOTYPE: NY!). *Cyperus uniflorus* Torr. & Hook., Ann. Lyceum Nat. Hist. New York 3: 431. 1836, non Thunb. 1825. *Mariscus uniflorus* (Torr. & Hook.) Steud., Synops. Cyper. 64. 1855. U.S.A. Texas: without locality, *Drummond 287* (HOLOTYPE: NY!; ISOTYPES: GH!, K!, OXF!).

3. **Cyperus pseudothyrsiflorus** (Kük.) R. Carter & S. D. Jones, *stat. nov.*

Cyperus uniflorus var. *pseudothyrsiflorus* Kük., Pflanzenreich IV. 20 (Heft 101): 521. 1936. TYPE: MEXICO. Nuevo Leon: Sierra Madre near Monterey, 30 Jun 1888, *Pringle 1966* (HOLOTYPE: B!; ISOTYPE: US!).

KEY TO *CYPERUS RETROFLEXUS* AND ALLIES

1. Floral scales on same side of spikelet not overlapping or spikelets with only 2 floral scales (best observed in mature spikelets); achenes (1.7–) 1.9–2.6 mm long; less than ⅐ (rarely as much as ¼ in *C. retroflexus*) of ventral achene edge extending beyond rachilla wing (free portion of achene measured from intersection of rachilla edge and achene ventral edge to achene apex); lower bracteoles in pedunculate spikes mostly triangular to narrowly triangular, equal to or shorter than associated secondary prophyll .... (2)

2. Longest spikelets 9.8–21.25 mm long, strongly flexuous-contorted; spikelet with strongly stipitate base 0.4–1.0 mm long; achenes more than 3 times as long as wide; distal fertile floral scales with prominent mucro 0.6–1.9 mm long; longest floral scale of spikelet (3.5–) 3.7–4.8

mm long; keel of distal fertile floral scales usually scabrid (30× magnification); anthers 0.5–1.3 mm long; plants restricted to lower Rio Grande valley and adjacent areas of southern Texas and northeastern Mexico, with outlier in Travis County, Texas .... *C. floribundus*

2. Longest spikelets 2.8–9.0 mm long, or if longer then at most flexuous with curved tips, but not strongly contorted; spikelet estipitate, or only weakly stipitate and stipe 0.1–0.3 (–0.5) mm long; achenes 2–3 (–3.3) times as long as wide; distal fertile floral scales obtuse to acute or with short mucro 0.1–0.3 (–0.5) mm long; longest fertile floral scale of spikelet (2.1–) 2.5–3.5 (–4.0) mm long; keel of distal fertile floral scales smooth (30× magnification), excluding cluster of small teeth at mucro tip; anthers 0.3–0.5 (–0.6) mm long; plants more widely distributed .... (3)

3. Fertile floral scales (2.8–) 3.0–3.9 mm long; rachilla wing usually chartaceous beyond clasped achene angle, border membranaceous; rachilla usually with two lateral nerves, one along each side of median; longest spikelets 4.9–9.0 (–11.3) mm long; terminal sterile floral scale usually not greatly reduced, ⅔ or more the length of fertile floral scales; longest peduncle (0.5–) 2.4–6.8 cm long; except for depauperate specimens, plants usually greater than 25 (–57) cm tall ...... *C. retroflexus* var. *retroflexus*

3. Fertile floral scales 1.9–3.0 (–3.3) mm long; rachilla wing usually membranaceous throughout; rachilla usually lacking lateral nerves; longest spikelets 2.8–5.8 (–8.0) mm long; terminal sterile floral scale of spikelet often much reduced, less than ⅔ the length of fertile floral scales; longest peduncle less than 2.7 (–3.9) cm long; plants diminutive, 3–35 (–45) cm tall .... *C. retroflexus* var. *pumilus*

1. Floral scales on same side of spikelet mostly overlapping or at least reaching base of next floral scale (best observed in mature spikelets); achenes 1.4–1.9 (–2.1) mm long; at least ⅕ of ventral achene edge extending beyond rachilla wing (free portion of achene measured from intersection of rachilla edge and achene ventral edge to achene apex); lower bracteoles in pedunculate spikes mostly narrowly

triangular to linear-triangular and setaceous, longer than associated secondary prophylls (except in *C. thyrsiflorus*). .... (4)

4. Spikelets remote, 6–10 (–15) per 5 mm rachis span in proximal half of rachis .... (5)
   5. Distal floral scales mucronate, mucros 0.2–0.5 mm long; scales (2.9–) 3.3–4.0 mm long; spikelets stipitate, stipes 0.3–0.5 mm long; scales mostly about 2× [(1.61–) 1.72–2.55] as long as achenes; spikelets 8.9–11 mm long; lower bracteoles in pedunculate spikes mostly narrowly triangular to linear-triangular and setaceous, longer than associated secondary prophylls; largest leaves and primary inflorescence bracts usually more than 3.0 mm wide; largest peduncles usually more than (0.4–) 0.5 mm wide; mature achene light brown with distinctly darker base and apex; floral scales chestnut to cinnamon brown sometimes yellow tinted .... *C. lentiginosus*
   5. Distal floral scales without mucros or mucros 0.1 mm or less long; floral scales 2.0–2.8 (–3.0) mm long; spikelets estipitate or stipes no more than 0.2 mm long; floral scales mostly about 1.5× [1.31–1.75 (–1.88)] as long as achenes; spikelets 3.4–7.4 (–17) mm long; lower bracteoles in pedunculate spikes mostly triangular to narrowly triangular and no longer than associated secondary prophylls; largest leaves and primary inflorescence bracts 1.0–2.8 (–3.0) mm wide; largest peduncles 0.2–0.5 (–0.55) mm wide; mature achene dark brown throughout; floral scales whitish along nerves and margins, with chocolate to liver brown undercolor mostly between nerves .... *C. thyrsiflorus*
4. Spikelets more congested, (9–) 11–45 per 5 mm span in distal half of rachis .... (6)
   6. Distal floral scales mucronate, mucros 0.2–0.5 mm long; floral scales predominately reddish, brownish, or whitish; rachis, spikelets, bracteoles, and prophylls usually conspicuously reddish brown maculate or striate (10× magnification) .... (7)
      7. Spikes loose, 8–12 spikelets per 5 mm span of upper half of rachis; floral scales (2.9–) 3.3–4.0 mm

long; spikelets stipitate, stipes 0.3–0.5 mm long; floral scales mostly twice [(1.61–) 1.72–2.5] as long as achenes; upper half of floral scale (excluding mucro) appressed and clasping spikelet (best observed in mature spikelets); spikelets and floral scales chestnut to cinnamon brown sometimes yellowish, color not bilaterally variable; spikelets mostly divaricate; spikes broadly oblong to oblong . . . . *C. lentiginosus*

7. Spikes tighter, 11–21 spikelets per 5 mm span of upper half of rachis; floral scales 2.4–3.4 mm long; spikelets estipitate, or stipes 0.1–0.2 mm long; floral scales mostly about 1.5× [1.33–1.74 (–1.81)] as long as achenes; upper half of lowest floral scale ascending, not tightly clasping spikelet (best observed in mature spikelets); spikelet and floral scale color usually bilaterally variable, from whitish to sanguineous or reddish brown sometimes tinted ferrugineous or yellowish; spikelets divaricate to ascending; spikes oblong to elliptical (rarely subglobose) . . . . *C. pseudothyrsiflorus*

6. Floral scale mucro absent or if present then less than 0.1 mm long; floral scales golden yellow to stramineous (to red-brown) or pale olivaceous with chocolate to liver brown undercolor; rachis, spikelets, bracteoles, and prophylls not conspicuously maculate or striate (10× magnification) . . . . . . (8)

8. Floral scales golden yellow to stramineous (to red-brown); inflorescence with 7–12 conspicuously pedunculate rays; achenes elliptic to oblong to narrowly obovate, 0.6–0.8 mm wide; spikes narrowly oblong to oblong; spikelets mostly divaricate . . . . *C. hermaphroditus*

8. Floral scales pale olivaceous with chocolate to liver brown undercolor; inflorescence of mostly sessile to subsessile spikes or at least peduncles obscure and no more than 3× (–3.3) as long as spike axis; achenes narrowly oblong, 0.4–0.45 mm wide; spikes oblong to subglobose; spikelets ascending to divaricate . . . . *C. tenuis*

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SYSTEMATIC NOTES ON *OLEANDRA*

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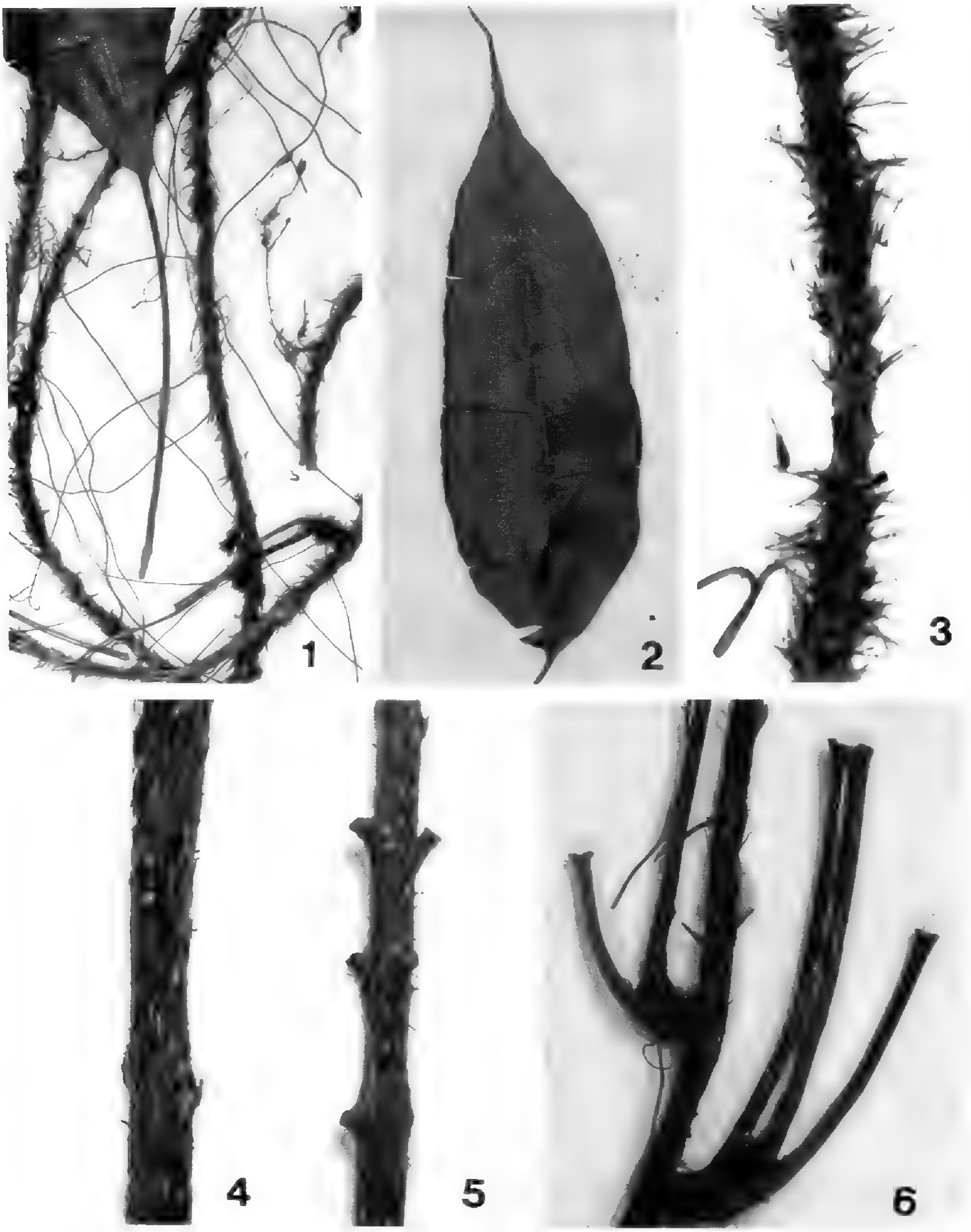
ABSTRACT. A classification of the American species of the tropical fern genus *Oleandra* is presented along with a review of previous work on the genus. This treatment contrasts with earlier work by reduction of a number of taxa that have been based on variable species. The American species are reduced to four; those that occur in Africa, Asia, and Pacific islands are also briefly noted.

Key Words: tropical, Oleandraceae, *Oleandra*, fern

Oleandra is one of the most distinctive of fern genera although its taxonomic position is uncertain. Hooker (1840 t. 45B) regarded it as "a highly beautiful and very natural genus"; somewhat later Greville (1848) reported that "The genus *Oleandra* of Cavanilles . . . is one of the most natural in habit of the families of ferns, and not less beautiful than well defined." The most distinctive features, although initially reported on meager material, still characterize the genus. These are long, branched roots or rhizophores (Figure 1), a simple, entire lamina (Figure 2) borne on an articulate petiole, and peltate stem scales. In addition, some species have a shrubby growth habit and, with the possible exception of *O. vulpina* C. Chr., all species have indusiate sori. Much later, Ogura (1938) stated, in an anatomical and morphological study, that ". . . the genus *Oleandra* stands far remote from other ferns and may be in an isolated phyletic position." Christensen (1938) recognized this distinctiveness by placing the genus in its own subfamily of the Polypodiaceae. Pichi-Sermolli (1965) treated the genus in its own family related to elements in the Davalliaceae and perhaps also to the Aspidiaceae (Dryopteridaceae).

In contrast, many authors have commented on the need for a clear definition of the species. For example, Kramer (1990) has stated that "Many species are similar in appearance, and a modern monograph is required." Palacios-Rios (1995) has noted, "El genero necesita un estudio monografico ya que han sido descritas muchas especies basandose y muy pocos ejamplares," and Smith



Figures 1–6. Morphological characters of *Oleandra*. 1. Long roots or rhizophores, *O. articulata*, Venezuela, *Maguire & Politi 27755* (MO), × ½. 2. Small lamina, *O. articulata*, Venezuela, *Maguire & Politi 27755* (MO), × ½. 3. Stem with patent scales, *O. articulata*, Bolivia, *Gentry & Solomon 44519* (MO), × 2. 4. Stem with appressed scales, *O. pilosa, van der Werff & Rivero 7849* (MO), × 2. 5. Short phyllopodia on stem, *O. pilosa, van der Werff & Rivero 7849* (MO), × 1 ½. 6. Long phyllopodia (3 to right and 1 to far left), *O. Lehmannii*, Colombia, *Betancur et al. 881* (MO), × 1 ½.

(1995) stated "The New World species are badly in need of a modern monograph."

The principal authors of new species or new combinations have been Ching, Copeland, Kunze, Maxon, and Presl. These, as well as others, have attempted to work toward a realistic classification of the species, but generally have been hampered by a lack of a complete monographic treatment. They likely hoped that future collections would verify the taxonomy that was provided. However, the taxonomic history of the genus has been as Palacios-Rios (1995) noted: too many species and too few specimens.

It is emphasized here that individual plants are placed in the same taxon because they share certain characters. Differences, especially at the level of genus and below, also concern the rank of a taxon. Which characters represent significant differences, as well as which characters are shared, needs to be evaluated.

Some authors have distinguished taxa on variable characters. For example, Maxon (1914), noted for his careful work, had too few specimens for his study of American *Oleandra* and his treatment provided no guidance concerning the variability of characters. The studies of Pichi-Sermolli (1965), based on African material in many herbaria, led to the conclusion that, in *O. distenta,* characters such as pilosity of the lamina, the costa, the petiole, and the indusium, as well as characters of the costa scales, are variable.

Field studies are needed in order to understand the stability and variability of characters within populations, and also the stage of development at which useful herbarium material should be collected. Such studies may provide evidence for recognition of additional taxa.

Here the American species have been reduced in number based on the comments in previous treatments, and on the basis of ample collections. Types that have been seen are indicated by affirmation (!). The taxonomy of species that occur beyond the American tropics has not been evaluated.

Oleandra Cav., Anal. Hist. Nat. 1: 115. 1799. Type and sole species: *Oleandra neriformis* Cav. corrected by Swartz (1806) to *neriiformis.* The species name is valid from the publication in 1799 (Tokyo Code, Art. 42.1 in Greuter et al. 1994).

Neuronia Don, Prod. Fl. Nepal. 6. 1825. Type and sole species: *Neuronia asplenioides* Don.

Ophiopteris Reinw., Syll. Pl. Nov. 2: 3. 1825. Type and sole species: *Ophiopteris verticillata* Reinw. The journal, published by the Soc. Ratisbona, was also cited as Regensburg Bot. Zeit. or other variations of the title. The first few pages of volume two were published late in 1825 or early in 1826, rather than 1828 as indicated on the cover.

Aspidium subgenus *Oleandra* (Cav.) Splitg., Tijds. Nat. Gesch. 7: 411. 1848.

AMERICAN SPECIES

1. Epiphytic; stem flexible, twining, with or without a whitish deposit, usually bearing many scales with the portion beyond the point of attachment patent or nearly so (Figure 3); phyllopodium (petiole below the joint) usually 6–30 mm long .... (2)
    2. Stem brown, lacking a whitish deposit; the scales usually concealing the stem; widespread in tropical America .... 1. *O. articulata*
    2. Stem, at least partially, with a whitish deposit; scales usually sparse; Costa Rica .... 2. *O. Bradei*
1. Terrestrial or epiphytic; stem rigid, and usually erect, rarely with some whitish deposit, bearing many scales that are fully and closely appressed (Figure 4); phyllopodia absent or to 30 mm long .... (3)
    3. All or most phyllopodia on a stem 1–5 mm long (Figure 5), or absent; Costa Rica and Panama, Trinidad, the Guianas, west to Colombia and south to Bolivia and in Amazonian Brazil .... 3. *O. pilosa*
    3. All or most phyllopodia on a stem 6–30 mm long (Figure 6); Haiti, Guatemala, Venezuela and Colombia, south to Peru .... 4. *O. Lehmannii*

1. **Oleandra articulata** (Sw.) Presl, Tent. Pterid. 78. 1836.

Aspidium articulatum Sw., Jour. Bot. (Schrader) 1800 (2): 30. 1801, not Willd. 1810. HOLOTYPE: Martinique, *Plumier*, Traité Foug. Amér. t. 136.

Polypodium articulatum (Sw.) Poir., in Lam. Encycl. 5: 514. 1804.

Polypodium articulatum Vahl, Eclog. Amer. 3: 51. 1807. LECTOTYPE (designated here): Montserrat, *Ryan* (C, photo A).

Aspidium nodosum Willd., Sp. Pl. ed. 4, 5: 211. 1810. *nom. superfl.* for *Aspidium articulatum* Sw. and with the same type.

Hypopeltis articulata (Sw.) Bory, in Bélan. Voy., Bot. 264. 1833.

Oleandra nodosa Presl, Tent. Pterid. 78. 1836, *nom. nov.* for *Aspidium nodosum* Willd. and with the same type.

Oleandra hirta Brack., U. S. Explor. Exped. (Wilkes) 16: 214. t. 29. 1854. HOLOTYPE: BRAZIL. Organ mountains, Rio de Janeiro (Guanabara), *U. S. Explor. Exped. 2* (US!; ISOTYPE: K, photo GH).

Oleandra neriiformis var. *hirta* (Brack.) Baker, Fl. Brasil. 1 (2): 495. 1870.

Oleandra nodosa var. *Magalhaesii* Christ, Bull. Herb. Boiss. II, 2: 236. 1902, as *Magalhaesi.* HOLOTYPE: BRAZIL. Serra do Itatiaia, *Magalhães Gomes 2259,* (Herb. Christ, P).

Oleandra Baetae Damazio, Bull. Herb. Boiss. II, 6: 892. 1906. HOLOTYPE: BRAZIL. Serra do Frasaò, Minas Geraes, *A. Baeta* (EM).

Oleandra articulata f. *eglandulosa* Domin, Pterid. Dominica 233. 1929. HOLOTYPE: Dominica, *Eggers 1036* (K). [PARATYPES: all Dominica, *Imray* (K), *Eggers 756* (K), *Nichols 253* (K)].

Oleandra zapatana Lell. Proc. Biol. Soc. Wash. 89: 719, f. 3. 1977. TYPES: COLOMBIA. Chocó, *Lellinger & de la Sota 300* (HOLOTYPE: US!, photo GH; ISOTYPES: COL, LP). [PARATYPE: Colombia, Chocó, *Lellinger & de la Sota 195* (US!; ISOPARATYPE: LP)].

The citation of the type of *Oleandra articulata* by Maxon (1914) was disputed by Morton (1968), but was maintained by Joncheere (1969). I agree with the original typification and use the basionym of Swartz for the species of the West Indies and elsewhere in tropical America.

In the West Indies this species is rather uniform with a long (usually 45 cm or more), broadly to narrowly elliptical lamina and scattered sori. It sometimes has a pubescent lamina, especially in southeastern Brazil. The scales on the stem are rarely sparse, as in *Dudley 13243,* GH.

The stem of *Oleandra hirta* was described as glaucous, but this character was not evident on the holotype.

Oleandra articulata ranges from Cuba and other of the Greater Antilles through the Lesser Antilles to Trinidad; from southern Mexico and British Honduras (Belize) to Panama; and from the Guianas west to Colombia and south to Bolivia; also Brazil, especially the southeast.

2. **Oleandra Bradei** Christ, Bull. Soc. Bot. Genève II, 1: 231. 1909. HOLOTYPE: COSTA RICA. La Palma, *C. Brade* 17, III, 1908 (Herb. Christ, P). The type of var. *caudata* was also cited.

Oleandra nodosa var. *caudata* Christ, Bull. Herb. Boiss. II, 4: 964. 1904. HOLOTYPE: COSTA RICA. Haut Uren, Talamanca, *Pittier 12699* (Herb. Christ, P).

The type of *Oleandra Bradei* is cited from the original publication. Scamman (1961) used the type of the variety, which Christ also cited with the species. The white deposit on the stem, emphasized by Maxon (1914), was not mentioned in the description of the variety.

Oleandra Bradei is confined to Costa Rica; it may well be a variant of *O. articulata.* There seems to be little reason for its recognition as a species. It is frequently collected and the numerous specimens may overemphasize its significance.

3. **Oleandra pilosa** Hook., Gen. Fil. t. 45B and text. 1840. HOLOTYPE: BRITISH GUIANA (GUAYANA). Berbice, *Schomburgk 416* (K, photo GH; ISOTYPE: L).

Aspidium pendulum Splitg., Tijds. Nat. Gesch. 7: 412. 1840, not Raddi, 1819. LECTOTYPE (designated here): SURINAM. Berlijn plantation, Para, *Splitgerber* (L, photo GH; ISOLECTOTYPE: K).

Oleandra micans Kunze Bot. Zeitung (Berlin) 9: 346. 1851. LECTOTYPE (designated here): "ad Mission. Tocache, flor. Huallaga superior, Peruviae. Sterile lectum Jul. Aug. 1830, (Diar. 1958)" (from Kunze 1834), Herb. *Poeppig,* Kunze, destroyed at LZ.

Oleandra trujillesis Karst., Fl. Columb. 1: 147, t. 73. 1861. HOLOTYPE: VENEZUELA. Near Escuque, *Karsten.*

Oleandra neriiformis var. *pilosa* (Hook.) Baker, Fl. Brasil. 1 (2): 494. 1870.

Oleandra decurrens Maxon, Contrib. U. S. Natl. Herb. 17: 396. 1914. HOLOTYPE: COSTA RICA. El General, *Pittier 10649* (US!).

Oleandra panamensis Maxon, Contrib. U. S. Natl. Herb. 17: 396. 1914. HOLOTYPE: PANAMA. Chiriqui, *Pittier 5322* (US!).

Oleandra trinitensis Maxon, Contrib. U. S. Natl. Herb. 17: 397. 1914. HOLOTYPE: Trinidad, *Fendler 114* (US!; ISOTYPE: US!, GH!, K, photo GH). [PARATYPE: Bot. Gard. Trinidad *333* (US!, 2 sheets; ISOPARATYPE: GH!, K, photo GH)].

Oleandra dura Maxon, Amer. Fern J. 35: 21. 1945. HOLOTYPE: COLOMBIA. Santander, *Haught 1329* (US!; ISOTYPE: GH!, K, photo GH).

The holotype of *Oleandra micans,* very briefly described, was destroyed at Leipzig and no other type has been located. Mettenius (1856) used the name and supplied a description for *Lechler 2539* (B!, K!) from Tatanara, Peru. In Herb. Mett. (B!) there is a pencil tracing of the sterile lectotype.

Oleandra pilosa has an extensive range from Costa Rica and Panama south to Bolivia, also in Trinidad and the Guianas, Venezuela and Amazonian Brazil.

4. **Oleandra Lehmannii** Maxon, Contrib. U. S. Natl. Herb. 17:

395. 1914. HOLOTYPE: COLOMBIA. Amalfi, *Lehman XLII* (US!; ISOTYPE: K, photo GH).

Oleandra guatemalensis Maxon, Contrib. U. S. Natl. Herb. 17: 395. 1914. HOLOTYPE: GUATEMALA. Alta Verapaz, *Maxon & Hay 3333* (US!).

Oleandra costaricensis Maxon, Contrib. U. S. Natl. Herb. 17: 397. 1914. HOLOTYPE: COSTA RICA. La Palma, *Tonduz 12551* (US!).

Oleandra Urbanii Brause, Ark. Bot. 17: 68. 1921. HOLOTYPE: Haiti, *Ekman 547* (B).

Oleandra duidae A. C. Sm., Bull. Torrey Bot. Club 58: 301. 1931. HOLOTYPE: VENEZUELA. Mount Duida, *Tate 580* (NY).

Oleandra trinitensis var. *subcostaricensis* Süsseng. & Losch, Mitt. Bot. Staatssamml. München 1: 23. 1950. HOLOTYPE: COSTA RICA. Turrialba, *Kupper 1613* (M).

Oleandra Archeri Maxon, Amer. Fern J. 24: 74. 1934. HOLOTYPE: COLOMBIA. Chocó, *Archer 1669* (US!).

Oleandra Lehmannii is selected over other available names because it is used most often. The type of the briefly described var. *subcostaricensis* has not been seen; it is placed here solely because of the epithet. *Oleandra Urbanii* was published in November, 1921, although the cover of the volume is dated 1922.

The species ranges from Guatemala to Panama and from Venezuela to Colombia, south to Peru, and in Haiti.

AFRICAN SPECIES

Pichi-Sermolli (1965) has discussed in some detail the species of Africa and adjacent islands. He notes that "A more abundant material than I have had at my disposal will perhaps lead us in the future to a re-arrangement of the African species, but for the time being I recognize the following species." These are: *Oleandra Anettii* Tard. (West Tropical Africa), *O. distenta* Kunze (Tropical and South Africa), O. *ejurana* Adams (Ghana), *O. madagascarica* Bonap. (Madagascar), and *O. Welwitschii* (Baker) Pichi-Sermolli (Angola, Congo, not *Welwitzchii* as originally published). Ample material of the species recognized by Pichi-Sermolli (except for *O. distenta* and probably *O. madagascarica*) is needed to confirm their taxonomic status. Kornaś (1977), on the basis of material from Zambia, has treated *O. Welwitschii* as a variety of *O. distenta*; however, the nomenclature is not correct.

ASIAN AND PACIFIC SPECIES

There are perhaps 40 species currently recognized in this vast region. A satisfactory classification of the species is not possible until more extensive collections are examined and types have been studied. In several studies of Chinese species about ten species are recognized. Only two are treated in the work on Java by Posthumus (1937). In this treatment seven are reduced to *Oleandra neriiformis* Cav. and four to *O. musifolia* (Bl.) Presl. Nine species, six of them endemics, are treated by Copeland in his work on the Philippine ferns (1958). Seven species are included in his New Guinea studies (1940) and three are considered endemic. Several species in the Asian and Pacific regions evidently have distinctive characters: *Oleandra Cumingii* J. Smith (not a nom. nud. as often indicated) has stems creeping; *O. pistillaris* (Sw.) C. Chr. has stems rigid, erect and shrublike; *O. Wallichii* (Hook.) Presl has patent stem scales; in *O. neriiformis* Cav. the scales are fully appressed and sori are arranged in two rows close to the costa; *O. Sibbaldii* Grev. has sori more or less scattered. Among the New Guinea species *O. Werneri* Ros. is recognized by its dimorphic leaves, and *O. vulpina* C. Chr. by the exindusiate condition, if this is truly so.

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RANGE EXPANSION NORTHWARD IN ILLINOIS AND INTO WISCONSIN OF *TRIDENS FLAVUS* (POACEAE)

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ABSTRACT. *Tridens flavus* is reported for the first time from Wisconsin, where specimens from 15 sites in eight southern counties were collected between 1961 and 1997. Nine of these sites were discovered after 1990. In 1997, this grass was collected in three northwestern Illinois counties from which it is previously unreported. Evidence of the recent spread north by this species is discussed.

Key Words: *Tridens,* Poaceae, biogeography

Tridens flavus (L.) A. S. Hitchc. (Poaceae) is native across the eastern U.S. from the Atlantic coast to Nebraska, Kansas, Oklahoma, and Texas, between the southern edge of the Great Lakes and the Gulf of Mexico (Hitchcock and Chase 1950). Its habitat has been described as open sandy areas, sandy prairies, disturbed prairies, dry fields, old fields, pastures, borders of woods, cutover woodland, open woods, rocky glades, waste places, and roadsides (Gress 1924; Small 1933; Deam 1940; Fernald 1950; Hitchcock and Chase 1950; Steyermark 1963; Seymour 1982; Great Plains Flora Association 1986; Mohlenbrock 1986; Eilers and Roosa 1994). Open or relatively open, rather dry, sandy, or disturbed sites are where *T. flavus* grows. Steyermark (1963) wrote, "Although this grass is one of the most abundant in Missouri, it is practically absent from the northern third of nearby Illinois and Indiana." Mohlenbrock (1986) wrote, of *T. flavus* in Illinois, ". . . common, except in the northern $\frac{1}{5}$ of the state where it is apparently very rare."

Tridens flavus was first collected in Wisconsin in 1961, when a single plant was found near the loading zone of the building housing the Botany Dept. at UW–Madison. Vehicular transportation of this propagule seems certain, and the apparent spread north in Illinois and Michigan of this species, particularly along roadways, has been suggested in the literature (Voss 1972; Swink and Wilhelm 1994; Young 1994). The author has repeatedly discovered this grass on roadsides in southern Wisconsin and northwestern Illinois during the years 1991–1997. Fifteen Wisconsin sites are known.

Regional herbaria were checked for Wisconsin specimens of *Tridens flavus.* No specimens other than duplicates are at F, IA, ILL, ILLS, ISC, MIL, MIN, OSH, SIU, UWL, UWSP, or UW-Green Bay. Data reported below are based on specimens deposited in the Herbarium of the University of Wisconsin–Madison (WIS). Nomenclature follows Kartesz (1994), except in the specimen label data which are presented without modification.

SPECIMENS EXAMINED

Illinois. Carroll Co.: Town of Savanna, beside Hwy. 84, 3.75 mi. S of jct. with Hwy. 64, 0.75 mi. S of jct. with Airport Rd., 42°04′15″N, 90°07′35″W, caespitose grass to 1 m high, scattered presence and uncommon along sandy state highway right-of-way on sand plain by Mississippi River, with *Bromus inermis,* 15 Jan 1997, *A. H. Williams 97-3* (WIS).

Illinois. Carroll Co.: On verge of road leading from Hwy. 84 to south gate of Savanna Army Depot, 42°11′16″N, 90°14′09″W, caespitose grass to 1 m high, few plants present, at edge of sand plain occupied by Savanna Army Depot, 15 Jan 1997, *A. H. Williams 97-4* (WIS).

Illinois. Jo Daviess Co.: On verge of Whitton Rd. at Hanover Bluff State Nature Preserve, 3.3 mi. from Hwy. 84, 42°12′28″N, 90°17′07″W, caespitose grass to 1 m high, few plants present, at edge of sand plain occupied by Savanna Army Depot, 15 Jan 1997, *A. H. Williams 97-5* (WIS).

Illinois. Rock Island Co.: Town of Albany, beside Hwy. 84 at 222nd Ave., 41°44′37″N, 90°17′16″W, caespitose grass to 1 m high, widespread and abundant on sandy state highway right-of-way on sand plain by Mississippi River, 15 Jan 1997, *A. H. Williams 97-1* (WIS).

Illinois. Whiteside Co.: Town of East Clinton, beside Hwy. 84 at jct. with Hwy. 30, 41°50′38″N, 90°09′27″W, caespitose grass to 1 m high, widespread and abundant on sandy state highway right-of-way on sand plain by Mississippi River, 15 Jan 1997, *A. H. Williams 97-2* (WIS).

Wisconsin. Dane Co.: City of Madison, one plant in crack of concrete just below steps at loading zone of Birge Hall and old animal house, 10 Oct 1961, *H. H. Iltis 19425* (WIS).

Wisconsin. Grant Co.: 4 mi. NW of Cassville, beside Hwy. VV, T3N R6W S11 SE¼, large patch on grassy roadside, with *Phleum pratense, Setaria glauca,* 7 Oct 1972, *M. Nee 5363* (WIS).

Wisconsin. Grant Co.: 1 mi. NW of Cassville, along Hwy. VV from Cassville to Nelson Dewey State Park, T3N R5W S19 NW¼ of NE¼, abundant and forming large colonies along grassy open roadside with *Bromus inermis, Agropyron repens, Digitaria ischaemum, Setaria viridis, Asclepias syriaca,* two other well-established colonies have been found this year in the vicinity of Cassville (*M. Nee 5363, M. Nee 5422*), 14 Oct 1972, *M. Nee 5402* (WIS).

Wisconsin. Grant Co.: T3N R5W S27 SW¼ of SE¼, abundant, forming large colonies and scattered clumps in grassy, sandy old field with *Eragrostis spectabilis, Setaria viridis, Ambrosia artemisiifolia, Paspalum, Leptoloma cognatum, Aster, Solidago,* 14 Oct 1972, *M. Nee 5422* (WIS).

Wisconsin. Grant Co.: 3 mi. NW of Cassville, along Hwy. VV, T3N R6W S11 NW¼ of SE¼, rocky or grassy roadside bank at base of Mississippi River bluff with thin woods of *Quercus* spp., *Juglans nigra, Rhus typhina,* the bank with a few prairie plants, *Rhus glabra, Sporobolus asper, Xanthoxylum americanum, Verbascum thapsus. Tridens flavus* forming patches of many plants, the largest patch 8 m long, a few smaller ones scattered, all on the steep bank on the upper side of the road, there is apparently a larger patch on the lower side of the road but mostly mowed off, this seems to be the only colony of *T. flavus* along Hwy. VV between entrance to Nelson Dewey State Park and where Hwy. VV turns NE out of the Mississippi River valley, this is the same colony collected 7 Oct 1972, as *M. Nee 5363,* 5 Oct 1981, *M. Nee 22034* (WIS).

Wisconsin. Grant Co.: 1 mi. NW of Cassville, along Hwy. VV, T3N R5W S18 SE¼ of SW¼, steep southwest facing grassy bank below the stone wall of Nelson Dewey State Park and base of Mississippi River bluff with thin woods of *Tilia americana, Gleditsia triacanthos, Quercus rubra,* the bank with mostly weedy plants such as *Physalis heterophylla, Kuhnia eupatorioides, Gnaphalium obtusifolium, Asparagus officinalis, Leptoloma cognatum; Tridens flavus* abundant, the dominant grass, common on both sides of Hwy. VV in the mile from entrance of power plant to entrance of Nelson Dewey State Park, on lower side of road common but mostly mowed off, this is the same colony collected 14 Oct 1972 as *M. Nee 5402,* 5 Oct 1981, *M. Nee 22051* (WIS).

Wisconsin. Grant Co.: 2 mi. E of Cassville along Hwy. 133, T3N R5W S27 SW¼ of SE¼, sandy soil of grassy roadside, old field and edges of cultivated corn field (*Zea mays*), with a mixture of weeds and native prairie species, *Eupatorium altissimum, Lespedeza capitata, Mirabilis nyctaginea, Asclepias verticillata, Leptoloma cognatum, Spartina pectinata; Tridens flavus* abundant on roadside and around edges of old field, this field now mostly planted to corn, not seen in nearby large alluvial gravel pit or from here to Cassville, this is the same colony collected 14 Oct 1972, as *M. Nee 5422,* 5 Oct 1981, *M. Nee 22063* (WIS).

Wisconsin. Grant Co.: In highway interchange where Eagle Point Rd. meets Hwy. 151, T1N R2W S16 SW¼ of SE¼, one robust plant, many culms, growing with a lot of *Sporobolus asper,* also *Panicum virgatum, Aster ericoides, A. novae-angliae, A. pilosus, Rosa* sp., *Rudbeckia hirta, Kuhnia eupatorioides,* 2 Oct 1991, *A. H. Williams 91-234a* (WIS).

Wisconsin. Grant Co.: Between Boscobel and Woodman on N side of Hwy. 133, T7N R3W S7 NW¼ of SE¼, dense stand 100 yd. long × 8 yd. wide, on highway right-of-way alongside red pine plantation and public hunting and fishing grounds, assoc. *Equisetum laevigatum, Lactuca canadensis, Monarda punctata, Ambrosia artemisiifolia, Bromus inermis, Verbena stricta, Daucus carota, Verbascum thapsus, Andropogon gerardii* (little), *A. scoparius* (little); smooth brome dominant, *Tridens flavus* subdominant, 20 Sep 1992, *T. S. Cochrane 12918* (WIS) w/ A. H. Williams, J. R. Sime & D. Hagar.

Wisconsin. Grant Co.: N of Cassville, S of Nelson Dewey State Park, T3N R5W S30 NE¼, imm. edge of road, where mowed occasionally, see *M. Nee 5402* (1972) at WIS, 24 Aug 1995, *A. H. Williams 95-51* (WIS). [The author chanced upon this, the second, of Nee's populations.]

Wisconsin. Green Co.: Vale Prairie owned by The Prairie Enthusiasts-Southwest Chapter, E of Monticello, W of Schneeberger Rd., S of Sugar River, T3N R8E S23 NW¼ of SE¼, rocky dry-mesic prairie remnant, mostly slopes north, diverse native flora and old field dominated by smooth brome, *Tridens flavus* has been here for some years, despite its new arrival in Wisconsin, 15 Jan 1996, *A. H. Williams 96-2* (WIS). [This grass was discovered here in the mid-1970s; G. Eldred, pers. comm.]

Wisconsin. Iowa Co.: T8N R4E S29 NW¼, sandy soil, 7 Oct 1973, *J. Meskill s. n.* (WIS).

Wisconsin. Iowa Co.: South verge of Hwy. 14, 0.6 mi. E of Sawle Rd., 0.4 mi. W of Hwy. K, T8N R5E S24 NW¼ of NW¼, loose colony of at least 50 plants in rather sandy soil with *Bromus inermis,* 24 Sep 1996, *A. H. Williams 96-34* (WIS). [Part of this population was mowed shortly prior to this collection.]

Wisconsin. Iowa Co.: South verge of Hwy. 14, 1.0 mi. W of Hwy. H, T8N R4E S24 NE¼ of NW¼, colony of at least 30 plants in rather sandy soil with *Paspalum setaceum, Poa pratensis, Schizachyrium scoparium, Cenchrus longispinus, Setaria glauca, Panicum capillare, Digitaria ischaemum* and *Sporobolus cryptandrus,* about half of this colony was recently mowed, 6 Sep 1997, *A. H. Williams 97-116* (WIS). [This site is 5.6 mi. W along Hwy. 14 from the site listed immediately above.]

Wisconsin. La Crosse Co.: Northwestern corner of the county, E side of Hwy. 53, just S of Black River, T18N R8W S1 SW¼ of SW¼, couple dozen plants on open grassy sloping right-of-way, 9 Jan 1996, *A. H. Williams 96-1* (WIS).

Wisconsin. Marquette Co.: Median strip of Hwy. 51, T17N R9E S1 W½ of NW¼, site had been planted to prairie species in 1988 or 1989, the seed obtained from a commercial dealer (Jock Engles), the seed itself from Illinois, site was also used for a mowing study on *Elytrigia repens* in which county equipment and crews were used, early Sep 1994, *D. R. Spuhler s. n.* (WIS).

Wisconsin. Rock Co.: T1N R11E S32, growing along a sandy roadside apparently spontaneously, 18 Sep 1994, *A. H. Williams 94-473* (WIS). [About 25 plants were present.]

Wisconsin. Rock Co.: Brockman Property, ca. 0.25 mi. S of Hwy. K, 200 yd. N of Wisconsin–Illinois border, T1N R11E S32 SW¼ of SW¼, sandy open roadside, 28 Sep 1996, *A. H. Williams 96-35* (WIS). [About 25 plants were present.]

Wisconsin. Sauk Co.: North verge of Kennedy Rd., scattered single plants and patches along 1.5 miles centered on the jct. with Big Hollow Rd., T8N R3E S10 & 11, growing only on the mowed roadside, not found on the adjacent unmowed railroad right-of-way which supports dry sandy prairie, species growing close to *T. flavus* on the mowed roadside include *Andropogon gerardii, Schizachyrium scoparium, Paspalum setaceum, Digitaria cognata, Panicum virgatum, P. capillare, Bouteloua hirsuta, Sorghastrum nutans, Eragrostis spectabilis, Cenchrus longispinus, Setaria glauca, S. viridis,* *Sporobolus cryptandrus, S. vaginiflorus, Ambrosia artemisiifolia, A. psilostachya, Monarda punctata, Helianthus occidentalis, Opuntia compressa, Verbena stricta, Euphorbia dentata, Amorpha canescens* and *Hieracium longipilum,* 6 Sep 1997, *A. H. Williams 97-114* (WIS).

DISCUSSION

Fernald (1950) lists the range of *Tridens flavus* as extending as far north as southern New Hampshire and Minnesota. This is partly in error, as Fassett (1951) does not list this grass for Wisconsin, Ownbey and Morley (1991) do not list it for Minnesota, and neither Hitchcock and Chase (1950) nor Gleason and Cronquist (1991) list it for either state.

Voss (1972), Swink and Wilhelm (1994), and Young (1994) suggest *Tridens flavus* may be adventive in northern Illinois and southern Michigan from farther south, particularly along roadways. Data presented here support the idea of vehicular introduction to 13 of 15 Wisconsin sites, but this is not definite. Even within this small sample, destruction of one of two old field sites by tillage was reported nine years after its discovery. Much of southern Wisconsin is tilled, and established populations are less likely to persist in tilled ground than along open roadsides. And the occurrence of *T. flavus* along roadsides has been reported from across its entire range (Gress 1924; Small 1933; Fernald 1950; Steyermark 1963; Great Plains Flora Association 1986), suggesting the relative openness, dryness, and disturbance characteristic of roadsides may better indicate habitat preference than vehicular transportation of propagules.

Two factors make *Tridens flavus* prominent on the verge in fall: its vertical culms stand up about 1 m, and anthesis is sufficiently late in this species that annual mowing on the right-of-way is often completed shortly prior to anthesis resulting in the taller vegetation on the roadside being, in places, almost exclusively *T. flavus.* The author discovered eight of the 15 Wisconsin sites between September and January while conducting prairie research on many sites around southwestern Wisconsin. Given such extensive travel, it's not surprising that new sites were discovered along roadsides, but it is noteworthy that all of the new sites were on roadsides rather than in prairies, whether or not propagules were transported by vehicles.

Most of these sites are sandy and dry. Mowing is noted on several specimen labels and surely occurs periodically over the entire width of the rights-of-way where this grass most often grows. County-owned mowing equipment may facilitate the spread of this grass from one roadside area to another. Roadside mowing often is completed in a given year prior to anthesis in this late-flowering grass, which may give this species a competitive advantage on these roadsides. This grass has persisted for years on some Wisconsin sites, and for at least 23 years in the oldest extant population.

In early spring, 1993, a portion of the off-road site in Green Co. was sprayed with Roundup herbicide to kill the dominant *Bromus inermis* in anticipation of a prairie planting the following fall. No other site preparation was done. *Tridens flavus* flourished here relative to the adjacent area that was not sprayed. It was still common and spreading at this site in 1997.

In Illinois, Mohlenbrock and Ladd (1978) showed Rock Island Co. as the northwestern range limit of *Tridens flavus,* where the author found it on a sand plain beside the Mississippi River in January, 1997. This sand plain, broken by riverine wetlands, stretches north through Whiteside Co. and much of Carroll Co. to Savanna, where limestone bluffs crowd the river. *Tridens flavus* was widespread and abundant in Rock Island and southern Whiteside Counties, growing in patches beside Illinois Highway 84, which parallels the river. Continuing north on this highway from its junction with U.S. Highway 30 in Whiteside Co., *T. flavus* was less frequently observed and in smaller colonies, but was found as far north as Savanna.

One more sand plain lies north of Savanna in Illinois. It is fully occupied by the Savanna Army Depot, to which immediate access was denied. Small patches of *Tridens flavus* were found on the periphery of this sand plain in Carroll and Jo Daviess Counties, suggesting it may occur in larger populations on this sand plain. This is the first report of *T. flavus* from Whiteside, Carroll, and Jo Daviess Counties, Illinois, as well as from eight counties in southern Wisconsin.

This grass is now abundant along sandy roadsides in northwestern Illinois, about 100 miles from the sandy area along the lower Wisconsin River in parts of Grant, Richland, Iowa, Sauk, and Dane Counties of Wisconsin. *Tridens flavus* currently occurs at four sites in this area and probably will become a prominent feature along sandy roadsides here in the near future. The La

Crosse Co. specimen suggests this process may occur in the sandy areas by the Mississippi River near La Crosse, and the Marquette Co. specimen suggests this may also occur in the "Central Sands" region of Wisconsin.

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NEW DISTRIBUTION NOTES ON THE MOSSES OF MASSACHUSETTS

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ABSTRACT. Eighteen moss species new to Massachusetts and 194 additional county records are reported. The new state records are briefly discussed. All county records are listed in an appendix. The moss flora of Massachusetts now stands at 356 species and 16 varieties.

Key Words: mosses, Massachusetts, state records, county records

Our knowledge of the moss flora of Massachusetts is substantially described in three previous papers (Hilferty 1960; Judd 1980; Mishler and Miller 1983). In addition, Welch (1960), Ireland (1969), Shaw (1981), and Crum and Anderson (1981) provided reports for certain Massachusetts mosses. Welch (1960) detailed state and county locality data for five taxa of the genus *Fontinalis* Hedw., *F. antipyretica* var. *oregonensis* Ren. & Card., *F. flaccida* Ren. & Card., *F. hypnoides* var. *duriaei* (Schimp.) Husn., *F. novae-angliae* var. *cymbifolia* (Aust.) Welch in Grout, and *F. sullivantii* Lindb. Ireland (1969) reported the first record of *Plagiothecium laetum* Schimp. in B.S.G. for the state from Essex County. Shaw (1981) reported Massachusetts records for *Pohlia andalusica* (Hohn.) Broth. (Berkshire County) and *Pohlia drummondii* (C. Mull.) Andrews. Crum and Anderson (1981) added records for *Orthotrichum speciosum* var. *elegans* (Schwaegr. ex Hook. & Grev.) Warnst., *F. filiformis* Sull. & Lesq. in Aust., *Sphagnum pylaisii* Brid., and *S. trinitense* C. Mull. For the last three taxa, we are unaware of any published county locality. Finally, Sorrie and Dunwiddie (1996) recently reported new state and county records for Nantucket.

The additions to the Massachusetts moss flora reported here are generated from eleven private collections. The identifications of specimens reported as new county or state records have been confirmed by the third author and are deposited in the Farlow Herbarium (FH) in Cambridge, Massachusetts. The collectors of these specimens and their affiliated institutions or home towns at the time the collections were made include the following: Jeanne E. Anderson (JEA) and Peter W. Dunwiddie (PWD)—Massachusetts Audubon Society; Sarah Cooper-Ellis (SC-E)—Smith College and Harvard Forest; Carol Knapp (CK)—Chilmark, Massachusetts; Glenn Motzkin (GM) and Paul Wilson (PW)—Harvard Forest; Lois Quillinan (LQ)—Glenville, New York; Sally Shaw (SS)—The Nature Conservancy; Nancy Slack (NS)—Russell Sage College; Susan A. Williams (SAW)—Rowe, Massachusetts; and Benito C. Tan (BCT) and Raymond Abair (RA)—Farlow Herbarium, Harvard University.

The moss flora of Massachusetts now consists of 356 species and 16 varieties. Overall, the flora consists predominantly of temperate species, with limited representation of circumboreal and polar/alpine species. To date, only six species on the state checklist, *Dicranella heteromalla* (Hedw.) Schimp., *Dicranum scoparium* Hedw., *Hypnum imponens* Hedw., *Polytrichum commune* Hedw., *P. piliferum* Hedw., and *Sphagnum palustre* L., are reported for every county in the state. In contrast, 82 taxa are known through only one county record and nearly half the taxa (ca. 182) are known from four or fewer counties. Not included in our count are two species introduced through the transport of planting materials and garden practices. *Callicostella pallida* (Hornsch.) Aongstr. and *Vesicularia vesicularis* (Schwaegr.) Broth., both widespread tropical American moss species, have been recently discovered growing on the soil of potted plants within greenhouses in Concord, Massachusetts.

Our compiled distribution records for Massachusetts mosses indicate that the local moss flora has not been thoroughly studied. For example, some common New England mosses such as *Polytrichum pallidisetum* and *Atrichum altecristatum* are reported here as additions to the state flora. In contrast, the Massachusetts record of *Desmatodon plinthobius* is the first report of the species north of New Jersey, representing a significant northward expansion of its range in eastern North America. One other species, *Pseudoleskeella tectorum* is also reported for the first time for New England. County level distribution in Massachusetts is best documented for Berkshire (231 taxa), Bristol (208), Essex (203), Middlesex (206), Norfolk (190), Worcester (185), Franklin (157), Suffolk (138), and Nantucket (83) Counties. The reported moss floras of Barnstable (52 taxa), Dukes (41), Hampden (89), Hampshire (106), and Plymouth (88) Counties are hardly complete. The authors are currently preparing a new state and county checklist that details these records.

A brief discussion of each of the eighteen state record species is presented below. New county records based on published information are listed as an appendix. Each species is cited with locality information and the initials of its collector(s) (see above). Nomenclature follows primarily that of Anderson, Crum, and Buck (1990). Exceptions include *Sphagnum* and *Leucodon andrewsianus* which use Anderson (1990) and Reese and Anderson (1997) respectively. Descriptions of worldwide species range and national distribution are taken from Crum and Anderson (1981) unless otherwise noted.

Atrichum altecristatum (Ren. & Card.) Smyth & Smyth (POLYTRICHACEAE)

Dukes County (Chilmark) CK
Essex County (Sagamore Hill Solar Observatory, Hamilton) BCT & RA
Franklin County (Rowe) SAW
Hampden County (Westover Air Force Base, Chicopee) BCT
Norfolk County (Blue Hills Reservation, MDC, Milton) BCT & RA

In North America, this species has a broad range from Saskatchewan, Nebraska, and Kansas eastward. Tan collected this species on two sites at Westover Air Force Base in Chicopee. One specimen was found in a mesic mixed-hardwood forest. The second was collected near Stoney Brook from the base of a tree along a path on disturbed ground near a deeply shaded red maple wetland. The Franklin County specimen was found growing with *Polytrichum piliferum* on exposed dirt and rock next to a brook.

Brachythecium turgidum (C. J. Hartm.) Kindb. (BRACHYTHECIACEAE)

Norfolk County (Hale Reservation, Trustees of Reservations, Westwood) BCT

Ireland (1982) described the habitat of this species as wet soil and rocks near streams, pools, or waterfalls, usually in calcareous habitats. Tan found this species in swampy sites on the Hale Reservation. This species is considered critically imperiled in New York State (Clemants and Ketchledge 1990). Although ranked as apparently secure throughout its global range, it is known from five or fewer sites in New York. The Massachusetts record appears among the most southern locations reported for this species in the eastern United States.

Bryum dichotomum Hedw. (BRYACEAE)

Essex County (Sagamore Hill Solar Observatory, Hamilton) BCT & RA

A large population of this species with the typical pendulous, short cylindrical capsules was found along the margin of an abandoned road inside the restricted compound of Sagamore Hill Solar Observatory and Antennae Complex in the town of Hamilton. Individual plants also bore 1 or 2 large, greenish bulbils in their leaf axils. The Massachusetts specimen matches the illustration of this species in Smith and Whitehouse (1978) and Crum and Anderson (1981). A widespread species in disturbed sites across the northern hemisphere, the local population of *Bryum dichotomum,* better known in old publications as *B. bicolor,* was found growing intermixed with *Bryum argenteum* Hedw., *Barbula unguiculata* Hedw. and *Ceratodon purpureus* (Hedw.) Brid.

Calliergon giganteum (Schimp.) Kindb. (AMBLYSTEGIACEAE)

Berkshire County (Mount Everett Wildlife Sanctuary, Massachusetts Audubon Society, Sheffield) JEA

Franklin County (Hawley Bog, Hawley) SC-E

Collected from a seasonal pond within a hardwood swamp in Berkshire County and from a red maple swamp at the south end of Hawley Bog in Franklin County. The latter site occurs within an area of wetland that contains some rare liverwort taxa, another state moss record, *Warnstorfia pseudostraminea,* and vascular plants characteristic of circumneutral conditions. Common and widespread at northern latitudes, this species extends as far south as Pennsylvania and Michigan. It is also wide-ranging in Europe and across Asia.

Desmatodon plinthobius Sull. & Lesq. in Sull. (POTTIACEAE)
Middlesex County (Harvard University campus, Cambridge) BCT

This species was collected from a brick wall of a campus building near the Harvard University Herbaria. Elsewhere, this species grows on concrete or mortared walls, preferring calcareous substrates in the wild. It is most common in the southern states of eastern North America. Crum and Anderson (1981) reported the northern end of its range as New Jersey and Pennsylvania. Consequently, this collection represents the first reported extension of the range of this species into New England.

Ditrichum rhynchostegium Kindb. (DITRICHACEAE)
Essex County (Sagamore Hill Solar Observatory, Hamilton) BCT & RA

This species was found at two sites at the observatory. Both are disturbed sites under shaded and semi-open tree and shrub communities in wet areas. Crum and Anderson (1981) reported this species as endemic to eastern North America with a range from Nova Scotia to Georgia and west to Ohio, Tennessee, and Arkansas.

Fissidens exilis Hedw., (FISSIDENTACEAE)
Essex County (Sagamore Hill Solar Observatory, Hamilton) BCT & RA

A small, fruiting population of this tiny moss was found growing on damp, semi-shaded clay soil at Sagamore Hill Solar Observatory and Antennae Complex. This site appears to be fertile ground for ephemeral mosses. In addition to *Fissidens exilis,* the second Massachusetts record of *Pleuridium ravenelii* Aust. was collected in the same vicinity. *Pleuridium ravenelii* is primarily a coastal plain species initially reported for Massachusetts from Nantucket (see Crum and Anderson 1981). Crum and Anderson (1981) reported *F. exilis* as a rare and local species with a range including Indiana, Kentucky, Maryland, Michigan, New York, Ohio, and Pennsylvania in North America. The specimen collected in Hamilton matches the illustration and description of *F. exilis* published by Steere (1950), who first observed and illustrated the bluntly and irregularly serrate margins of vaginant laminae with an intramarginal border somewhat differentiated from that of North American specimens. This observation led to his comment that the New World populations possibly represent a species distinct from the Old World *F. exilis.* This is in contrast to several modern European floras (Nyholm 1954; Smith 1978; Frahm and Frey 1987) which continue to describe the leaf margins of vaginant laminae on all *F. exilis* specimens as finely and evenly serrulate or crenulate.

Haplocladium microphyllum (Hedw.) Broth. (LESKEACEAE)
Berkshire County (Florida) SC-E

Cooper-Ellis (1994) collected this species from a decaying log in an old-growth hardwood forest as part of her graduate research on the bryophytes of western Massachusetts old-growth forests. This research also generated several county records for sites in Berkshire and Franklin Counties. Additional ecological information on these species is provided by Cooper-Ellis (in press). This moss can be considered somewhat weedy in calcareous habitats, although that habitat is not limiting. The species is widespread in continental North America. It is also known from southeast Asia and northern Europe. This species was previously reported as doubtful for Massachusetts by Hilferty (1960).

Plagiomnium ellipticum (Brid.) T. Kop. (MNIACEAE)
Franklin County (High Ledges Wildlife Sanctuary, Massachusetts Audubon Society, Shelbourne Falls) JEA

This moss was collected under shaded conditions in the vicinity of Spring Brook. Another state record (*Rhizomnium appalachianum*), also from the family Mniaceae, was collected from this location as well. The range of the species is circumpolar, generally more common northward. It has been encountered in rich fens elsewhere in its range.

Polytrichum pallidisetum Funck (POLYTRICHACEAE)
Hampden County (Westover Air Force Base, Chicopee) SC-E
Norfolk County (Blue Hills Reservation, MDC, Milton) BCT & RA

At Westover Air Force Base, this species was collected on a log in a young hardwoods wetland. Although this species has long been confused with *Polytrichum ohioense* Ren. & Card., it is common in much of eastern North America, as well as central

Europe. It is typically found in more northern latitudes or at higher elevations in coniferous forest.

Pseudoleskeella tectorum (Funck ex Brid.) Kindb. in Broth. (LESKEACEAE)

Worcester County (Harvard Forest, Petersham) PW

This species was collected from the trunk of an oak within the Prospect Hill Tract of Harvard Forest in Petersham. This and other Worcester County moss records were collected in conjunction with the long-term ecological research being conducted at Harvard Forest. *Pseudoleskeella tectorum* has a disjunct distribution in the East, being more characteristic of the western mountains of North America (Wilson and Norris 1989). It is reported by Clemants and Ketchledge (1990) as rare in New York State. This is the first record for this species in the New England states.

Rhabdoweisia crispata (With.) Lindb. (DICRANACEAE)

Franklin County (Adams Mountain, Rowe) SAW

This species was collected from soil over rock at Adams Mountain in Rowe. It is widespread in eastern North America, northern and central Europe, Southeast Asia, Africa, and the Pacific Islands.

Rhizomnium appalachianum T. Kop. (MNIACEAE)

Franklin County (High Ledges Wildlife Sanctuary, Massachusetts Audubon Society, Shelbourne Falls) JEA & PWD

This species, along with another state record moss species, *Plagiomnium ellipticum,* was collected under shaded conditions in the vicinity of Spring Brook at High Ledges Wildlife Sanctuary. In the Appalachian system, this species grows mainly in seepage and particularly on rock and ledges in the spray of waterfalls. It occurs throughout eastern North America and westward to Manitoba.

Scorpidium scorpioides (Hedw.) Limpr. (AMBLYSTEGIACEAE)

Berkshire County (Kampoosa Bog, Stockbridge) SS

Hampden County (Wilbraham) GM

Motzkin (1994) listed this species in his study of calcareous fens in western Massachusetts and adjacent New York and Connecticut. It has also been recently located in at least five sites in

New Hampshire. (N. Slack, pers. comm., 1997). Motzkin's collections of *Scorpidium scorpioides,* as well as that of another state record, *Sphagnum contortum,* were made at the same site in Wilbraham. The species is primarily circumpolar. These new locales are among the more southern sites in eastern North America. The State of New York includes this species on its list of rarities (Clemants and Ketchledge 1990).

Sphagnum centrale C. Jens. in Arnell & C. Jens. (SPHAGNACEAE)

Franklin County (Hawley Bog, Hawley) SC-E

At Hawley Bog, this *Sphagnum* species is found at the margins of the wetland. Crum and Anderson (1981) noted the species' tendency at the southern end of its range to be found among shrubs at the margins of bog mats. Commonly found in rich boggy woods in Michigan and New York, it is readily confused with *S. palustre* given the lack of reliable field characters (N. Slack, pers. comm., 1997). Its range in North America is from Newfoundland to Alaska, south through Washington, Iowa, Illinois, Indiana, West Virginia, and New Jersey. It is also known from Europe and reported from Greenland and northern Asia.

Sphagnum contortum Schultz (SPHAGNACEAE)

Hampden County (Wilbraham) GM

Motzkin (1994) listed this species in his study of calcareous fens in western Massachusetts and adjacent New York and Connecticut. His collections of *Sphagnum contortum,* as well as that of another state record, *Scorpidium scorpioides,* were from the same site in Wilbraham. This species is apparently circumpolar and is known in the east from Nova Scotia to New York and Michigan, although the distribution is considered poorly understood.

Sphagnum wulfianum Girg. (SPHAGNACEAE)

Berkshire County (Canoe Meadows Wildlife Sanctuary, Massachusetts Audubon Society, Pittsfield) JEA

This species was collected in 1990 from a small swamp at Canoe Meadows Wildlife Sanctuary. Nearly all of the tamarack in this wetland had died recently from what remain undetermined causes. This species has a broad range through northern North

America, northern Europe, and northern Asia. The most southern reported locale on the east coast is Connecticut.

Warnstorfia pseudostraminea (C. Muell.) Tuom. & T. Kop. (AMBLYSTEGIACEAE)

Franklin County (Hawley Bog, Hawley) SC-E

This moss species was found in a red maple swamp at the south end of the wetland, where sedges and mosses characteristic of neutral-basic conditions dominate. Some rare liverwort taxa also occur in this area. This species, previously known as *Calliergidium pseudostramineum,* is considered rare by Crum and Anderson (1981) and has been reported from Maine, New Hampshire, Michigan, and Alaska, as well as Germany, Scandinavia, and Greenland.

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APPENDIX: MOSSES OF MASSACHUSETTS, NEW COUNTY RECORDS (VOUCHER SPECIMENS DEPOSITED IN FH)

BARNSTABLE COUNTY (Cape Cod Air Force Base, Bourne)
Callicladium haldanianum (Grev.) Crum BCT & RA
Dicranum condensatum Hedw. BCT & RA

Dicranum montanum Hedw. BCT & RA
Ditrichum lineare (Sw.) Lindb. BCT & RA
Hypnum pallescens (Hedw.) P. Beauv. BCT & RA
Plagiothecium laetum Schimp. in B.S.G. BCT & RA
Pleurozium schreberi (Brid.) Mitt. BCT & RA

BERKSHIRE COUNTY

Drepanocladus aduncus (Hedw.) Warnst. SS (Kampoosa Bog, Stockbridge)
Helodium blandowii (Web. & Mohr) Warnst. GM (Williamstown)
Helodium blandowii var. *helodioides* (Ren. & Card. in Röll) Crum et al. SS (Egremont)
Oncophorus wahlenbergii Brid. LQ (west of Williamstown)
Sphagnum fimbriatum Wils. GM (Stockbridge)

DUKES COUNTY

Anomodon rostratus (Hedw.) Schimp. SC-E (Cedar Tree Neck Sanctuary, Chilmark)
Atrichum undulatum (Hedw.) P Beauv. PWD 1327 (Chilmark)
Aulacomnium palustre (Hedw.) Schwaegr. SC-E (Cedar Tree Neck Sanctuary) and JEA (Felix Neck Wildlife Sanctuary)
Brachythecium salebrosum (Web. & Mohr) Schimp. in B.S.G. CK (Chilmark)
Bryoandersonia illecebra (Hedw.) Robins. PWD 1330 (Chilmark)
Dicranella heteromalla (Hedw.) Schimp. PWD 1335 (Chilmark)
Dicranum condensatum Hedw. PWD 1358 (Lobsterville)
Dicranum fulvum Hook. PWD 1339, 1343 (Chilmark)
Ditrichum lineare (Sw.) Lindb. PWD 1384 (Long Point Reservation, Chilmark)
Hedwigia ciliata (Hedw.) P. Beauv. PWD 1345 (Chilmark)
Hypnum cupressiforme Hedw. PWD 1323 (Chilmark)
Hypnum imponens Hedw. PWD 1347 (Chilmark)
Leucobryum albidum (Brid.) Lindb. JEA (Felix Neck Wildlife Sanctuary, Edgartown)
Leucobryum glaucum (Hedw.) Schimp. PWD 1311 (Long Point Reservation, Chilmark)
Mnium hornum Hedw. SC-E (Cedar Tree Neck Sanctuary, Chilmark)
Platygyrium repens (Brid.) B.S.G. PWD 1354 (Menemsha Hills)
Pogonatum pensilvanicum (Hedw.) P. Beauv. PWD 1350 (Menemsha Hills)
Polytrichum commune Hedw. PWD 1301 (West Tisbury)
Polytrichum ohioense Ren. & Card. PWD 1360, 1314 (Lobsterville & Long Point Reservation, Chilmark)
Polytrichum piliferum Hedw. PWD 1302, 1359 (Lobsterville & West Tisbury)
Sphagnum capillifolium (Ehrh.) Hedw. PWD 1366, 1383 (Chilmark)
Sphagnum fimbriatum Wils. PWD 1365 (Chilmark)
Tetraphis pellucida Hedw. PWD 1342 (Chilmark)
Thelia hirtella (Hedw.) Sull. JEA (Felix Neck Wildlife Sanctuary, Edgartown) and PWD 1320 (Chilmark)

Thuidium delicatulum (Hedw.) Mitt. SC-E (Cedar Tree Neck Sanctuary, Chilmark)
Warnstorfia exannulata (Schimp.) Loeske PWD 1370 (Chilmark)

ESSEX COUNTY (Sagamore Hill Solar Observatory, Hamilton)
Campylium polygamum (B.S.G.) Bryhn. BCT & RA
Fissidens bushii Card. & Thér. BCT & RA
Pseudotaxiphyllum elegans (Brid.) Iwats. BCT & RA
Pleuridium ravenelii Aust. BCT & RA

FRANKLIN COUNTY
Andreaea rothii Web. & Mohr SAW (Rowe)
Aulacomnium palustre (Hedw.) Schwaegr. SC-E (Hawley Bog, Hawley)
Barbula unguiculata Hedw. SAW (Rowe)
Brachythecium digastrum C. Muell. & Kindb. NS 2480 (Mt. Toby State Forest)
Brachythecium oedipodium (Mitt.) Jaeg. JEA & PWD (High Ledges Wildlife Sanctuary) and SAW (Rowe)
Brachythecium reflexum (Starke) B.S.G. SAW (Rowe)
Brachythecium velutinum (Hedw.) B.S.G. JEA (High Ledges Wildlife Sanctuary, Shelbourne Falls)
Bryum argenteum Hedw. SAW (Rowe)
Bryum caespiticium Hedw. SAW (Rowe)
Bryum capillare Hedw. SAW (Rowe)
Calliergon cordifolium (Hedw.) Kindb. SC-E (Hawley Bog)
Campylium stellatum (Hedw.) Lange & Jens. SC-E (Rowe)
Climacium dendroides (Hedw.) Web. & Mohr. SAW (Rowe)
Dicranella heteromalla (Hedw.) Schimp. JEA & PWD (High Ledges Wildlife Sanctuary, Shelbourne Falls)
Dicranum fuscescens Turn. JEA (Bear Swamp Reservation, Ashfield)
Dicranum undulatum Brid. SC-E (Rowe)
Drepanocladus aduncus (Hedw.) Warnst. var. *aduncus* SC-E (Hawley Bog, Hawley)
Entodon compressus (Hedw.) C. Muell. SAW (Rowe)
Entodon seductrix (Hedw.) C. Muell. SAW (Rowe)
Fissidens bushii Card. & Thér. SAW (Rowe)
Fontinalis antipyretica var. *gigantea* Sull. SAW (Rowe)
Fontinalis novae-angliae Sull. SAW (Rowe)
Forsstroemia trichomitria (Hedw.) Lindb. SAW (Rowe)
Funaria hygrometrica Hedw. SAW (Rowe)
Haplocladium virginianum (Brid.) Broth. SAW (Rowe)
Helodium blandowii (Web. & Mohr) Warnst. SC-E (Hawley Bog, Hawley)
Hygrohypnum ochraceum (Turn.) Loeske SAW (Rowe)
Hymenostylium recurvirostre (Hedw.) Dix. NS 2472 (Mt. Toby State Forest)
Hypnum lindbergii Mitt. GM (Deerfield & Greenfield)
Isopterygiopsis muelleriana (Schimp.) Iwats. SAW (Rowe)
Leptodictyum riparium (Hedw.) Warnst. SAW (Rowe)
Leskea polycarpa Hedw. NS 2373 (Mt. Toby State Forest)

Leucobryum albidum (Brid.) Lindb. JEA (High Ledges Wildlife Sanctuary, Shelbourne Falls)
Neckera pennata Hedw. SAW (Rowe)
Orthotrichum sordidum Sull. & Lesq. SAW (Rowe)
Philonotis fontana (Hedw.) Brid. SC-E and GM (Deerfield)
Physcomitrium pyriforme (Hedw.) Hampe SAW (Rowe)
Plagiothecium laetum Schimp. in B.S.G. SAW (Rowe)
Pleurozium schreberi (Brid.) Mitt. SAW (Rowe)
Pohlia cruda (Hedw.) Lindb. SC-E (Mt. Toby. Sunderland)
Polytrichum piliferum Hedw. SAW (Rowe)
Pseudobryum cinclidioides (Hüb.) T. Kop. JEA (Orange)
Pylaisiella selwynii (Kindb.) Crum et al. SAW (Rowe)
Racomitrium aciculare (Hedw.) Brid. SAW (Rowe)
Rhizomnium punctatum (Hedw.) T. Kop. SC-E (Hawley Bog, Hawley)
Sanionia uncinatus (Hedw.) Loeske SAW (Rowe)
Schistidium agassizii Sull. & Lesq. in Sull. SAW (Rowe)
Sphagnum angustifolium (C. Jens. ex Russ.) C. Jens. in Tolf. SC-E (Hawley Bog, Hawley)
Sphagnum fimbriatum Wils. SC-E (Hawley Bog, Hawley)
Sphagnum fuscum (Schimp.) Klinggr. JEA (High Ledges Wildlife Sanctuary, Shelbourne Falls)
Steerecleus serrulatus (Hedw.) Robins. SAW (Rowe)
Thuidium recognitum (Hedw.) Lindb. SAW (Rowe)
Trematodon ambiguus (Hedw.) Broth. SAW (Rowe)
Ulota coarctata (P. Beauv.) Hammar SAW (Rowe)
Ulota crispa (Hedw.) Brid. JEA & PWD (High Ledges Wildlife Sanctuary, Shelbourne Falls)
Weissia controversa Hedw. SAW (Rowe)

HAMPDEN COUNTY (Westover Air Force Base, Chicopee)
Amblystegium serpens (Hedw.) Schimp. in B.S.G. BCT
Aulacomnium androgynum (Hedw.) Schwaegr. BCT
Brachythecium salebrosum (Web. & Mohr) Schimp. in B.S.G. BCT
Bryhnia novae-angliae (Sull. & Lesq.) Grout BCT and SC-E
Bryum caespiticium Hedw. BCT
Calliergon cordifolium (Hedw.) Kindb. SC-E
Calliergonella cuspidata (Brid.) Loeske BCT
Campylium chrysophyllum (Brid.) Bryhn BCT
Campylium radicale (P. Beauv.) Grout SC-E
Climacium dendroides (Hedw.) Web. & Mohr BCT
Dicranum flagellare Hedw. BCT
Dicranum montanum Hedw. BCT
Entodon seductrix (Hedw.) C. Muell. BCT
Hedwigia ciliata (Hedw.) P. Beauv. BCT
Helodium blandowii (Web. & Mohr) Warnst. SC-E
Helodium paludosum (Sull.) Aust. BCT
Hypnum cupressiforme Hedw. BCT
Hypnum imponens Hedw. BCT
Leskea gracilescens Hedw. BCT

Mnium hornum Hedw. BCT
Orthotrichum anomalum Hedw. BCT
Orthotrichum obtusifolium Brid. BCT
Orthotrichum sordidum Sull. & Lesq. BCT
Physcomitrium pyriforme (Hedw.) Hampe BCT & SC-E
Plagiothecium cavifolium (Brid.) Iwats. BCT
Plagiothecium laetum Schimp. in B.S.G. SC-E
Pohlia nutans (Hedw.) Lindb. BCT
Polytrichum piliferum Hedw. BCT
Rhizomnium magnifolium (Horik.) T. Kop. SC-E
Rhizomnium punctatum (Hedw.) T. Kop. BCT
Schistidium agassizii Sull. & Lesq. in Sull. BCT
Sphagnum compactum DC. BCT
Sphagnum fimbriatum Wils. BCT and SC-E
Sphagnum palustre L. BCT
Ulota crispa (Hedw.) Brid. BCT

HAMPSHIRE COUNTY
Brachythecium oedipodium (Mitt.) Jaeg. SC-E (Arcadia Wildlife Sanctuary, Easthampton)
Brotherella recurvans (Michx.) Fleisch. JEA (Graves Farm Wildlife Sanctuary, Williamsburg)
Bryhnia novae-angliae (Sull. & Lesq.) Grout SC-E (Arcadia Wildlife Sanctuary, Easthampton)
Calliergon cordifolium (Hedw.) Kindb. JEA (Arcadia Wildlife Sanctuary, Easthampton)
Cyrto-hypnum minutulum (Hedw.) Buck & Crum SC-E (Williamsburg)
Dichelyma capillaceum (With.) Myr. JEA (Arcadia Wildlife Sanctuary, Easthampton)
Dicranum montanum Hedw. SC-E (Unquomonk Mt., Williamsburg)
Dicranum polysetum Sw. JEA (Graves Farm Wildlife Sanctuary, Williamsburg)
Dicranum scoparium Hedw. SC-E (Graves Farm Wildlife Sanctuary, Williamsburg)
Drepanocladus aduncus (Hedw.) Warnst. SC-E (Arcadia Wildlife Sanctuary, Easthampton)
Fissidens bushii Card. & Thér. SC-E (Williamsburg)
Herzogiella striatella (Brid.) Iwats. JEA (Graves Farm Wildlife Sanctuary, Williamsburg)
Hypnum cupressiforme Hedw. SC-E (Arcadia Wildlife Sanctuary, Easthampton)
Hypnum fertile Sendtn. JEA (Graves Farm Wildlife Sanctuary, Williamsburg)
Hypnum imponens Hedw. SC-E (Arcadia Wildlife Sanctuary, Easthampton)
Hypnum lindbergii Mitt. SC-E (Graves Farm Wildlife Sanctuary, Williamsburg)
Leptodictyum riparium (Hedw.) Warnst. SC-E (Williamsburg)
Leskea gracilescens Hedw. SC-E (Hadley)

Leucodon andrewsianus (Crum & Anders.) Reese & Anders. SC-E (Graves Farm Wildlife Sanctuary, Williamsburg)

Neckera pennata Hedw. SC-E (Graves Farm Wildlife Sanctuary, Williamsburg)

Orthotrichum obtusifolium Brid. SC-E (Graves Farm Wildlife Sanctuary, Williamsburg)

Plagiomnium ciliare (C. Muell.) T. Kop. SC-E (Unquomonk Mt., Williamsburg)

Plagiomnium medium (Bruch & Schimp. in B.S.G.) T. Kop. SC-E (Arcadia Wildlife Sanctuary, Easthampton)

Plagiothecium laetum Schimp. in B.S.G. SC-E (Arcadia Wildlife Sanctuary, Easthampton)

Pogonatum pensilvanicum (Hedw.) P. Beauv. SC-E (Williamsburg)

Polytrichum commune Hedw. SC-E (Sawmill Hills, Florence)

Polytrichum juniperinum Hedw. SC-E (Unquomonk Mt., Williamsburg)

Polytrichum ohioense Ren. & Card. SC-E (Williamsburg)

Steerecleus serrulatus (Hedw.) Robins. SC-E (Williamsburg)

Ulota crispa (Hedw.) Brid. SC-E (Arcadia Wildlife Sanctuary, Easthampton)

MIDDLESEX COUNTY

Orthotrichum pumilum Mitt. BCT (Harvard University, Cambridge)

NANTUCKET COUNTY

Sematophyllum demissum (Wils.) Mitt. PWD 1389

NORFOLK COUNTY

Andreaea rupestris Hedw. BCT & RA (Blue Hills Reservation, Milton)

Aulacomnium androgynum (Hedw.) Schwaegr. LQ (Blue Hills Reservation, Milton)

Brachythecium digastrum C. Muell. & Kindb. BCT & RA (Blue Hills Reservation, Milton)

Climacium dendroides (Hedw.) Web. & Mohr BCT (Hale Reservation, Westwood)

Dicranum condensatum Hedw. BCT & RA (Blue Hills Reservation, Milton)

Dicranum muehlenbeckii B.S.G. BCT & RA (Blue Hills Reservation, Milton)

Isopterygium tenerum (Sw.) Mitt. BCT & RA (Blue Hills Reservation, Milton)

Leucobryum albidum (Brid.) Lindb. BCT (Hale Reservation, Westwood)

Orthotrichum anomalum Hedw. BCT & RA (Blue Hills Reservation, Milton)

Pohlia cruda (Hedw.) Lindb. BCT & RA (Blue Hills Reservation, Milton)

Polytrichastrum alpinum (Hedw.) G.L. Sm. BCT (Hale Reservation, Westwood)

Pseudotaxiphyllum elegans (Brid.) Iwats. LQ and BCT & RA (Blue Hills Reservation, Milton)

Pylaisiella polyantha (Hedw.) Grout BCT & RA (Blue Hills Reservation, Milton)

Racomitrium heterostichum (Hedw.) Brid. BCT & RA (Blue Hills Reservation, Milton)

Schistidium agassizii Sull. & Lesq. in Sull. BCT & RA (Blue Hills Reservation, Milton)

WORCESTER COUNTY

Brachythecium reflexum (Starke) B.S.G. PW (Harvard Forest, Petersham)

Bryoerythrophyllum recurvirostre (Hedw.) Chen PW (Harvard Forest, Petersham)

Campylostelium saxicola (Web. & Mohr) B.S.G. PW (Harvard Forest, Petersham)

Climacium dendroides (Hedw.) Web. & Mohr JEA (Cooks Canyon Wildlife Sanctuary, Barre)

Fontinalis antipyretica Hedw. var. *antipyretica* PW (Harvard Forest, Petersham)

Leskea gracilescens Hedw. PW (Harvard Forest, Petersham)

Paraleucobryum longifolium (Hedw.) Loeske PW (Harvard Forest, Petersham)

Plagiothecium cavifolium (Brid.) Iwats. PW (Harvard Forest, Petersham)

Plagiothecium laetum Schimp. in B.S.G. PW (Harvard Forest, Petersham)

Pterigynandrum filiforme Hedw. PW (Harvard Forest, Petersham)

Sphagnum angustifolium (C. Jens. ex Russ.) C. Jens. in Tolf. JEA (Flat Rock Wildlife Sanctuary, Fitchburg)

Sphagnum fallax (Klinggr.) Klinggr. PW (Harvard Forest, Petersham)

Sphagnum fuscum (Schimp.) Klinggr. PW (Harvard Forest, Petersham)

Sphagnum papillosum Lindb. JEA (Flat Rock Wildlife Sanctuary, Fitchburg)

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MICROMORPHOLOGICAL STUDIES OF *CAREX* SECTION *MITRATAE* (CYPERACEAE) IN TURKEY

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ABSTRACT. Scanning electron microscopy was used to examine achene epidermal features in species of *Carex* section *Mitratae* and the allied section *Acrocystis* found in Turkey. Members of section *Mitratae* share a particular achene phenotype. Micromorphological characters appear to be conservative, and show little variation between species of section *Mitratae*. Comparative data of achene micromorphology support the placement of *C. tomentosa* within section *Acrocystis*.

Key Words: *Carex, Mitratae,* Cyperaceae, systematics, achene, SEM

Carex section *Mitratae* Kük. has comprised three taxa in Turkey: *C. umbrosa* subsp. *huetiana, C. caryophyllea,* and *C. depressa* subsp. *transsilvanica.* One species was recognized within section *Acrocystis* Dumort. [= *Montanae* (Fries) Carey]: *C. tomentosa* (Nilsson 1985). These sections (*Mitratae* and *Acrocystis*) have been combined into one unit, as section *Onkerma* (Rafin) Krecz. (Kreczetovicz 1935). Chater (1980) and Nilsson (1985) outlined several morphological features that distinguish the species of section *Mitratae.* Members of *Carex* section *Mitratae* are distinguished from taxa in other sections of *Carex* by achenes with annular, whitish apical discs.

Achene epidermis characters have been used in many studies on *Carex* taxonomy at both the specific and the sectional levels (Crins and Ball 1988; Menapace and Wujek 1985, 1987; Menapace et al. 1986; Rettig 1986, 1990; Salo et al. 1994; Standley 1985, 1987a, b, 1990; Tallent and Wujek 1983; Toivonen and Timonen 1976; Waterway 1990; Wujek and Menapace 1986). Usually these characters have provided criteria useful for delimitation of taxa at various levels. They have also been used for distinguishing species within critical groups (Rettig 1990; Standley 1987a, b). However, studies on taxa within the *C. crinita* complex (Bruederle et al. 1989) and the *C. flava* complex (Salo et al. 1994) indicated that achene micromorphology was not useful in distinguishing taxa because of the considerable amount of

Table 1. Collection data for *Carex* species used for SEM observations.

Section *Mitratae*
C. umbrosa Host. subsp. *huetiana* Boiss.
RÍZE: Kaçkar, *Olgun 58*; Cimil, *Olgun 63*; TRABZON: Solma y., *Olgun 83*; Çakilgöl, *Olgun 85.*
C. caryophyllea Latourr.
RÍZE: Balliköy, *Olgun 15*; Ovit, *Olgun 57*; Cimil, *Olgun 64.*
C. depressa Link. subsp. *transsilvanica* Schur.
TRABZON: Sümela, *Olgun 2*; KTÜ Kampüs, *Olgun 11*; RÍZE: Balliköy, *Olgun 16*; Cimil, *Olgun 74.*
Section *Acrocystis*
C. tomentosa L.
TRABZON: Zingana, *Olgun 9*; Kiremithaneler, *Olgun 13*; Erikbeli, *Olgun 76.*

variation within species. Studies on the sections *Heleonastes* (Toivonen and Timonen 1976), *Folliculatae* (Wujek and Menapace 1986) and *Lupulinae* (Menapace et al. 1986) illustrated that achene micromorphology may differ more drastically from one section to another than from species to species. In other studies, variation within well-defined sections was found to be as great as variation between sections (Menapace and Wujek 1985; Rettig 1986; Waterway 1990). Salo et al. (1994) indicated that the utility of achene epidermis characters as a basis of taxonomic decisions varies greatly in the different sections of *Carex.*

In the present work, achene micromorphology of section *Mitratae* was examined by SEM and *Carex tomentosa* (from the related section *Acrocystis*) was used for comparison.

MATERIALS AND METHODS

Perigynia containing mature achenes of all species of *Carex* sections *Mitratae* and *Acrocystis* were taken from herbarium specimens deposited at the Karadeniz Technical University Herbarium (KTUB). Three or four accessions of each species were examined. Observations were made on six to eight achenes from each accession. Collection data for SEM studies are given in Table 1.

Achenes were treated with a 1 : 9 (v/v) mixture of concentrated sulfuric acid: acetic anhydride and sonicated in ultrasonic cleaner for 1 to 2 hours to remove the outer cell walls (Tallent and Wujek 1983; Toivonen and Timonen 1976). Dried achenes were sputter coated with 200–300 Å of gold before observation with a JSM-6400 SEM. Upper shoulders of achenes were photographed at an accelerating voltage of 5 kV. Micrographs were usually obtained at magnifications of 1500×. Terminology used in describing the anticlinal walls and the silica deposits follows Rettig (1990).

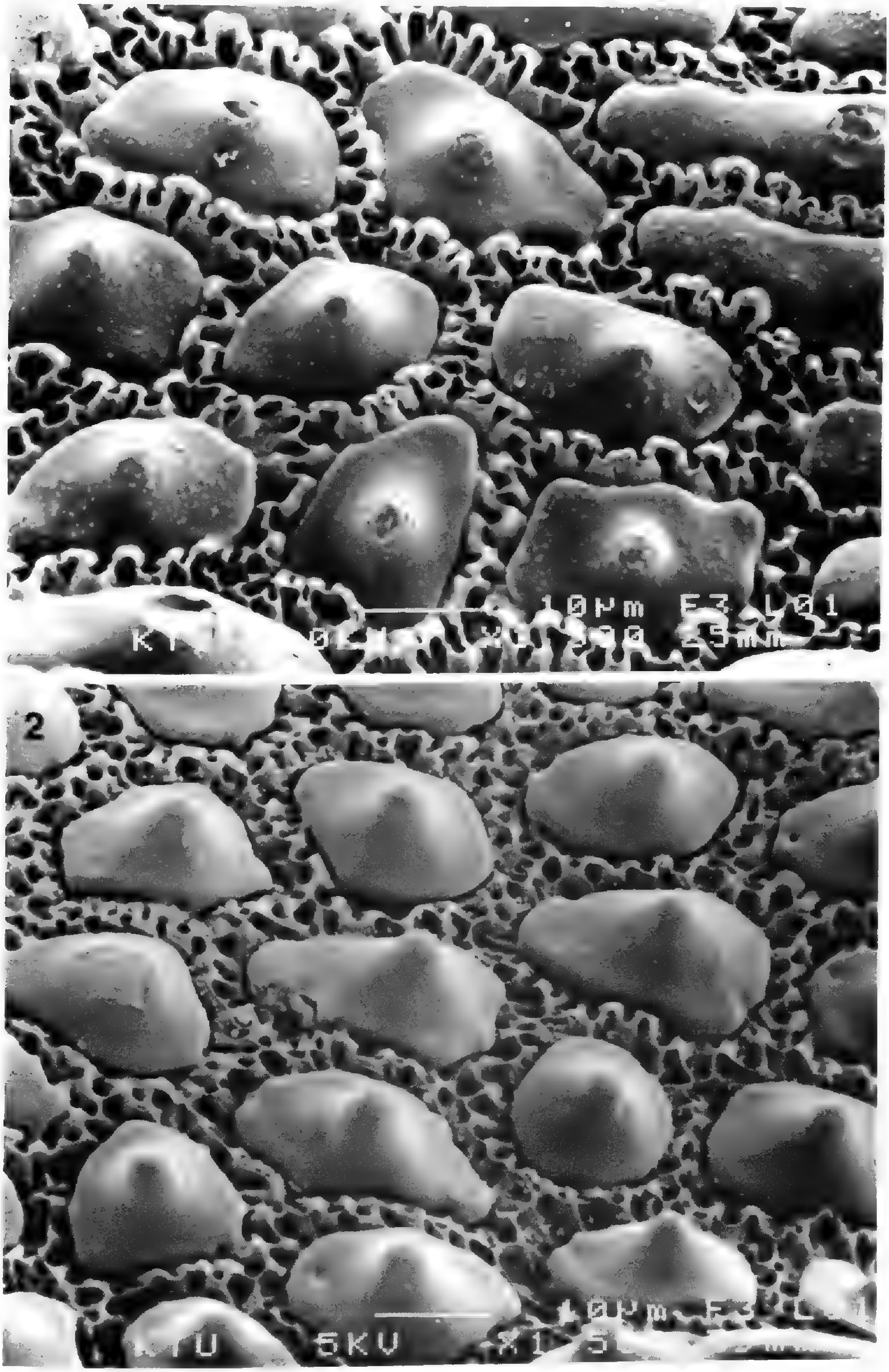
RESULTS AND DISCUSSION

Representative scanning electron micrographs of four taxa are shown in Figures 1 through 6. As can be seen from the figures, the species of section *Mitratae* share a particular achene micromorphology. *Carex umbrosa* subsp. *huetiana, C. caryophyllea,* and *C. depressa* subsp. *transsilvanica* have convex silicon platforms with round corners and honeycombed anticlinal walls. These characters were constant for all cells of achenes of these species.

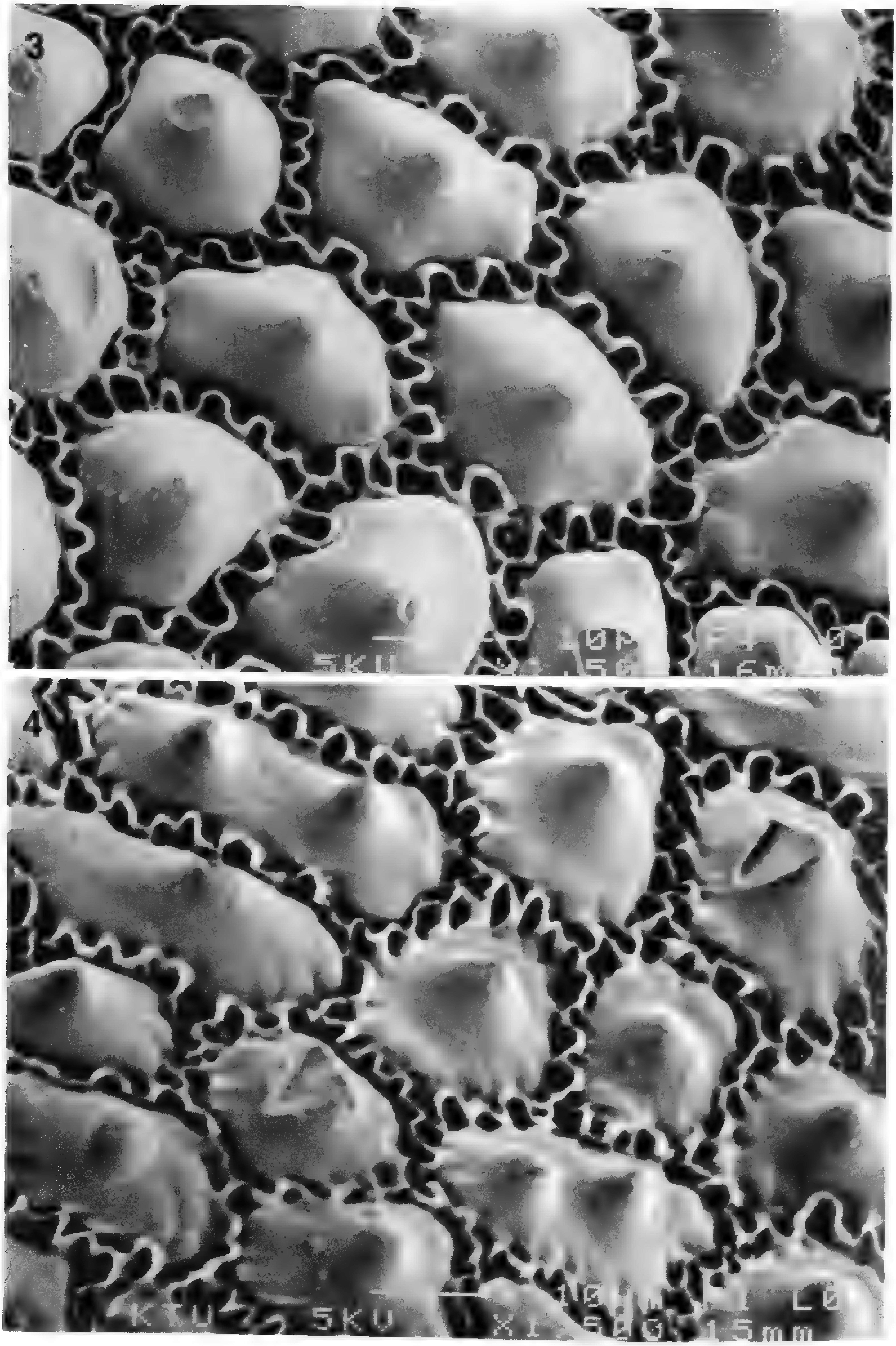
Carex caryophyllea (Figure 1) and *C. depressa* subsp. *transsilvanica* (Figure 2) are different from *C. umbrosa* subsp. *huetiana* based on the presence of a silicon body. The achene cells of *C. caryophyllea* and *C. depressa* subsp. *transsilvanica* always have one silicon body, while the cells of *C. umbrosa* typically have one (Figure 3), rarely two (Figure 4), or sometimes no silicon body (Figure 5).

The achene micromorphology of *Carex tomentosa* (Figure 6) is in contrast to species of section *Mitratae* by having thin, straight anticlinal walls. Furthermore, the silicon platforms are concave with sharp corners.

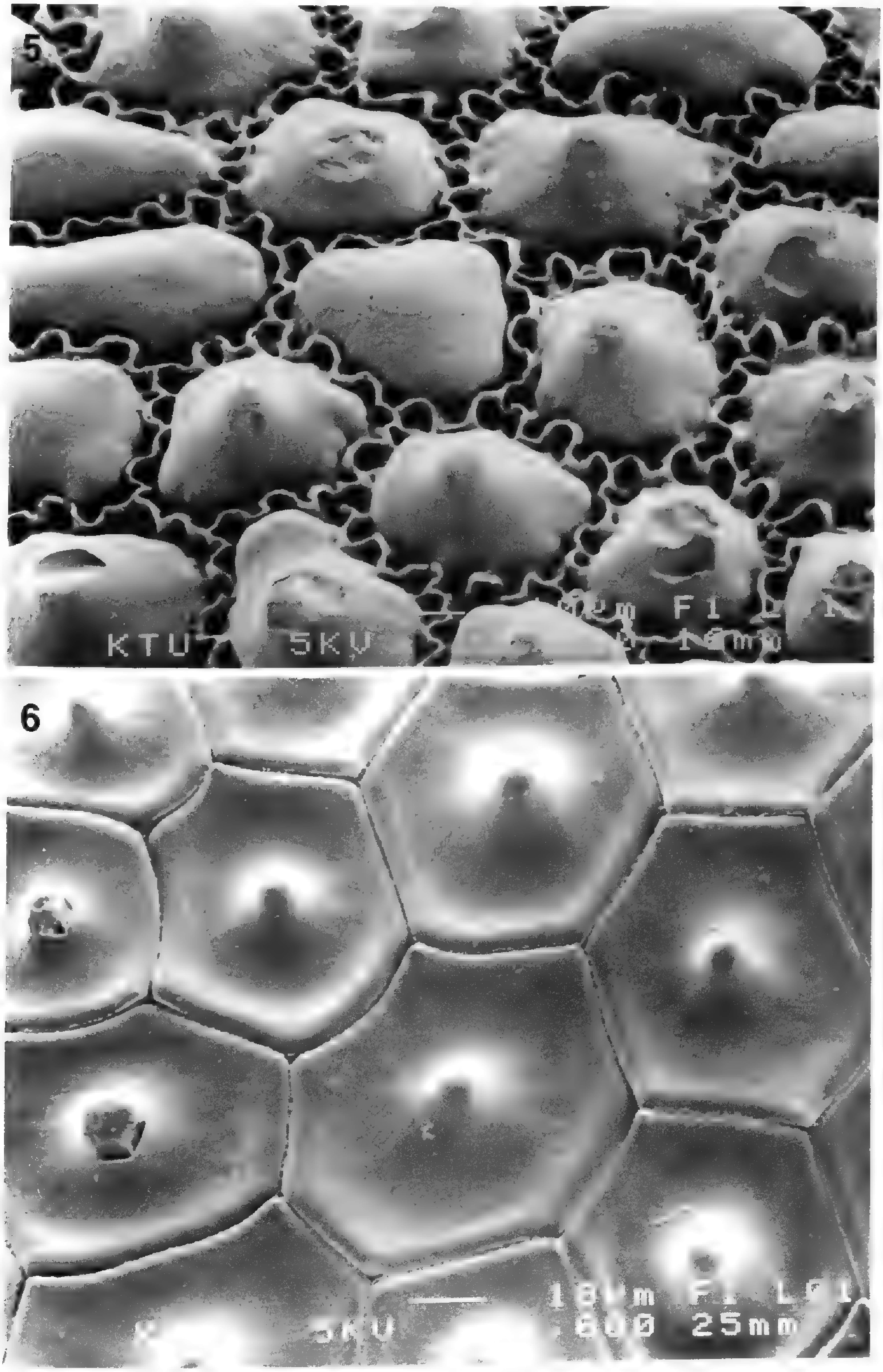
In this study, no significant variation in micromorphological characters within species was observed and variation also was minimal within section *Mitratae.* Achene micromorphology of section *Mitratae* is characterized by special anticlinal walls, and these characters may provide useful data to delineate the section rather than to distinguish species. Epidermal features of *Carex tomentosa* are significantly different from the taxa of section *Mitratae.* These examples illustrate the correspondence between achene epidermal features and sectional classifications of the species examined. Our observations are concordant with classifications of these species at the sectional level (Chater 1980; Nilsson 1985). However, the honeycomb anticlinal wall structure has been reported on the achene cells of *C. emmonsii* Dewey ex Torrey var. *muhlenbergii* (A. Gray) J. Rettig from section *Acrocystis*



Figures 1–2. SEM photographs of *Carex* achenes. 1. (top) *C. caryophyllea* 2. (bottom) *C. depressa* subsp. *transsilvanica*. Scale bar = 10 µm.



Figures 3–4. SEM photographs of *Carex umbrosa* subsp. *huetiana* achenes. Scale bar = 10 μm.



Figures 5–6. SEM photographs of *Carex* achenes. 5. (top) *C. umbrosa* subsp. *huetiana* 6. (bottom) *C. tomentosa*. Scale bar = 10 μm.

(Rettig 1990). This similarity supports the hypothesis that there is a close relationship between the species of these two sections.

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BOOK REVIEW

New England's Mountain Flowers: A High Country Heritage by J. Wallner and M. J. DiGregorio. 1997. xiii + 221 pp. illus. ISBN 0-87842-337-0 $17.00 (paper). Mountain Press Publishing Company, Missoula, MT (in cooperation with the New England Wild Flower Society).

This book is intended to attract and hold the attention of people who may simply enjoy the beauty of flowers or are beginning a deeper interest in plants. While readers are admiring the handsome full page photographs, the informal text on the facing page introduces different botanical and ecological concepts, in addition to information on the species illustrated. The introduction packs in much information on botanical exploration of New England, particularly the northern regions, conservation efforts, and geology and its major role in forming different habitats which enable the diversity of plant communities to flourish. The book is not intended to serve as a field guide, but more as an enticement to the deeper knowledge of plants.

Eighty-five of the showiest wild flowers are grouped into habitat categories of Forest Slopes, Streambanks and Ponds, Bogs and Fens, Cliffs, Ledges and Talus Slopes, The Alpine Zone, Alien Species, and Rare and Endangered Flowers. The title is a little misleading as many of the species are lowland inhabitants. Each section has an informative introduction which discusses the unique characteristics of each habitat. One of the main themes throughout the book is the plant's need of specific conditions to survive. Conservation of habitat equals, possibly, conservation of the plant. Aspects of rarity are discussed in the Rare and Endangered Flowers section, where seven of the very rarest plants are included.

Text opposite each photograph covers a multitude of subjects, from lore, uses, ecology, pollination, conservation, role of soils and nutrients, associated species and characteristics of certain plant families, to evolution and aesthetics. The excitement of botanizing, exploration, and discovery and even the fun of drive-by botany, are stressed.

The inclusion of six alien species is somewhat mysterious, although it gives the authors a chance to expand on the beauty but also the dangers of introduced species. The cheerful yellow of coltsfoot (*Tussilago farfara*) is enjoyed by all, but how many will come upon grecian foxglove (*Digitalis lanata*)? Two photos of garden lupine (*Lupinus polyphyllus, L. nootkatensis*) seem a waste of valuable space that could have been dedicated to another rare native species.

The purposes of this book are important: raising people's awareness of the beauty of our native plants, broadening their enjoyment, encouraging their powers of observation, and stressing the plants' need of wild, undisturbed habitat. The book should be made available to those in charge of our vast public lands. In accomplishing these goals, it should take its place in the struggle to save our natural environments.

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RHODORA, Vol. 99, No. 900, pp. 378–379, 1997

BOOK REVIEW

The Forgotten Pollinators by Stephen L. Buchmann and Gary Paul Nabhan. 1996 (paper 1997). 292 pp. 33 illus. ISBN 1-55963-353-0 $27.50 (cloth) $16.95 (paper). Island Press/Shearwater Books, Washington, DC/Covelo, CA.

In the Berlin/Dahlem Botanical Garden there stands a small stone memorial inscribed with the title page of a book by Christian Conrad Sprengel entitled *Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen* (*The secret of Nature revealed in the structure and fertilization of flowers*), published in 1793. It illustrates a wide range of floral mechanisms and the insects that operate them and pays tribute to the founder of detailed and comprehensive descriptive studies in pollination ecology over 200 years ago, continued by Hermann Müller and Paul Knuth in the nineteenth and early twentieth centuries.

In the first five chapters of *The Forgotten Pollinators,* Buchmann and Nabhan review some of these early descriptions and add more recent information on floral function derived experimentally. The next three chapters deal with human disruptions of natural pollination associations including disruptions in fragmented habitats, threats to migratory pollinators, and destruction of natural populations by clearing of forests and application of herbicides and insecticides. Chapters nine and ten draw a stark comparison between sustainable resource gathering from native insect colonies and the disruptive effect of introduced hives of honeybees, pejoratively labelled "almost camp followers of man." The next chapter favorably views the "economics of pollination" in terms of cultivation of native pollinators with examples from alkali and leafcutter bees. Running through the entire volume is the theme of conservation of native plant–pollinator associations by preserving habitats and biotic communities. It culminates in a final chapter advocating "pollinator gardens" and "ecological restoration" with a "call for a national policy on pollination" as an appendix.

Buchmann and Nabhan raise some fundamental issues in the conflict between commercial and conservation interests regarding reciprocal reproductive associations of native plants and pollinating animals, mostly insects. They recommend cultivation of specific crops within the geographic ranges of their native, i.e., "forgotten," pollinators and cultivation and transport of pollinators within their native ranges. Where pollinators are migratory and habitats are fragmented, vegetation corridors linking discrete plant populations are suggested. The difficulty of maintaining genetic integrity in cultivated crops grown adjacent to native taxa with which they are reproductively compatible is also discussed.

Controversial concepts needing corroborative data are introduced including competition between pollinators for floral resources, "diffuse coevolution," and pollination syndromes. The authors correctly recognize the unwarranted establishment of pollination syndromes solely on the basis of floral morphology. The inclusion of a table of pollinator syndromes (pp. 66–67) with many floral characteristics demonstrates the limited applicability of such generalizations. The difficulty of demonstrating competition and its persistence in pollination associations is also recognized. The claim that sequential anthesis on the alpine tundra reduces pollinator competition, however, seems unlikely in view of the short growing season of temperate and subarctic alpine tundras.

The narrative style of the book is informal and idiomatic. The authors have succeeded in weaving the warp of scientific expression with the woof of popular understanding without losing technical accuracy. Technical terms are italicized in the text and explained, with some omissions, in a glossary. Appendices include "a call for a national policy on pollination," a list of pollinators of major crop plants, a list of conservation and research organizations, a list of sources of supplies for pollination techniques, a summary of pollinator classes for the world's wild flowering plants, and a list of common agricultural pesticides with their toxicity to pollinators. A detailed index is included. The book is a useful addition to conservation literature. Reading *The Forgotten Pollinators* is an unforgettable experience.

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RHODORA, Vol. 99, No. 900, pp. 380–381, 1997

BOOK REVIEW

Common Families of Flowering Plants by M. Hickey and C. King. 1997. xii + 212 pp. illus. ISBN 0-521-57281-9 $64.95 (cloth), 0-521-57609-1 $22.95 (paper). Cambridge University Press, New York, NY.

This book is a follow-up to the authors' popular 1981 *100 Families of Flowering Plants.* Scaled down to concentrate on 25 common families, it is designed to acquaint botany students with the general features of select angiosperm families and relationships among them.

The book is essentially divided into two sections. The first section represents an expansion from the previous title. It offers a 30 page component on essential basic botany and is intended to cater to amateur botanists and field biologists, or to serve as a refresher course to professional botanists. Included is a short account on the evolution of the Plant Kingdom and a diagram summarizing the classification and characteristic features of dicots and monocots, followed by a comprehensive treatment of flowering plant classification and morphology. The structures of vegetative, flowering, and fruiting portions of plants are fully diagramed by well-labeled, simple line drawings. Over 80 illustrations are dedicated to stem and foliar features, and over 100 to inflorescence, perianth, androecium, gynoecium, seed, seedling, and fruit characteristics. Key vocabulary words are highlighted in bold print throughout the text.

The second section of the book concentrates on detailed descriptions of 25 common angiosperm families, chosen for their economic, ornamental, and ecological importance. This part comprises the majority of the book and covers 19 dicot and 6 monocot families, taxonomically arranged. Each family treatment includes overall distribution, general features, economic and ornamental aspects, and intrafamilial classification. Every family account is followed by a detailed description of at least one (up to four) representative species. The species accounts include information on distribution, vegetative and floral characteristics (including floral formulas), and pollination, and offer alternate species for further study. Each species is fully illustrated by original line drawings of internal or external floral details and/or full habit.

A useful feature is a section composed of four comparative tables. Each table contains three families which have superficially similar characters. The table compares features of flowers and fruits and, in some instances, leaves and inflorescence types. An example of compared families includes Ranunculaceae-Saxifragaceae-Rosaceae and Liliaceae-Amaryllidaceae-Iridaceae. A selected bibliography and comprehensive glossary also complement the treatments in the book.

The most pleasing attribute of the book is its prolific use of illustrations. Both detailed and diagrammatic illustrations are well prepared and usually dedicated to a full page. One feature that may be distressing to North American users is the authors' adoption of unfamiliar representative species. Most species in the book are common in the Old World, and merely introduced into parts of North America. *Common Families of Flowering Plants* offers fundamental knowledge of flowering plant form and terminology. It presents concise, useful taxonomic descriptions of many important plant families and would be a welcome addition to any botanist's references, as well as to those with a need to understand flower structure (illustrators, gardeners, etc.).

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RHODORA, Vol. 99, No. 900, pp. 382–384, 1997

BOOK REVIEW

The Ferns and Allied Plants of New England by A. F. Tryon and R. C. Moran. 1997. xv + 325 pp. black and white photos, SEM micrographs, line drawings, silhouettes, and maps. ISBN 0-932691-23-4 $49.95 (cloth). Massachusetts Audubon Society, Lincoln, MA.

Scientific writing is one of the many forms of literary expression. It is the art of communicating one's understanding of the nature and workings of our physical and biological surroundings. In their book. *The Ferns and Allied Plants of New England,* Tryon and Moran demonstrate a real talent for conveying their knowledge of the biology and their appreciation of the natural beauty of these distinctive members of our flora. This handsomely bound and richly illustrated treatment of our native ferns, horsetails, and lycopods is worth owning for its wonderful photographs and illustrations alone. The color photograph of the Hay-Scented Fern colony on the jacket is especially alluring; it evokes memories of the splendor of a walk through the woods on a beautiful summer day.

The Ferns and Allied Plants of New England is the first book devoted to the free-sporing vascular plants of New England in 50 years and includes treatments for 92 species in 31 genera belonging to 14 families. The authors have skillfully employed a combination of fine black and white photographs, leaf silhouettes, and line drawings to illustrate the characteristics of these plants. Each species is illustrated with a photograph. The majority of these are from the collection of Robert L. Coffin, an amateur naturalist and photographer from Amherst, Massachusetts, who photographed most of the ferns of his region between 1918 and 1942. Leaf silhouettes are included to clarify aspects of leaf shape and dissection which are difficult to describe, but are useful in distinguishing species belonging to the same genus. Line drawings prepared by Robbin Moran illustrate technical characteristics that need to be observed in order to discriminate between species of the more difficult groups, such as the woodsias and horsetails.

It is evident that much thought went into planning the format of the text. Following the Table of Contents, Foreword, Introduction and Acknowledgements, is the List of Families, Genera and Species with both Latin and common names. The list is followed by the Key to Genera and a description of the General Plan of Generic Treatments. The next two hundred and fifty pages enumerate the genera and species of ferns and allied plants. Five Appendices include material on subjects relevant to the ferns treated in the main text. These comprise Scanning Electron Micrographs of Spores, Geology and Climate, Ferns for the Garden, a Glossary and a list of References. The book concludes with an index to both Latin and common names with the currently accepted Latin names listed in bold type.

It should be remembered that it is not usually possible to prepare a monographic or floristic treatment that can be regarded as the "final word" on the subject. Additional exploration often leads to the discovery of new localities for species so distribution maps are almost never final. In this regard, the authors refer to the work of Angelo and Boufford (1996) where new information on the distribution of species and hybrids may be found. New research methods provide new data that change our understanding of the taxa that comprise a flora. New species are recognized and some of our old concepts must change if we are to portray biological diversity as accurately as is possible. And, the interpretation of how the new data are best translated into a classification system varies somewhat from one taxonomist to the next. This is affected, to some degree, by the authors' objectives in preparing the book. For example, if the primary objective is to provide an easy-to-use reference that will enable more people to explore, enjoy, and hopefully develop the desire to conserve the diversity of ferns and other free-sporing plants in our region, the authors may choose to omit some of the technical research detail in order to make the book accessible to a larger number of readers. There is a real need for books that increase the awareness and interest of the people of New England to appreciate and conserve our biodiversity. Thus, although we might be tempted to fault the authors for omitting a few taxa which many fern specialists would recognize, or for omitting descriptions of the families included in the list in the front of the book, I believe they have achieved a remarkably good balance between maintaining accessibility to the non-specialist and the inclusion of detail of interest to the expert. Not everyone who becomes interested in ferns does so because these plants have unusually high chromosome numbers or because they have life histories that provide unique research opportunities. Many people first become interested because ferns are beautiful and this aspect of fern diversity is exceptionally well portrayed in Tryon and Moran's work.

Several features of this book are especially noteworthy. The use of world distribution maps along with New England county-level maps enables the reader to appreciate the biogeographic context of each species at a glance. Some of our locally abundant species such as the Christmas Fern and the Marginal Wood Fern take on new significance. These are not just common ferns, they are taxa that are endemic to Eastern North America. Others, such as the Male Fern, a rarity in New England, have a much broader distribution and it can be seen that such plants are more widespread in other parts of the world. The inclusion of scanning electron micrographs of the spores of each species will be especially useful to amateur and professional ferners alike. The reader will have a clear image of the appearance and size of a "normal" spore. This will help users to identify abnormal spores typical of hybrids and the larger than usual spores characteristic of polyploids. There are undoubtedly a few polyploids still waiting to be discovered in the fern flora of New England. The Appendix on the Geology and Climate of New England reveals the complexity and great age of the historical events that have shaped our landforms, soils, and climate and have thus affected the distributions of ferns, both fossil and extant. This helps to explain why some ferns grow where they do.

Although the price is higher than one might expect to pay for a field guide, this book is a great value at $50.00. The book is beautifully designed, it is packed with information, and will be the main reference work on the ferns, horsetails, and lycopods of New England for a long time to come.

LITERATURE CITED

ANGELO, R. AND D. E. BOUFFORD. 1996. Atlas of the Flora of New England: Pteridophytes and Gymnosperms. Rhodora 98: 1–79.

—DAVID S. CONANT, Department of Natural Science, Lyndon State College, Lyndonville, VT 05851.

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1997

The editors of *Rhodora* are grateful to each of the following specialists for their participation in the review process.

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FLORAS AND TAXONOMIC TREATMENTS: Specimen citation should be selected critically, especially for common species of broad distribution. Keys and synonymy for systematic revisions should be prepared in the style of "A Monograph of the Genus *Malvastrum*," S. R. Hill, RHODORA 84: 159–264, 1982. Designation of a new taxon should carry a Latin diagnosis (rather than a full Latin description), which sets forth succinctly how the new taxon differs from its congeners.

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22 Divinity Avenue
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The New England Botanical Club is a nonprofit organization that promotes the study of plants of North America, especially the flora of New England and adjacent areas. The Club holds regular meetings, and has a large herbarium of New England plants and a library. It publishes a quarterly journal, RHODORA, which is now in its 99th year and contains about 400 pages per volume. Visit our web site at http://www.herbaria.harvard.edu/nebc/

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