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ATLAS OF THE FLORA OF NEW ENGLAND: MONOCOTS EXCEPT POACEAE AND CYPERACEAE

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ABSTRACT. Dot maps are provided to depict the distribution at the county level of the families of Monocotyledons except Poaceae and Cyperaceae growing outside of cultivation in the six New England states of the northeastern United States. The 325 of the 329 taxa (species, subspecies, varieties, and hybrids, but not forms) treated are mapped based on specimens in the major herbaria of Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, and Connecticut, with primary emphasis on the holdings of the New England Botanical Club Herbarium (NEBC). Brief synonymy to account for names used in recent manuals and floras for the area, habitat and chromosome information, and common names are also provided.

Key Words: flora, New England, atlas, distribution, Juncaceae, Liliaceae, Orchidaceae, Potamogetonaceae, aquatic plants, rushes, lilies, orchids

This article is the third in a series that will present the distributions of the vascular flora of New England in the form of dot distribution maps at the county level (Figure 1). The atlas is posted on the internet at http://www.herbaria.harvard.edu/~rangelo/Neatlas0/WebIntro.html where we will attempt to keep it updated.

This project encompasses all vascular plants (pteridophytes and spermatophytes) at the rank of species, subspecies, and variety growing outside of cultivation in the six New England states. Hybrids are also included, but forms and other ranks below the level of variety are not. The dots are based primarily on voucher specimens in the herbaria of New England representing reproducing populations, or plants persisting long after cultivation when it is uncertain that they are actually naturalized. This third installment includes the families of the Monocotyledoneae except the Poaceae and Cyperaceae. The number of taxa treated is 329, of which 325 are mapped. Of these 329 taxa, 56 (mostly in Liliaceae) are not native to the region. Future accounts will treat the distribution of the rest of the angiosperms.

We intend to gather this series of articles, together with additional background material, into a separate volume upon completion of all the maps. It is our hope, in the meantime, that these articles will stimulate additional field work to supplement the distributions portrayed in the maps. The New England Botanical Club herbarium, which has proven to be the most important resource for this project, is especially eager to receive specimens documenting range extensions. We also would like to be informed of such specimens in other herbaria. Similarly, because the atlas of the New England flora will be continuously updated as new information becomes available, we are eager to receive notification of published corrections of cytological information and new, documented chromosome counts for taxa in the New England flora.

MATERIALS AND METHODS

Materials and methods are as outlined in Angelo and Boufford (1996) and are not repeated here.

TAXONOMY AND FORMAT

The taxonomy and nomenclature adopted for this work essentially follow that of the Flora of North America project in progress, except that families, genera, and species are arranged alphabetically. Named and unnamed hybrid taxa are placed alphabetically at the end of the genus. Unnamed hybrids combine the names of the progenitors alphabetically by epithet. Taxa that are not native to New England are indicated by uppercase text. Unpublished names are not used, even if publication is pending.

Cited chromosome numbers are taken from indices prepared by Cave (1958a, b, 1959a, b, 1960, 1961, 1962, 1963, 1964, 1965), Goldblatt (1981, 1984, 1985, 1988), Goldblatt and Johnson (1990, 1991, 1994, 1996), Löve and Löve (1975), Moore (1973, 1974, 1977), and Ornduff (1967, 1968, 1969). Very few of the counts are based on material from New England, but instead reflect counts made from throughout the range of the taxon.

Synonymy is provided primarily with respect to names accepted in standard manuals covering New England published from 1950 onward, including Fernald (1950), Gleason (1952), Gleason and Cronquist (1991), and Seymour (1982). Synonyms have not been provided where the distribution for the synonymized name does not include New England.

The following list will aid readers in finding familiar names that have been transferred to other taxa:

ARACEAE (*Acorus*) ⇒ ACORACEAE
AMARYLLIDACEAE ⇒ LILIACEAE
Habenaria (in part) ⇒ *Coeloglossum*
Habenaria (in part) ⇒ *Platanthera*
LILIACEAE (*Smilax*) ⇒ SMILACACEAE
LILIACEAE (*Yucca*) ⇒ AGAVACEAE
Lophotocarpus ⇒ *Sagittaria*
Orchis (in part) ⇒ *Amerorchis*
Orchis (in part) ⇒ *Galearis*
Potamogeton (in part) ⇒ *Stuckenia*
Smilacina ⇒ *Maianthemum*

The following species are reported from our area in manuals, but no specimens were seen, or the substantiating specimens were misidentified:

Melanthium hybridum Walter (no specimen seen)
Smilax bona-nox Linnaeus [misidentified: = *S. rotundifolia* Linnaeus (Sorrie 1987)]

ANGIOSPERMAE (MAGNOLIOPSIDA)—ANGIOSPERMS

MONOCOTYLEDONEAE (LILIIDAE)

ACORACEAE

Acorus americanus (Rafinesque) Rafinesque—Sweet Flag (Figure 2). $2n = 24$. Marshes, shores, wet meadows. [*A. calamus* misapplied; The mapped distribution may include specimens of the introduced sterile triploid, *A. CALAMUS*, which is not generally distinguished in herbaria.]

ACORUS CALAMUS Linnaeus—Sweet Flag (Figure 2). $2n = 36$. Marshes, shores, wet meadows. From Europe. [This sterile triploid is not separated from the native species in most herbaria.]

AGAVACEAE

YUCCA FILAMENTOSA Linnaeus—Yucca (Figure 2). 2*n* = 60. Roadsides. From farther south.

ALISMATACEAE

Alisma gramineum Lejeune—(Figure 2). 2*n* = 14, 16. Muddy shores and shallow water of basic lakes and streams.

Alisma subcordatum Rafinesque—Southern Water-plantain (Figure 3). 2*n* = 14. Muddy or sandy shores, marshes, ditches, shallow water. [*A. plantago-aquatica* Linnaeus var. *parviflorum* (Pursh) Torrey]

Alisma triviale Pursh—Northern Water-plantain (Figure 3). 2*n* = 14, 28. Muddy shores, marshes, ditches, shallow water. [*A. plantago-aquatica* Linnaeus var. *americana* J. A. Schultes & Schultes]

Echinodorus tenellus (Martius) Buchenau—(Figure 3). 2*n* = ?. Sandy shores of streams and lakes. [*E. parvulus* Engelmann]

Sagittaria cuneata Sheldon—Wapato (Figure 3). 2*n* = 22. Alkaline waters of muddy shores and shallow water of rivers.

Sagittaria engelmanniana J. G. Smith—(Figure 4). 2*n* = 22. Acidic waters of shores, marshes, and bogs.

Sagittaria filiformis J. G. Smith—(Figure 4). 2*n* = ?. Deep water of streams and in rapids. [*S. subulata* (Linnaeus) Buchenau var. *gracillima* (S. Watson) J. G. Smith]

Sagittaria graminea Michaux subsp. *graminea*—(Figure 4). 2*n* = 22. Muddy or sandy shores, shallow water. [*S. eatonii* J. G. Smith]

Sagittaria latifolia Willdenow—(Figure 4). 2*n* = 22. Muddy shores, ditches, bogs. [*S. latifolia* Willdenow var. *obtusa* (Muhlenberg) Wiegand]

Sagittaria montevidensis Chamisso & Schlechtendahl subsp.

spongiosa (Engelmann) Bogin—(Figure 5). 2*n* = 22. Tidal mud flats of estuaries and salt marshes. [*S. spatulata* (J. G. Smith) Buchenau; *Lophotocarpus spongiosus* (Engelmann) J. G. Smith]

Sagittaria rigida Pursh—(Figure 5). 2*n* = 22. Alkaline or brackish shores and shallow water.

Sagittaria subulata (Linnaeus) Buchenau—(Figure 5). 2*n* = 22. Tidal mud.

Sagittaria teres S. Watson—(Figure 5). 2*n* = 22. Acid sandy pond shores.

ARACEAE

Arisaema dracontium (Linnaeus) Schott—Green Dragon (Figure 6). 2*n* = 28, 56. Rich or alluvial soil.

Arisaema triphyllum (Linnaeus) Schott—Jack-in-the-pulpit (Figure 6). 2*n* = 28, 36, 56. Rich damp-to-wet woods, boggy places. [*A. triphyllum* var. *pusillum* Peck; *A. triphyllum* var. *stewardsonii* (Britton) Stevens ex Wiegand & Eames; *A. atrorubens* (Aiton) Blume; *A. pusillum* (Peck) Nash; *A. stewardsonii* Britton]

—*Arisaema* hybrids—

Arisaema dracontium (Linnaeus) Schott × *Arisaema triphyllum* (Linnaeus) Schott—(Figure 6).

Calla palustris Linnaeus—Wild Calla (Figure 6). 2*n* = 36, 60, 72. Bogs, marshes, swampy woods, pond margins, shallow water.

Orontium aquaticum Linnaeus—Golden Club (Figure 7). 2*n* = 26. Shallow water of ponds, sandy, muddy, or sphagnous shores.

Peltandra virginica (Linnaeus) Schott—Arrow Arum (Figure 7). 2*n* = 112. Shallow water or mud at margins of ponds and streams, swamps, bogs, damp meadows.

Symplocarpus foetidus (Linnaeus) Nuttall—Skunk Cabbage (Figure 7). $2n = 26, 60$. Swamps, damp thickets and woods, wet meadows, shores.

BUTOMACEAE

BUTOMUS UMBELLATUS Linnaeus—Flowering Rush (Figure 7). $2n = 16, 20, 24, 26, 30, 39$. Muddy shores and marshes. From Eurasia.

COMMELINACEAE

COMMELINA COMMUNIS Linnaeus—Asiatic Dayflower (Figure 8). $2n = 16, 22, 28, 32, 36–90$. Waste places, roadsides, disturbed moist soil in shade. From eastern Asia. [*C. COMMUNIS* var. *LUDENS* (Miquel) C. B. Clarke]

COMMELINA DIFFUSA Burman f.—Creeping Dayflower (Figure 8). $2n = 18, 28–60$. Waste places. From the Old World.

TRADESCANTIA BRACTEATA Small—Sticky Spiderwort (Figure 8). $2n = 12, 18, 24$. Roadsides. From farther west.

Tradescantia ohiensis Rafinesque—Smooth Spiderwort (Figure 8). $2n = 12, 24$. Roadsides, waste places, thickets.

Tradescantia virginiana Linnaeus—Widow's Tears (Figure 9). $2n = 12, 18, 24, 24 + 6B$. Roadsides, waste places, thickets.

—*Tradescantia* hybrids—

Tradescantia ohiensis Rafinesque × *TRADESCANTIA SUBASPERA* Ker Gawler—(Figure 9).

Tradescantia ohiensis Rafinesque × *Tradescantia virginiana* Linnaeus—(Figure 9).

DIOSCOREACEAE

DIOSCOREA BATATAS Decaisne—Cinnamon-vine (Figure 9). $2n =$ ca. 140–144. Thickets, waste places. From China.

Dioscorea villosa Linnaeus—Wild Yam (Figure 10). $2n = 60$. Damp thickets, wet woods, roadsides.

ERIOCAULACEAE

Eriocaulon aquaticum (Hill) Druce—White-buttons (Figure 10). $2n$ = 32, 64. Acid shores, shallow water, and bogs. [*E. septangulare* Withering]

Eriocaulon parkeri B. L. Robinson—(Figure 10). $2n$ = 48. Tidal mud and estuaries.

HAEMODORACEAE

Lachnanthes caroliniana (Lamarck) Dandy—Redroot (Figure 10). $2n$ = 24, 48. Sandy or sphagnous pond shores. [*L. tinctoria* (J. F. Gmelin) Elliott]

HYDROCHARITACEAE

EGERIA DENSA Planchon—(Figure 11). $2n$ = 46, 48. Ponds. From Brazil and Argentina. [*ELODEA DENSA* (Planchon) Caspary; *ANACHARIS DENSA* (Planchon) Marie-Victorin]

Elodea canadensis Michaux—(Figure 11). $2n$ = 24, 48. Ponds, lakes, and quiet streams, mostly basic. [*Anacharis canadensis* (Michaux) Richardson]

Elodea nuttallii (Planchon) St. John—(Figure 11). $2n$ = 48. Ponds, lakes, and streams, acidic to moderately basic. [*Anacharis nuttallii* Planchon]

HYDRILLA VERTICILLATA (Linnaeus f.) Royle—(Figure 11). $2n$ = 16, 24, 32. Ponds, lakes, and streams. From the Old World.

Vallisneria americana Michaux—Water-celery (Figure 12). $2n$ = 20. Ponds and quiet streams.

IRIDACEAE

BELAMCANDA CHINENSIS (Linnaeus) de Candolle—(Figure 12). $2n$ = 16, 27, 28, 30, 32, 128. Fields, roadsides, thickets, open woods. From eastern Asia.

CROCUS VERNUS (Linnaeus) J. Hill subsp. *VERNUS*—Dutch

Crocus (Figure 12). 2*n* = 8, 10, 12, 16, 16 + 2B, 18, 19, 20, 22, 23, 32. Grasslands. From Europe.

IRIS CRISTATA Aiton—Dwarf Crested Iris (Figure 12). 2*n* = 24, 32. Rich woods, in acid soils. From farther south and west.

IRIS GERMANICA Linnaeus—Fleur-de-lis (Figure 13). 2*n* = 28, 36–48. Roadsides, waste places. From Europe.

IRIS KAEMPFERI Siebold ex Lemaire—Japanese Iris (Figure 13). 2*n* = 24. Habitat? From Japan.

Iris prismatica Pursh—Slender Blue Flag (Figure 13). 2*n* = 42. Marshes, meadows, swamps, sands, shores, seacoasts.

IRIS PSEUDACORUS Linnaeus—Yellow Iris (Figure 13). 2*n* = 24–34. Swamps, wet meadows, marshes, brooksides, waste places. From Europe.

IRIS PUMILA Linnaeus subsp. *PUMILA*—(Figure 14). 2*n* = 20, 24, 30, 31, 32. Dry rocky knolls. From Eurasia.

Iris setosa Pallas—Beachhead Iris (Figure 14). 2*n* = 34–38. Rocky slopes, upper borders of beaches, moist fields, always near salt water. [*Iris hookeri* Penny ex G. Don]

IRIS SIBIRICA Linnaeus—Siberian Iris (Figure 14). 2*n* = 28. Wet meadows, waste lots. From Eurasia.

IRIS TECTORUM Maximowicz—Wall Iris (Figure 14). 2*n* = 28, 36. Habitat? From China.

Iris versicolor Linnaeus—Blue Flag (Figure 15). 2*n* = 108. Swamps, marshes, meadows, shores, ditches.

—*Iris* hybrids—

Iris prismatica Pursh × *Iris versicolor* Linnaeus—(Figure 15).

Sisyrinchium albidum Rafinesque—(Figure 15). 2*n* = 32, 64. Dry, sandy, open soil and thin woodlands.

Sisyrinchium angustifolium Miller—Stout Blue-eyed Grass (Figure 15). 2*n* = 48. Meadows, fields, low woods, thickets, damp shores. [*S. bermudiana* misapplied; *S. graminoides* Bicknell]

Sisyrinchium atlanticum Bicknell—Eastern Blue-eyed Grass (Figure 16). 2*n* = 16, 32, 96. Meadows, marshes, low woods.

Sisyrinchium fuscatum Bicknell—(Figure 16). 2*n* = 32. Grasslands, mostly sandy soils. [*S. arenicola* Bicknell]

Sisyrinchium montanum Greene var. *crebrum* Fernald—Common Blue-eyed Grass (Figure 16). 2*n* = 32, 96. Fields, meadows, open woods.

Sisyrinchium mucronatum Michaux—Slender Blue-eyed Grass (Figure 16). 2*n* = 30, 32. Meadows, fields, sandy places, open woods.

JUNCACEAE

Juncus acuminatus Michaux—(Figure 17). 2*n* = 40. Tidal mud flats, salt marsh borders, ditches, shores, meadows.

Juncus alpinoarticulatus Chaix—Alpine Rush (Figure 17). 2*n* = 40. Shores, meadows, usually basic. [*J. alpinus* Villars; *J. alpinus* Villars var. *fuscescens* Fernald; *J. alpinus* Villars var. *rariflorus* Hartmann]

Juncus anthelatus (Wiegand) R. E. Brooks—(Figure 17). 2*n* = 80. Moist sandy or clay soils. [*J. tenuis* Willdenow var. *anthelatus* Wiegand]

Juncus arcticus Willdenow var. *balticus* (Willdenow) Trautvetter—Wire Rush (Figure 17). 2*n* = 40, 80. Sandy shores, sphagnous meadows. [*J. balticus* Willdenow var. *littoralis* Engelmann]

Juncus articulatus Linnaeus—(Figure 18). 2*n* = 40, 80. Shores, springy spots, ditches. [*J. articulatus* var. *obtusatus* Engelmann]

Juncus brachycarpus Engelmann—(Figure 18). 2*n* = 44. Salt marshes, ocean beaches.

Juncus brachycephalus (Engelmann) Buchenau—(Figure 18). 2*n* = 80. Basic shores, marshes, meadows, swamps.

Juncus brevicaudatus (Engelmann) Fernald—(Figure 18). 2*n* = 80. Shores, bogs, marshes.

Juncus bufonius Linnaeus—Toad Rush (Figure 19). 2*n* = 27–37, 40, ca. 54, 58–81, 106, 108–115, 120. Shores, salt marshes, roadsides, moist to wet borrow pits. [*J. bufonius* var. *halophilus* Buchenau & Fernald]

Juncus canadensis J. Gay—(Figure 19). $2n = 80$. Shores, swamps, marshes, meadows. [*J. canadensis* var. *sparsiflorus* Fernald]

JUNCUS COMPRESSUS Jacques—(Figure 19). $2n = 40, 44$. Disturbed wet ground, especially ditches, roadsides, frequently saline or basic soils. From Europe. [*J. bulbosus* Linnaeus]

Juncus debilis A. Gray—(Figure 19). $2n = ?$. Ditches, pools, shores.

Juncus dichotomus Elliott—(Figure 20). $2n = 80$. Sandy or sphagnous shores, salt marsh borders. [*J. platyphyllus* (Wiegand) Fernald; *J. tenuis* Willdenow var. *dichotomus* (Elliott) A. Wood]

JUNCUS DIFFUSISSIMUS Buckley. $2n = ?$. Disturbed open barrens. From farther south. [Voucher discovered while mss. in press. South Windsor, Hartford County, CT (CONN).]

Juncus dudleyi Wiegand—(Figure 20). $2n = 42, 80$, ca. 84. Shores, boggy meadows, in basic soils. [*J. tenuis* Willdenow var. *dudleyi* (Wiegand) F. J. Hermann]

Juncus effusus Linnaeus—Tufted Rush (Figure 20). $2n = 5, 40, 42$. Marshy ground, low spots. [*J. effusus* var. *compactus* Lejeune & Courtois; *J. effusus* var. *conglomeratus* (Linnaeus) Engelmann; *J. effusus* var. *costulatus* Fernald; *J. effusus* var. *decipiens* Buchenau; *J. effusus* var. *pylaei* (Laharpe) Fernald & Wiegand; *J. effusus* var. *solutus* Fernald & Wiegand; *J. conglomeratus* Linnaeus; *J. pylaei* Laharpe]

Juncus filiformis Linnaeus—(Figure 20). $2n = 40, 70, 80, 84$. Shores, swamps, bogs, alpine meadows.

Juncus gerardii Loiseleur-Deslongchamps—Black Grass (Figure 21). $2n = 80, 84$. Salt marshes. [*J. gerardii* var. *pedicellatus* Fernald]

Juncus greenei Oakes & Tuckerman—(Figure 21). $2n = 80$. Dry open places, usually well-drained, sandy soil. In pine lands near lake shores, dunes.

JUNCUS INFLEXUS Linnaeus—(Figure 21). $2n$ = 38, 40. Meadows, damp roadsides. From Eurasia and northern Africa.

Juncus marginatus Rostkovius—Grass Rush (Figure 21). $2n$ = 38, 40. Sandy pond margins, wet meadows. [*J. biflorus* Elliott]

Juncus militaris Bigelow—Bayonet Rush (Figure 22). $2n$ = ?. Shallow water of ponds and streams with sandy, gravelly, or sphagnous margins.

Juncus nodosus Linnaeus var. *nodosus*—(Figure 22). $2n$ = 40. Shores, marshes, meadows, swamps, especially basic soils.

Juncus pelocarpus E. Meyer—(Figure 22). $2n$ = 40. Sandy shores, marshes, ditches.

Juncus secundus Beauvois ex Poiret—(Figure 22). $2n$ = ca. 80. Ledges, dry open sterile soils.

Juncus stygius Linnaeus var. *americanus* Buchenau—(Figure 23). $2n$ = ?. Bogs, bog pools.

Juncus subcaudatus (Engelmann) Coville & S. F. Blake—(Figure 23). $2n$ = ?. Swamps, bogs, shaded spring-heads, mossy woods.

JUNCUS SUBNODULOSUS Schrank—(Figure 23). $2n$ = 40. Salt marsh borders. From Europe. [*J. PERVETUS* Fernald]

Juncus subtilis E. Meyer—Creeping Rush (Figure 23). $2n$ = 40. Muddy shores.

Juncus tenuis Willdenow—Path Rush (Figure 24). $2n$ = 40, 80, 84. Roadsides, paths. [*J. tenuis* var. *williamsii* Fernald]

JUNCUS TORREYI Coville—(Figure 24). $2n$ = 40. Shores, ditches, roadsides. From farther west and south.

Juncus trifidus Linnaeus—Highland Rush (Figure 24). $2n$ = 20, 30, 40. Exposed, rocky, or sterile summits. [*J. trifidus* var. *monanthos* (Jacquin) Bluff & Fingerhuth]

Juncus vaseyi Engelmann—(Figure 24). $2n$ = 42, ca. 80. Swamps, shores, thickets.

—*Juncus* hybrids—

Juncus articulatus Linnaeus × *Juncus brevicaudatus* (Engelmann) Fernald—(Figure 25).

Juncus brevicaudatus (Engelmann) Fernald × *Juncus nodosus* Linnaeus var. *nodosus*—(Figure 25).

Juncus × *oronensis* Fernald—(Figure 25). Alder swamps, thickets. [*J. tenuis* Willdenow × *J. vaseyi* Engelmann ?]

Juncus secundus Beauvois ex Poiret × *Juncus tenuis* Willdenow—(Figure 25).

Juncus tenuis Willdenow × *Juncus vaseyi* Engelmann—(Figure 26).

Luzula acuminata Rafinesque var. *acuminata*—(Figure 26). $2n = 18$. Thickets, clearings, woods.

Luzula acuminata Rafinesque var. *carolinae* (S. Watson) Fernald—$2n = 18$. Limy wooded slopes. [Reported (Flora of North America, in press); no voucher seen.]

Luzula bulbosa (Wood) Rydberg—(Figure 26). $2n = 12$. Dry, sandy, open woods and fields.

LUZULA CAMPESTRIS (Linnaeus) de Candolle—(Figure 26). $2n = 12, 12 + 1B, 13, 14, 16$. Lawns. From Europe.

Luzula confusa Lindeberg—Northern Woodrush (Figure 27). $2n = 36, 44–48$. Alpine areas.

Luzula echinata (Small) Hermann—(Figure 27). $2n = 12$. Woods, thickets, clearings. [*L. campestris* (Linnaeus) de Candolle var. *echinata* (Small) Fernald & Wiegand]

LUZULA LUZULOIDES (Lamarck) Dandy & Wilmott subsp. *LUZULOIDES*—Forest Woodrush (Figure 27). $2n = 12$. Rocky woods, roadsides, lawns. From Europe.

Luzula multiflora (Ehrhart) Lejeune subsp. *multiflora*—Common Woodrush (Figure 27). $2n = 12, 24, 28, 36$. Open woods, dry fields, meadows. [*L. multiflora* var. *acadiensis* Fernald; *L. campestris* (Linnaeus) de Candolle var. *multiflora* (Ehrhart) Čelakovský]

Luzula multiflora (Ehrhart) Lejeune subsp. *frigida* (Buchenau)

Kreczetowicz—(Figure 28). 2*n* = 36. Sphagnous barrens, clearings, fields. [*L. multiflora* var. *fusconigra* Čelakovský]

LUZULA PALLIDULA Kirschner—(Figure 28). 2*n* = 12–18. Meadows, open woods, clearings, rocky places. From Eurasia. [*L. pallescens* (Wahlenberg) Besser]

Luzula parviflora (Ehrhart) Desvaux var. *melanocarpa* (Michaux) Buchenau—(Figure 28). 2*n* = 24. Mossy wooded banks, dry woods, damp thickets, often rocky places.

Luzula spicata (Linnaeus) de Candolle—Alpine Woodrush (Figure 28). 2*n* = 12, 14, 18, 24, 36. Alpine areas.

JUNCAGINACEAE

Triglochin gaspense Lieth & D. Löve—(Figure 29). 2*n* = 96. Salt marshes.

Triglochin maritima Linnaeus—(Figure 29). 2*n* = 12, 24, 30, 36, 48, 96, 120. Salt, brackish, and freshwater marshes.

Triglochin palustre Linnaeus—(Figure 29). 2*n* = 24, 28, 36. Salt marshes and river shores.

LEMNACEAE

Lemna minor Linnaeus—(Figure 29). 2*n* = 20, 30, 40, 42, 50, 63, 80, 126. Floating on quiet water of ponds and streams, muddy shores.

Lemna perpusilla Torrey—(Figure 30). 2*n* = 20, 40, 42, 50, 60, 80. Floating on quiet water of ponds and streams.

Lemna trisulca Linnaeus—(Figure 30). 2*n* = 20, 40, 42, 44, 56–60, 63, 80. Surface of quiet often basic water of ponds and streams.

Lemna turionifera Landolt—(Figure 30). 2*n* = 40, 42, 50, 80. Quiet waters.

Lemna valdiviana Philippi—(Figure 30). 2*n* = 36, 40, 42. Quiet waters or swift currents of streams.

Spirodela polyrrhiza (Linnaeus) Schleiden—Water Flaxseed (Figure 31). $2n = 30, 32, 38, 40, 50, 80$. Surface of quiet water of lakes, ponds, ditches, and streams; muddy shores.

SPIRODELA PUNCTATA (G. F. W. Meyer) C. H. Thompson—$2n = 40, 43–44, 46, 50$. Quiet waters. From subtropical regions. [*S. OLIGORRHIZA* (Kurtz) Hegelmaier; reported from Massachusetts (Flora of North America, in press); no voucher seen]

Wolffia borealis (Engelmann ex Hegelmaier) Landolt—(Figure 31). $2n = 20, 22, 30, 40$. Floating on quiet waters of ditches, ponds, lakes, and streams. [*W. punctata* misapplied]

WOLFFIA BRASILIENSIS Weddell—(Figure 31). $2n = 20, 40, 42, 50, 60, 80$. Floating on quiet waters. From farther south. [*W. PAPULIFERA* C. H. Thompson]

Wolffia columbiana Karsten—(Figure 31). $2n = 30, 40, 42, 50, 70$. Quiet mostly basic waters of lakes, ponds, ditches, and streams.

Wolffiella gladiata (Hegelmaier) Hegelmaier—(Figure 32). $2n = 40, 42$. Quiet acidic waters. [*W. floridana* (J. D. Smith) C. H. Thompson]

LILIACEAE

Note: The Liliaceae are here treated mostly in their traditional sense with the understanding that numerous smaller families will be recognized within the very near future.

Aletris farinosa Linnaeus—Unicorn-root (Figure 32). $2n = 26$. Moist, open, sandy soil and barrens.

Allium canadense Linnaeus var. *canadense*—Wild Garlic (Figure 32). $2n = 14, 21, 28, 82$. Low woods, alluvial thickets, meadows.

ALLIUM CEPA Linnaeus—Onion (Figure 32). $2n = 14, 16, 28, 32, 64$. Waste ground. From southwest Asia.

ALLIUM OLERACEUM Linnaeus—Wild Onion (Figure 33). $2n = 24, 32, 40, 48$. Wood borders, thickets, roadside banks. From Europe.

ALLIUM SATIVUM Linnaeus—Garlic (Figure 33). 2*n* = 12, 16. Roadsides, pastures, fields. From western Asia.

Allium schoenoprasum Linnaeus—Chives (Figure 33). 2*n* = 16, 16 + (1–18)B, 24, 32. Gravelly and rocky shores. [*A. schoenoprasum* var. *sibiricum* (Linnaeus) Hartman]

Allium tricoccum Aiton var. *tricoccum*—Wild Leek (Figure 33). 2*n* = 16. Rich basic woods and bottoms.

Allium tricoccum Aiton var. *burdickii* Hanes—(Figure 34). 2*n* = 16. Dry soil in upland woods.

ALLIUM VINEALE Linnaeus—Field Garlic (Figure 34). 2*n* = 16, 32, 32 + (0–2)s, 40. Dry grasslands, fallow fields, lawns, waste places. From Europe.

ASPARAGUS OFFICINALIS Linnaeus—Asparagus (Figure 34). 2*n* = 20, 40. Roadsides, near buildings, fields, fence rows. From Europe.

Chamaelirium luteum (Linnaeus) Gray—Blazing-star (Figure 34). 2*n* = ?. Meadows, thickets, rich woods.

Clintonia borealis (Aiton) Rafinesque—Yellow Clintonia (Figure 35). 2*n* = 28, 28 + 2B, 32. Woods, usually moist, thickets.

COLCHICUM AUTUMNALE Linnaeus—Autumn Crocus (Figure 35). 2*n* = 36, 38, 42. Meadows, fields. From Europe.

CONVALLARIA MAJALIS Linnaeus var. *MAJALIS*—European Lily-of-the-Valley (Figure 35). 2*n* = 36, 38. Roadsides, old house sites, thickets, open woods. From Europe.

Erythronium americanum Ker—Trout Lily (Figure 35). 2*n* = 48. Rich moist woods and thickets.

GALANTHUS NIVALIS Linnaeus subsp. *NIVALIS*—Snowdrop (Figure 36). 2*n* = 18, 24, 24 + (1–10)B, 26. Abandoned gardens. From Europe.

HEMEROCALLIS FULVA (Linnaeus) Linnaeus—Orange Daylily (Figure 36). 2*n* = 22, 33, 36. Roadsides, waste places. From Asia.

HEMEROCALLIS LILIOASPHODELUS Linnaeus—Yellow Daylily (Figure 36). 2*n* = 22. Roadsides, waste places. From Asia. [*H. FLAVA* (Linnaeus) Linnaeus]

HOSTA LANCIFOLIA Trattinnick—(Figure 36). $2n = 60$. Thickets, roadsides, waste places. From eastern Asia. [*H. JAPONICA* Voss]

HOSTA VENTRICOSA (Salisbury) Stearn—Blue Plantain-lily (Figure 37). $2n = 60$, 120. Rich woods along streams, moist banks. From eastern Asia.

Hypoxis hirsuta (Linnaeus) Coville—Common Stargrass (Figure 37). $2n = 28$. Open woods, fields.

LEUCOJUM AESTIVUM Linnaeus—Summer Snowflake (Figure 37). $2n = 22$, 24. Meadows, low woods. From Europe.

Lilium canadense Linnaeus—Canada Lily (Figure 37). $2n = 24$. Meadows, low woods, thickets.

LILIUM LANCIFOLIUM Thunberg—Tiger Lily (Figure 38). $2n = 24$, 36. Old house sites, roadsides, dry thickets. From eastern Asia. [*L. TIGRINUM* Ker]

Lilium philadelphicum Linnaeus—Wood Lily (Figure 38). $2n = 24$. Dry open woods, thickets, clearings.

Lilium superbum Linnaeus—Turk's-cap Lily (Figure 38). $2n = 24$. Meadows, damp thickets, swampy woods.

Maianthemum canadense Desfontaines—Canada Mayflower (Figure 38). $2n = 36$. Woods, clearings. [*M. canadense* var. *interius* Fernald]

Maianthemum racemosum (Linnaeus) Link subsp. *racemosum*—False Solomon's-seal (Figure 39). $2n = 36$, 72, 144. Woods, clearings. [*Smilacina racemosa* (Linnaeus) Desfontaines; *Smilacina racemosa* (Linnaeus) Desfontaines var. *cylindrata* Fernald]

Maianthemum stellatum (Linnaeus) Link—(Figure 39). $2n = 36$, 54. Sandy soil of shores, hillsides, fields, thickets. [*Smilacina stellata* (Linnaeus) Desfontaines; *Smilacina stellata* (Linnaeus) Desfontaines var. *crassa* Victorin]

Maianthemum trifolium (Linnaeus) Sloboda—(Figure 39). $2n = 36$. Sphagnum bogs, sphagnous shores and woods. [*Smilacina trifolia* (Linnaeus) Desfontaines]

Medeola virginiana Linnaeus—Indian Cucumber Root (Figure 39). $2n = 14$. Rich woods.

MUSCARI BOTRYOIDES (Linnaeus) Miller—Grape-hyacinth (Figure 40). $2n = 18$, 36, ca. 40, 48. Pastures, fields, roadsides, waste places. From Europe.

MUSCARI NEGLECTUM Gussone ex Tenore—Blue-bottle (Figure 40). $2n = 18$–72. Fields, roadsides, lawns, waste places. From Europe. [*M. ATLANTICUM* Boissier & Reuter; *M. RACEMOSUM* Lamarck & de Candolle]

NARCISSUS POETICUS Linnaeus—Poet's Narcissus (Figure 40). $2n = 14$, 21, 28. Fields, moist meadows. From Europe.

NARCISSUS PSEUDONARCISSUS Linnaeus—Daffodil (Figure 40). $2n = 14$, $14 + (1–2)$B, 15, 21, 26–30, 35, 43. Fields, open groves, moist meadows. From Europe.

ORNITHOGALUM NUTANS Linnaeus—(Figure 41). $2n = 14$, 15, 40, 41, 45. Low meadows, fields. From western Asia.

ORNITHOGALUM UMBELLATUM Linnaeus—Star-of-Bethlehem (Figure 41). $2n = 18$–108. Old house sites, roadsides, thickets, fields, meadows. From Europe.

Polygonatum biflorum (Walter) Elliott var. *biflorum*—Great Solomon's-seal (Figure 41). $2n = 20$, 40. Rocky woods.

Polygonatum biflorum (Walter) Elliott var. *commutatum* (J. A. & J. H. Schultes) Morong—Giant Solomon's-seal (Figure 41). $2n = 40$. Rich woods, alluvial thickets, riverbanks, hedgerows. [*P. canaliculatum* misapplied; *P. commutatum* (J. A. & J. H. Schultes) A. Dietrich]

POLYGONATUM LATIFOLIUM (Jacquin) Desfontaines—(Figure 42). $2n = 18$, 20. Roadside thickets. From Europe.

Polygonatum pubescens (Willdenow) Pursh—Small Solomon's-seal (Figure 42). $2n = 20$. Dry-to-rich woods.

SCILLA SIBERICA Haworth ex Andrews—(Figure 42). $2n = 12$, $12 + B$, $12 + 4B$, 18, 24, 30. Roadsides, pastures. From Eurasia.

Streptopus amplexifolius (Linnaeus) de Candolle—Twisted Stalk

(Figure 42). 2*n* = 16, 32. Rich damp woods and thickets. [*S. amplexifolius* var. *americanus* Schultes]

Streptopus lanceolatus (Aiton) Reveal—Rose Mandarin (Figure 43). 2*n* = 16, 48. Rich, damp, cool woods and thickets. [*S. roseus* Michaux var. *longipes* (Fernald) Fassett; *S. roseus* Michaux var. *perspectus* Fassett]

—*Streptopus* hybrids—

Streptopus × *oreopolus* Fernald—(Figure 43). 2*n* = 24. Subalpine woods and meadows. [*S. amplexifolius* (Linnaeus) de Candolle × *S. lanceolatus* (Aiton) Reveal; *S. amplexifolius* (Linnaeus) de Candolle var. *oreopolus* (Fernald) Fassett]

Tofieldia glutinosa (Michaux) Persoon—(Figure 43). 2*n* = 30. Marshes (basic), bogs, shores.

TRICYRTIS HIRTA (Thunberg) Hooker—Toad Lily (Figure 43). 2*n* = 24, 26, 37. Open woods. From eastern Asia.

Trillium cernuum Linnaeus—Nodding Trillium (Figure 44). 2*n* = 10. Rich damp woods, most often in acid soil. [*T. cernuum* var. *macranthum* A. J. Eames & Wiegand]

Trillium erectum Linnaeus—Purple Trillium (Figure 44). 2*n* = 10. Rich woods. [*T. erectum* var. *blandum* Jennison]

Trillium grandiflorum (Michaux) Salisbury—Snowy Trillium (Figure 44). 2*n* = 10. Rich usually basic woods and thickets.

Trillium undulatum Willdenow—Painted Trillium (Figure 44). 2*n* = 10. Rich usually wet woods in acidic soils.

TULIPA GESNERIA Linnaeus—Garden Tulip (Figure 45). 2*n* = 24, 25, 26, 36, 48. Waste areas. From Eurasia.

TULIPA SYLVESTRIS Linnaeus—(Figure 45). 2*n* = 24, 48. Meadows. From Europe.

Uvularia grandiflora J. E. Smith—Big Merry-bells (Figure 45). 2*n* = 14. Rich moist woods and thickets, chiefly basic.

Uvularia perfoliata Linnaeus—Perfoliate Bellwort (Figure 45). 2*n* = 14. Rich usually dry woods and thickets, preferring acid soils.

Uvularia sessilifolia Linnaeus—Wild-oats (Figure 46). $2n = 14$. Woods, thickets, clearings.

Veratrum viride Aiton—White Hellebore (Figure 46). $2n = 32$. Swampy woods, wet meadows.

Zigadenus elegans Pursh var. *glaucus* (Nuttall) Preece—White Camass (Figure 46). $2n = 32$. Basic gravel, cliffs, shores, bogs. [*Z. glaucus* Nuttall]

NAJADACEAE

Najas flexilis (Willdenow)—Northern Water-nymph (Figure 46). $2n = 24$. Quiet shallow water of ponds and streams, usually rooting in mud.

Najas gracillima (A. Braun ex Engelmann) Magnus—(Figure 47). $2n = 12$. Muddy, sandy, or sphagnous ponds and shores.

Najas guadalupensis (Sprengel) Magnus subsp. *guadalupensis*—Southern Water-nymph (Figure 47). $2n = 12, 36, 48, 54, 60$. Ponds and streams.

Najas guadalupensis (Sprengel) Magnus subsp. *olivacea* (Rosendahl & Butters) R. R. Haynes & Hellquist—(Figure 47). $2n$ = ?. Habitat? [*N. olivacea* Rosendahl & Butters]

NAJAS MINOR Allioni—(Figure 47). $2n = 12, 24, 46, 56$. Quiet basic water of lakes and streams. From the Old World.

ORCHIDACEAE

Amerorchis rotundifolia (Banks) Hultén—Small Round-leaved Orchis (Figure 48). $2n = 42$. Bogs, swamps, boggy woods, in basic soil. [*Orchis rotundifolia* Banks]

Aplectrum hyemale (Muhlenberg ex Willdenow) Nuttall—Putty-root (Figure 48). $2n$ = ?. Rich rocky woods.

Arethusa bulbosa Linnaeus—Arethusa (Figure 48). $2n = 40$. Sphagnous bogs, meadows, and swamps.

Calopogon tuberosus (Linnaeus) Britton, Sterns & Poggenberg—Grass-pink (Figure 48). $2n = 26, 42$. Sphagnous bogs, swamps, and meadows. [*C. pulchellus* (Salisbury) R. Brown]

Calypso bulbosa (Linnaeus) Oakes var. *americana* (R. Brown ex Aiton f.) Luer—Calypso (Figure 49). 2*n* = 28. *Thuja* swamps.

Coeloglossum viride (Linnaeus) Hartman var. *virescens* (Muhlenberg ex Willdenow) Luer—Bracted Orchis (Figure 49). 2*n* = 40, 42. Rich moist woods, thickets, meadows. [*Habenaria viridis* (Linnaeus) R. Brown var. *bracteata* (Muhlenberg) A. Gray]

Corallorhiza maculata (Rafinesque) Rafinesque—Spotted Coral-root (Figure 49). 2*n* = 42, 84. Dry-to-moist woods.

Corallorhiza odontorhiza (Willdenow) Poiret—Autumn Coral-root (Figure 49). 2*n* = ?. Rich dry woods, in basic soil.

Corallorhiza trifida Chatelain—Early Coral-root (Figure 50). 2*n* = 38, 40, 42. Rich wet woods, swamps with *Thuja*. [*C. trifida* var. *verna* (Nuttall) Fernald]

Cypripedium acaule Aiton—Pink Lady's-slipper (Figure 50). 2*n* = 20. Dry woods, acid soils.

Cypripedium arietinum R. Brown—Ram's-head Lady's-slipper (Figure 50). 2*n* = 20. Rich damp woods, usually on hillsides, usually acid soils in coniferous woods.

Cypripedium parviflorum Salisbury var. *parviflorum*—Small Yellow Lady's-slipper (Figure 50). 2*n* = 20. Rich usually swampy basic woods, bogs (chiefly basic), shores. [*C. calceolus* Linnaeus var. *parviflorum* (Salisbury) Fernald]

Cypripedium parviflorum Salisbury var. *makasin* (Farwell) Sheviak. 2*n* = ?. *Thuja* bogs and fens. [There are no distribution data for this relatively newly described taxon since it is not yet distinguished in New England herbaria. The author of this combination reports that "Virtually everything reported from NE as var. *parviflorum* is in fact var. *makasin*" (pers. comm.).]

Cypripedium parviflorum Salisbury var. *pubescens* (Willdenow) Knight—Large Yellow Lady's-slipper (Figure 51). 2*n* = 20. Rich woodlands. [*C. calceolus* Linnaeus var. *pubescens* (Willdenow) Correll]

Cypripedium reginae Walter—Showy Lady's-slipper (Figure 51). 2*n* = 20. Bogs, swamps, swampy woods, in basic soils.

EPIPACTIS HELLEBORINE (Linnaeus) Crantz—Helleborine (Figure 51). $2n = 36–44$. Woods, thickets, roadsides. From Europe.

Galearis spectabilis (Linnaeus) Rafinesque—Showy Orchis (Figure 51). $2n = 42$. Rich woods, mostly in basic soils. [*Orchis spectabilis* Linnaeus]

Goodyera oblongifolia Rafinesque—Giant Rattlesnake-plantain (Figure 52). $2n = 22, 30$. Dry coniferous and mixed woods.

Goodyera pubescens (Willdenow) R. Brown—Downy Rattlesnake-plantain (Figure 52). $2n = 26$. Dry-to-moist woods.

Goodyera repens (Linnaeus) R. Brown var. *ophioides* Fernald—Dwarf Rattlesnake-plantain (Figure 52). $2n = 30, 40$. Damp mossy woods, especially under conifers.

—*Goodyera* hybrids—

Goodyera × *tesselata* Loddiges—(Figure 52). $2n = 59–61$. Rich woods, often pine. [*G. oblongifolia* Rafinesque × *G. repens* (Linnaeus) R. Brown var. *ophioides* Fernald]

Isotria medeoloides (Pursh) Rafinesque—Small Whorled Pogonia (Figure 53). $2n = 18$. Open second growth, rich woods, often near *Fagus*.

Isotria verticillata (Muhlenberg ex Willdenow) Rafinesque—Large Whorled Pogonia (Figure 53). $2n = 18$. Acidic woods, usually damp, often with *Medeola*.

Liparis liliifolia (Linnaeus) Richard ex Lindley—Large Twayblade (Figure 53). $2n = ?$. Rich moist woods.

Liparis loeselii (Linnaeus) Richard—Loesel's Twayblade (Figure 53). $2n = 26, 32$. Swamps, bogs, damp thickets, sphagnous meadows, ditches.

Listera auriculata Wiegand—Auricled Twayblade (Figure 54). $2n = ?$. Moist woods and thickets.

Listera australis Lindley—Southern Twayblade (Figure 54). $2n = ?$. Sphagnous thickets and bogs.

Listera convallarioides (Swartz) Elliott—Broad-lipped Twayblade (Figure 54). $2n = 36$. Wet or swampy woods, often with *Thuja,* shores.

Listera cordata (Linnaeus) R. Brown—Heartleaf Twayblade (Figure 54). $2n = 34$, 34 + (1–9)B, 36–42, 44. Mossy knolls in wet woods.

Malaxis bayardii Fernald—(Figure 55). $2n = ?$. Dry sandy woods and clearings.

Malaxis monophyllos (Linnaeus) Swartz var. *brachypoda* (A. Gray) F. Morris & Eames—(Figure 55). $2n = 28$, 30. *Thuja* swamps and thickets. [*M. brachypoda* (A. Gray) Fernald]

Malaxis unifolia Michaux—Green Adder's-mouth (Figure 55). $2n = ?$. Woods, borders of swamps or bogs.

Platanthera blephariglottis (Willdenow) Lindley var. *blephariglottis*—White Fringed Orchis (Figure 55). $2n = 42$. Sphagnum bogs, wet sphagnous soil. [*Habenaria blephariglottis* (Willdenow) Hooker]

Platanthera ciliaris (Linnaeus) Lindley—Yellow Fringed Orchis (Figure 56). $2n = ?$. Swampy woods, wet thickets, bogs. [*Habenaria ciliaris* (Linnaeus) R. Brown]

Platanthera clavellata (Michaux) Luer—Green Woodland Orchis (Figure 56). $2n = 42$. Swampy woods, bogs, spring-heads, shores, typically sphagnous. [*Habenaria clavellata* (Michaux) Sprengel; *H. clavellata* var. *ophioglossoides* Fernald]

Platanthera cristata (Michaux) Lindley—Crested Yellow Orchis (Figure 56). $2n = ?$. Damp acid woods, low moist meadows. [*Habenaria* cristata (Michaux) R. Brown]

Platanthera dilatata (Pursh) Lindley ex Beck var. *dilatata*—Bog Candle (Figure 56). $2n = 42$. Springy woods, bogs, shores, meadows. [*Habenaria dilatata* (Pursh) Hooker]

Platanthera flava (Linnaeus) Lindley var. *herbiola* (R. Brown ex Aiton f.) Luer—Tubercled Orchis (Figure 57). $2n = 42$. Springy meadows, shores. [*Habenaria flava* (Linnaeus) R. Brown var. *herbiola* (R. Brown) Ames & Correll]

Platanthera grandiflora (Bigelow) Lindley—Large Purple Fringed Orchis (Figure 57). $2n = 42$. Rich swampy woods, spring-heads, along streams, thickets. [*Habenaria fimbriata* (Aiton) R. Brown; *H. psycodes* (Linnaeus) Sprengel var. *grandiflora* (Bigelow) A. Gray]

Platanthera hookeri (Torrey ex A. Gray)—Hooker's Orchis (Figure 57). 2*n* = 42. Rich dry woods. [*Habenaria hookeri* Torrey]

Platanthera hyperborea (Linnaeus) Lindley—Northern Green Orchis (Figure 57). 2*n* = 42, 84, 84 ± 1. Springy woods, sphagnum bogs, ditches. [*P. hyperborea* var. *huronensis* (Nuttall) Luer; *Habenaria hyperborea* (Linnaeus) R. Brown; *H. hyperborea* (Linnaeus) R. Brown var. *huronensis* (Nuttall) Farwell]

Platanthera lacera (Michaux) G. Don—Ragged Orchis (Figure 58). 2*n* = 42. Meadows, damp fields, alluvial or wet woods. [*Habenaria lacera* (Michaux) Loddiges]

Platanthera leucophaea (Nuttall) Lindley—Prairie Fringed Orchis (Figure 58). 2*n* = 42. Bogs, open tamarack swamps. [*Habenaria leucophaea* (Nuttall) A. Gray]

Platanthera obtusata (Banks ex Pursh) Lindley—Blunt-leaf Orchis (Figure 58). 2*n* = 42. Sphagnum bogs, damp woods, especially coniferous or mixed. [*Habenaria obtusata* (Banks ex Pursh) Richards]

Platanthera orbiculata (Pursh) Lindley var. *orbiculata*—Round-leaved Orchis (Figure 58). 2*n* = 42. Rich woods. [*Habenaria orbiculata* (Pursh) Torrey]

Platanthera orbiculata (Pursh) Lindley var. *macrophylla* (Goldie) Luer—(Figure 59). 2*n* = ?. Rich woods. [*Habenaria macrophylla* Goldie; *H. orbiculata* (Pursh) Torrey var. *macrophylla* (Goldie) B. Boivin]

Platanthera psycodes (Linnaeus) Lindley—Small Purple Fringed Orchis (Figure 59). 2*n* = 42. Wet woods, damp thickets, along streams. [*Habenaria psycodes* (Linnaeus) Sprengel]

—*Platanthera* hybrids—

Platanthera × *andrewsii* (M. White) Luer—(Figure 59). 2*n* = 42. [*P. lacera* (Michaux) G. Don × *P. psycodes* (Linnaeus) Lindley]

Platanthera grandiflora (Bigelow) Lindley × *Platanthera hyperborea* (Linnaeus) Lindley—(Figure 59).

Platanthera grandiflora (Bigelow) Lindley × *Platanthera lacera* (Michaux) G. Don—(Figure 60).

Platanthera × *media* (Rydberg) Luer—(Figure 60). [*P. dilatata* (Pursh) Lindley ex Beck var. *dilatata* × *P. hyperborea* (Linnaeus) Lindley]

Pogonia ophioglossoides (Linnaeus) Ker—Rose Pogonia (Figure 60). $2n = 18$. Sphagnum bogs, swamps, wet meadows, pond shores, sphagnous thickets.

Spiranthes casei Catling & Cruise—(Figure 60). $2n = 60, 75$. Sandy acid soils, roadsides, fields.

Spiranthes cernua (Linnaeus) Richard—Nodding Ladies'-tresses (Figure 61). $2n = 30, 45$, ca. 50, 60, 61. Damp banks, meadows, bogs, shores, low thickets, open moist sandy places.

Spiranthes lacera (Rafinesque) Rafinesque var. *lacera*—Northern Slender Ladies'-tresses (Figure 61). $2n = 30$. Open sandy places.

Spiranthes lacera (Rafinesque) Rafinesque var. *gracilis* (Bigelow) Luer—Southern Slender Ladies'-tresses (Figure 61). $2n = 30$. Sterile open soils, thickets, and open woods. [*S. gracilis* (Bigelow) Beck]

Spiranthes lucida (H. H. Eaton) Ames—(Figure 61). $2n = 44$. Damp rocky shores, meadows, rich damp thickets, usually in basic soils.

Spiranthes ochroleuca (Rydberg) Rydberg—(Figure 62). $2n = 30$. Sterile fields, dry barrens, rocky slopes, open woods, roadsides. [*S. cernua* (Linnaeus) Richard var. *ochroleuca* (Rydberg) Ames]

Spiranthes romanzoffiana Chamisso—Hooded Ladies'-tresses (Figure 62). $2n = 30, 44, 60$. Swampy places, often along rivers and ponds, thickets.

Spiranthes tuberosa Rafinesque—Little Ladies'-tresses (Figure 62). $2n = ?$. Dry sandy fields, woodland borders, cemeteries, roadsides. [*S. tuberosa* var. *grayi* (Ames) Fernald]

Spiranthes vernalis Engelmann & A. Gray—Spring Ladies'-tresses (Figure 62). $2n = 30$. Grasslands, sandy fields, clearings.

—*Spiranthes* hybrids—

Spiranthes × *intermedia* Ames—(Figure 63). [*S. lacera* (Rafinesque) Rafinesque var. *lacera* × *S. vernalis* Engelmann & A. Gray]

Spiranthes lacera (Rafinesque) Rafinesque var. *lacera* × *Spiranthes romanzoffiana* Chamisso—(Figure 63).

Spiranthes lacera (Rafinesque) Rafinesque var. *gracilis* (Bigelow) Luer × *Spiranthes tuberosa* Rafinesque—(Figure 63).

Tipularia discolor (Pursh) Nuttall—Crane-fly Orchid (Figure 63). $2n = ?$. Rich, damp, oak-holly-beech woods.

Triphora trianthophora (Swartz) Rydberg subsp. *trianthophora*—Nodding Pogonia (Figure 64). $2n = 44$. Deep humus of rich moist woods with *Fagus*, often on rotten logs.

PONTEDERIACEAE

EICHHORNIA CRASSIPES (Martius) Solms-Laubach—Water-hyacinth (Figure 64). $2n = 30, 32, 58$. Floating in ponds and quiet streams. From South America.

Heteranthera dubia (Jacquin) MacMillan—Water Stargrass (Figure 64). $2n = 30$. Shallow, quiet, basic water. [*Zosterella dubia* (Jacquin) Small]

Heteranthera reniformis Ruiz & Pavón—(Figure 64). $2n = 48$. Muddy river shores (in mud or floating in shallow water).

Pontederia cordata Linnaeus—Pickerelweed (Figure 65). $2n = 16$. Shallow water of ponds, lakes, and river shores, rooting in mud.

POTAMOGETONACEAE

Potamogeton alpinus Balbis—Red Pondweed (Figure 65). $2n = 26, 52$. Slow-moving streams, shallow water of ponds and lakes. [*P. alpinus* var. *subellipticus* (Fernald) Ogden; *P. alpinus* var. *tenuifolius* (Rafinesque) Ogden]

Potamogeton amplifolius Tuckerman—(Figure 65). 2*n* = 52. Deep water of lakes and river coves.

Potamogeton bicupulatus Fernald—(Figure 65). 2*n* = ?. Acidic shallow water of rivers and ponds. [*P. diversifolius* Rafinesque var. *trichophyllus* Morong; *P. capillaceus* Poiret]

Potamogeton confervoides Reichenbach—Alga Pondweed (Figure 66). 2*n* = ?. Acidic sandy or sphagnous ponds, mountain pools, and lakes.

POTAMOGETON CRISPUS Linnaeus—Curly Pondweed (Figure 66). 2*n* = 26, 36, 42, 50, 52, 72, 78. Shallow basic or brackish water. From Europe.

Potamogeton diversifolius Rafinesque—Common Snailseed Pondweed (Figure 66). 2*n* = ?. Acidic shallow water. [*P. capillaceus* Poiret]

Potamogeton epihydrus Rafinesque—Ribbonleaf Pondweed (Figure 66). 2*n* = 26. Shallow quiet and moving water. [*P. epihydrus* var. *nuttallii* (Chamisso & Schlechtendahl) Fernald; *P. epihydrus* var. *ramosus* (Peck) House]

Potamogeton foliosus Rafinesque subsp. *foliosus*—Leafy Pondweed (Figure 67). 2*n* = 26, 28. Basic still water of ponds, lakes, and streams. [*P. foliosus* var. *macellus* Fernald]

Potamogeton friesii Ruprecht—(Figure 67). 2*n* = 26. Alkaline deep water of lakes and ponds.

Potamogeton gramineus Linnaeus—(Figure 67). 2*n* = 52. Shallow water. [*P. gramineus* var. *maximus* Morong; *P. gramineus* var. *myriophyllus* Robbins]

Potamogeton hillii Morong—(Figure 67). 2*n* = 26. Alkaline water of ponds and streams.

Potamogeton illinoensis Morong—(Figure 68). 2*n* = 104. Alkaline water of ponds and streams.

Potamogeton natans Linnaeus—Floating Pondweed (Figure 68). 2*n* = 42, 52. Ponds and slow streams.

Potamogeton nodosus Poiret—Longleaf Pondweed (Figure 68). $2n = 52$. Streams.

Potamogeton oakesianus Robbins—Oakes Pondweed (Figure 68). $2n =$?. Acidic ponds and lakes.

Potamogeton obtusifolius Mertens & Koch—(Figure 69). $2n = 26$. Quiet basic water, usually cold.

Potamogeton ogdenii Hellquist & R. L. Hilton—Ogden's Pondweed (Figure 69). $2n =$?. Basic water of ponds and lakes.

Potamogeton perfoliatus Linnaeus—Redhead-grass (Figure 69). $2n = 14$, ca. 40, 52, 78. Shallow water. [*P. perfoliatus* var. *bupleuroides* (Fernald) Farwell]

Potamogeton praelongus Wulfen—White-stem Pondweed (Figure 69). $2n = 52$. Moderately alkaline still water, usually deep.

Potamogeton pulcher Tuckerman—Spotted Pondweed (Figure 70). $2n =$?. Acidic shallow water of ponds and muddy shores.

Potamogeton pusillus Linnaeus subsp. *pusillus*—(Figure 70). $2n = 26$. Alkaline water of ponds and streams. [*P. pusillus* var. *minor* (Bivona-Bivardi) Fernald & B. G. Schubert]

Potamogeton pusillus Linnaeus subsp. *gemmiparus* (Robbins) R. R. Haynes & Hellquist—(Figure 70). $2n = 26$. Quiet acidic water of ponds and streams. [*P. gemmiparus* (Robbins) Robbins ex Morong]

Potamogeton pusillus Linnaeus subsp. *tenuissimus* (Mertens & Koch) R. R. Haynes & Hellquist—(Figure 70). $2n = 26$. Quiet shallow water of ponds and streams. [*P. berchtoldii* Fieber; *P. berchtoldii* Fieber var. *acuminatus* Fieber; *P. berchtoldii* Fieber var. *lacunatus* (Hagström) Fernald; *P. berchtoldii* Fieber var. *polyphyllus* (Morong) Fernald; *P. berchtoldii* Fieber var. *tenuissimus* (Mertens & Koch) Fernald]

Potamogeton richardsonii (A. Bennett) Rydberg—Redhead Pondweed (Figure 71). $2n = 26$, 52. Alkaline water of lakes and streams.

Potamogeton robbinsii Oakes—Fern Pondweed (Figure 71). $2n = 52$. Ponds, lakes, and slow streams.

Potamogeton spirillus Tuckerman—Northern Snailseed Pondweed (Figure 71). $2n$ = ?. Neutral-to-acidic quiet water of ponds and streams.

Potamogeton strictifolius A. Bennett—(Figure 71). $2n = 52$. Alkaline water of lakes and slow streams. [*P. strictifolius* var. *rutiloides* Fernald]

Potamogeton vaseyi Robbins—Vasey's Pondweed (Figure 72). $2n = 28$. Quiet water of ponds and streams, of low-to-moderate alkalinity. [*P. lateralis* Morong]

Potamogeton zosteriformis Fernald—Flatstem Pondweed (Figure 72). $2n = 52$. Quiet often alkaline water of ponds and slow streams.

—*Potamogeton* hybrids—

Potamogeton alpinus Balbis × *Potamogeton epihydrus* Rafinesque—(Figure 72).

Potamogeton amplifolius Tuckerman × *Potamogeton illinoensis* Morong—(Figure 72).

Potamogeton amplifolius Tuckerman × *Potamogeton praelongus* Wulfen—(Figure 73).

Potamogeton × *argutulus* Hagström—(Figure 73). [*P. gramineus* Linnaeus × *P. nodosus* Poiret]

Potamogeton × *faxonii* Morong—(Figure 73). [*P. illinoensis* Morong × *P. nodosus* Poiret]

Potamogeton × *haynesii* Hellquist & G. E. Crow—(Figure 73). [*P. strictifolius* A. Bennett × *P. zosteriformis* Fernald; *P. longiligulatus* misapplied]

Potamogeton illinoensis Morong × *Potamogeton perfoliatus* Linnaeus—(Figure 74).

Potamogeton illinoensis Morong × *Potamogeton richardsonii* (A. Bennett) Rydberg—(Figure 74).

Potamogeton × *mysticus* Morong—(Figure 74). [*P. perfoliatus* Linnaeus × *P. pusillus* Linnaeus subsp. *tenuissimus* (Mertens & Koch) R. R. Haynes & Hellquist]

Potamogeton × *nericius* Hagström—(Figure 74). [*P. alpinus* Balbis × *P. gramineus* Linnaeus]

Potamogeton × *nitens* G. Weber—(Figure 75). [*P. gramineus* Linnaeus × *P. perfoliatus* Linnaeus]

Potamogeton perfoliatus Linnaeus × *Potamogeton richardsonii* (A. Bennett) Rydberg—(Figure 75).

Potamogeton praelongus Wulfen × *Potamogeton richardsonii* (A. Bennett) Rydberg—(Figure 75).

Potamogeton × *prussicus* Hagström—(Figure 75). [*P. alpinus* Balbis × *P. perfoliatus* Linnaeus]

Potamogeton × *spathuliformis* (Robbins)—(Figure 76). [*P. gramineus* Linnaeus × *P. illinoensis* Morong]

Stuckenia filiformis (Persoon) Börner subsp. *alpina* (Blytt) R. R. Haynes, Les & M. Král—(Figure 76). 2*n* = 78. Highly alkaline water of cold springs and lakes. [*Potamogeton filiformis* Persoon var. *borealis* (Rafinesque) St. John; *P. filiformis* Persoon var. *macounii* Morong]

Stuckenia filiformis (Persoon) Börner subsp. *occidentalis* (J. W. Robbins) R. R. Haynes, Les & M. Král—(Figure 76). 2*n* = ?. Highly alkaline water of cold streams.

Stuckenia pectinata (Linnaeus) Börner—Sago (Figure 76). 2*n* = 42, ca. 66, 70–87. Brackish or alkaline waters. [*Potamogeton pectinatus* Linnaeus]

RUPPIACEAE

Ruppia maritima Linnaeus—(Figure 77). 2*n* = 14, 16, 20, 24, 28, 40. Saline or brackish water. [*R. maritima* var. *longipes* Hagström; *R. maritima* var. *obliqua* (Schur) Ascherson & Graebner; *R. maritima* var. *rostrata* Agardh; *R. maritima* var. *subcapitata* Fernald & Wiegand]

SCHEUCHZERIACEAE

Scheuchzeria palustris Linnaeus—(Figure 77). 2*n* = 22. Sphagnum bogs. [*S. palustris* var. *americana* Fernald]

SMILACACEAE

Smilax glauca Walter—Sawbrier (Figure 77). 2*n* = 32. Sandy thickets, open woods. [*S. glauca* Walter var. *leurophylla* Blake]

Smilax herbacea Linnaeus—Carrion-flower (Figure 77). 2*n* = 26. Rich thickets, low woods.

Smilax pulverulenta Michaux—(Figure 78). 2*n* = ?. Rich mostly basic woods and thickets. [*S. herbacea* Walter var. *pulverulenta* (Michaux) A. Gray]

Smilax rotundifolia Linnaeus—Common Greenbrier (Figure 78). 2*n* = 32. Woods and thickets.

Smilax tamnoides Linnaeus—China-root (Figure 78). 2*n* = 32. Low woods and thickets. [*S. tamnoides* var. *hispida* (Muhlenberg) Fernald; *S. hispida* Muhlenberg ex Torrey]

SPARGANIACEAE

Sparganium americanum Nuttall—(Figure 78). 2*n* = ?. Muddy shores, shallow water.

Sparganium androcladum (Engelmann) Morong—(Figure 79). 2*n* = ?. Muddy shores, marshes, shallow water.

Sparganium angustifolium Michaux—(Figure 79). 2*n* = 30. Shallow-to-deep water, shores. [*S. multipedunculatum* (Morong) Rydberg]

Sparganium emersum Rehmann—(Figure 79). 2*n* = 30. Muddy shores, marshes, shallow water. [*S. chlorocarpum* Rydberg; *S. chlorocarpum* Rydberg var. *acaule* (Beeby) Fernald]

Sparganium eurycarpum Engelmann—(Figure 79). 2*n* = 30. Mostly basic muddy shores, marshes, shallow water.

Sparganium fluctuans (Engelmann ex Morong) B. L. Robinson—(Figure 80). 2*n* = ?. Nonbasic lakes and ponds.

Sparganium natans Linnaeus—(Figure 80). 2*n* = 30. Shallow pools, streams, shores, bogs. [*S. minimum* (Hartman) Fries]

—*Sparganium* hybrids—

Sparganium americanum Nuttall × *Sparganium fluctuans* (Engelmann ex Morong) B. L. Robinson—(Figure 80).

Sparganium angustifolium Michaux × *Sparganium emersum* Rehmann—(Figure 80).

TYPHACEAE

Typha angustifolia Linnaeus—(Figure 81). 2*n* = 30. Salt marshes, inland marshes, mostly alkaline, and near highways.

Typha latifolia Linnaeus—Common Cat-tail (Figure 81). 2*n* = 30. Marshes, shores, roadside ditches.

—*Typha* hybrids—

Typha × *glauca* Godron—(Figure 81). [*T. angustifolia* Linnaeus × *T. latifolia* Linnaeus]

XYRIDACEAE

Xyris difformis Chapman var. *difformis*—Common Yellow-eyed Grass (Figure 81). 2*n* = 18. Sandy shores of acid ponds, lakes, and bogs. [*X. caroliniana* misapplied]

Xyris montana Ries—Small Yellow-eyed Grass (Figure 82). 2*n* = ?. Sandy mostly acidic shores and bogs.

Xyris smalliana Nash—(Figure 82). 2*n* = 18. Muddy shores, bogs, swamps, sandy or sphagnous shallows. [*X. caroliniana* Walter; *X. congdoni* Small]

Xyris torta Smith—(Figure 82). 2*n* = 18. Sandy shores, sphagnous depressions, meadows.

ZANNICHELLIACEAE

Zannichellia palustris Linnaeus—Horned Pondweed (Figure 82). 2*n* = 12, 24, 28, 32, 34, 36, 48. Fresh-to-brackish water of lakes, streams, and estuaries. [*Z. palustris* var. *major* (Hartman) W. D. J. Koch]

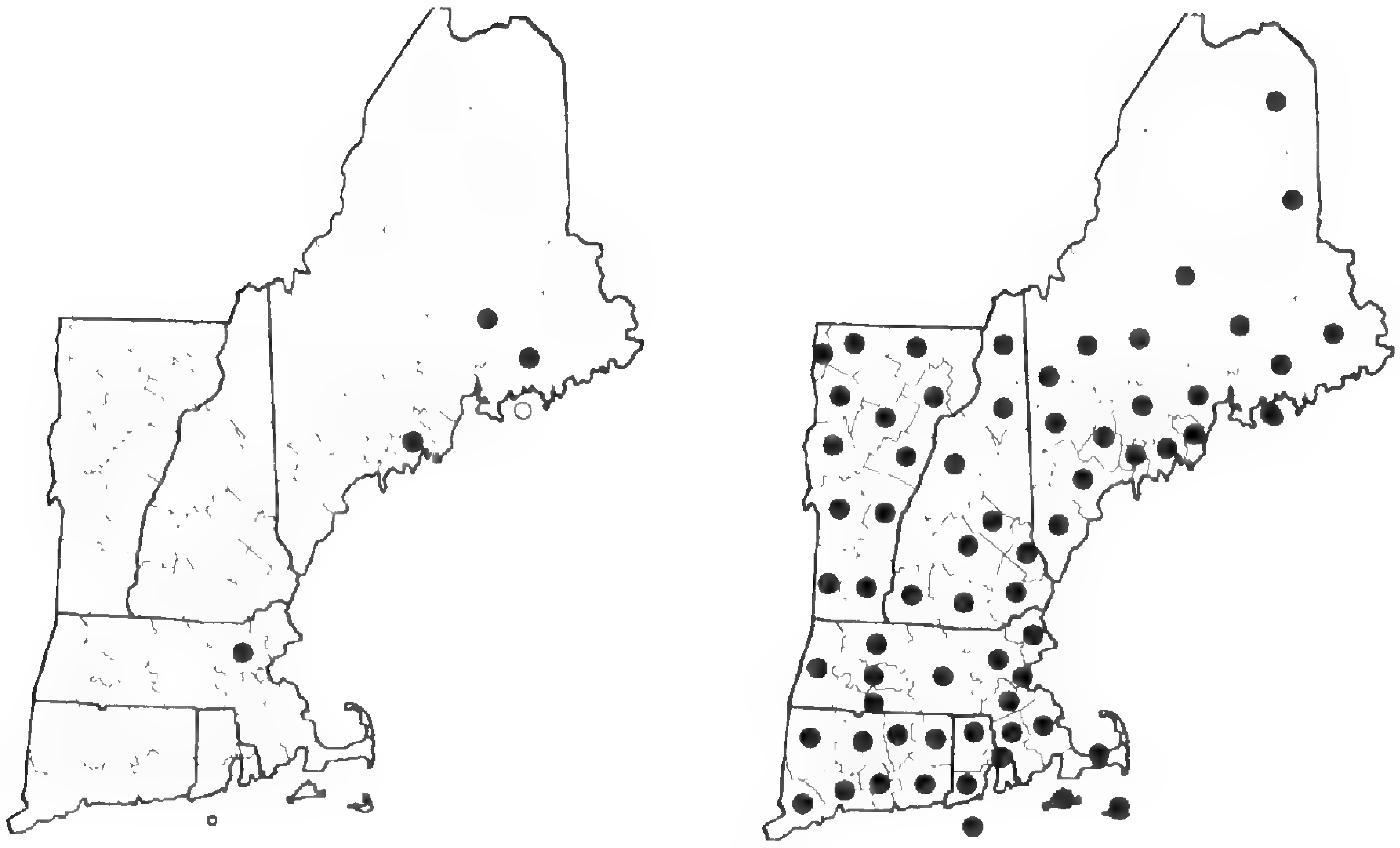
ZOSTERACEAE

Zostera marina Linnaeus—Common Eel-grass (Figure 83). $2n = 12$. Shallow waters of coastal estuaries, coves, and bays. [*Z. marina* var. *stenophylla* Ascherson & Graebner]

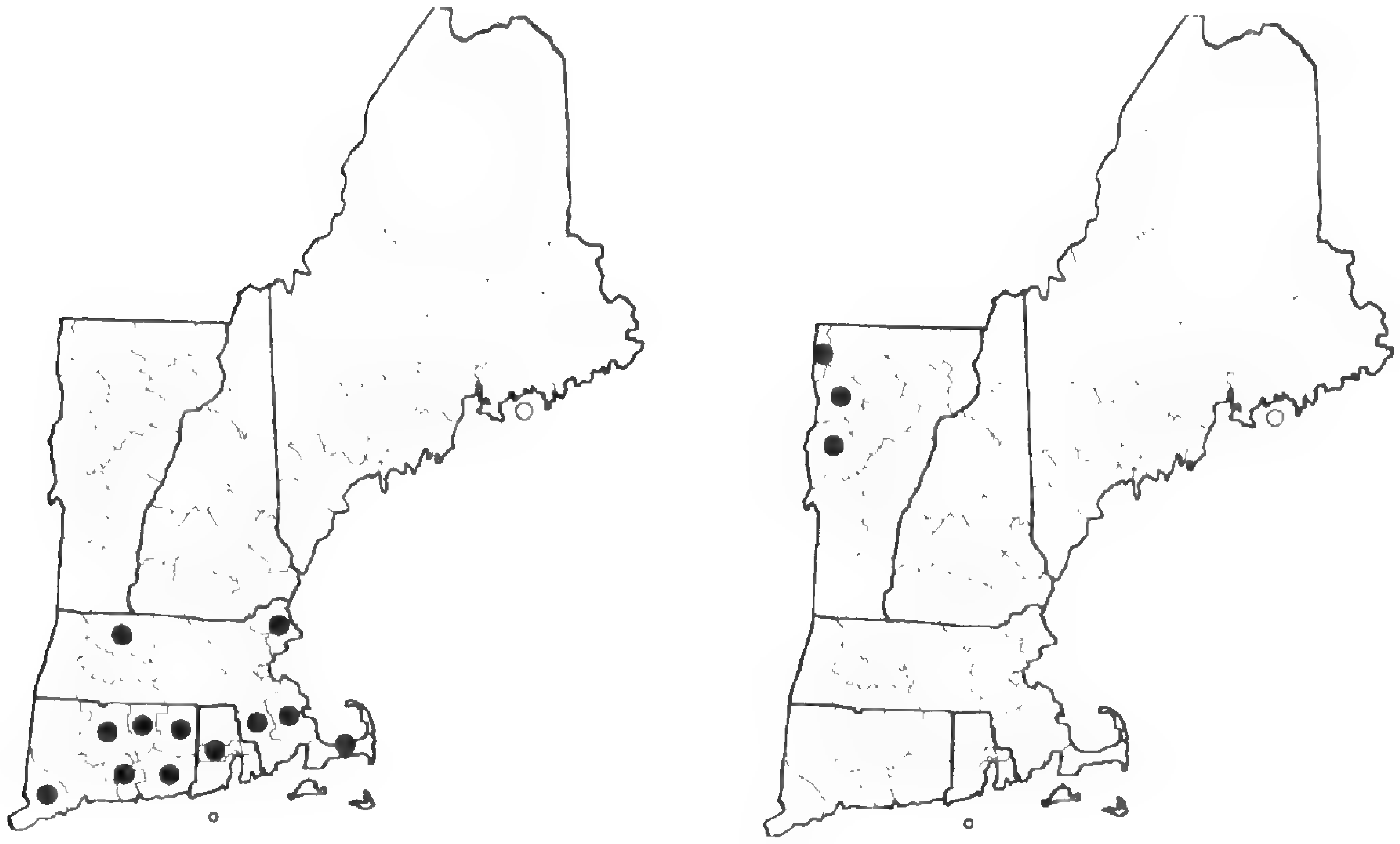
ACKNOWLEDGMENTS. We thank the curators and directors of the herbaria of Harvard University, the University of Maine, the University of Massachusetts, and the University of Vermont for allowing us access to their collections. We particularly appreciate the kindness of David Barrington, Chris Campbell, and Karen Searcy for allowing use of the collections in their care outside of normal hours of operation. We are grateful also to Karen Searcy for allowing access to the notebooks of Harry E. Ahles at the University of Massachusetts and for verifying some voucher specimens there. We also appreciate the research into voucher specimens by Arthur Haines. Barre Hellquist gave especially generously of his time and knowledge to provide much information on the aquatic groups. Kancheepuram Gandhi provided valuable assistance in settling nomenclatural issues. Les Mehrhoff also was very helpful in reviewing our Connecticut data and providing many additional records. Janet Sullivan verified records at NHA. Charles Sheviak provided information relative to *Cypripedium parviflorum*. Anthony Reznicek searched for a voucher specimen at MICH.

ADDENDUM. As this paper went to press an article in Rhodora (101:419–423, 1999) by Donald H. Les and Robert S. Capers reported the collection of *Limnobium spongia* (Bosc) Steudel (Hydrocharitaceae) from Tolland County, Connecticut. The voucher specimen is deposited at CONN.

Figure 1. Key map for counties of the New England states (and Mt. Desert Island, Maine; Block Island, Rhode Island; arbitrary divisions of larger Maine counties and of Coös County, New Hampshire).

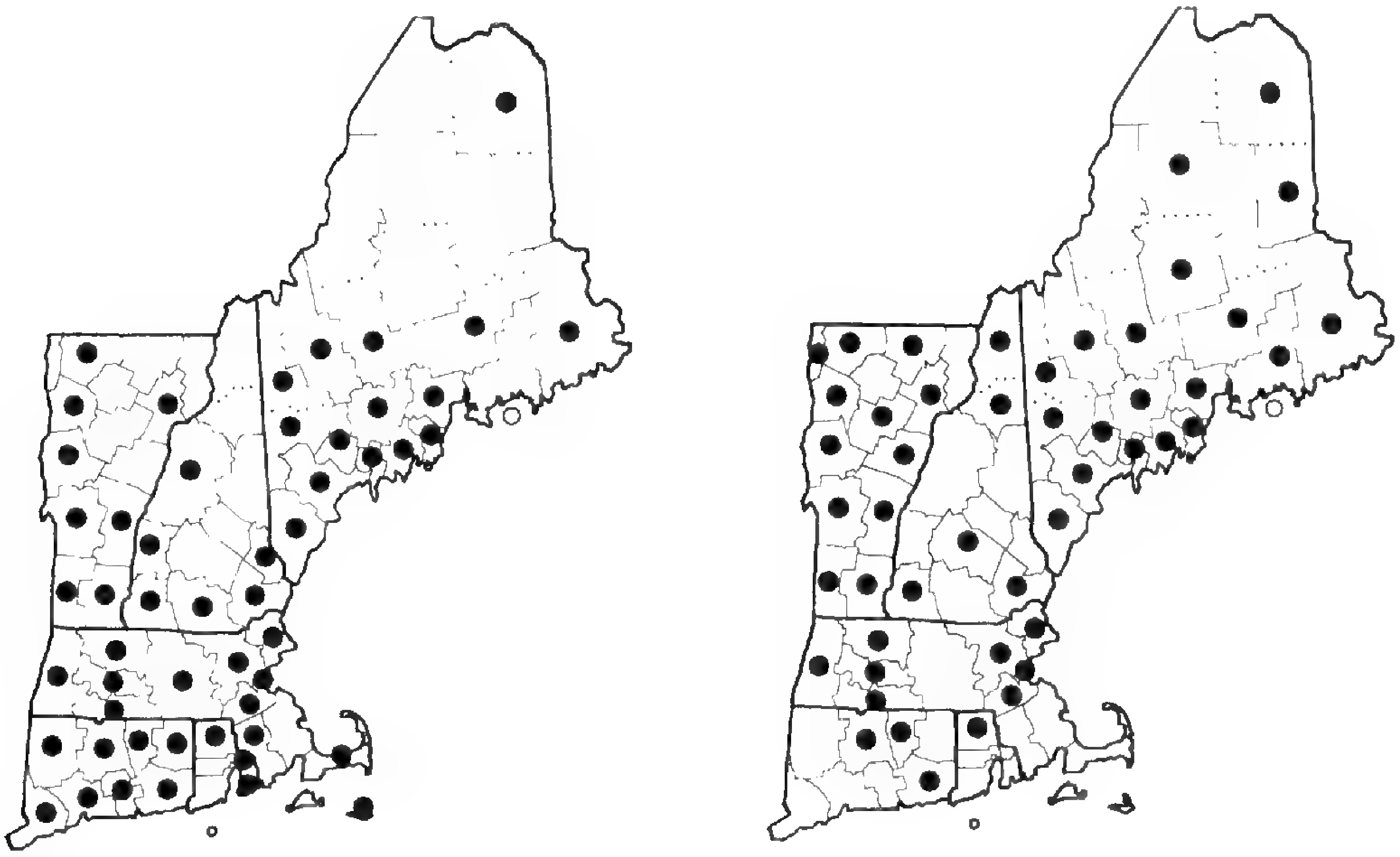


Acorus americanus *ACORUS CALAMUS*



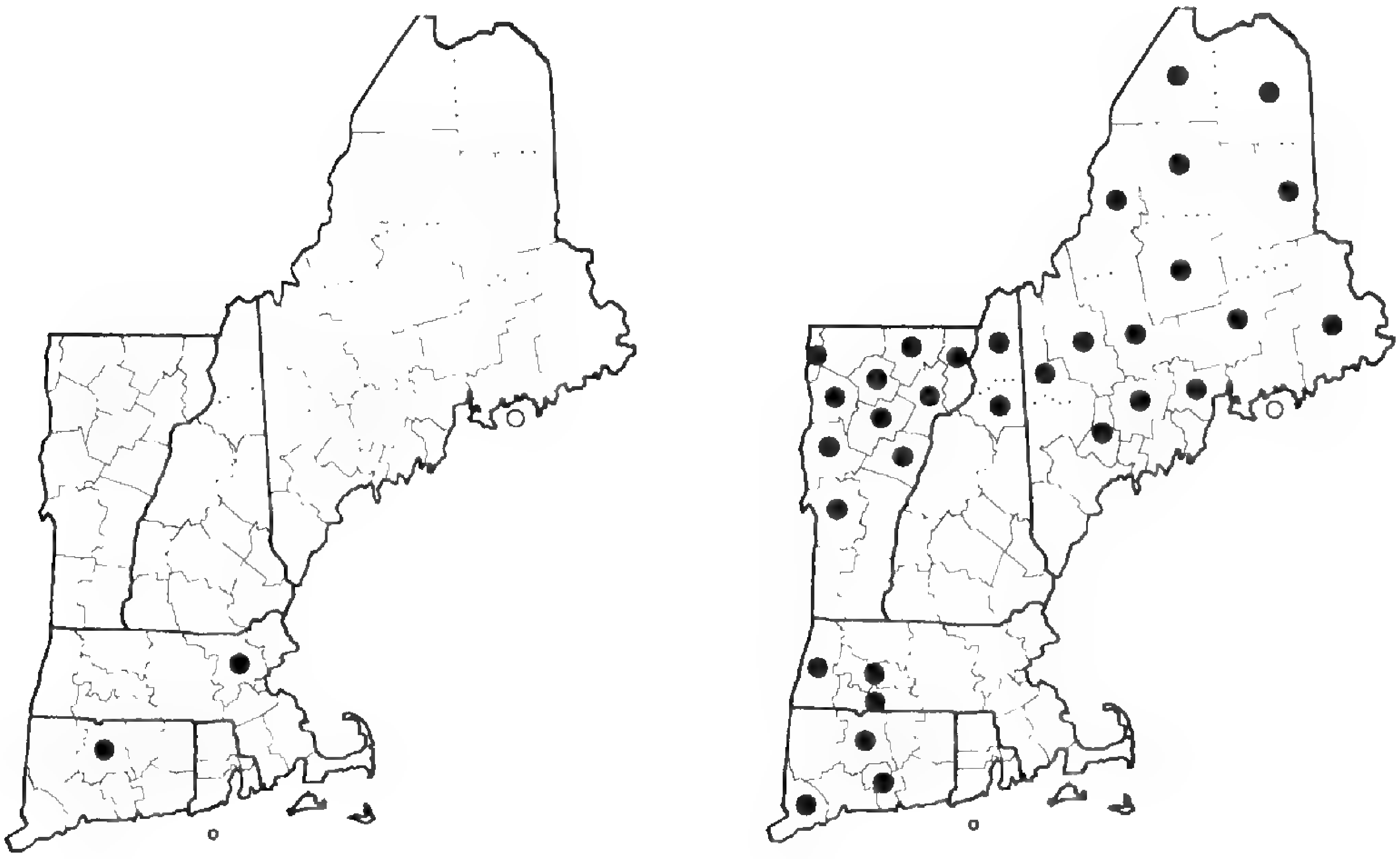
YUCCA FILAMENTOSA *Alisma gramineum*

Figure 2. Distribution maps for *Acorus americanus, A. CALAMUS, YUCCA FILAMENTOSA,* and *Alisma gramineum.*



Alisma subcordatum

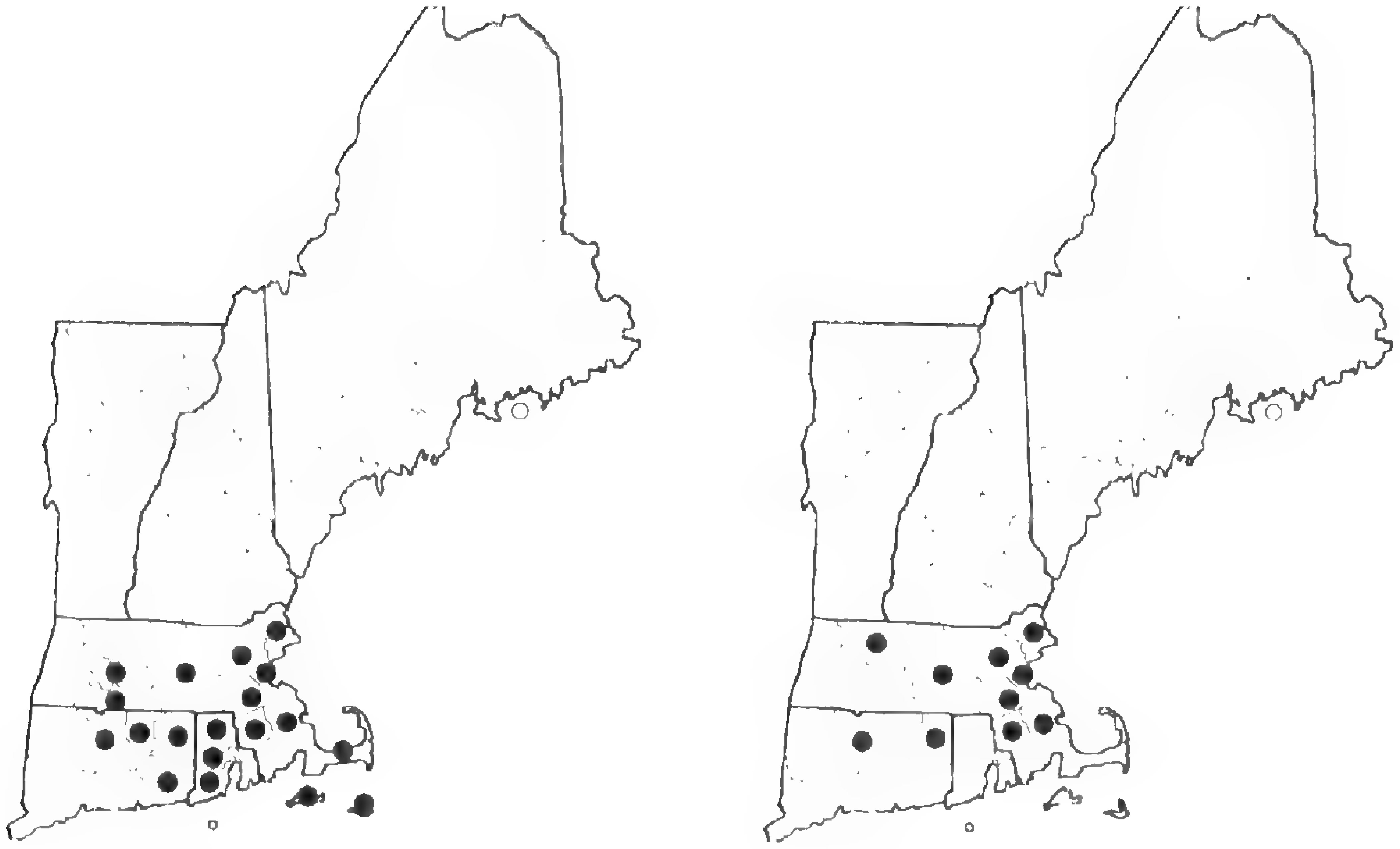
Alisma triviale



Echinodorus tenellus

Sagittaria cuneata

Figure 3. Distribution maps for *Alisma subcordatum*, *A. triviale*, *Echinodorus tenellus*, and *Sagittaria cuneata*.



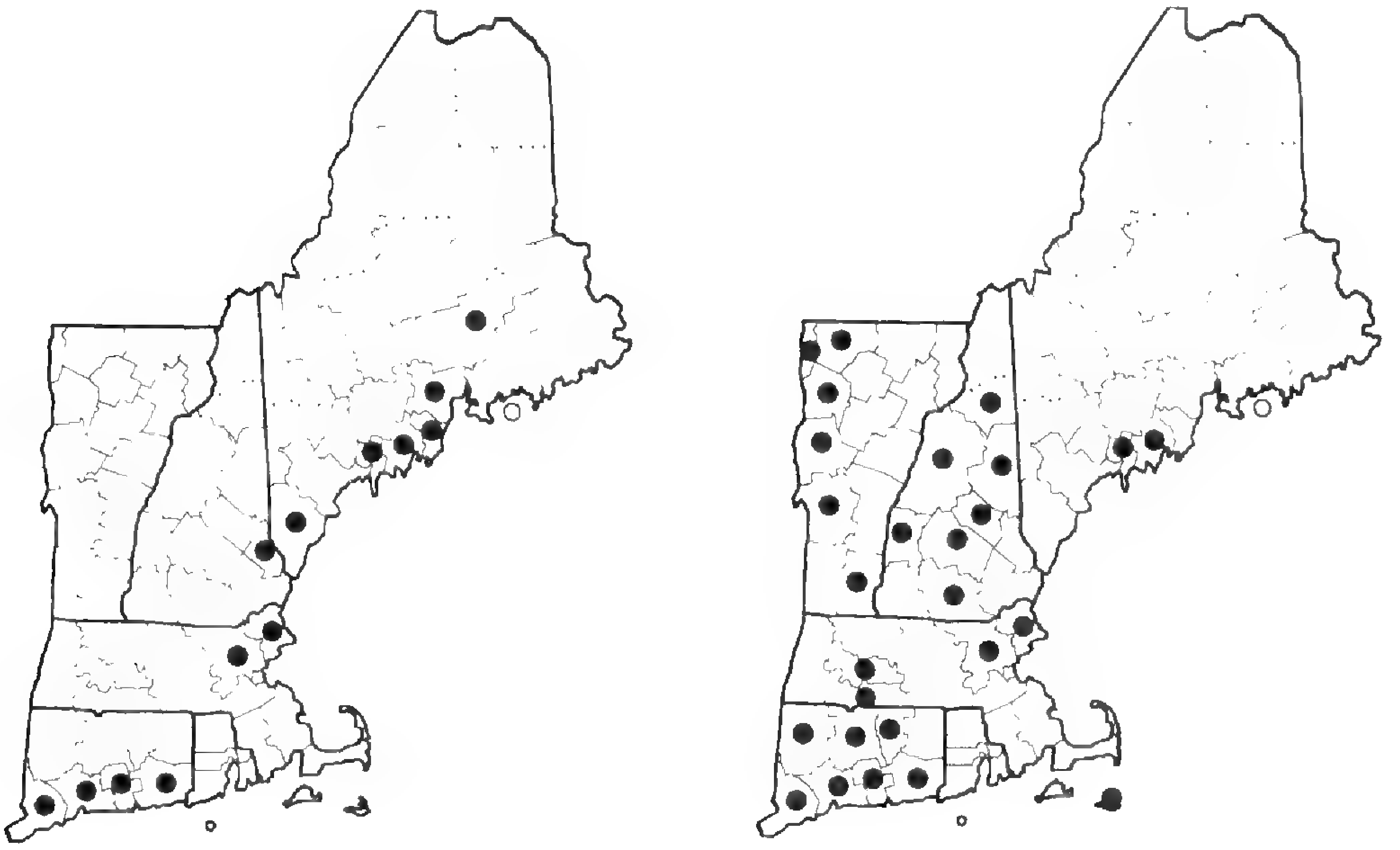
Sagittaria engelmanniana

Sagittaria filiformis

Sagittaria graminea subsp. *graminea*

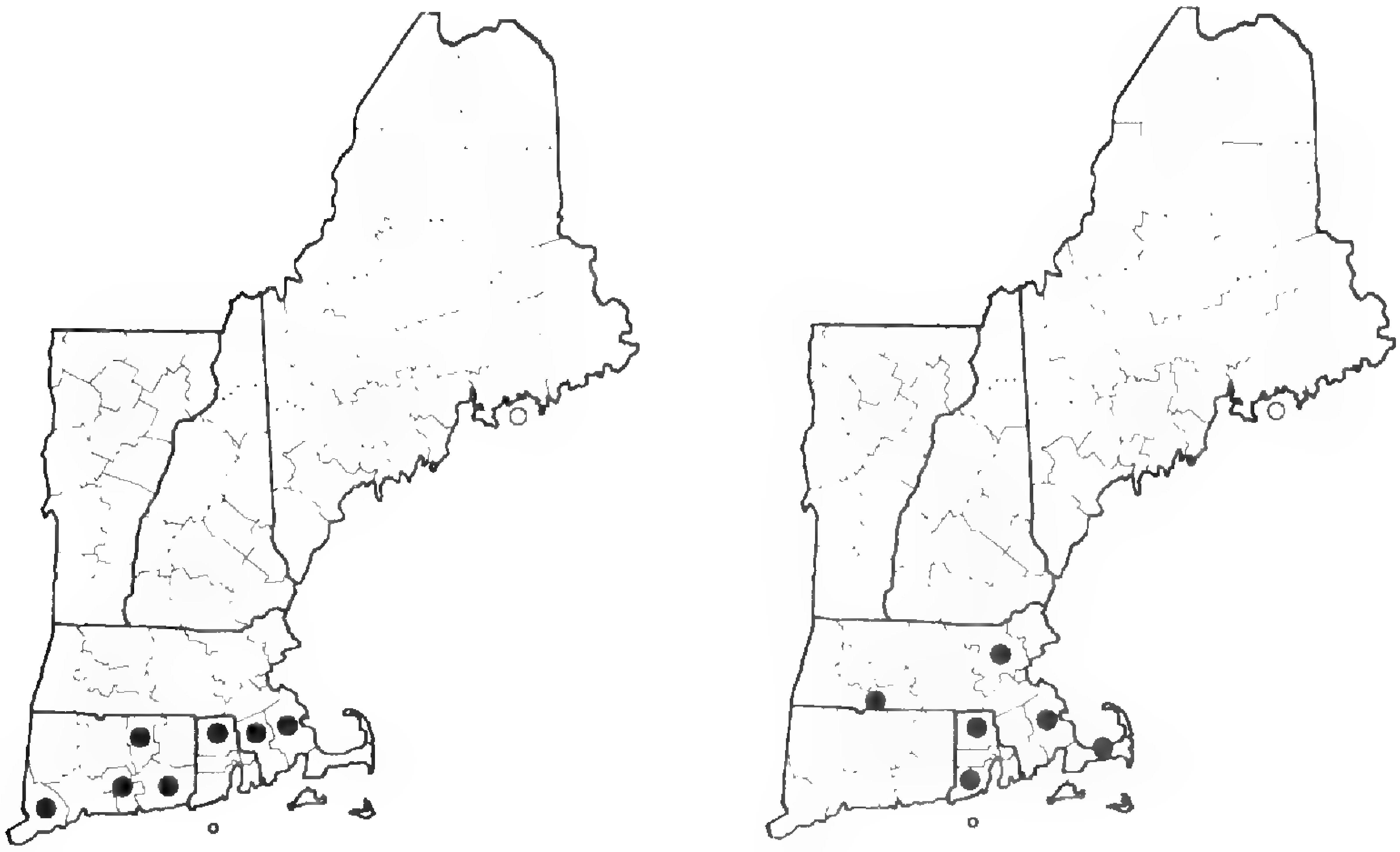
Sagittaria latifolia

Figure 4. Distribution maps for *Sagittaria engelmanniana, S. filiformis, S. graminea* subsp. *graminea,* and *S. latifolia.*



Sagittaria montevidensis subsp. *spongiosa*

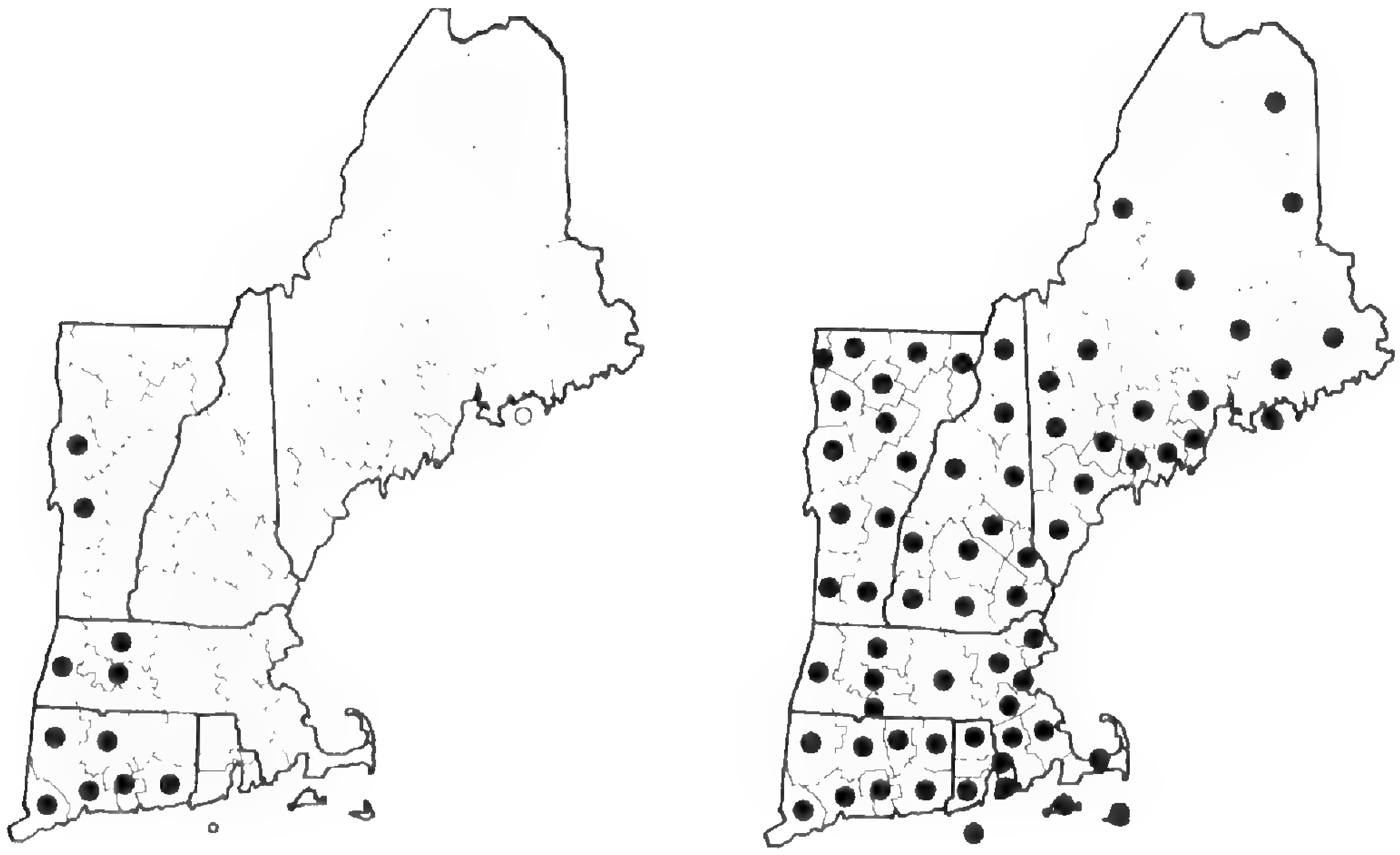
Sagittaria rigida



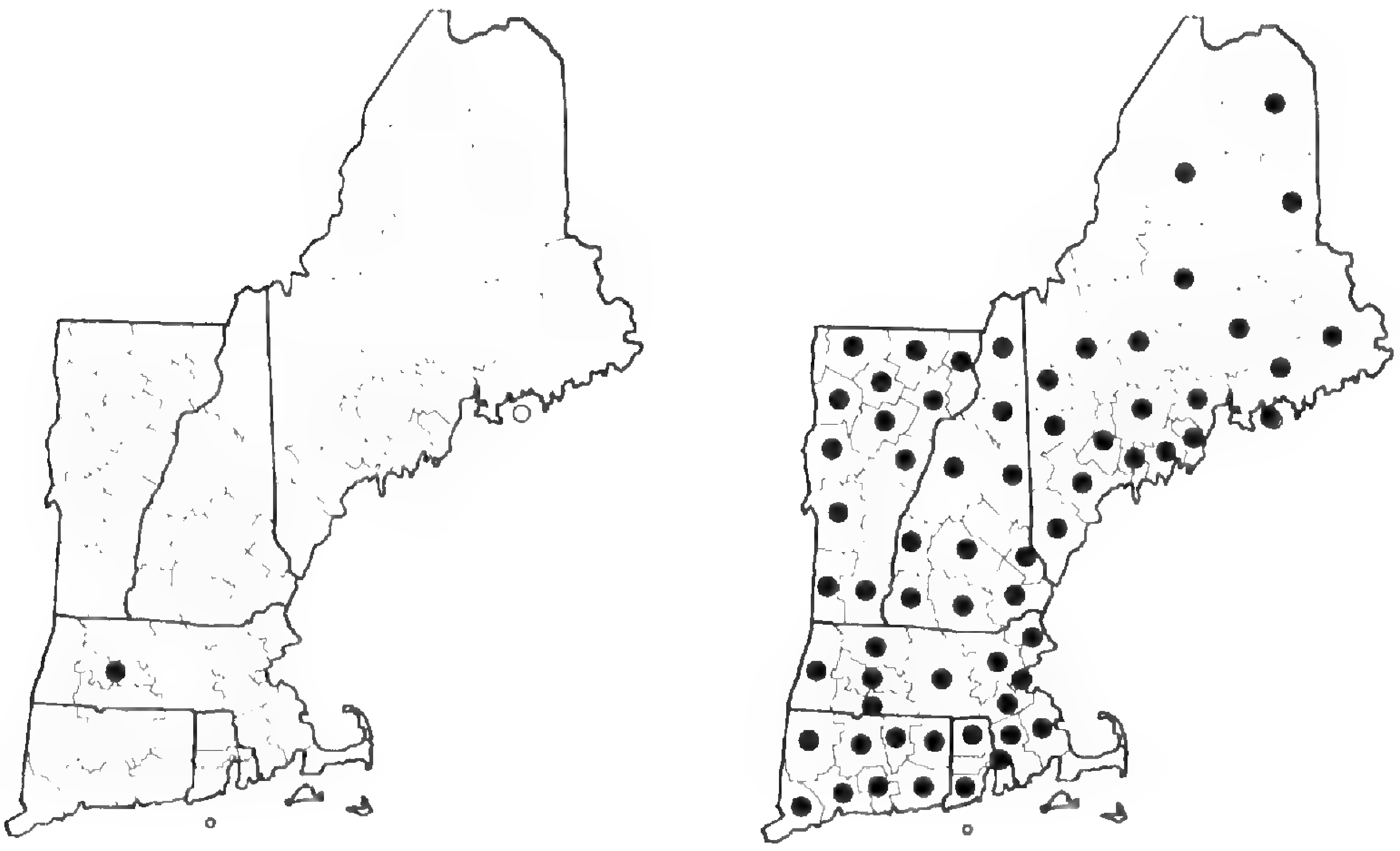
Sagittaria subulata

Sagittaria teres

Figure 5. Distribution maps for *Sagittaria montevidensis* subsp. *spongiosa*, *S. rigida*, *S. subulata*, and *S. teres*.



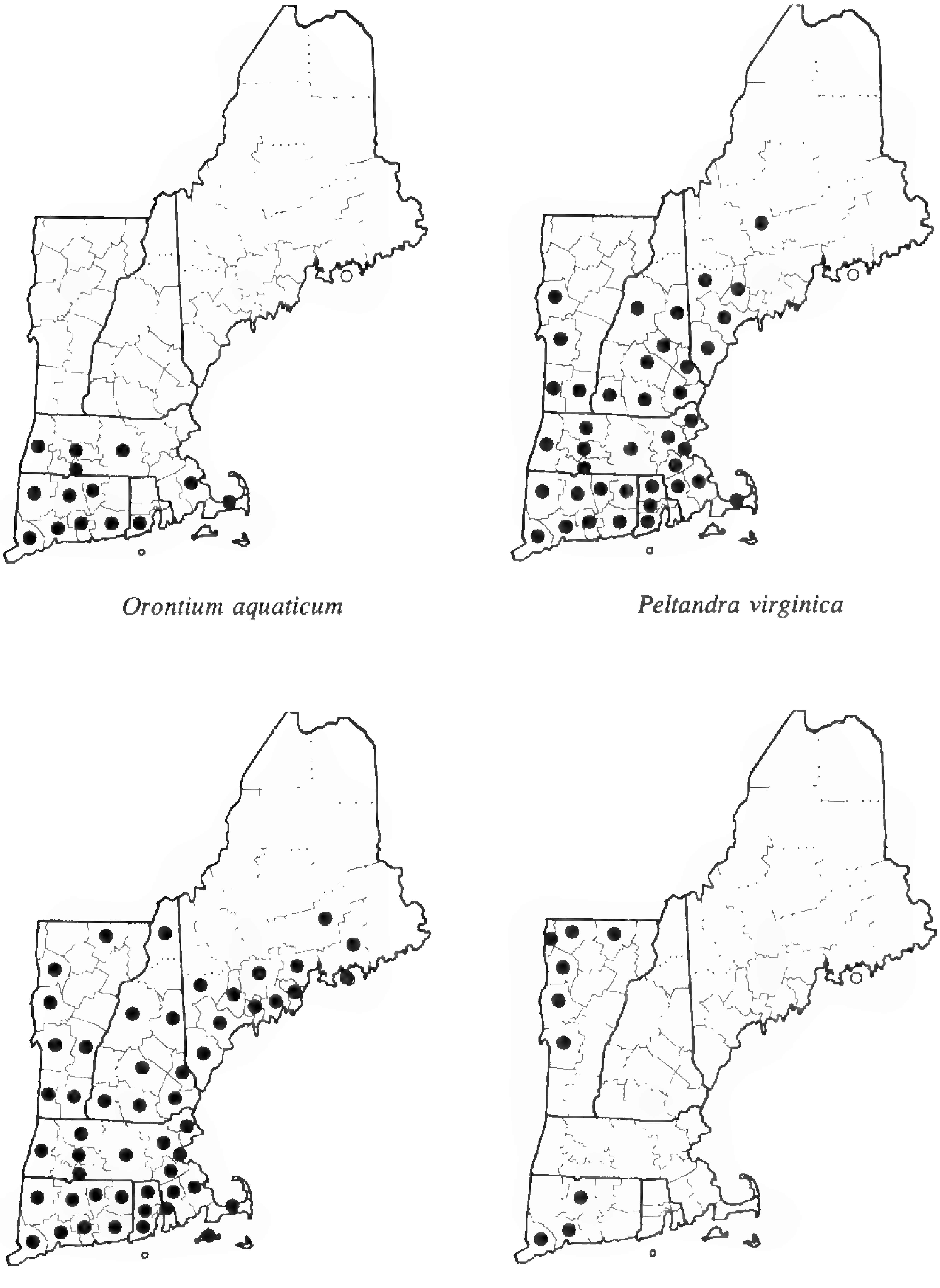
Arisaema dracontium *Arisaema triphyllum*



Arisaema dracontium
X *A. triphyllum*

Calla palustris

Figure 6. Distribution maps for *Arisaema dracontium*, *A. triphyllum*, *A. dracontium* X *A. triphyllum*, and *Calla palustris*.



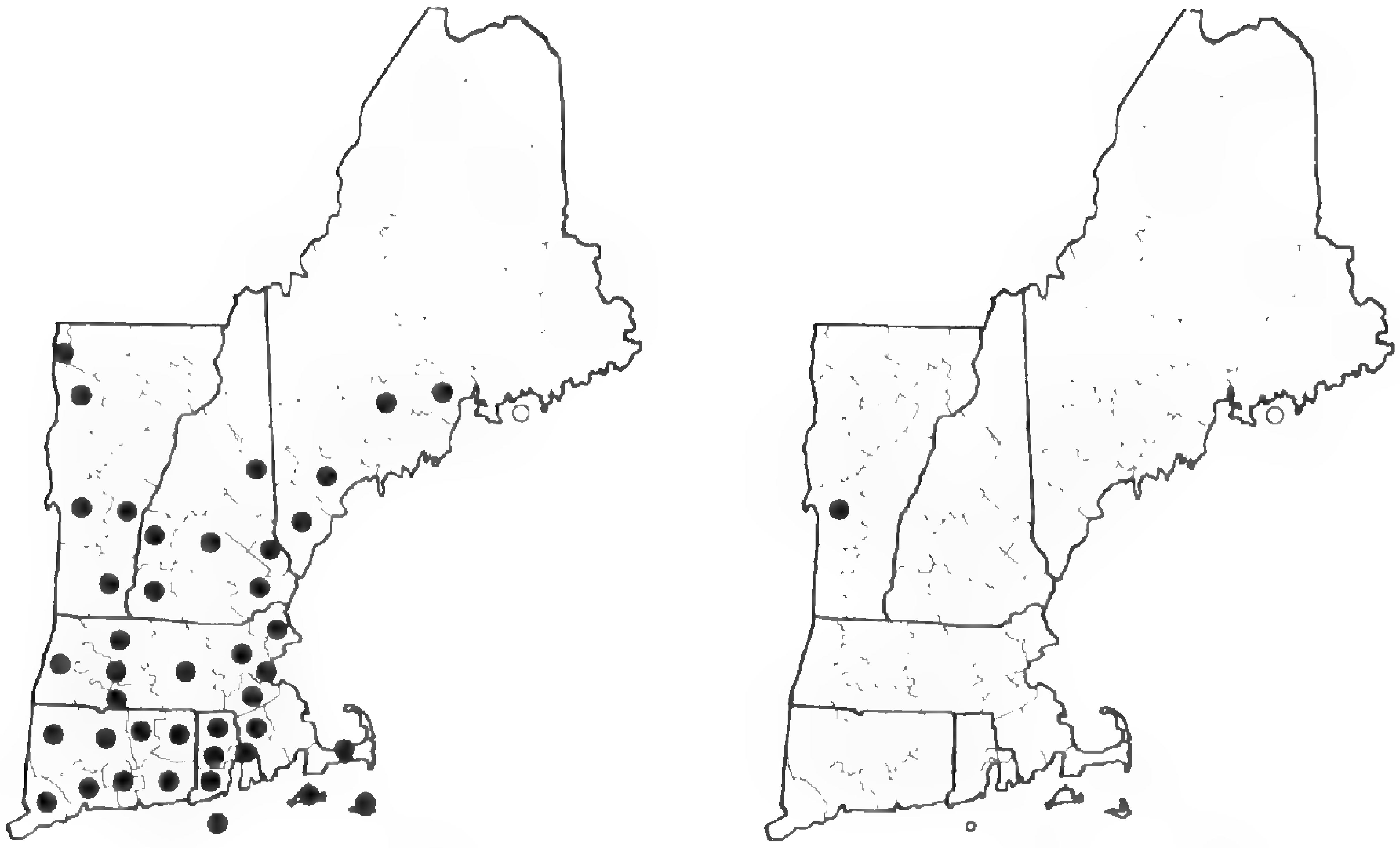
Orontium aquaticum

Peltandra virginica

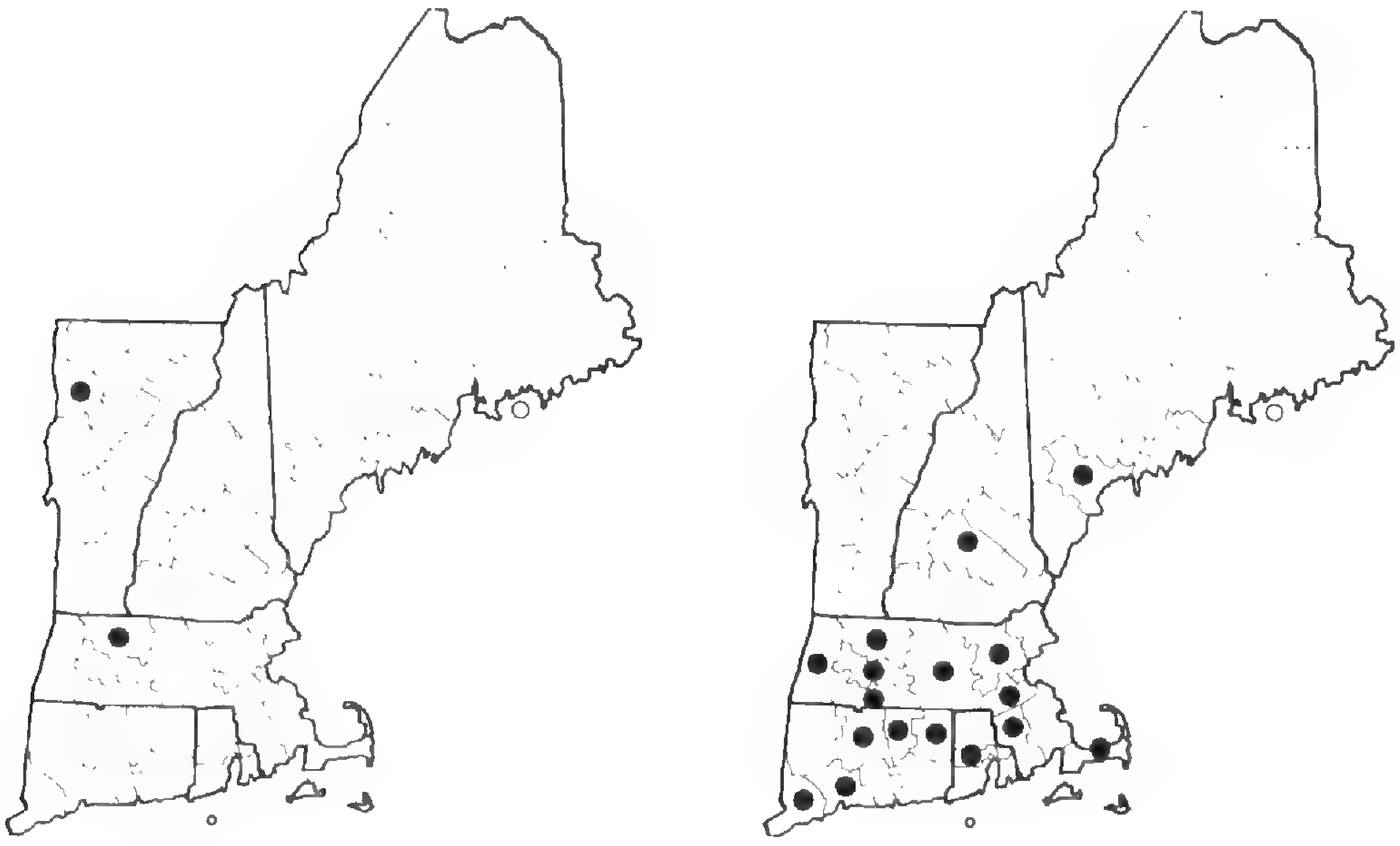
Symplocarpus foetidus

BUTOMUS UMBELLATUS

Figure 7. Distribution maps for *Orontium aquaticum, Peltandra virginica, Symplocarpus foetidus,* and *BUTOMUS UMBELLATUS.*

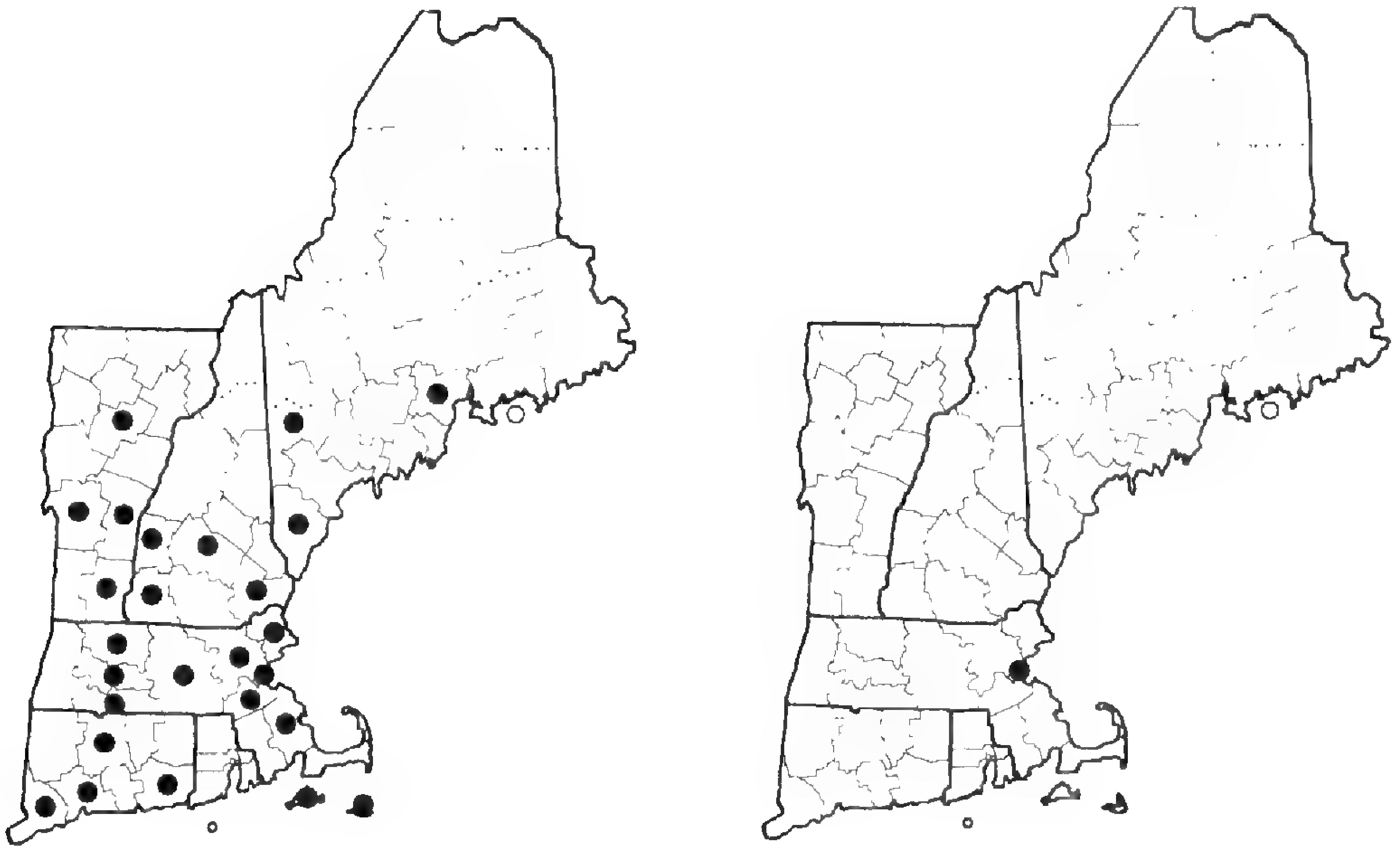


COMMELINA COMMUNIS *COMMELINA DIFFUSA*



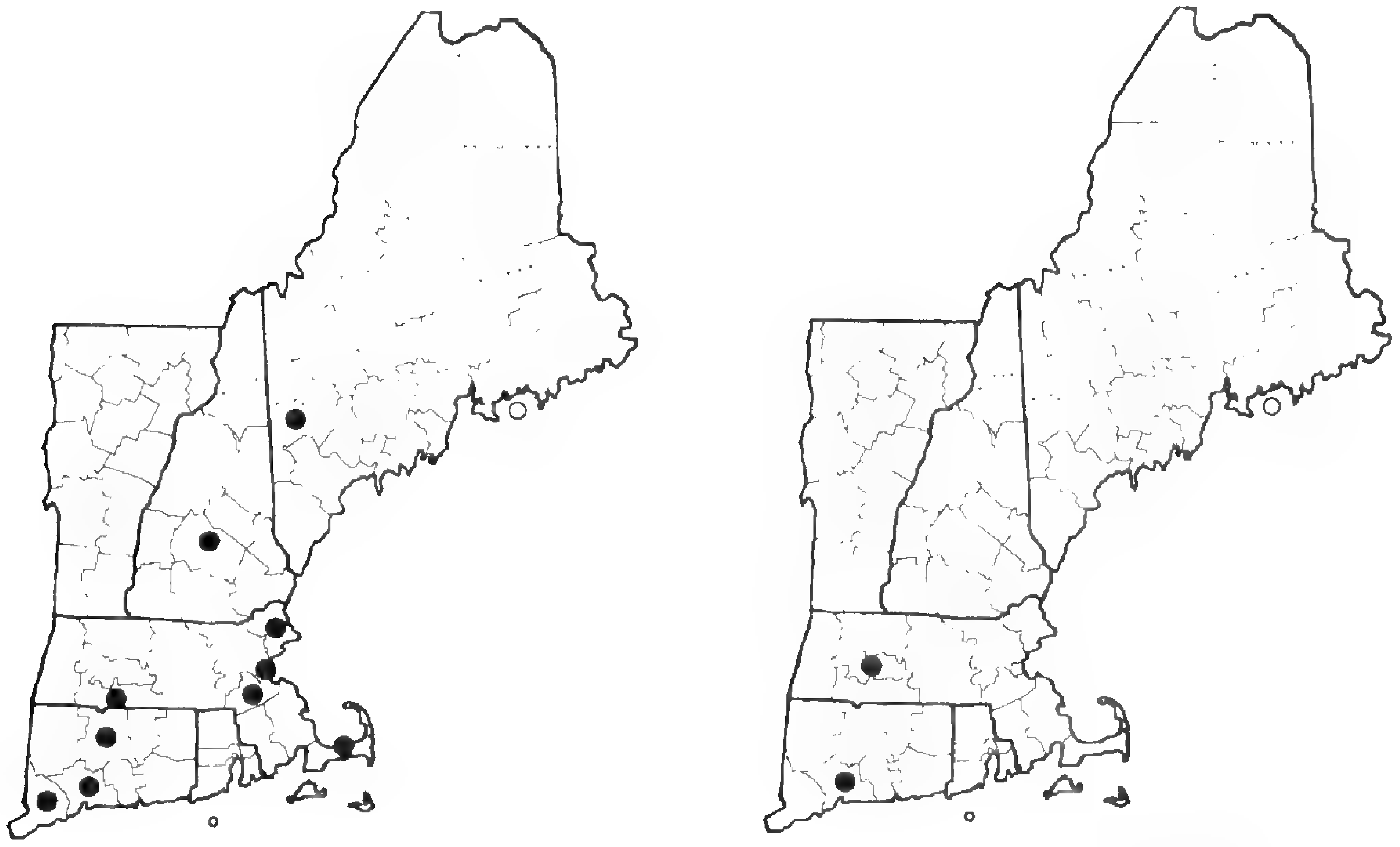
TRADESCANTIA BRACTEATA *Tradescantia ohiensis*

Figure 8. Distribution maps for *COMMELINA COMMUNIS, C. DIFFUSA, TRADESCANTIA BRACTEATA*, and *T. ohiensis*.



Tradescantia virginiana

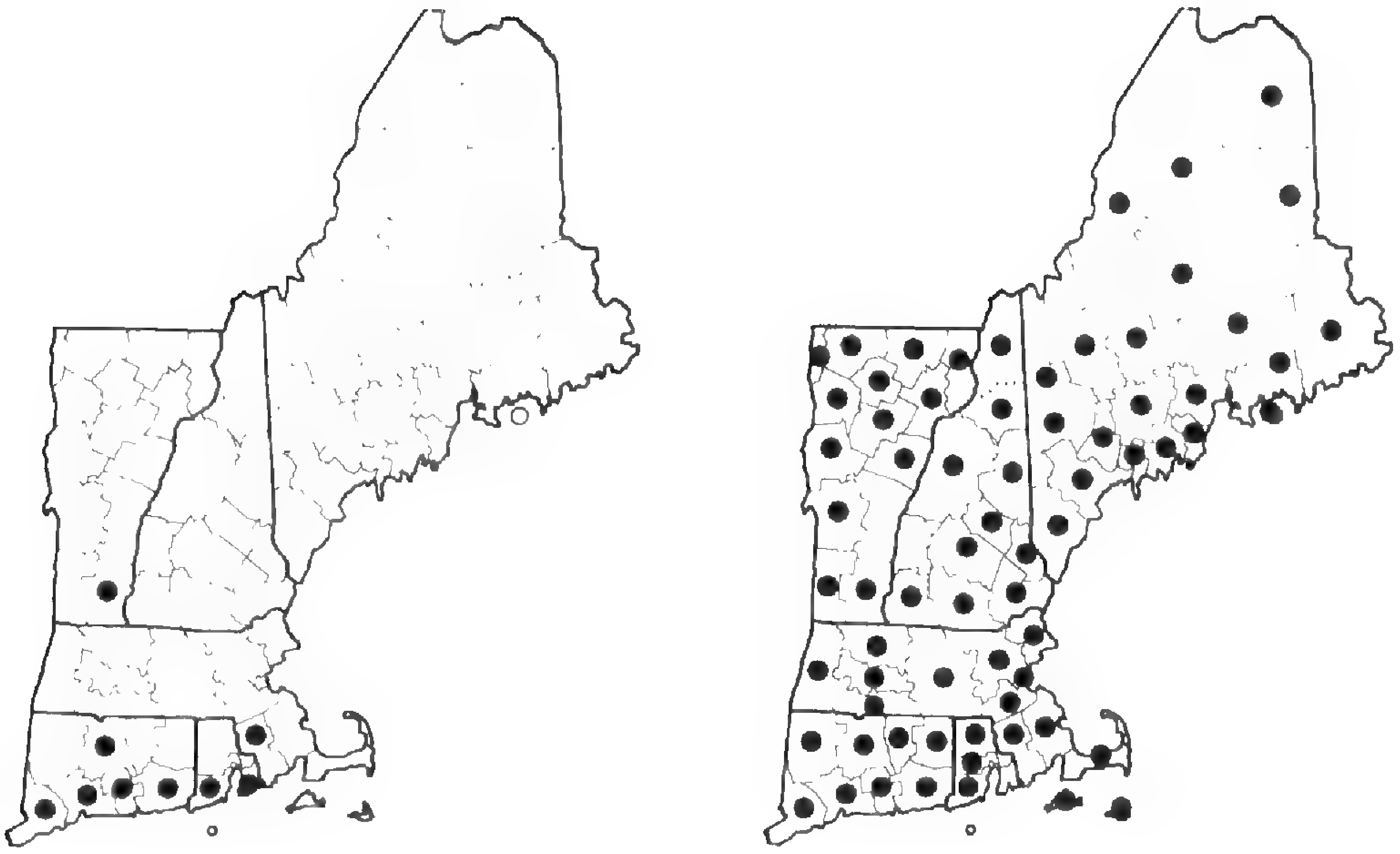
Tradescantia ohiensis
X *T. SUBASPERA*



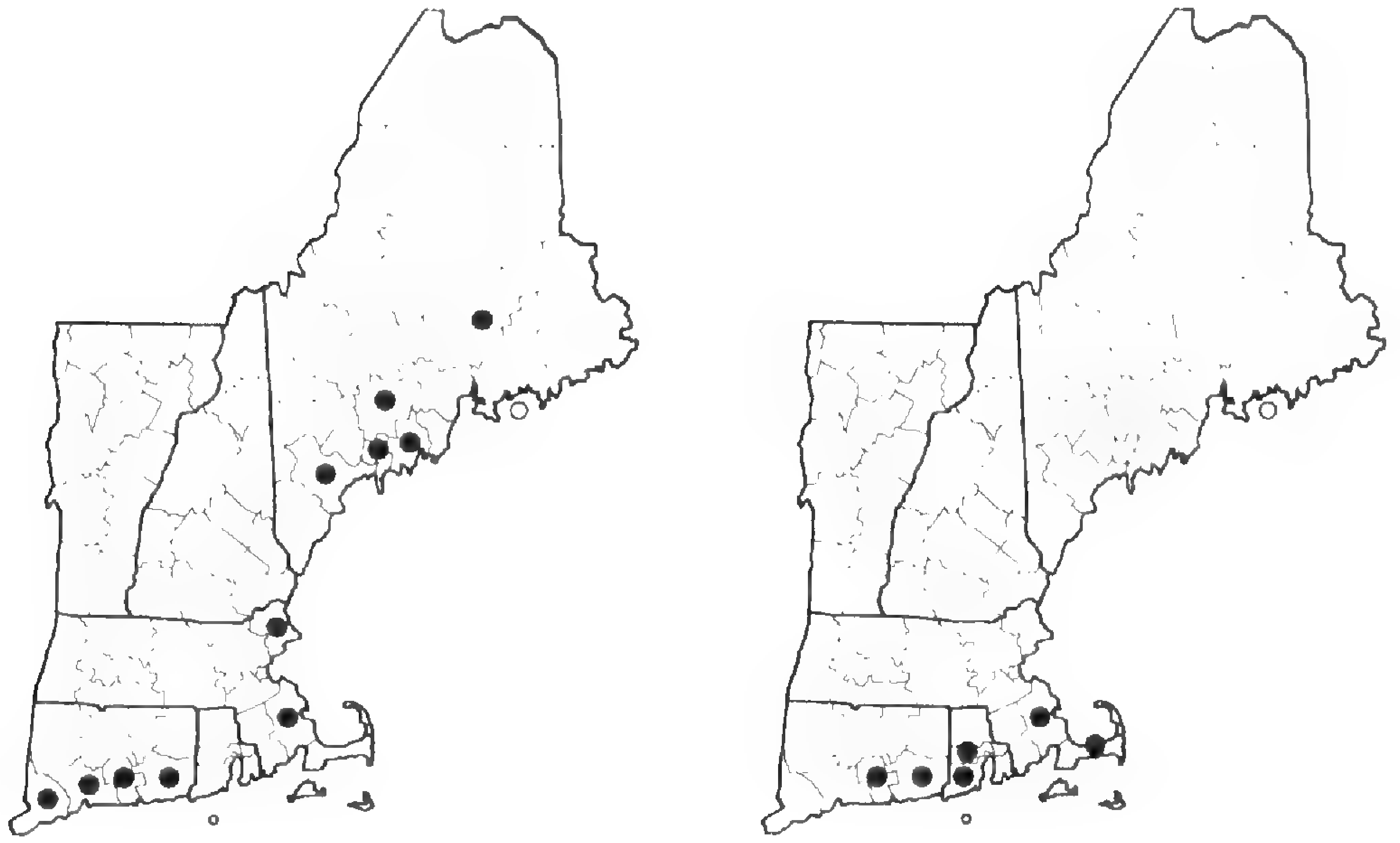
Tradescantia ohiensis
X *T. virginiana*

DIOSCOREA BATATAS

Figure 9. Distribution maps for *Tradescantia virginiana*, *T. ohiensis* X *T. SUBASPERA*, *T. ohiensis* X *T. virginiana*, and *DIOSCOREA BATATAS*.

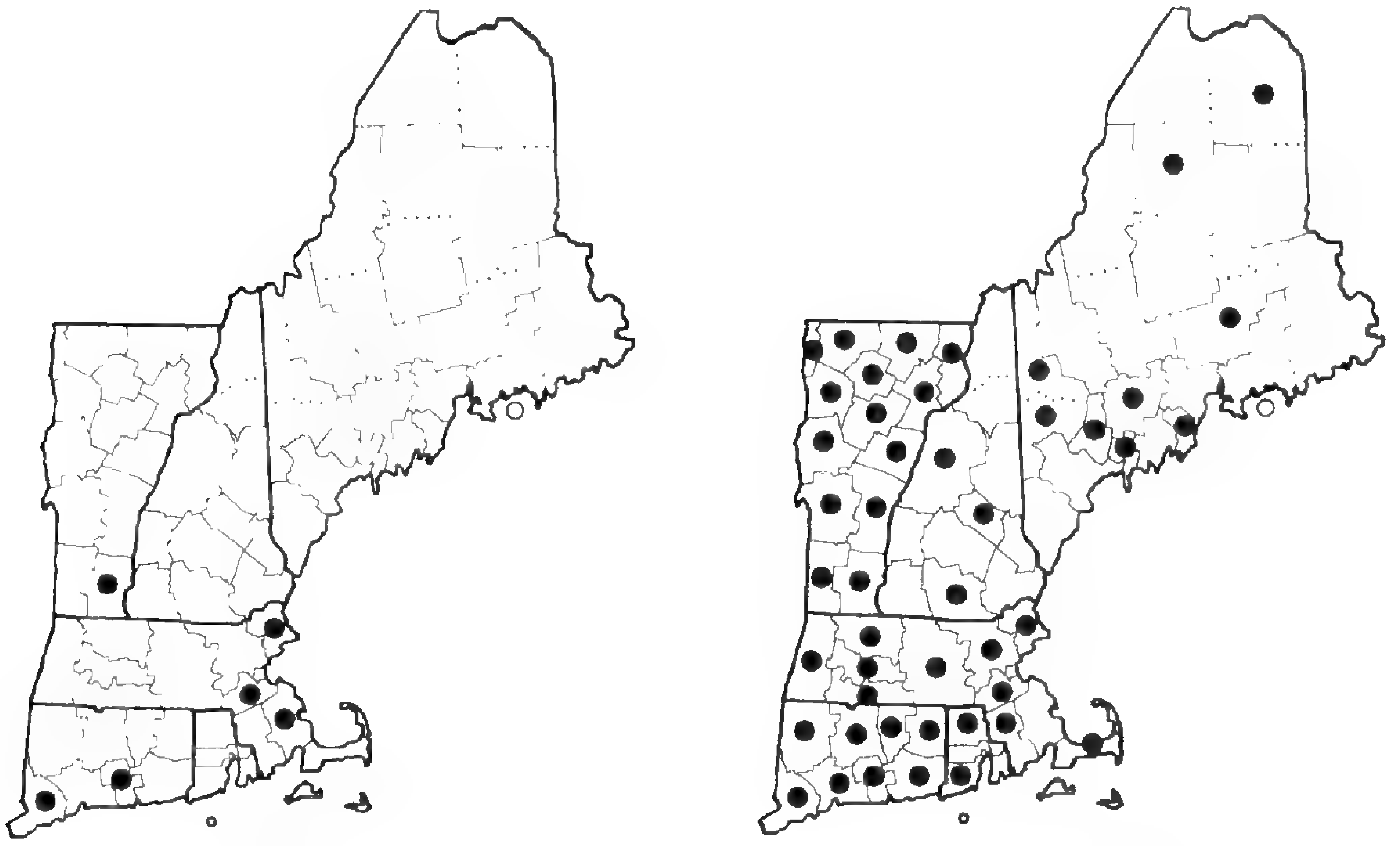


Dioscorea villosa *Eriocaulon aquaticum*



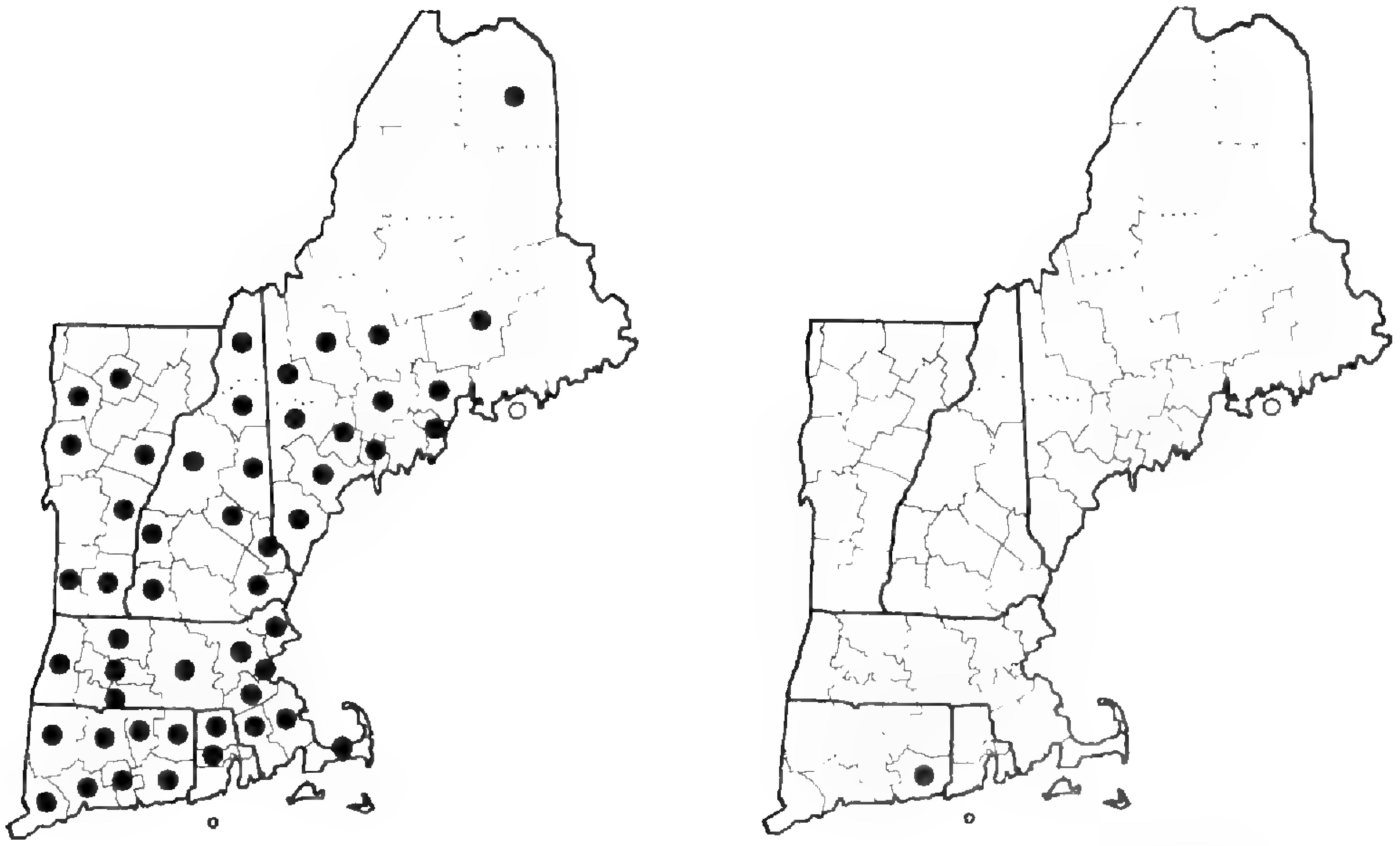
Eriocaulon parkeri *Lachnanthes caroliniana*

Figure 10. Distribution maps for *Dioscorea villosa, Eriocaulon aquaticum, E. parkeri,* and *Lachnanthes caroliniana.*



EGERIA DENSA

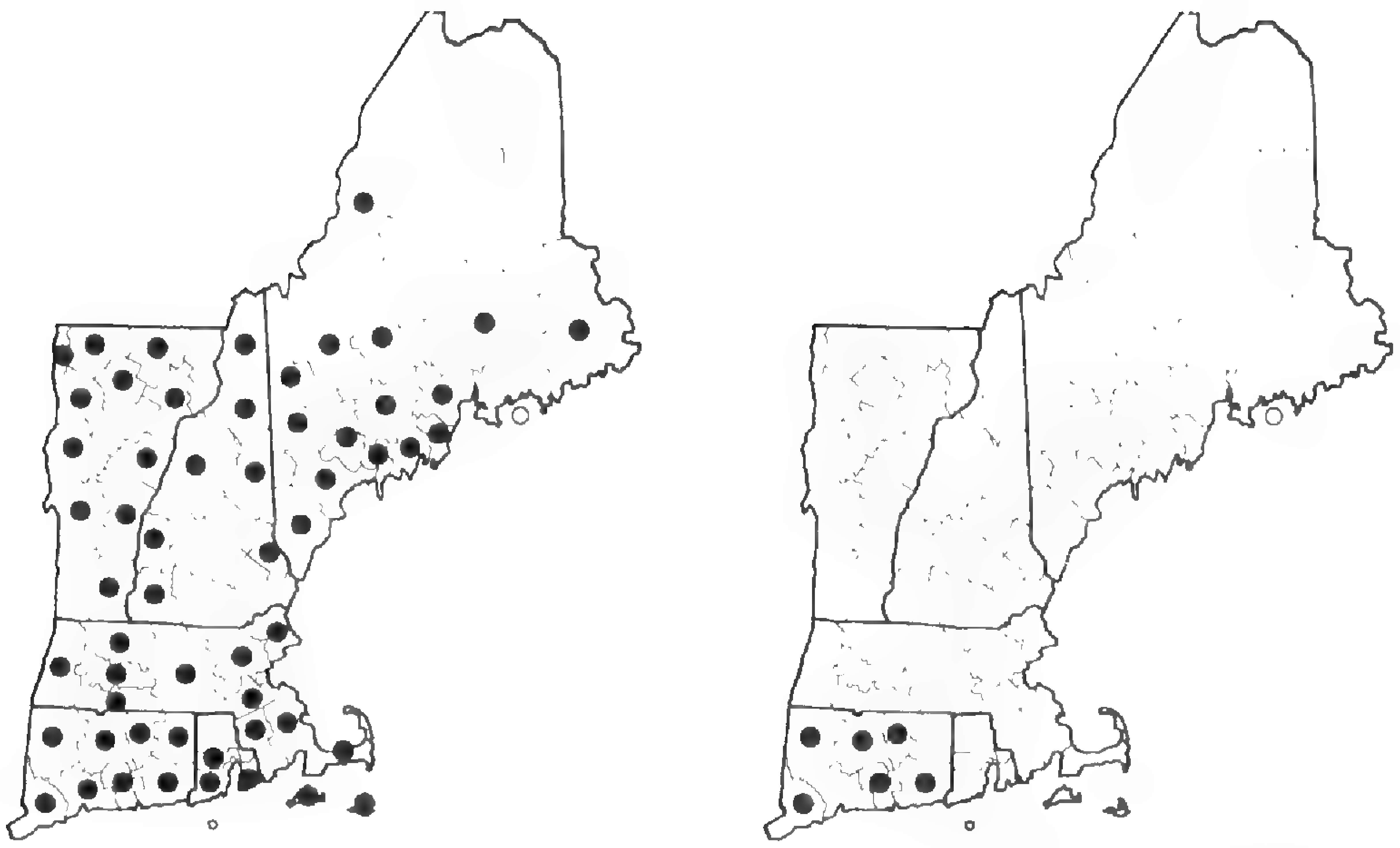
Elodea canadensis



Elodea nuttallii

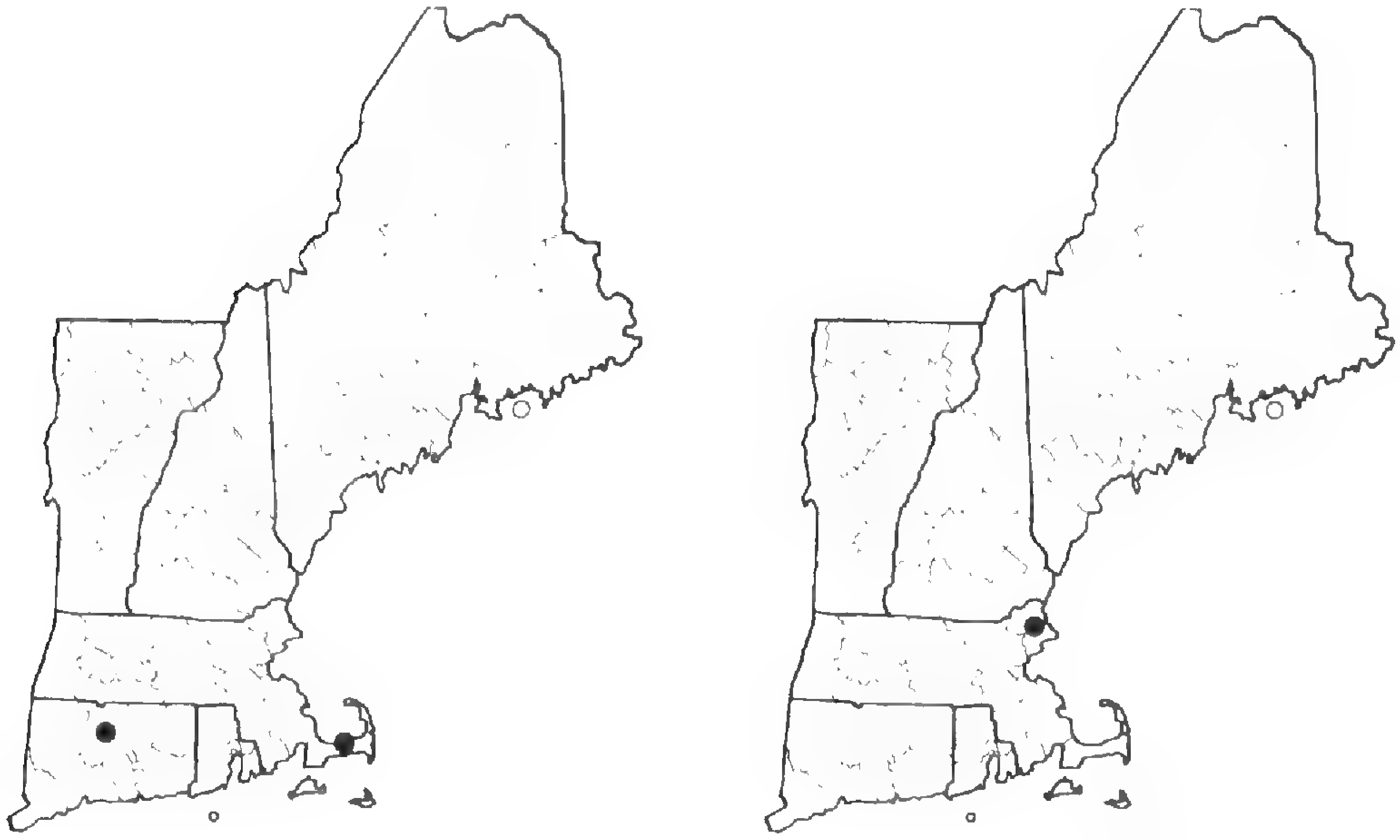
HYDRILLA VERTICILLATA

Figure 11. Distribution maps for *EGERIA DENSA*, *Elodea canadensis*, *E. nuttallii*, and *HYDRILLA VERTICILLATA*.



Vallisneria americana

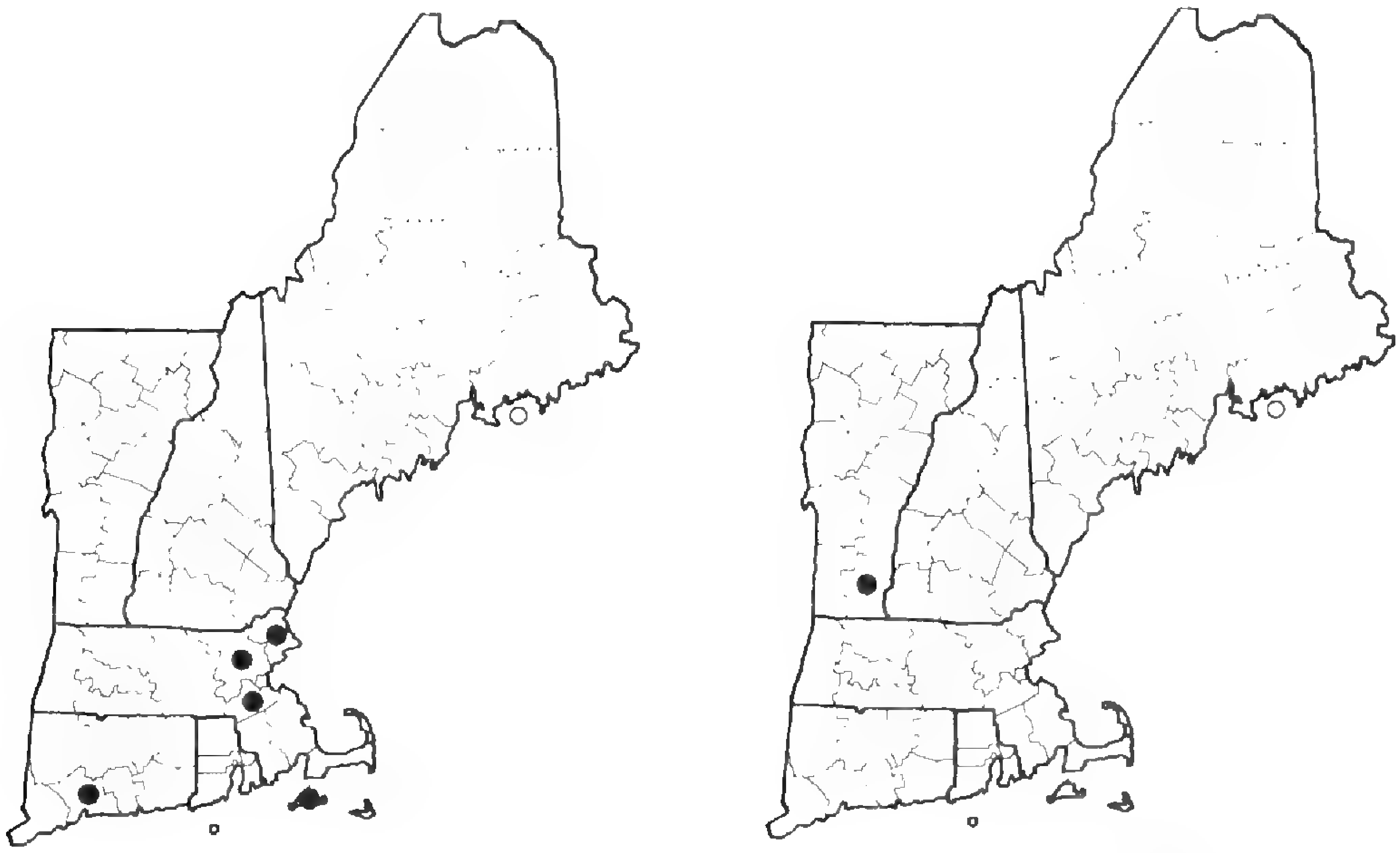
BELAMCANDA CHINENSIS



CROCUS VERNUS
subsp. *VERNUS*

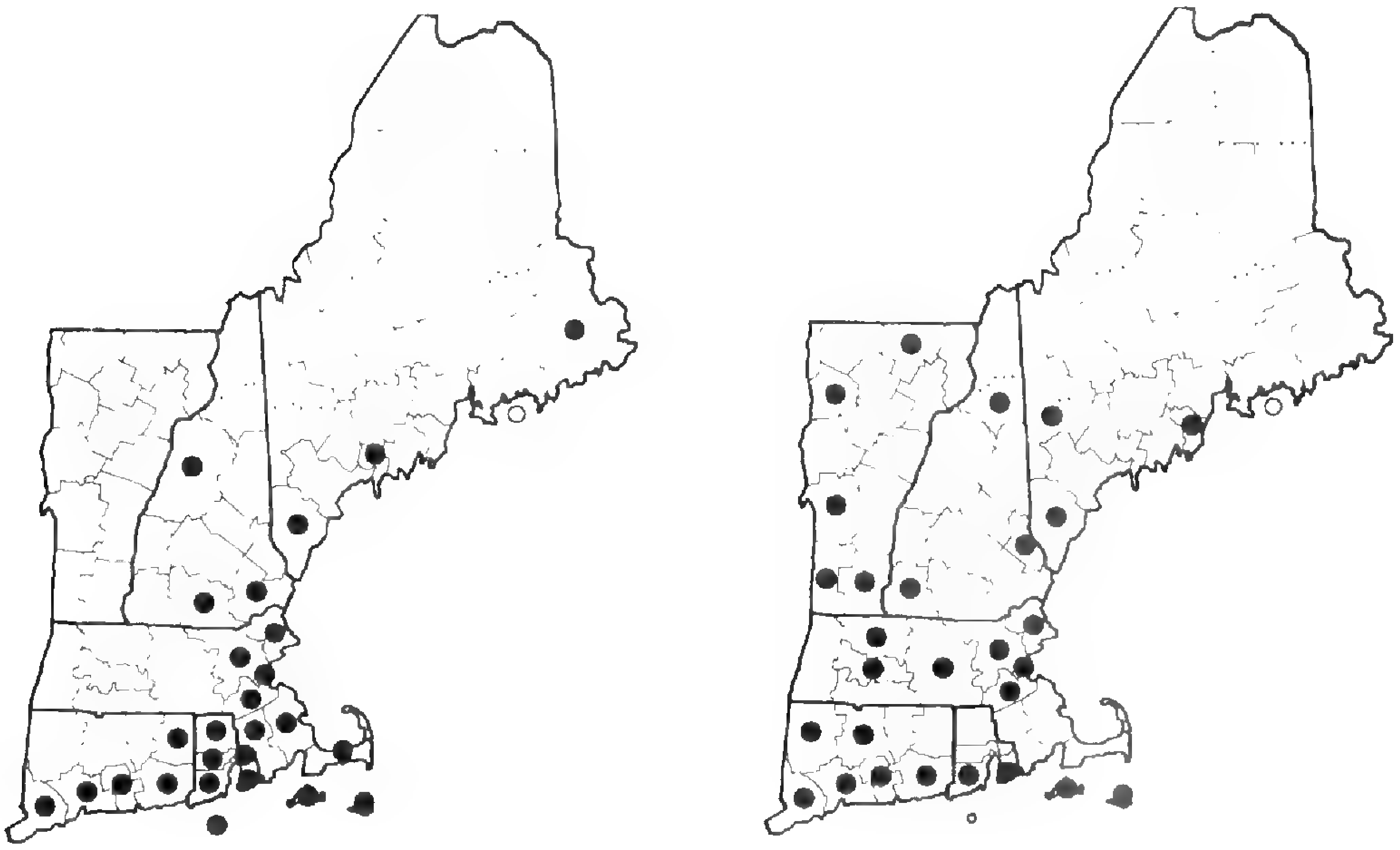
IRIS CRISTATA

Figure 12. Distribution maps for *Vallisneria americana, BELAMCANDA CHINENSIS, CROCUS VERNUS* subsp. *VERNUS,* and *IRIS CRISTATA.*



IRIS GERMANICA

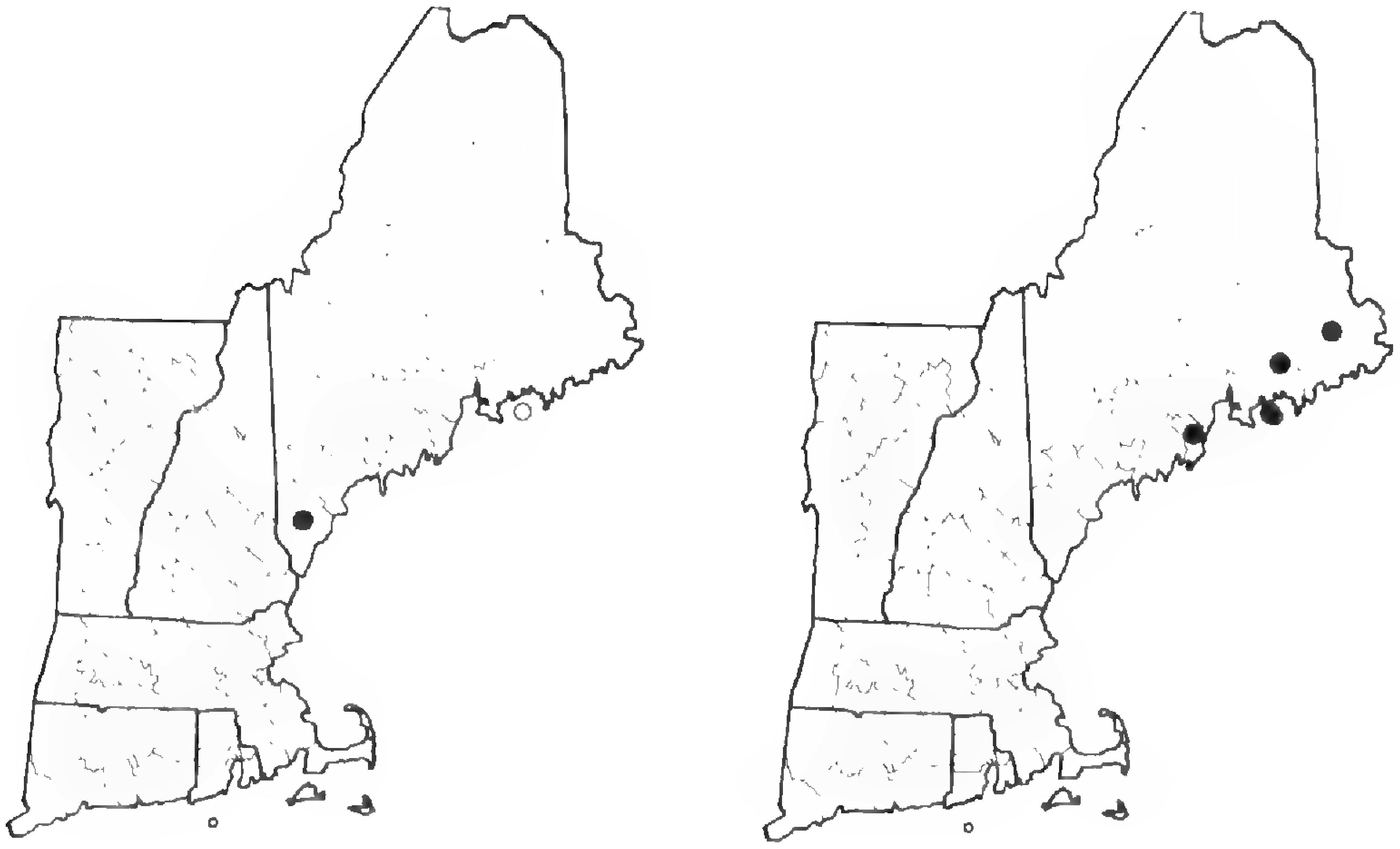
IRIS KAEMPFERI



Iris prismatica

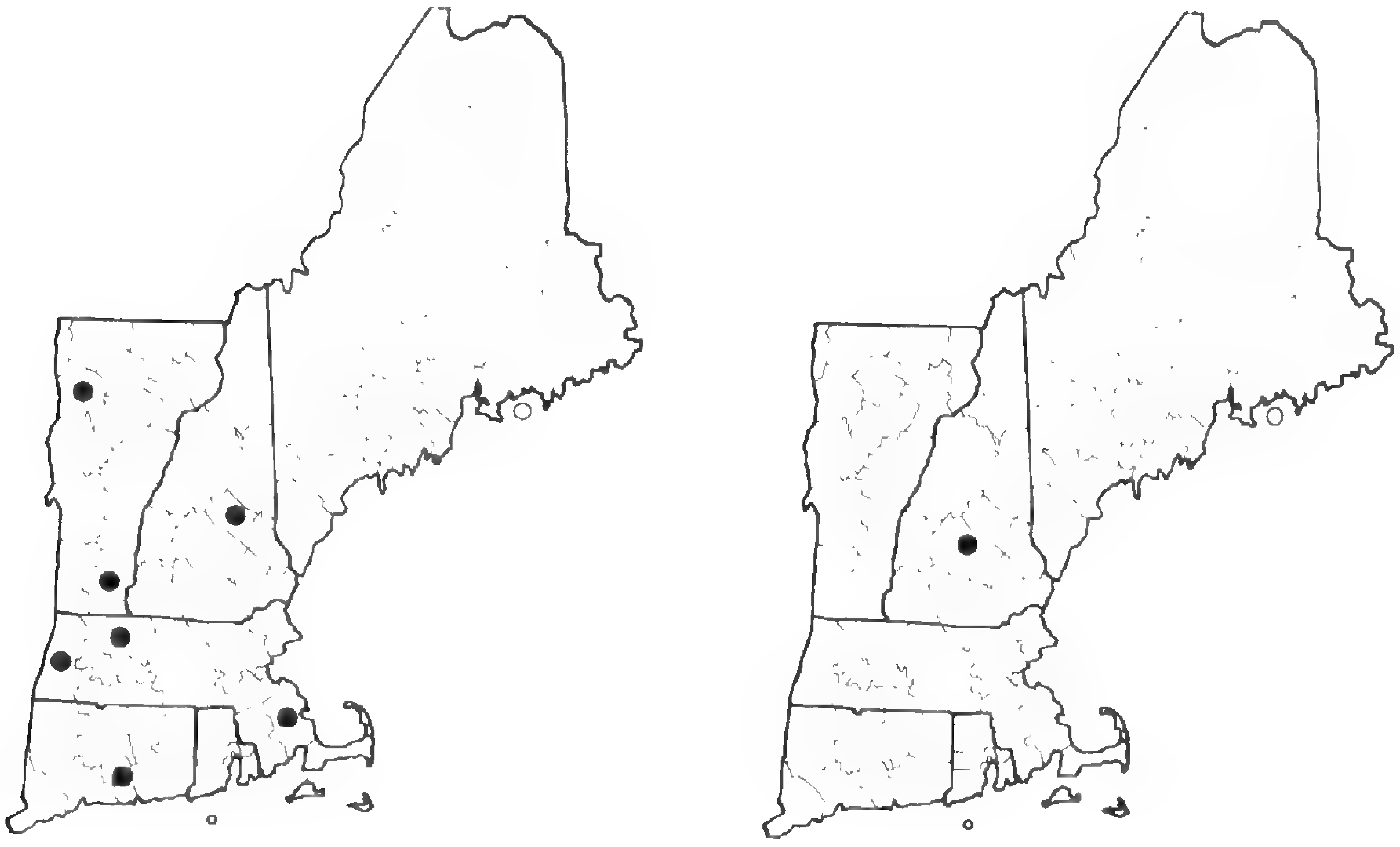
IRIS PSEUDACORUS

Figure 13. Distribution maps for *IRIS GERMANICA, I. KAEMPFERI, I. prismatica,* and *I. PSEUDACORUS.*



IRIS PUMILA
subsp. *PUMILA*

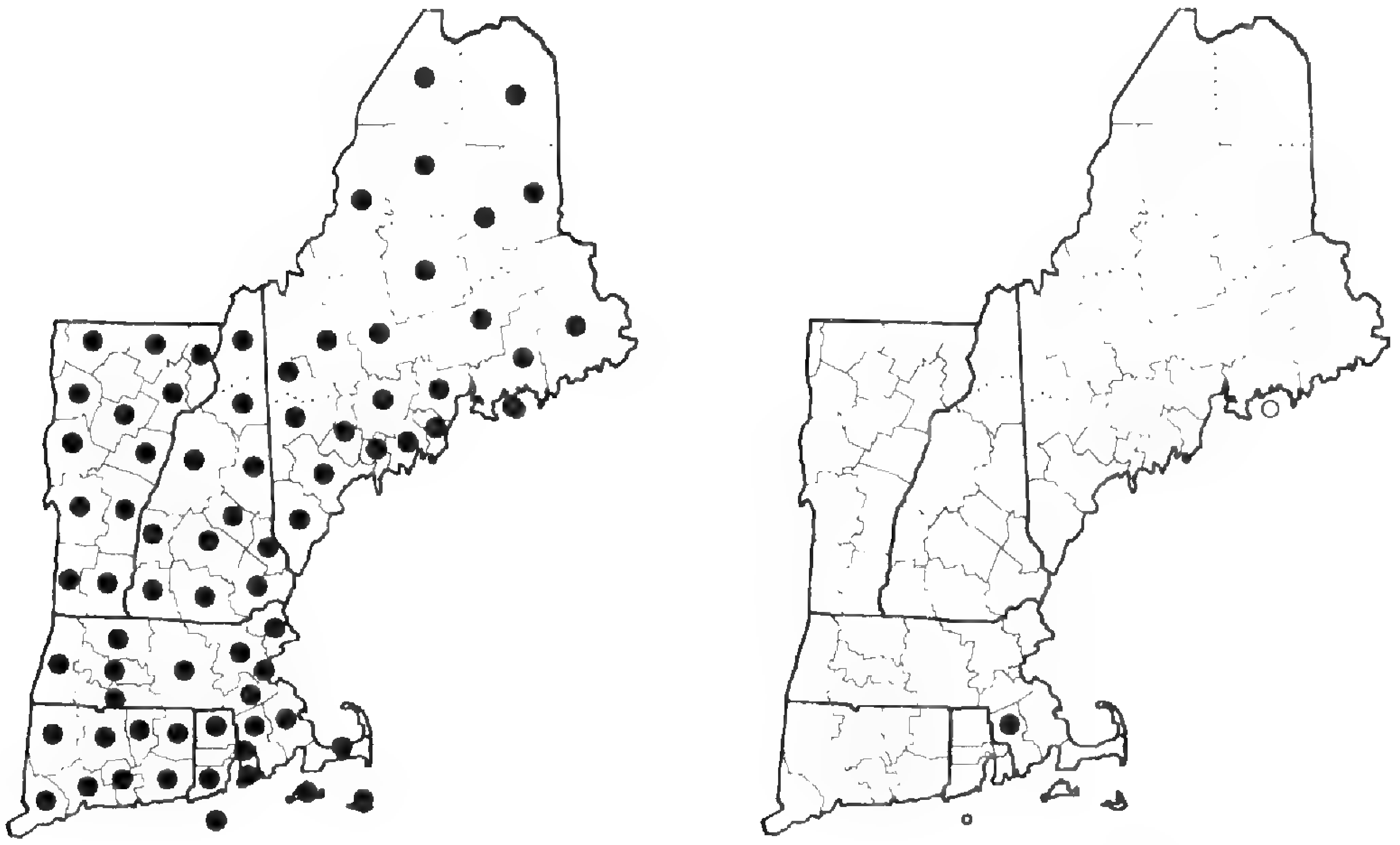
Iris setosa



IRIS SIBIRICA

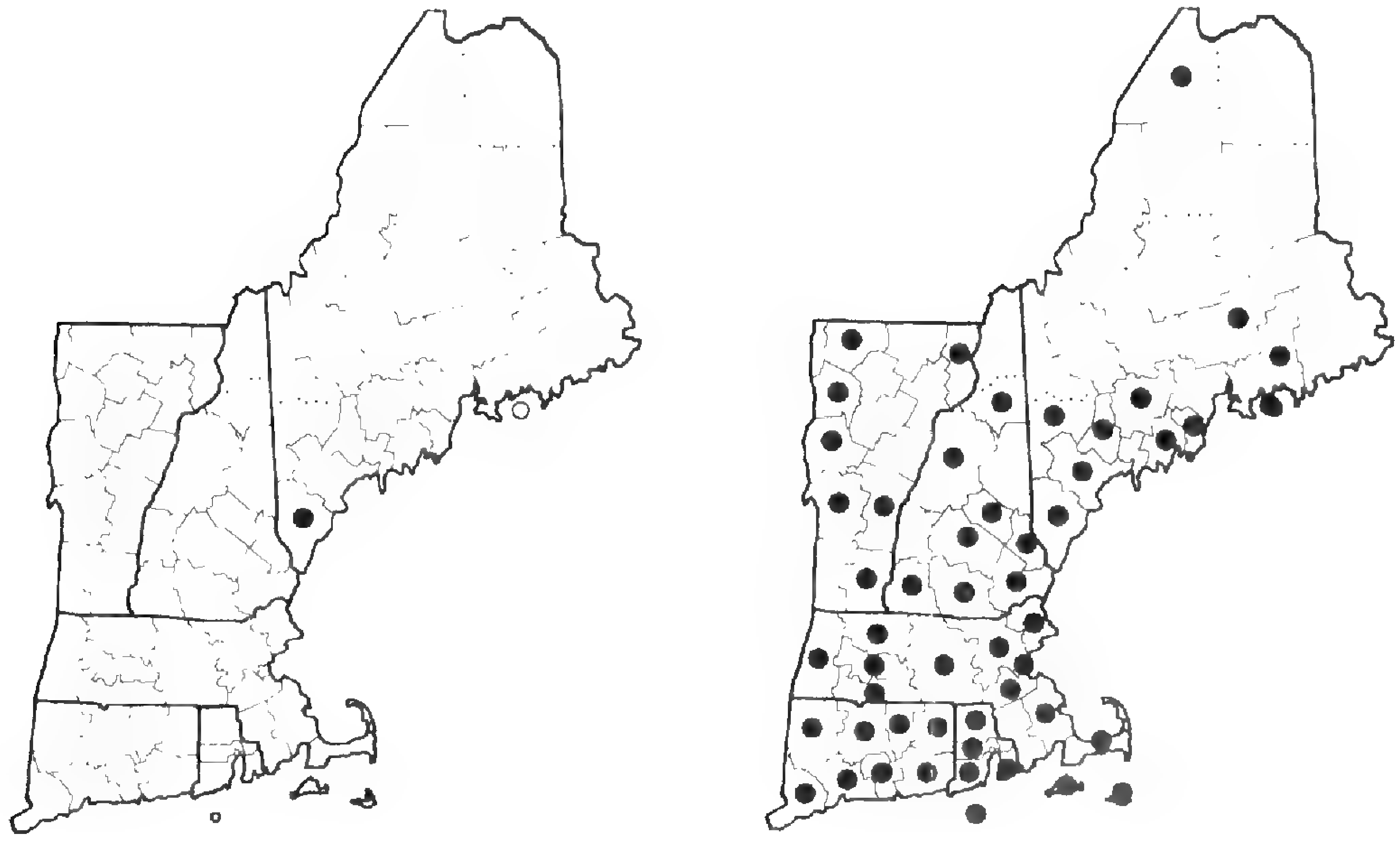
IRIS TECTORUM

Figure 14. Distribution maps for *IRIS PUMILA* subsp. *PUMILA*, *I. setosa*, *I. SIBIRICA*, and *I. TECTORUM*.



Iris versicolor

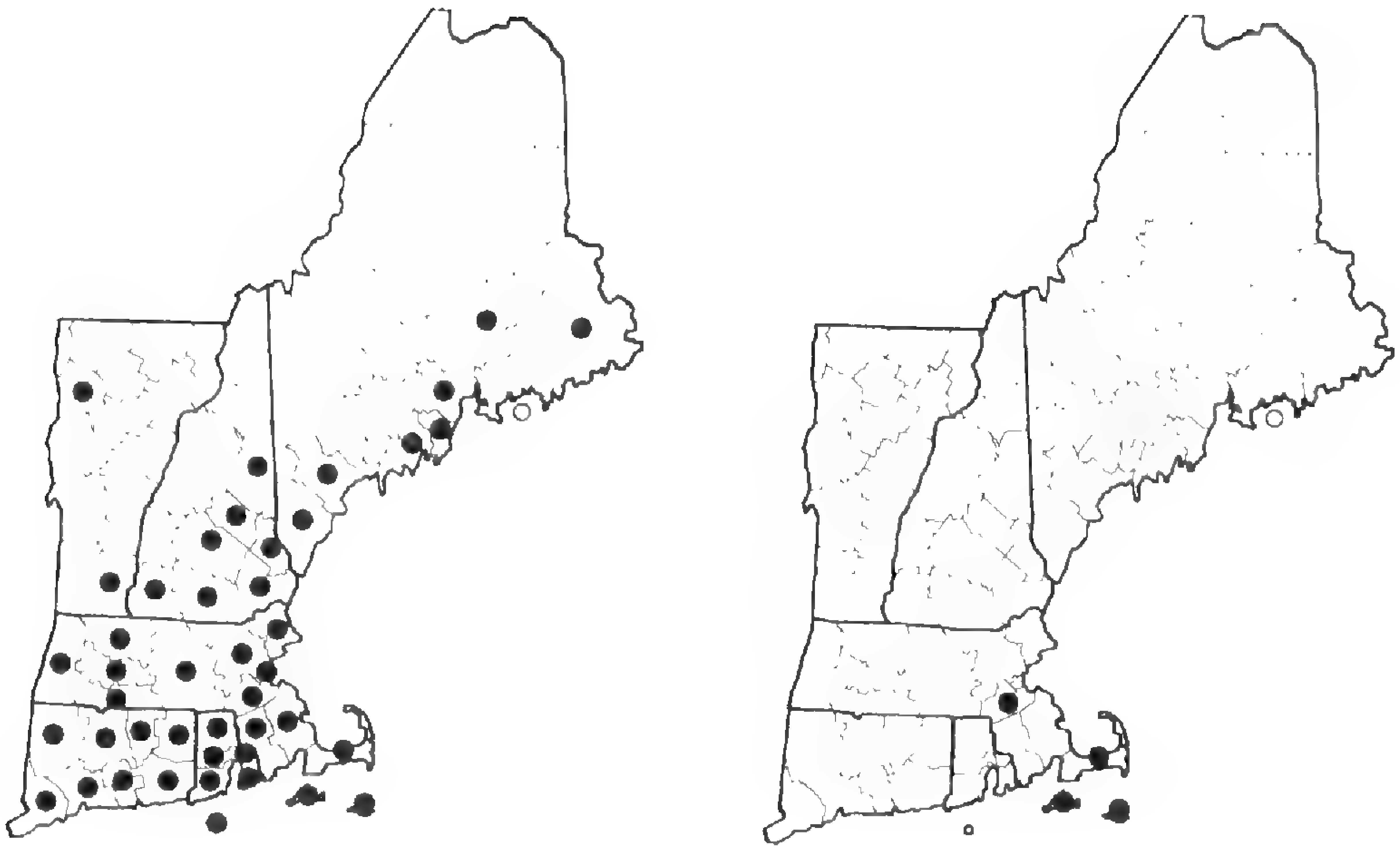
Iris prismatica
X *I. versicolor*



Sisyrinchium albidum

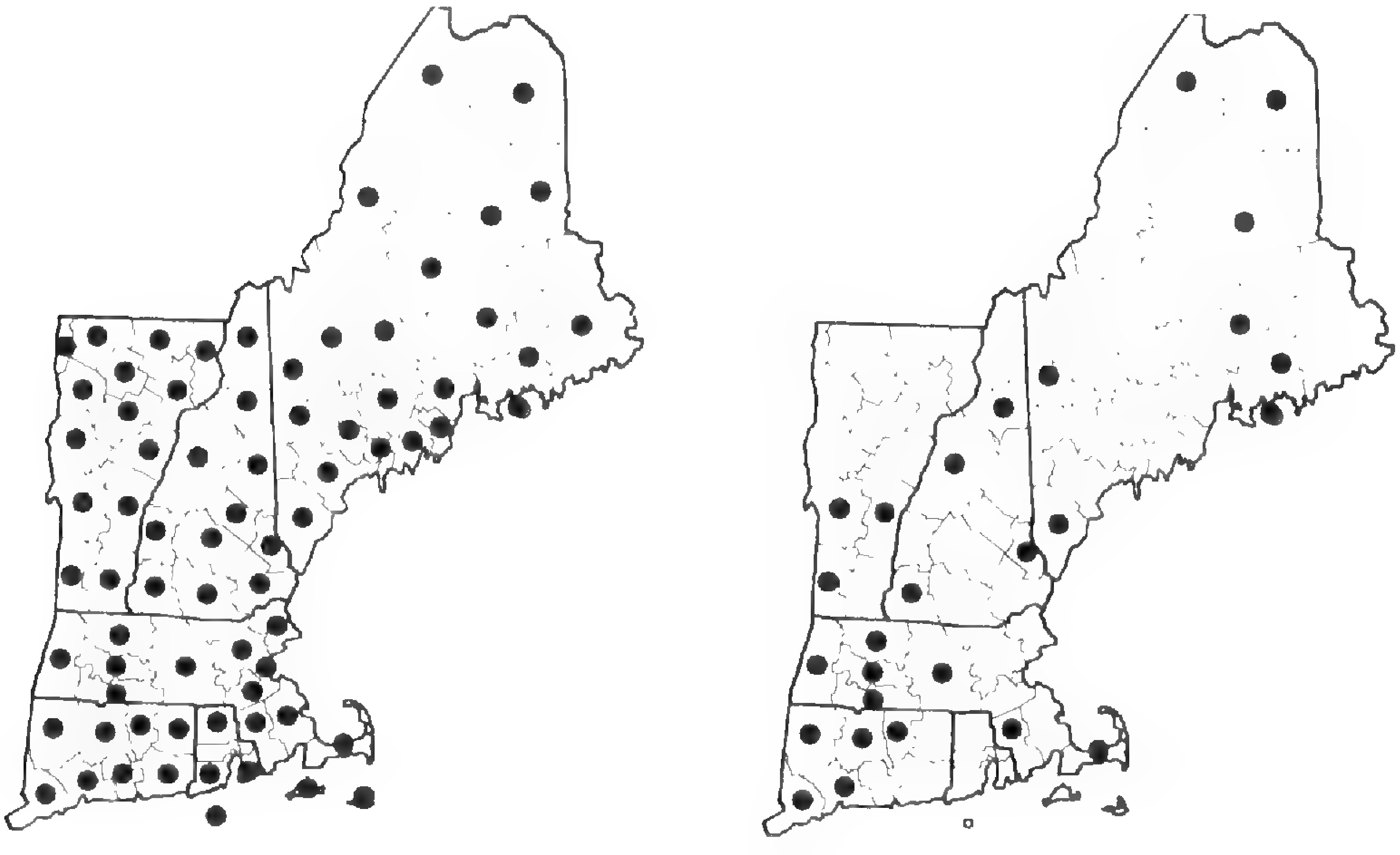
Sisyrinchium angustifolium

Figure 15. Distribution maps for *Iris versicolor, I. prismatica* X *I. versicolor, Sisyrinchium albidum,* and *S. angustifolium.*



Sisyrinchium atlanticum

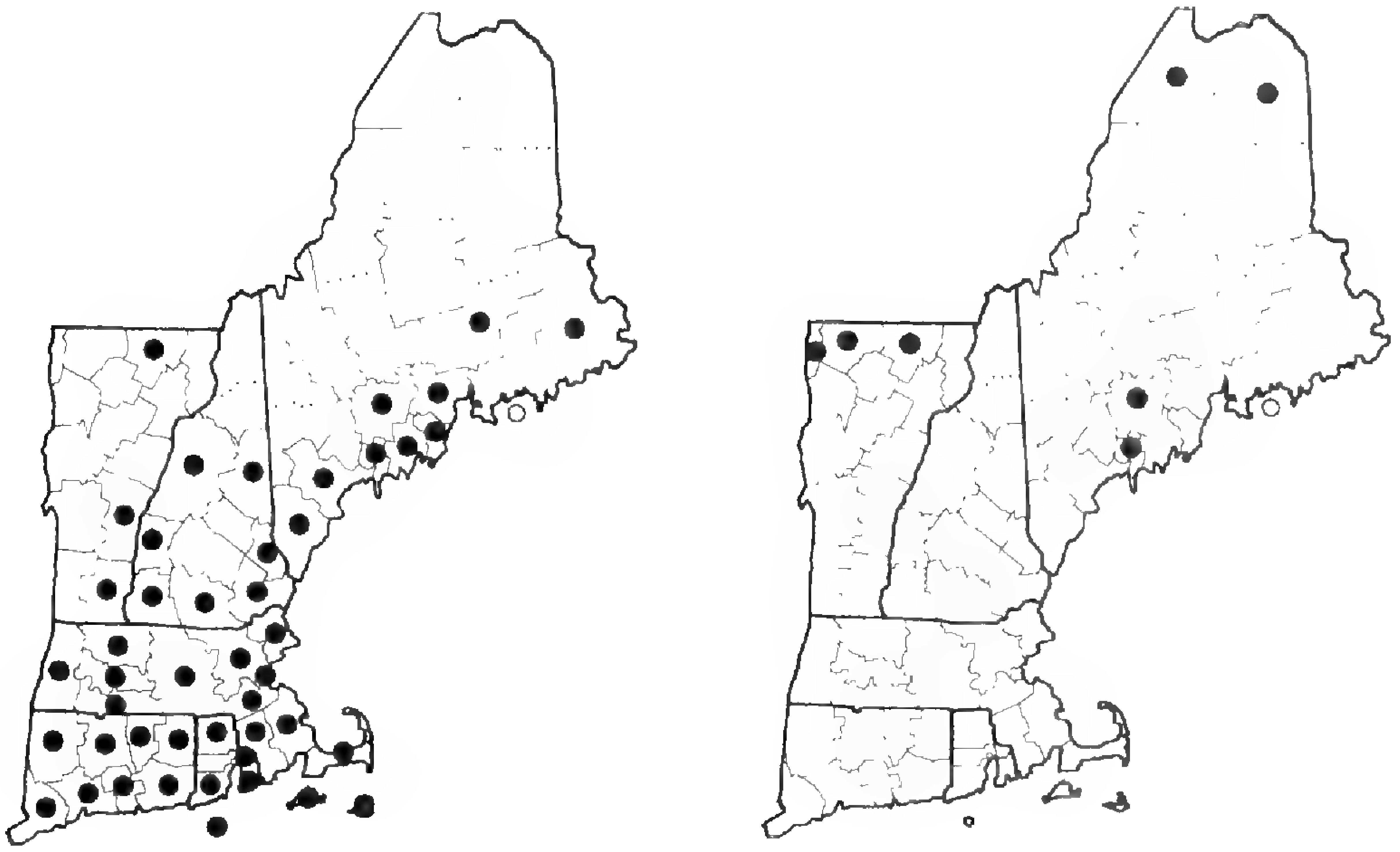
Sisyrinchium fuscatum



Sisyrinchium montanum
var. *crebrum*

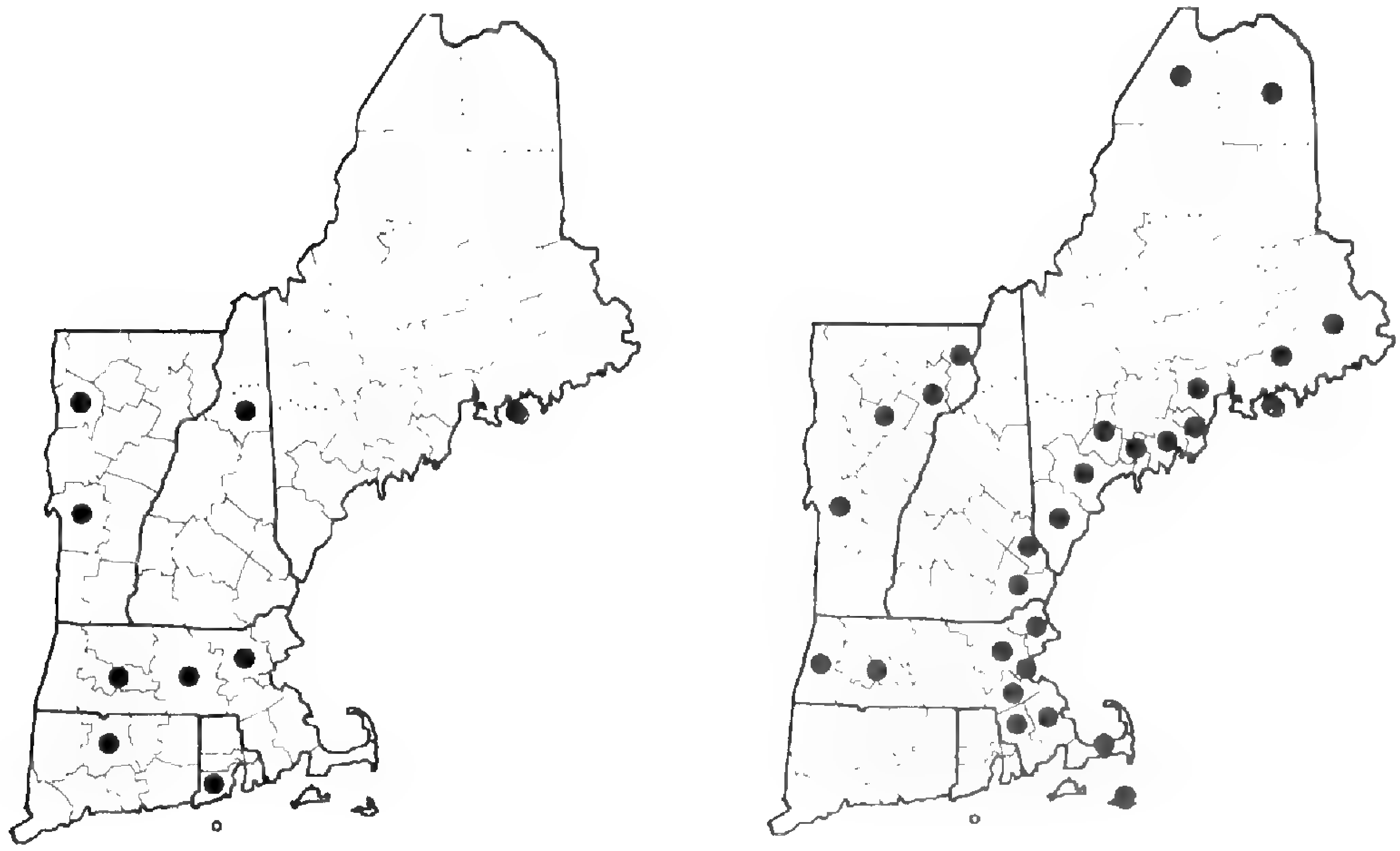
Sisyrinchium mucronatum

Figure 16. Distribution maps for *Sisyrinchium atlanticum, S. fuscatum, S. montanum* var. *crebrum,* and *S. mucronatum.*



Juncus acuminatus

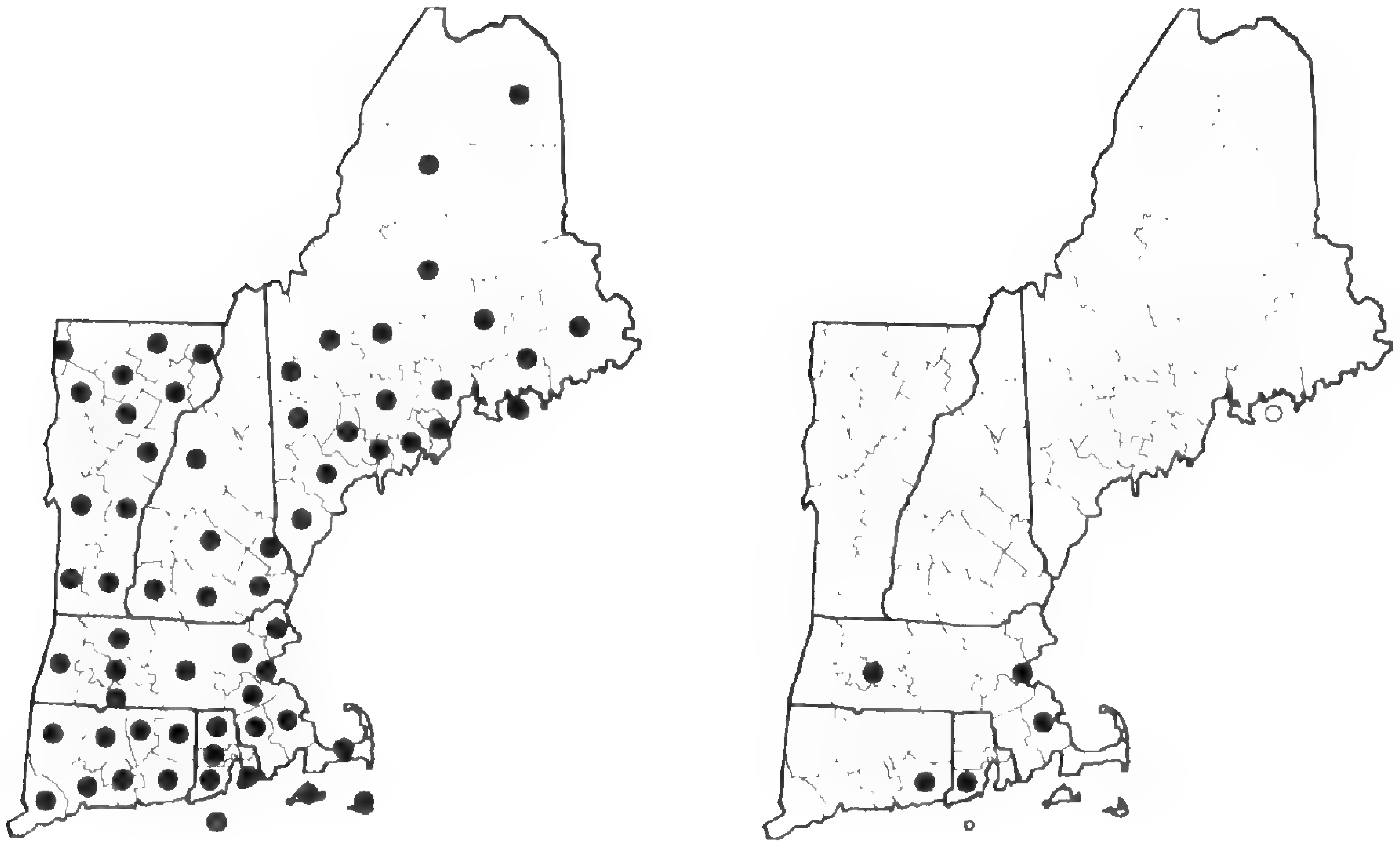
Juncus alpinoarticulatus



Juncus anthelatus

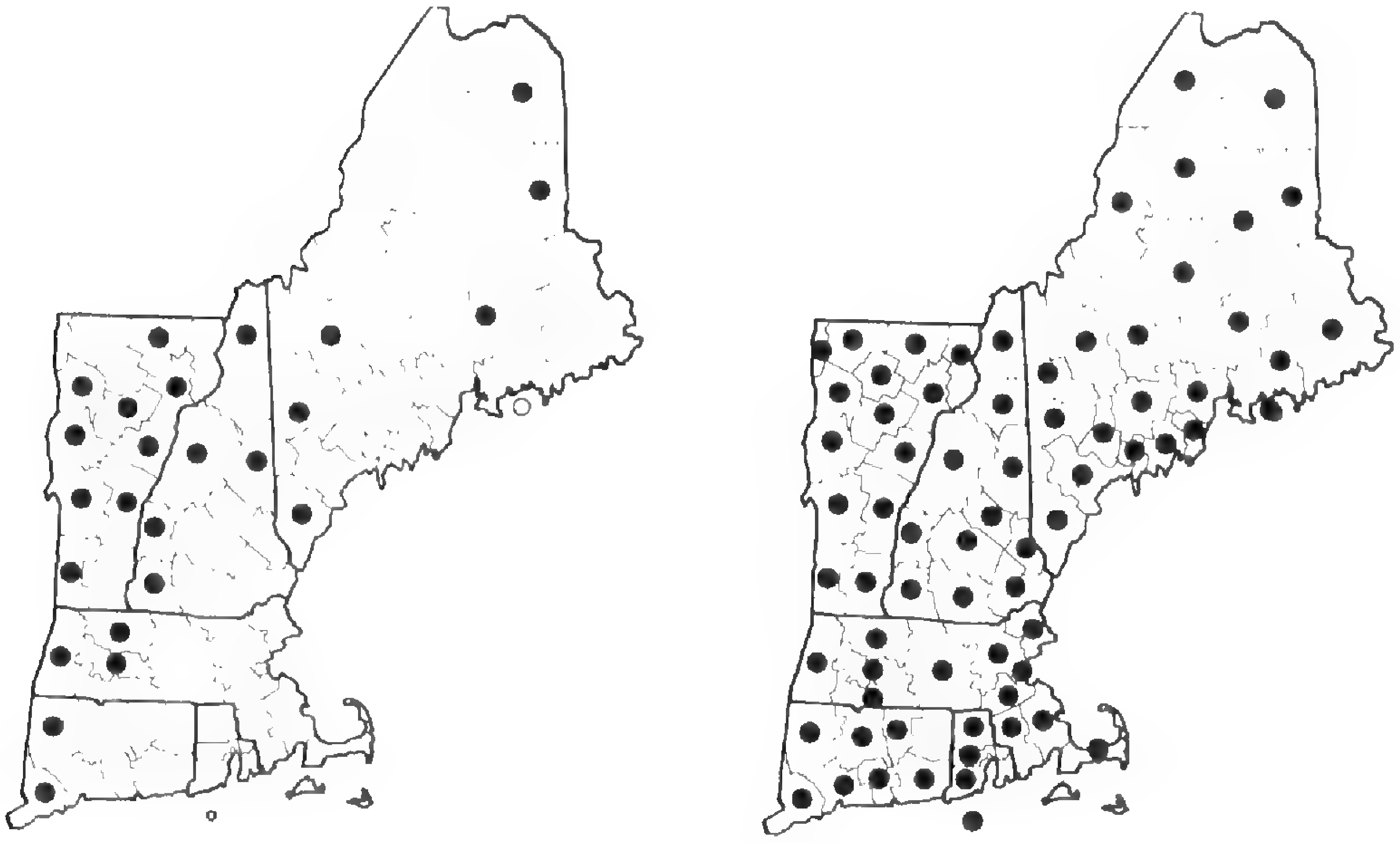
Juncus arcticus
var. *balticus*

Figure 17. Distribution maps for *Juncus acuminatus*, *J. alpinoarticulatus*, *J. anthelatus*, and *J. arcticus* var. *balticus*.



Juncus articulatus

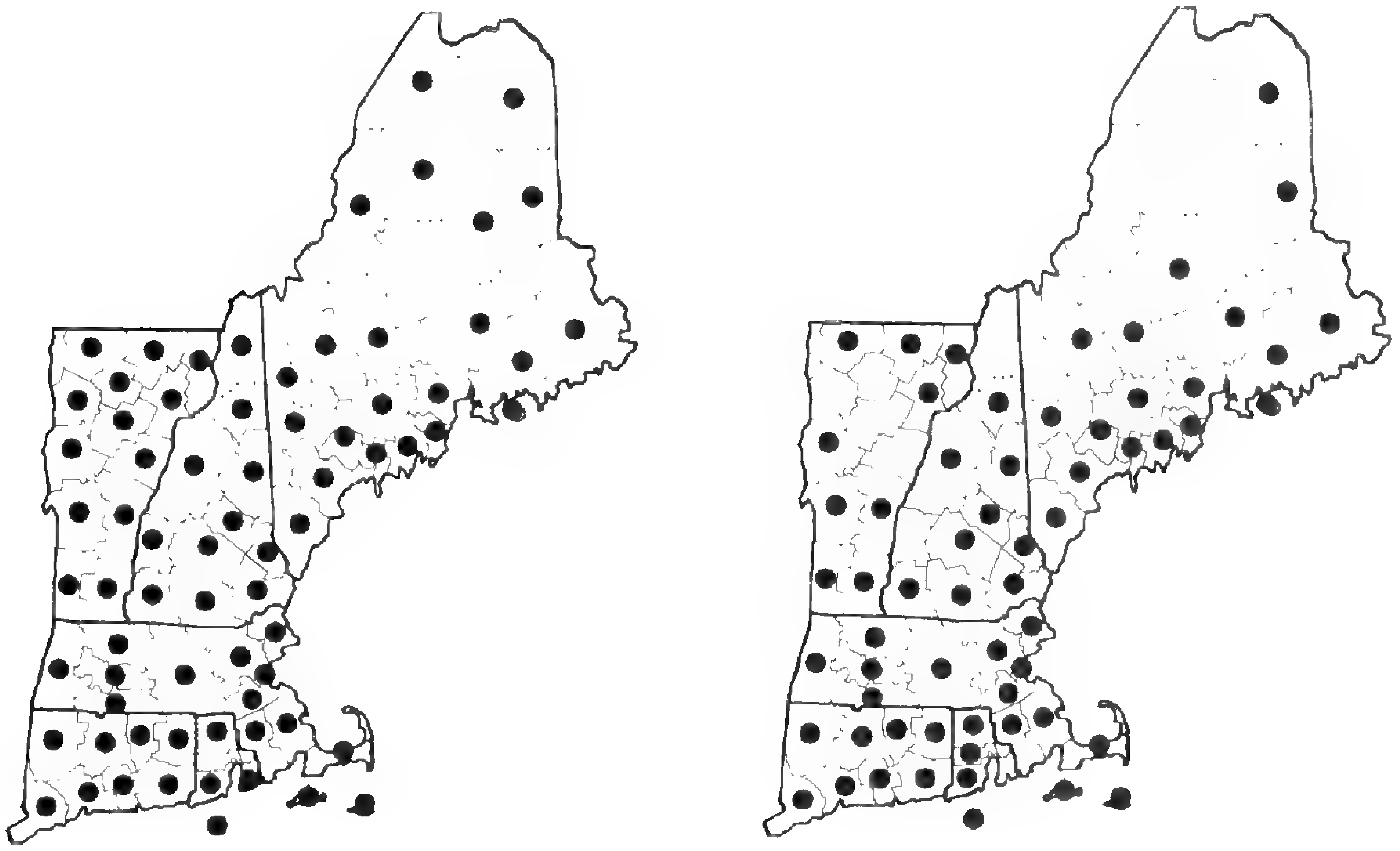
Juncus brachycarpus



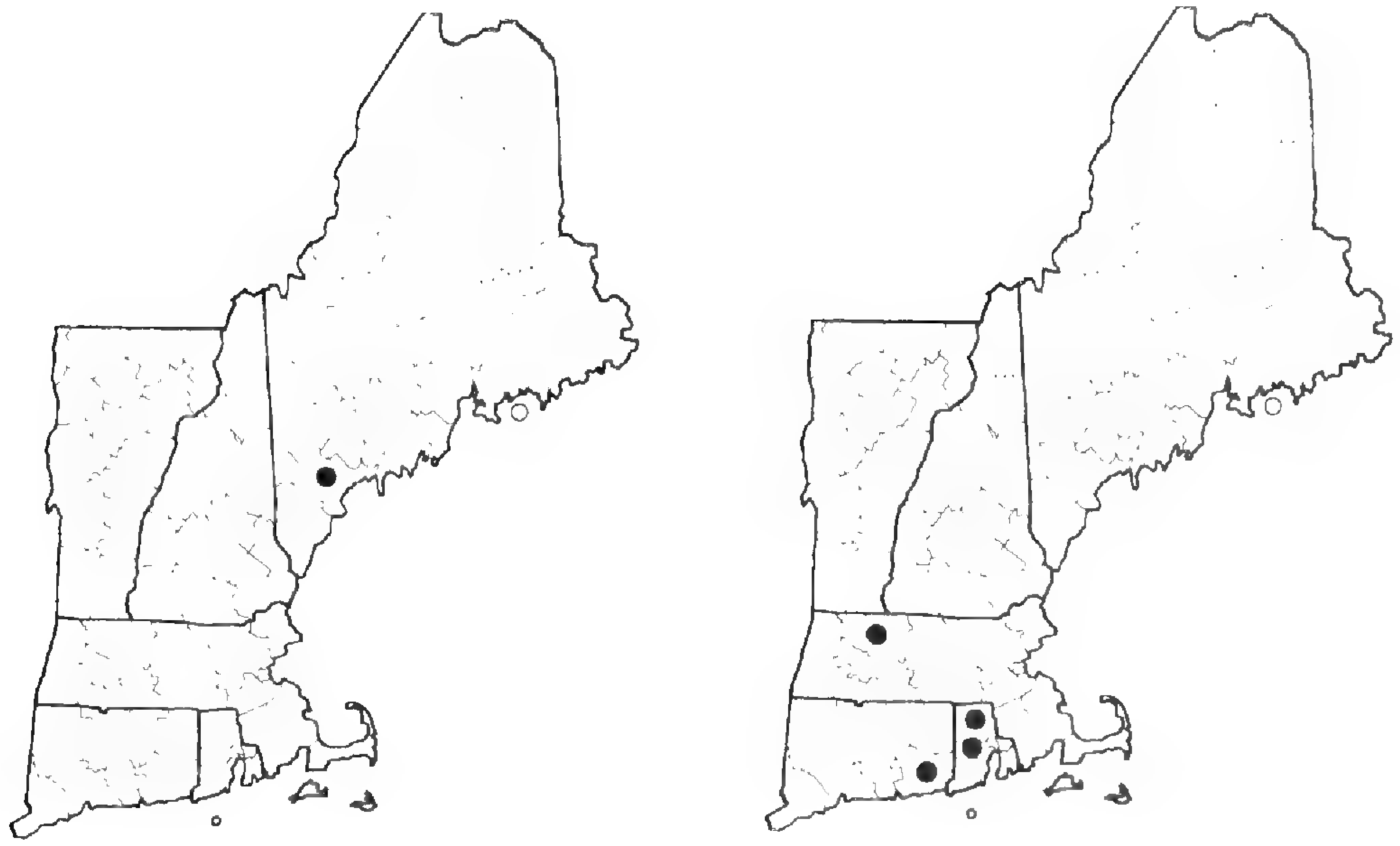
Juncus brachycephalus

Juncus brevicaudatus

Figure 18. Distribution maps for *Juncus articulatus*, *J. brachycarpus*, *J. brachycephalus*, and *J. brevicaudatus*.

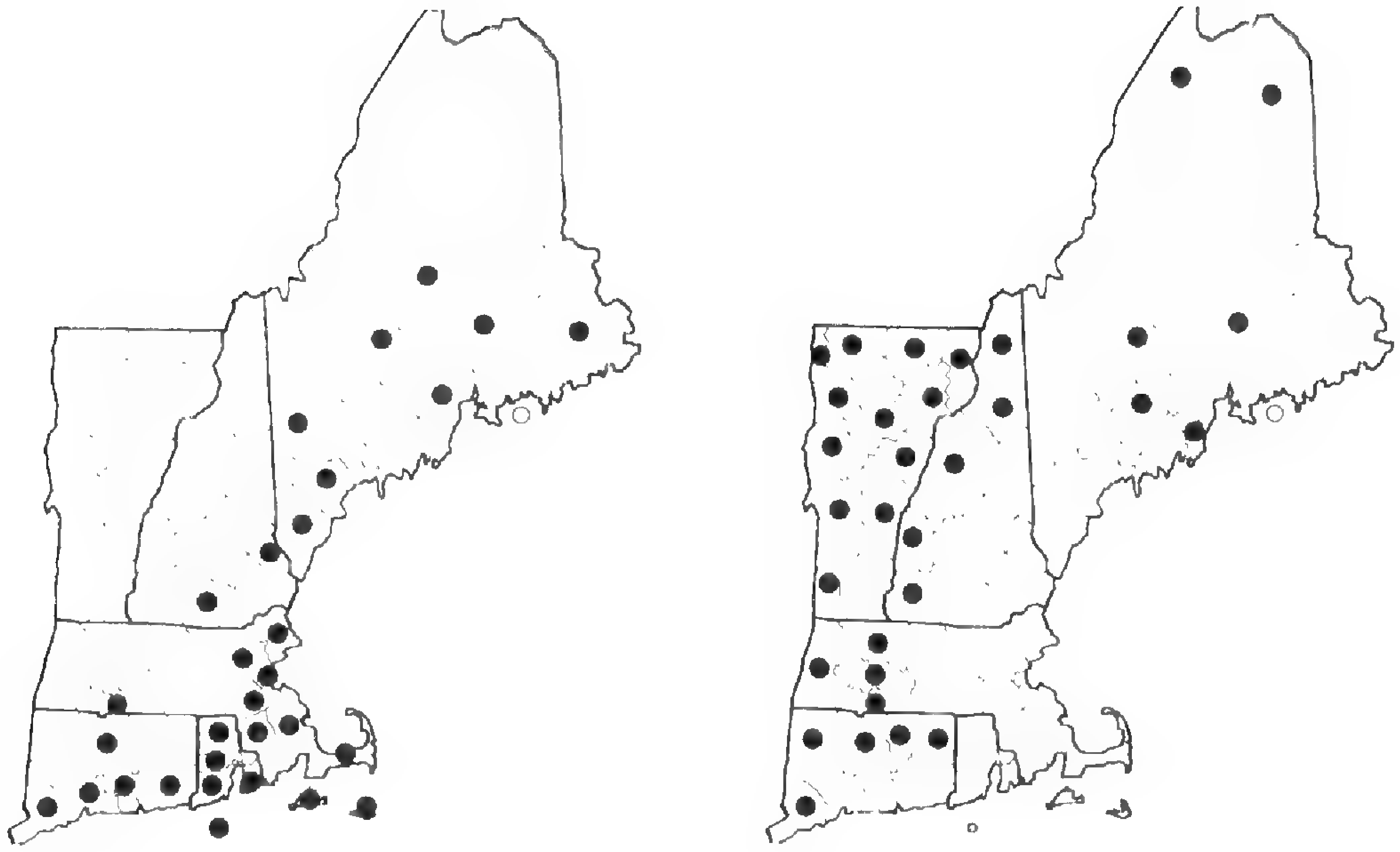


Juncus bufonius *Juncus canadensis*

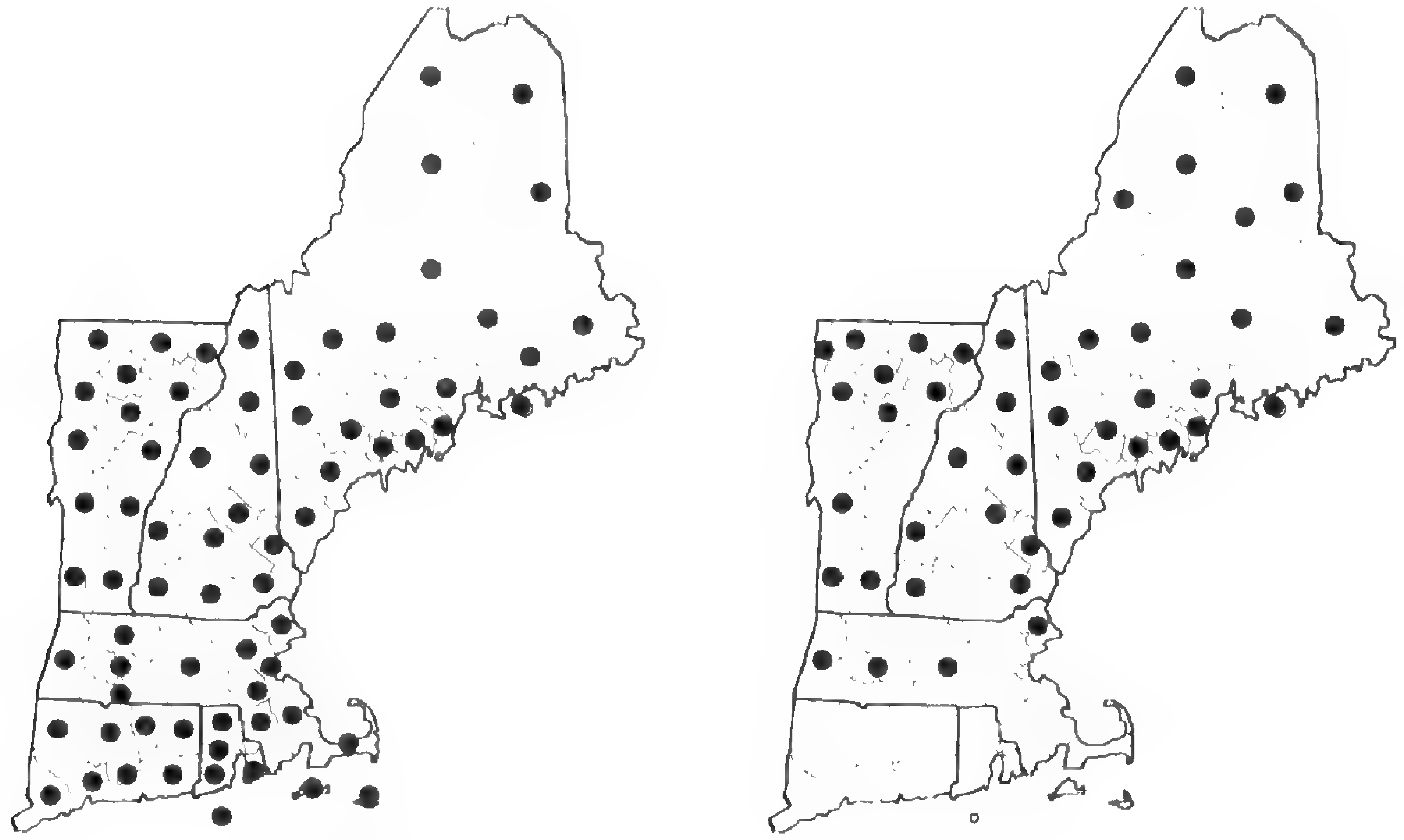


JUNCUS COMPRESSUS *Juncus debilis*

Figure 19. Distribution maps for *Juncus bufonius*, *J. canadensis*, *J. COMPRESSUS*, and *J. debilis*.

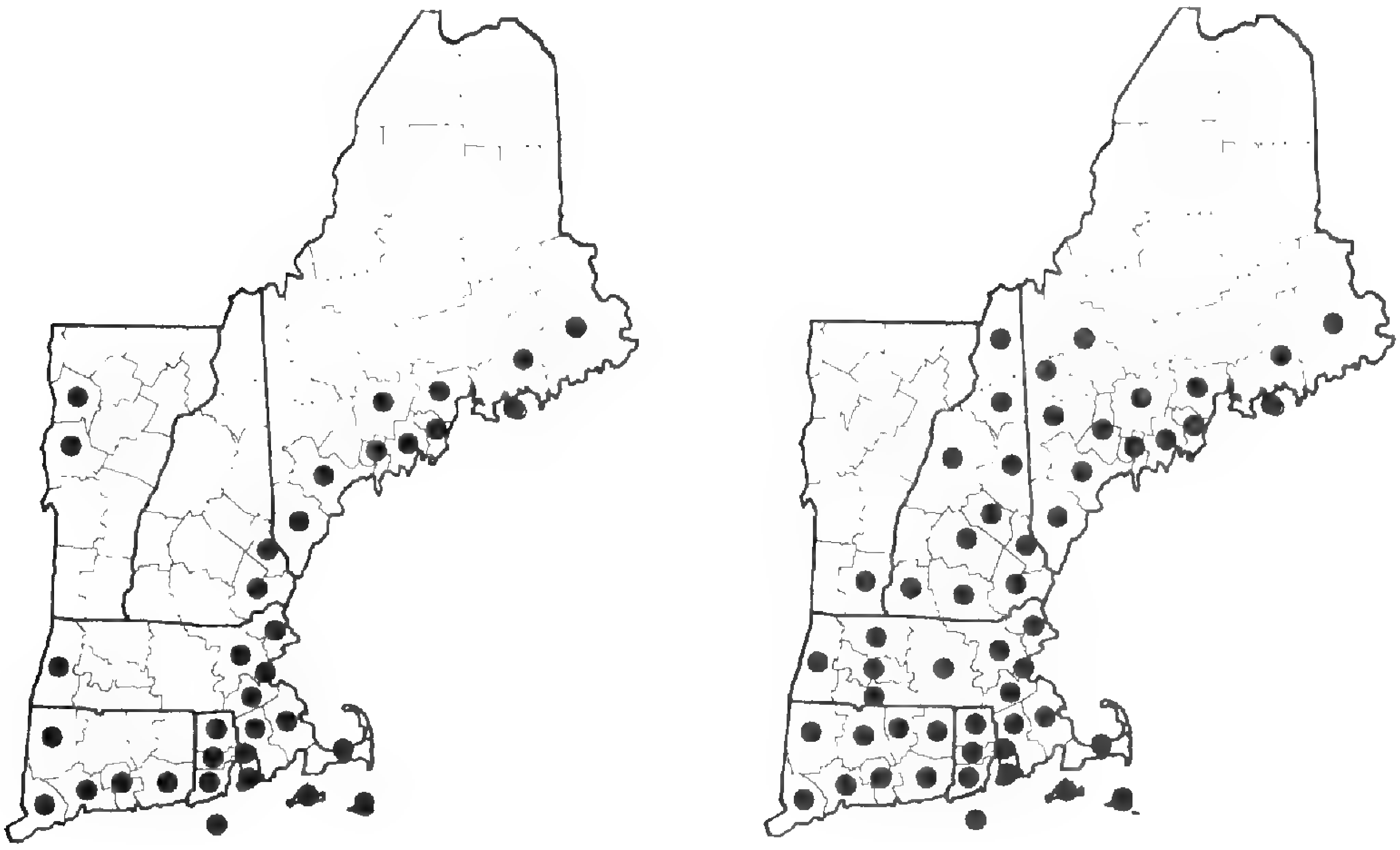


Juncus dichotomus *Juncus dudleyi*

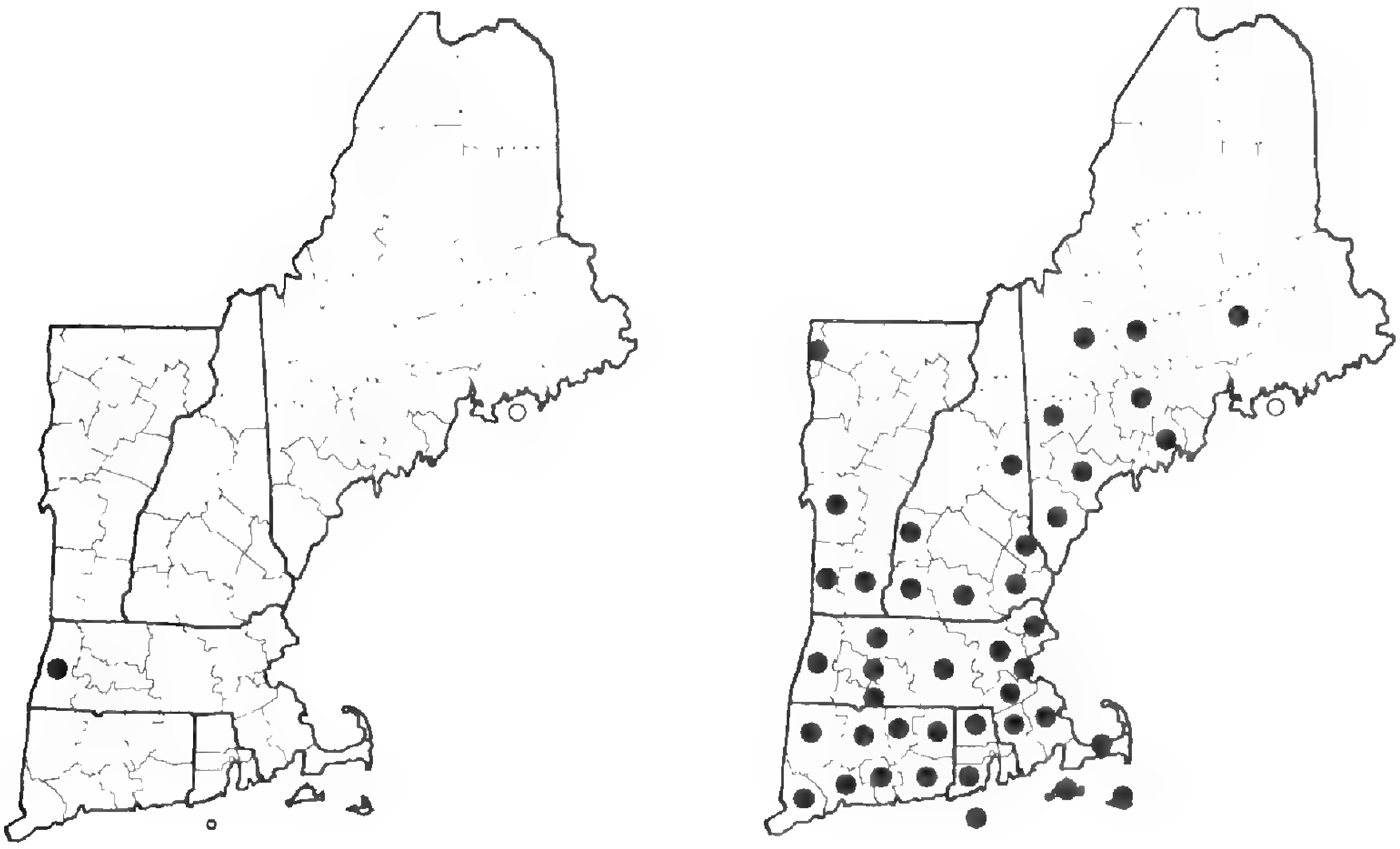


Juncus effusus *Juncus filiformis*

Figure 20. Distribution maps for *Juncus dichotomus*, *J. dudleyi*, *J. effusus*, and *J. filiformis*.

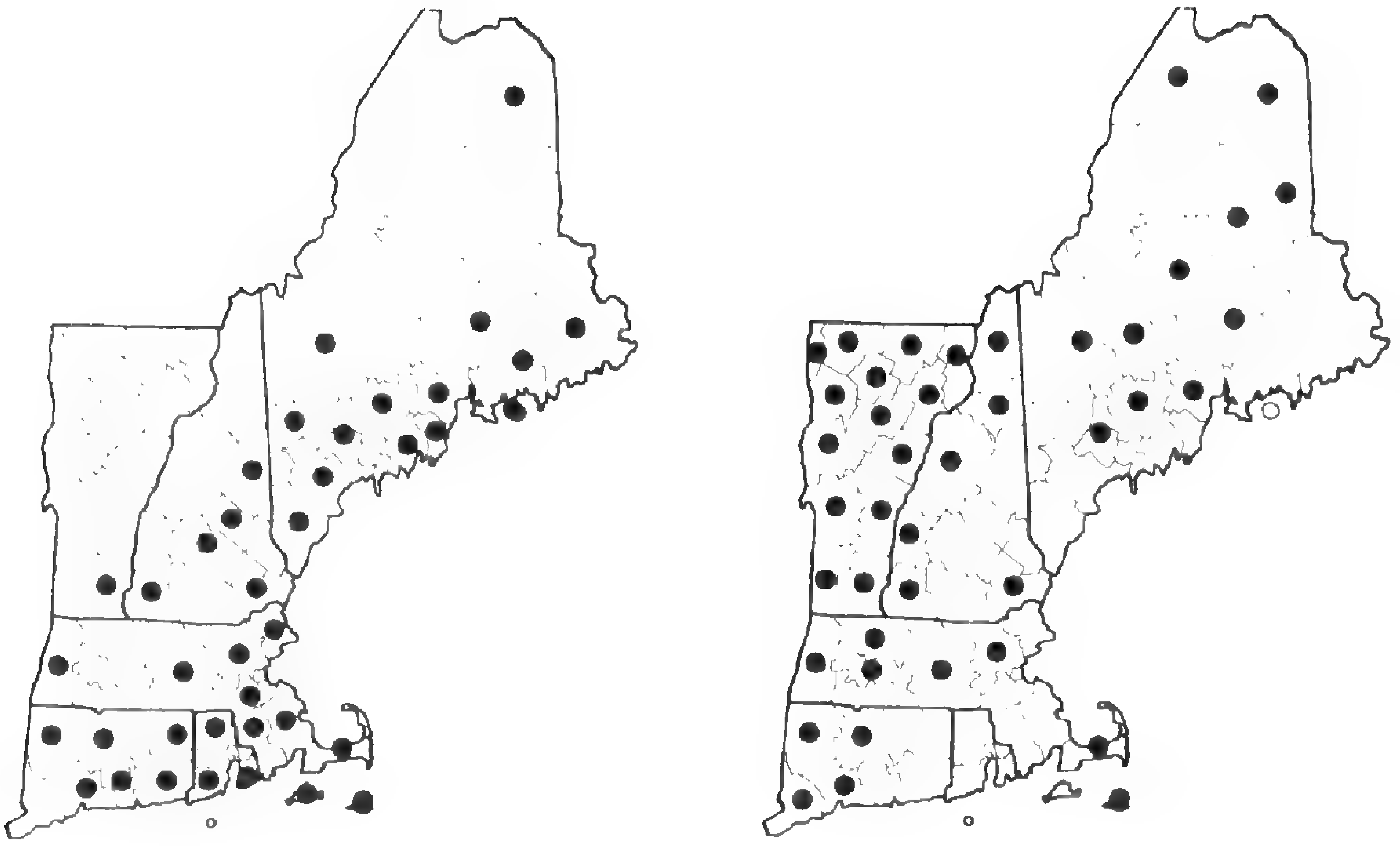


Juncus gerardii *Juncus greenei*



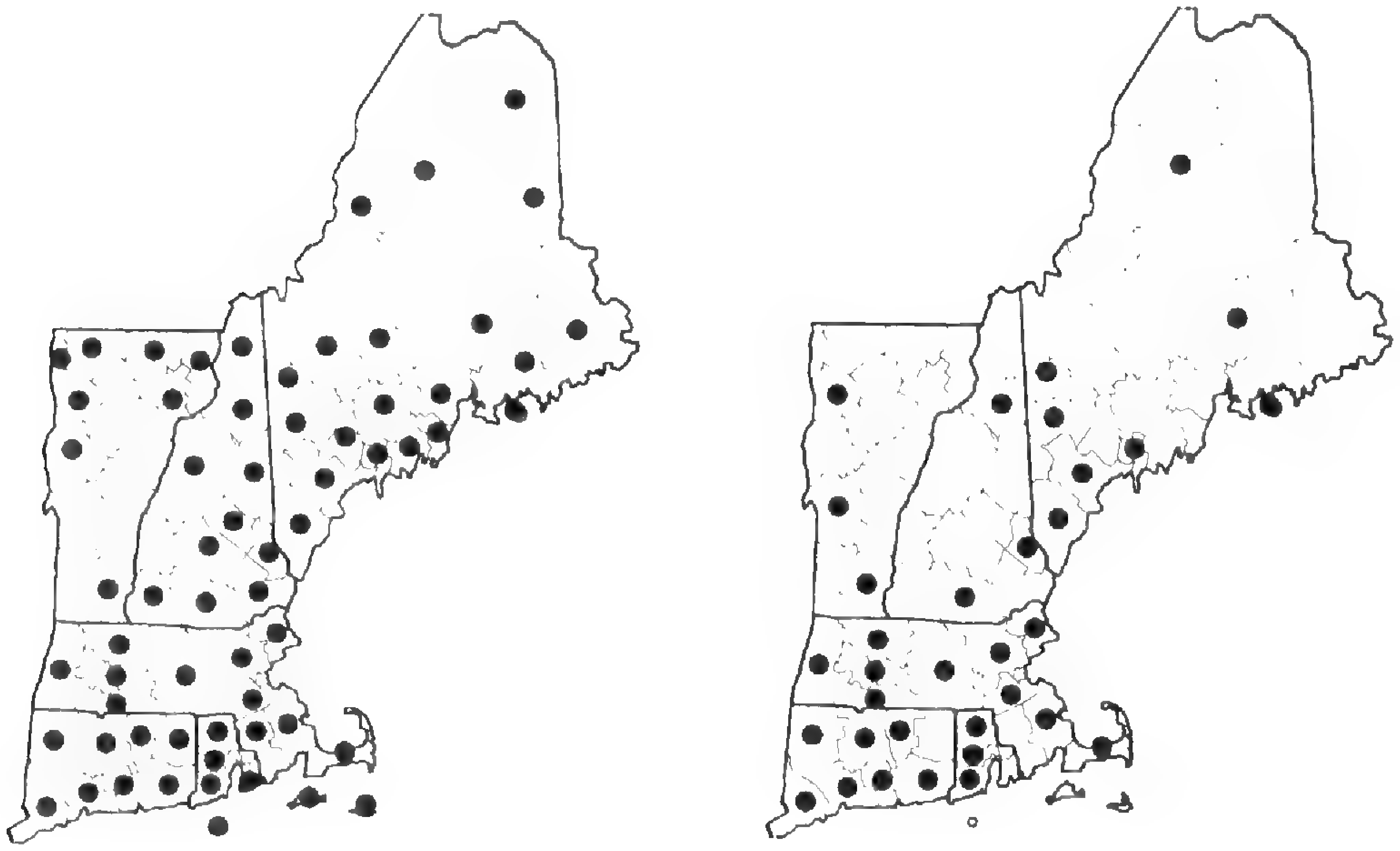
JUNCUS INFLEXUS *Juncus marginatus*

Figure 21. Distribution maps for *Juncus gerardii, J. greenei, J. INFLEXUS,* and *J. marginatus.*



Juncus militaris

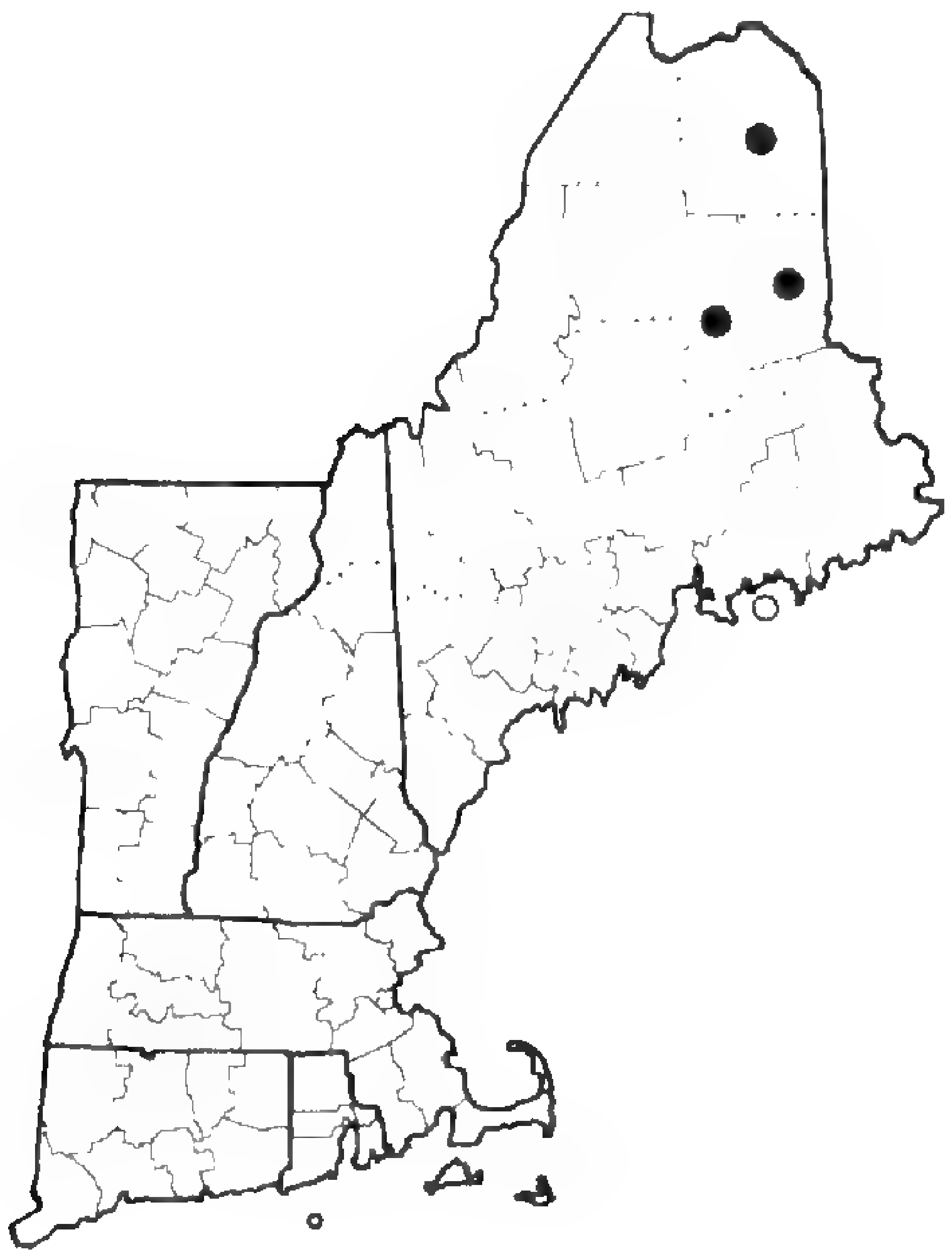
Juncus nodosus var. *nodosus*



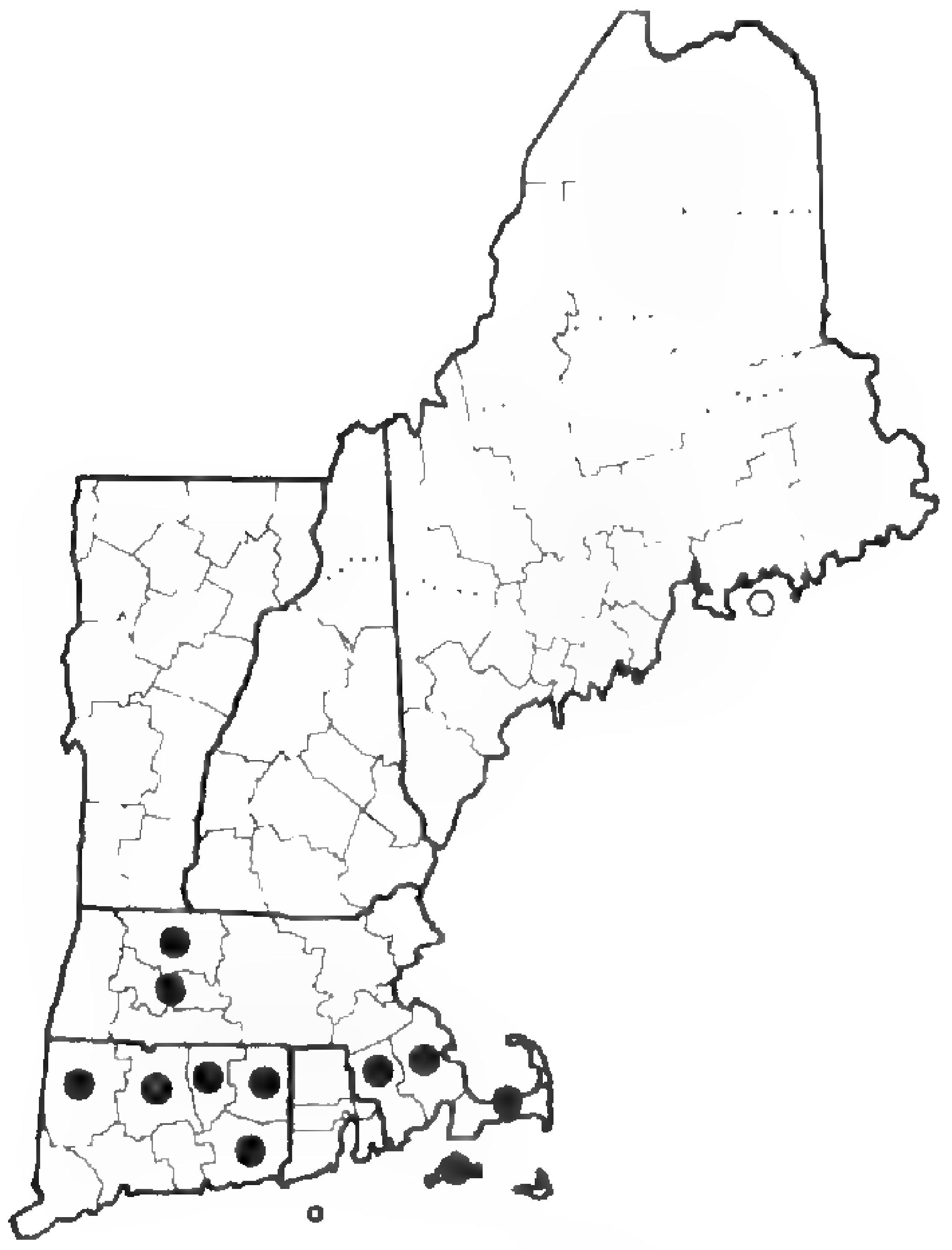
Juncus pelocarpus

Juncus secundus

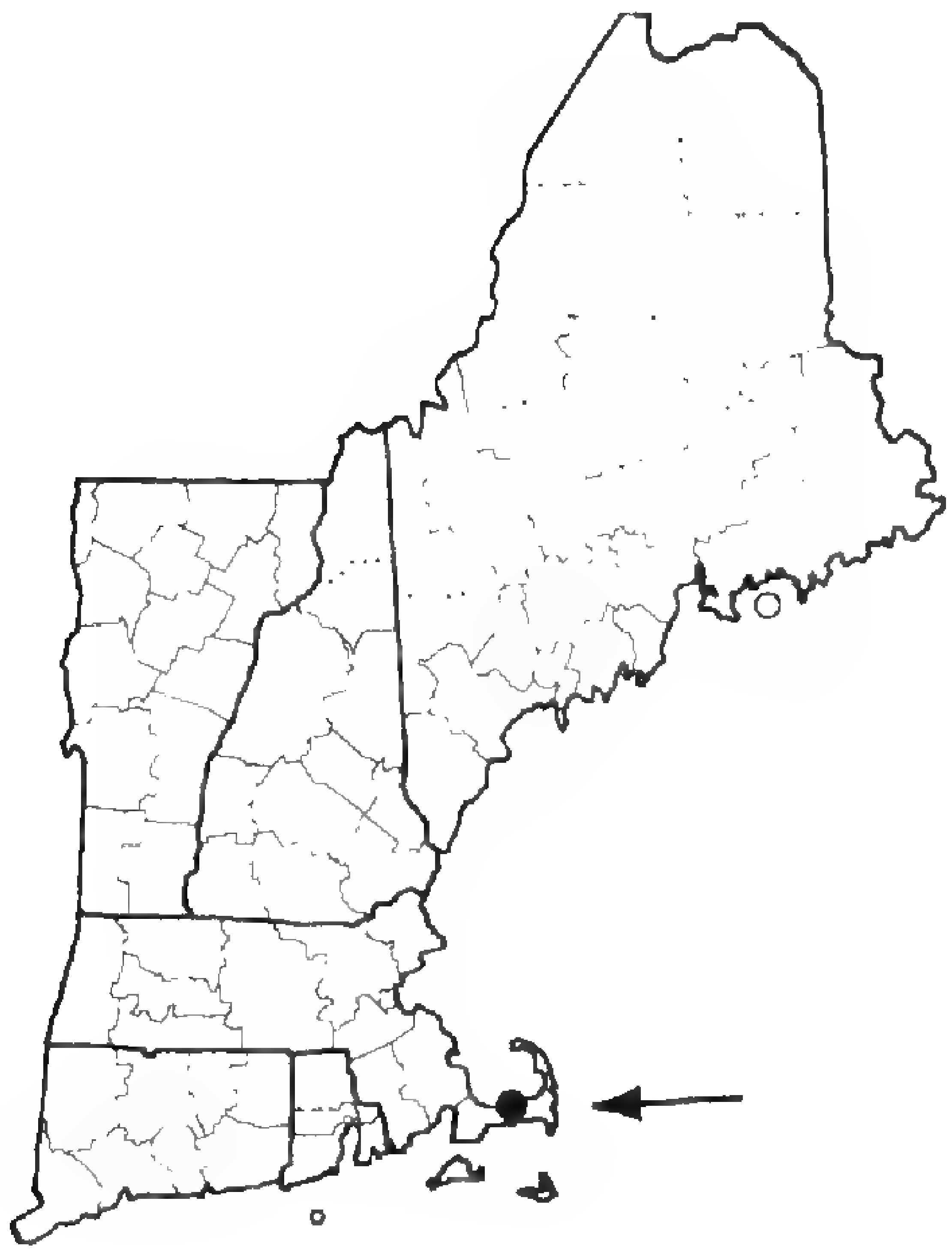
Figure 22. Distribution maps for *Juncus militaris, J. nodosus* var. *nodosus, J. pelocarpus,* and *J. secundus.*



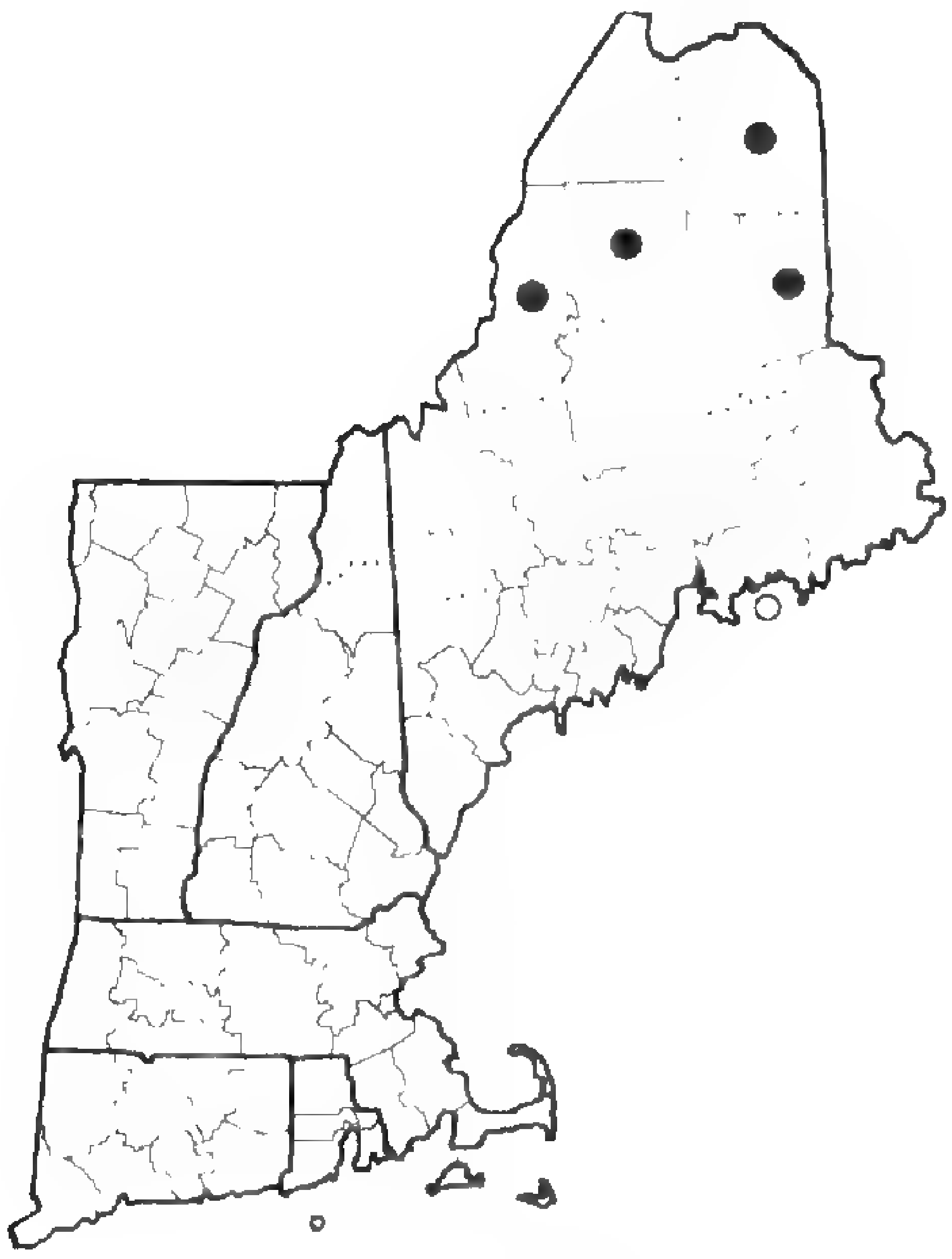
Juncus stygius
var. *americanus*



Juncus subcaudatus

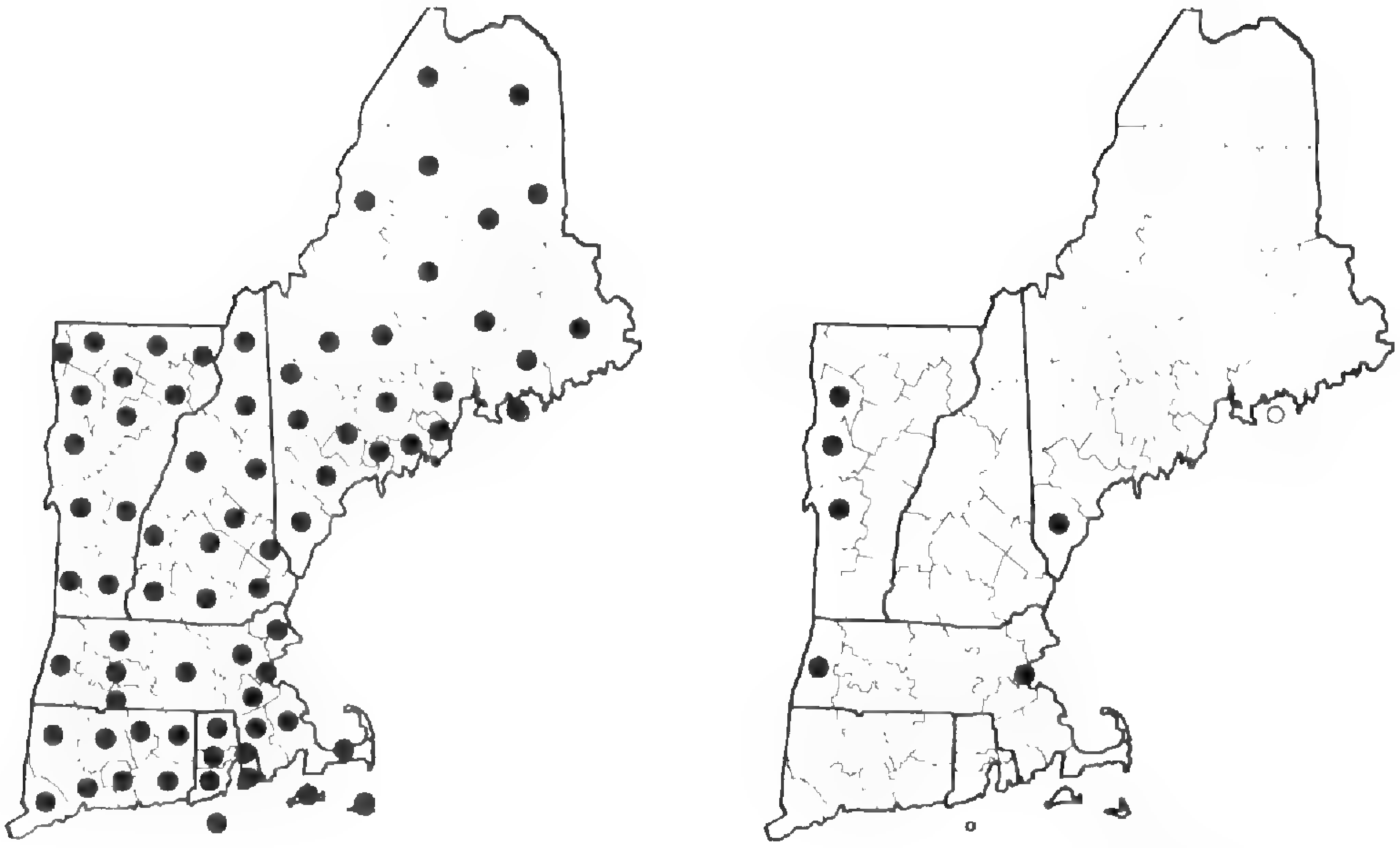


JUNCUS SUBNODULOSUS



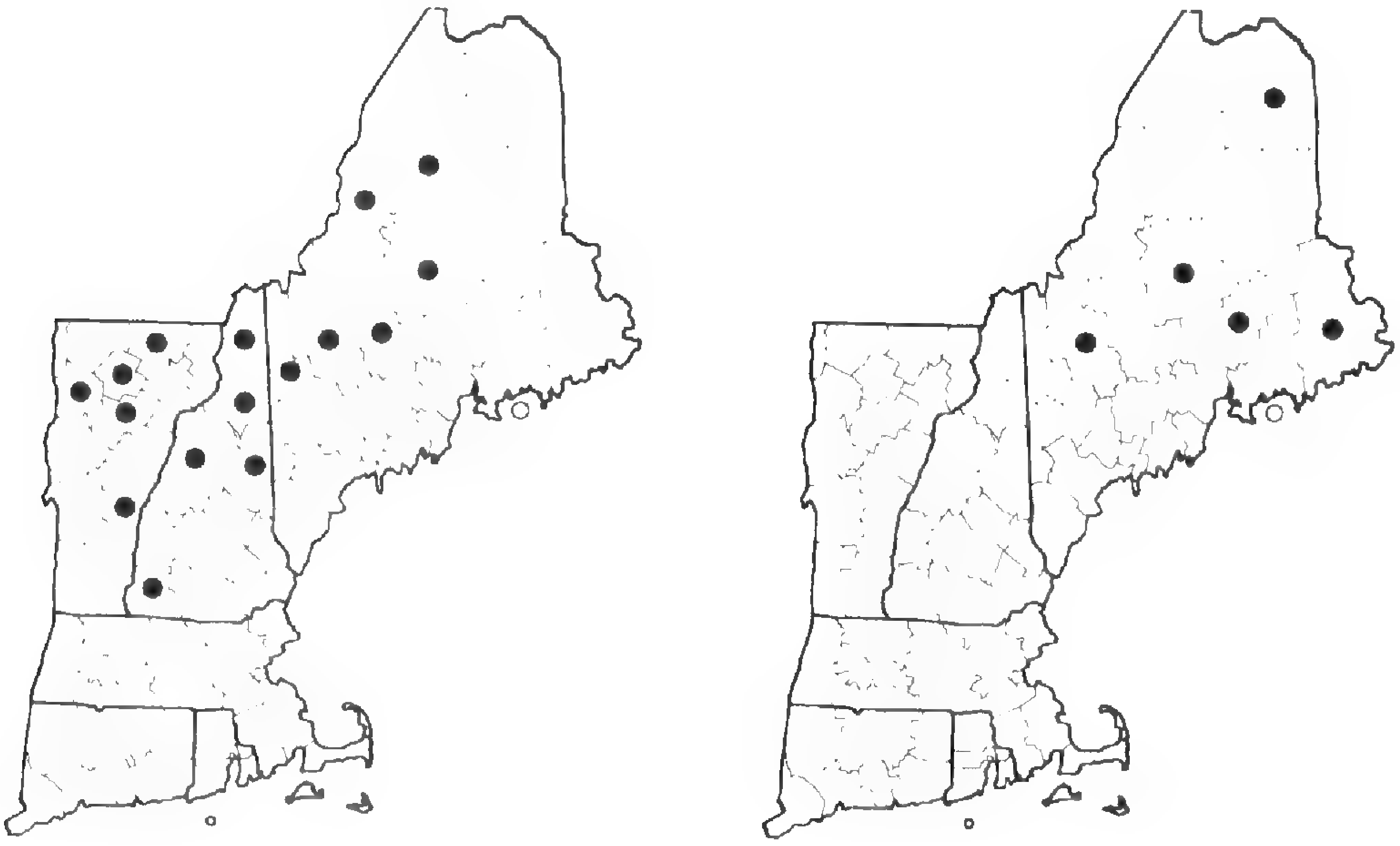
Juncus subtilis

Figure 23. Distribution maps for *Juncus stygius* var. *americanus*, *J. subcaudatus*, *J. SUBNODULOSUS*, and *J. subtilis*.



Juncus tenuis

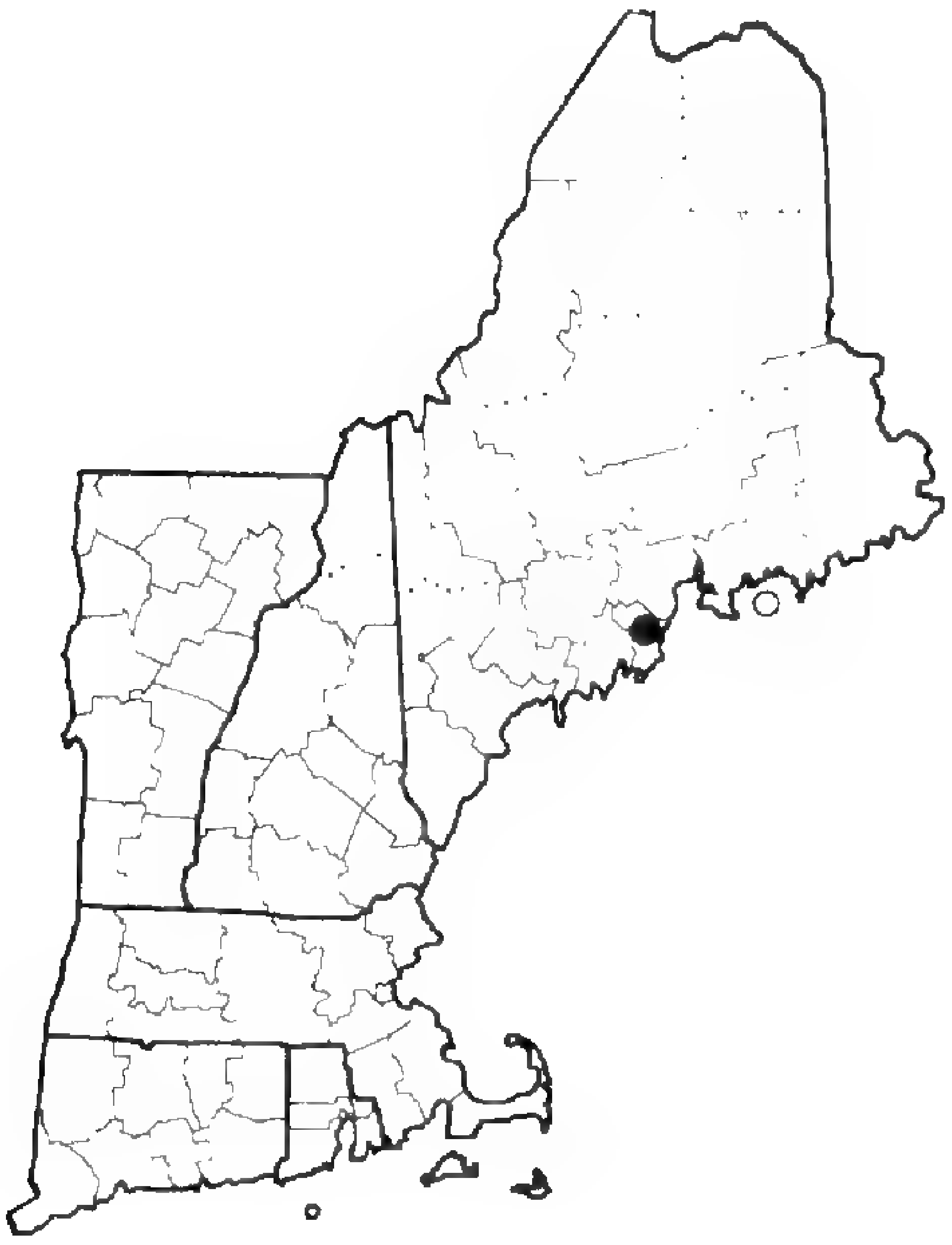
JUNCUS TORREYI



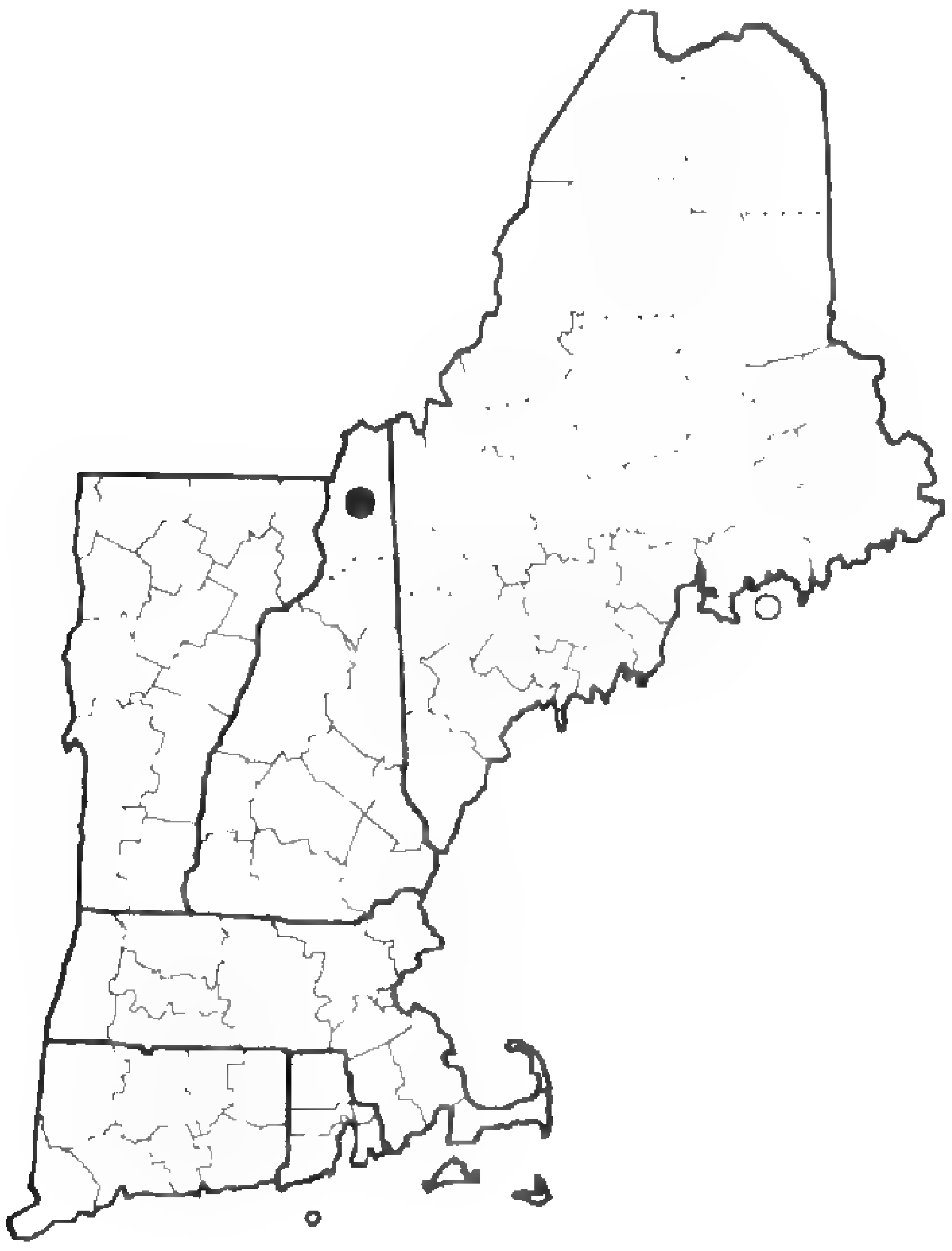
Juncus trifidus

Juncus vaseyi

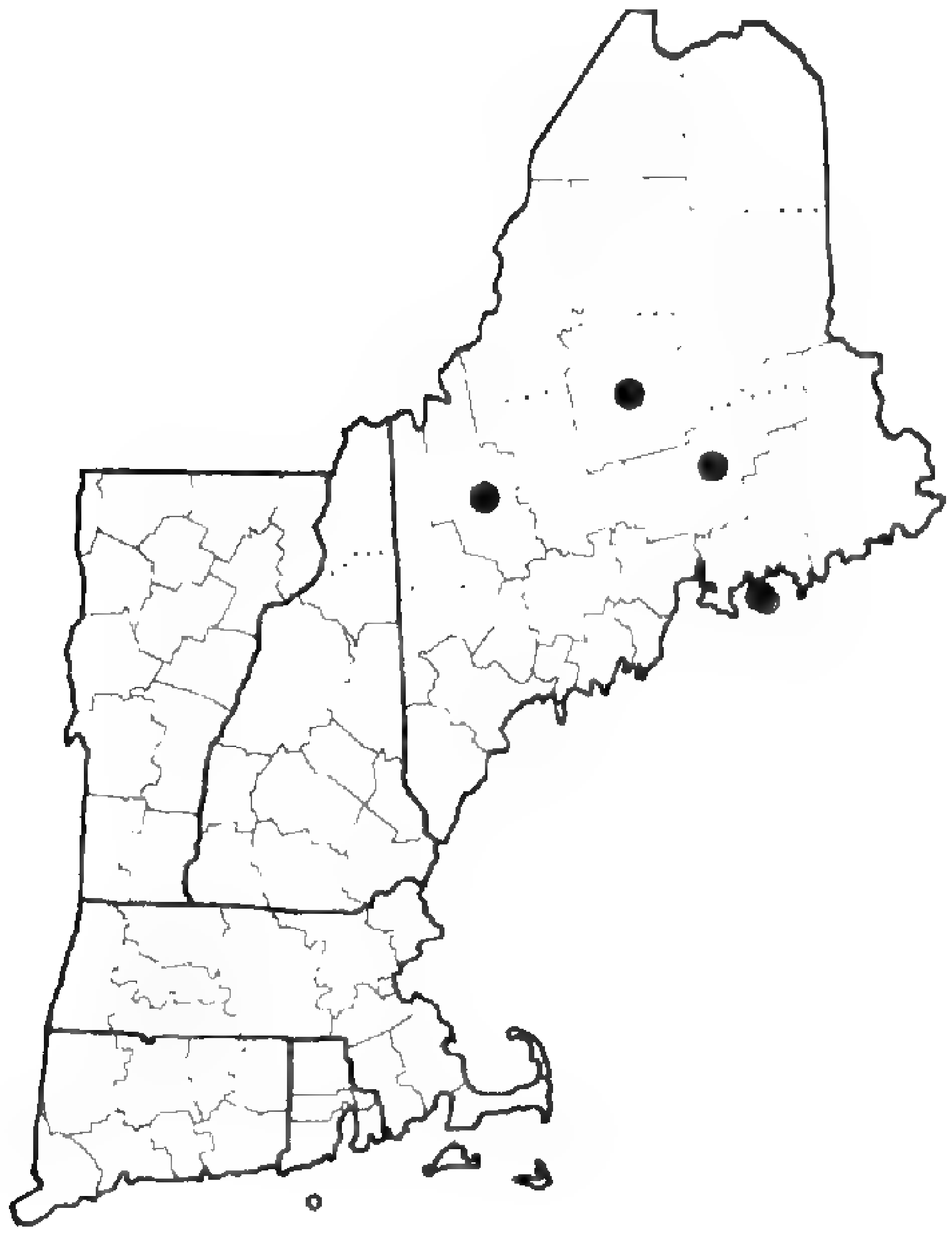
Figure 24. Distribution maps for *Juncus tenuis, J. TORREYI, J. trifidus,* and *J. vaseyi.*



Juncus articulatus
X *J. brevicaudatus*



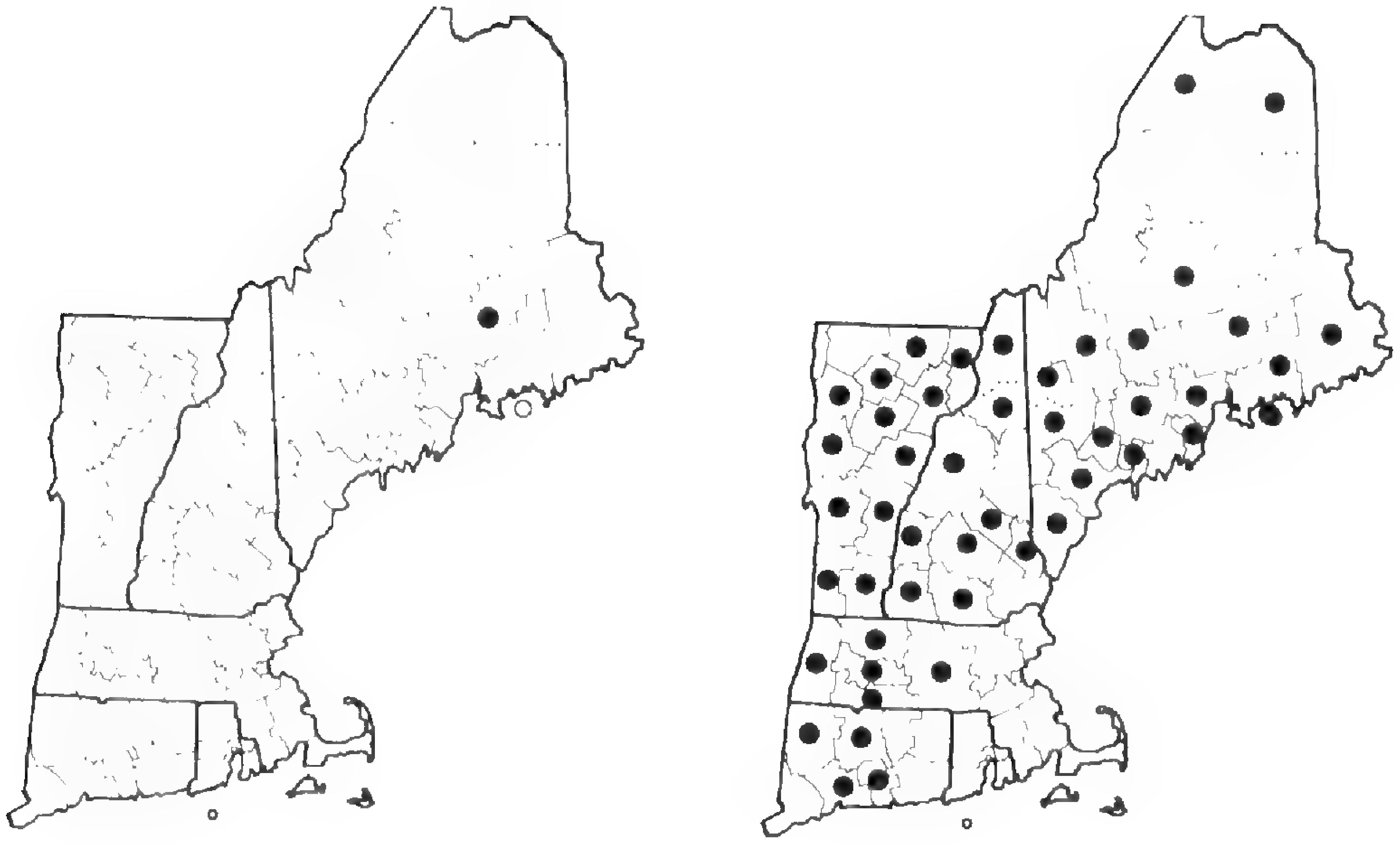
Juncus brevicaudatus
X *J. nodosus* var. *nodusus*



Juncus X *oronensis*

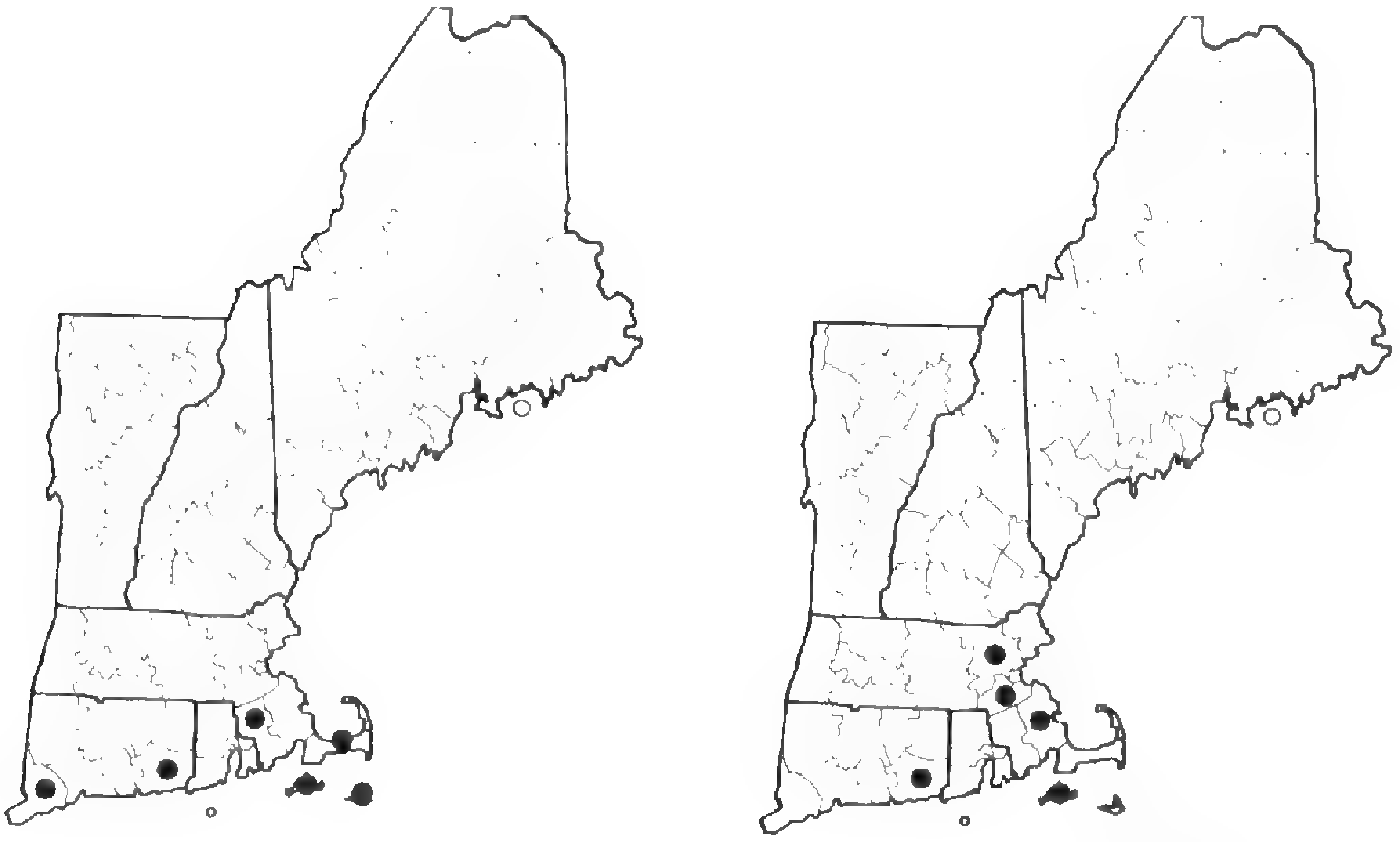
Juncus secundus
X *J. tenuis*

Figure 25. Distribution maps for *Juncus articulatus* X *J. brevicaudatus*, *J. brevicaudatus* X *J. nodosus* var. *nodosus*, *J.* X *oronensis*, and *J. secundus* X *J. tenuis*.



Juncus tenuis X *J. vaseyi*

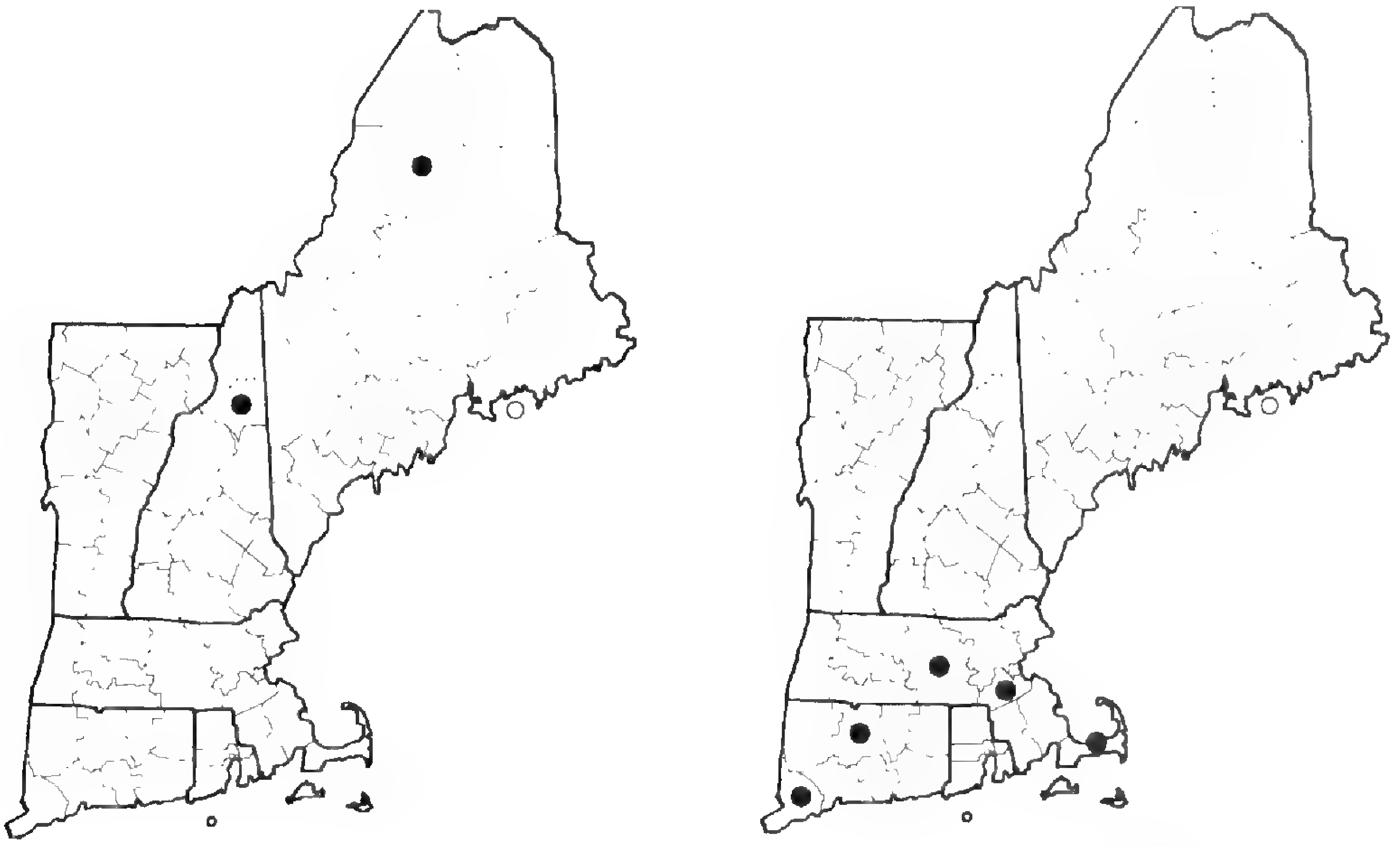
Luzula acuminata var. *acuminata*



Luzula bulbosa

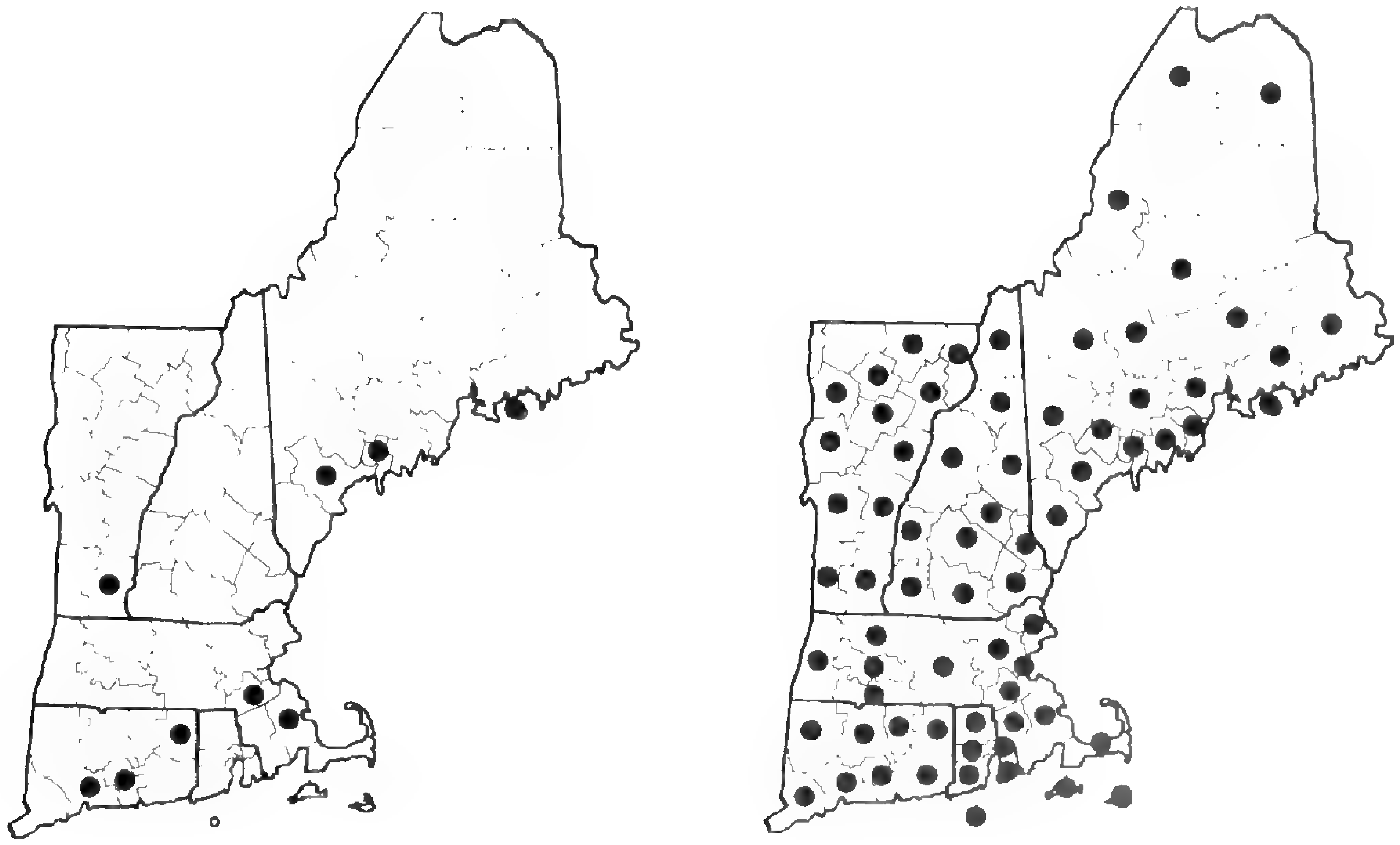
LUZULA CAMPESTRIS

Figure 26. Distribution maps for *Juncus tenuis* X *J. vaseyi*, *Luzula acuminata* var. *acuminata*, *L. bulbosa*, and *L. CAMPESTRIS*.



Luzula confusa

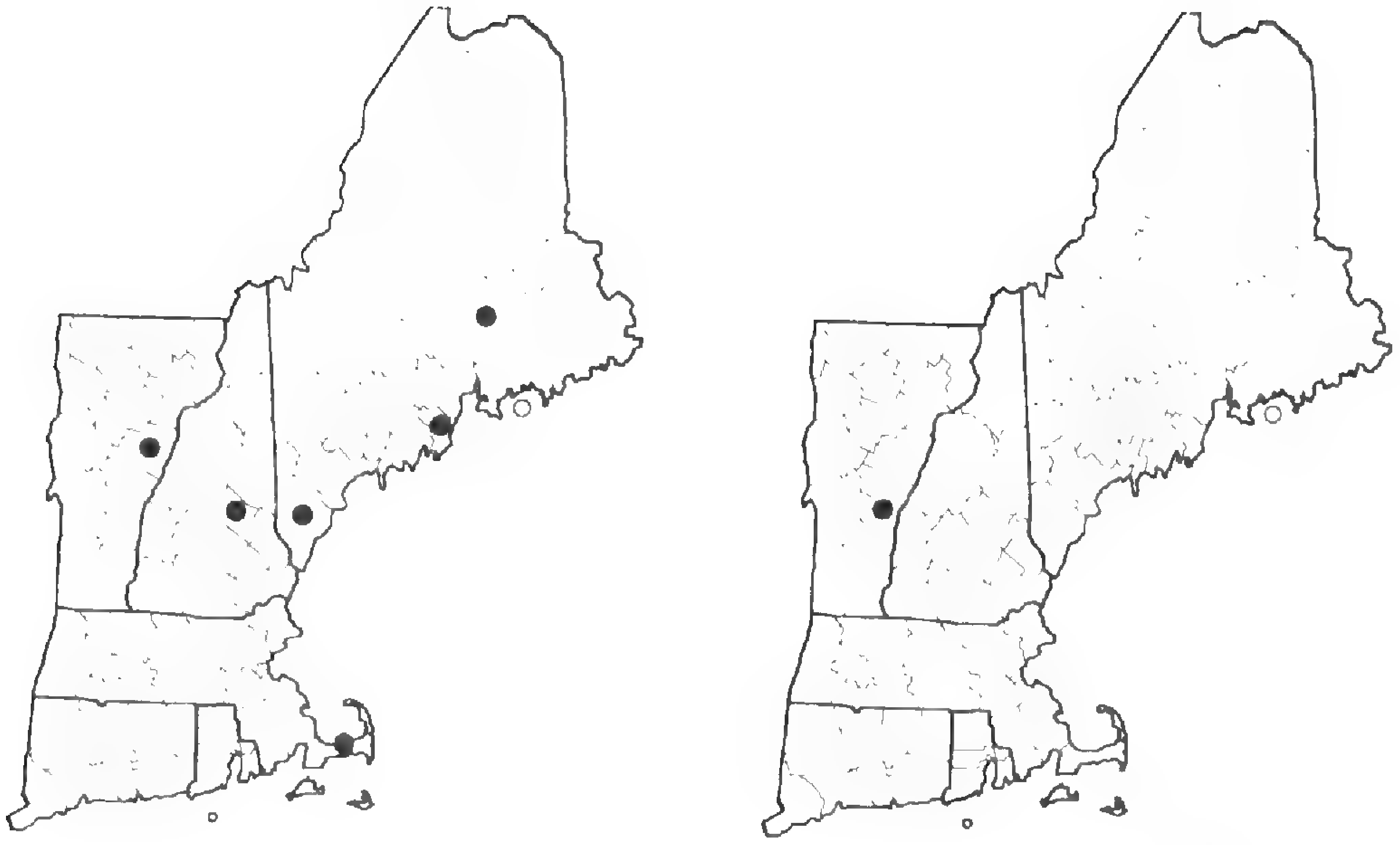
Luzula echinata



LUZULA LUZULOIDES
subsp. *LUZULOIDES*

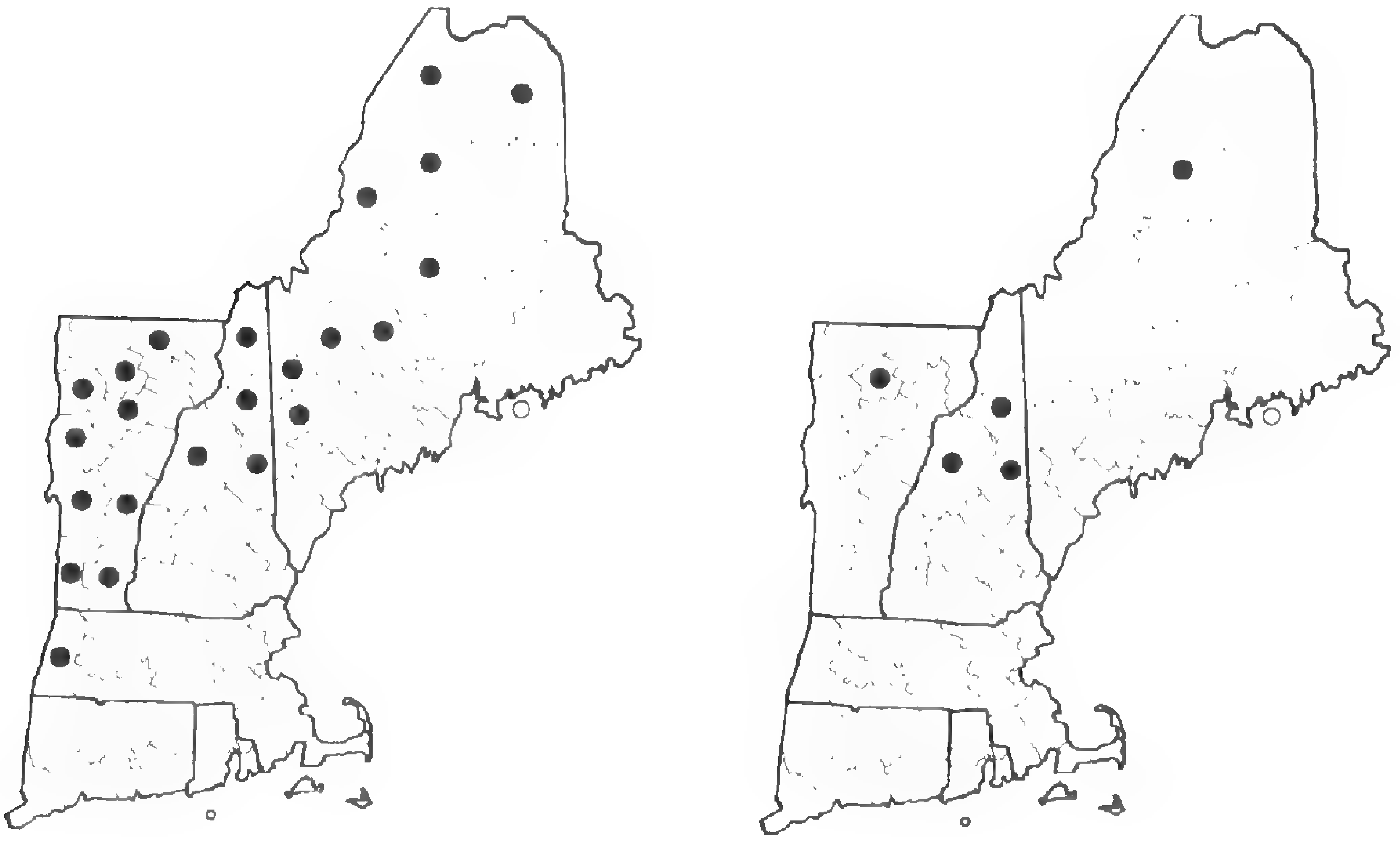
Luzula multiflora
subsp. *multiflora*

Figure 27. Distribution maps for *Luzula confusa, L. echinata, L. LUZULOIDES* subsp. *LUZULOIDES,* and *L. multiflora* subsp. *multiflora.*



Luzula multiflora subsp. *frigida*

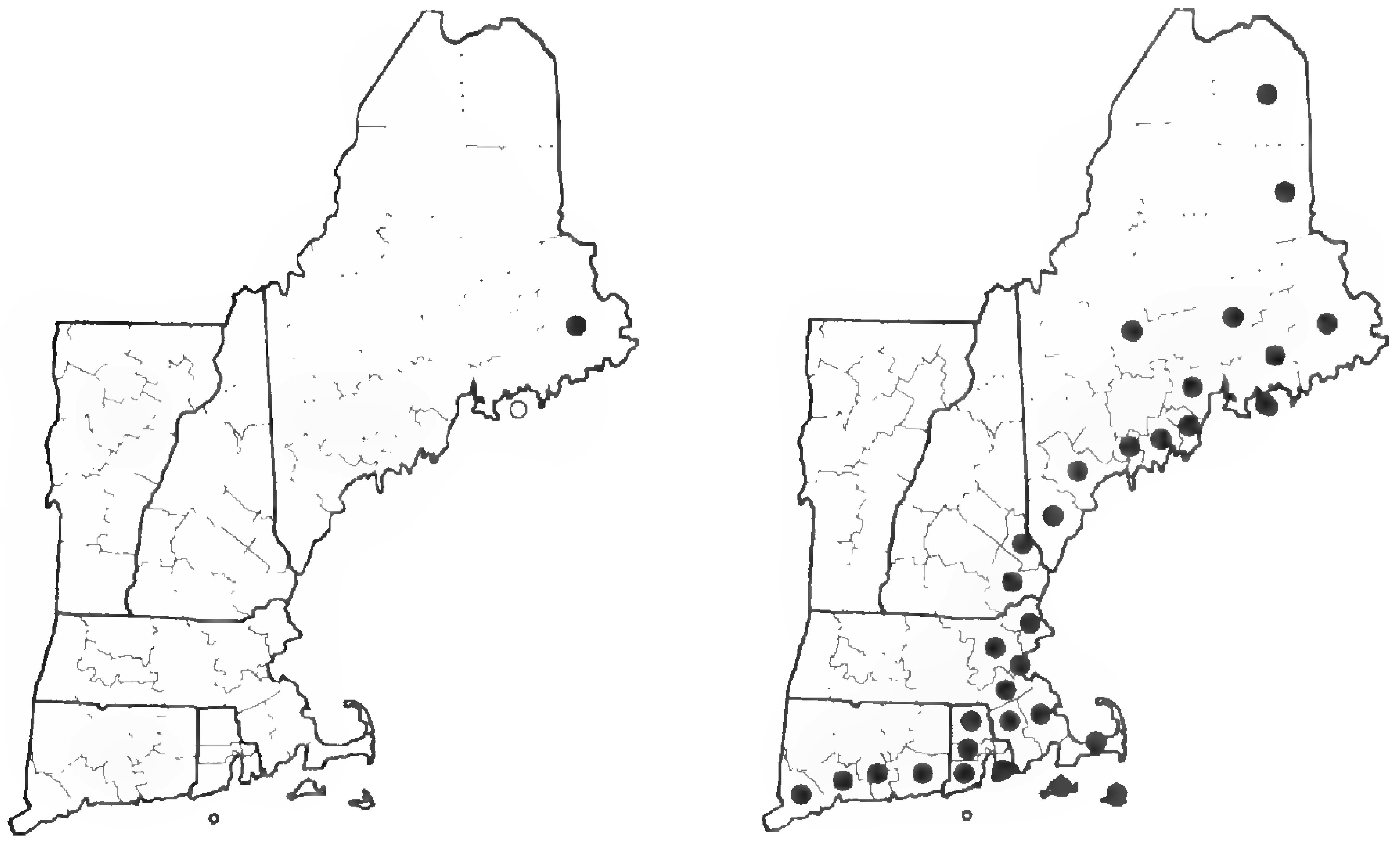
LUZULA PALLIDULA



Luzula parviflora var. *melanocarpa*

Luzula spicata

Figure 28. Distribution maps for *Luzula multiflora* subsp. *frigida*, *L. PALLIDULA*, *L. parviflora* var. *melanocarpa*, and *L. spicata*.



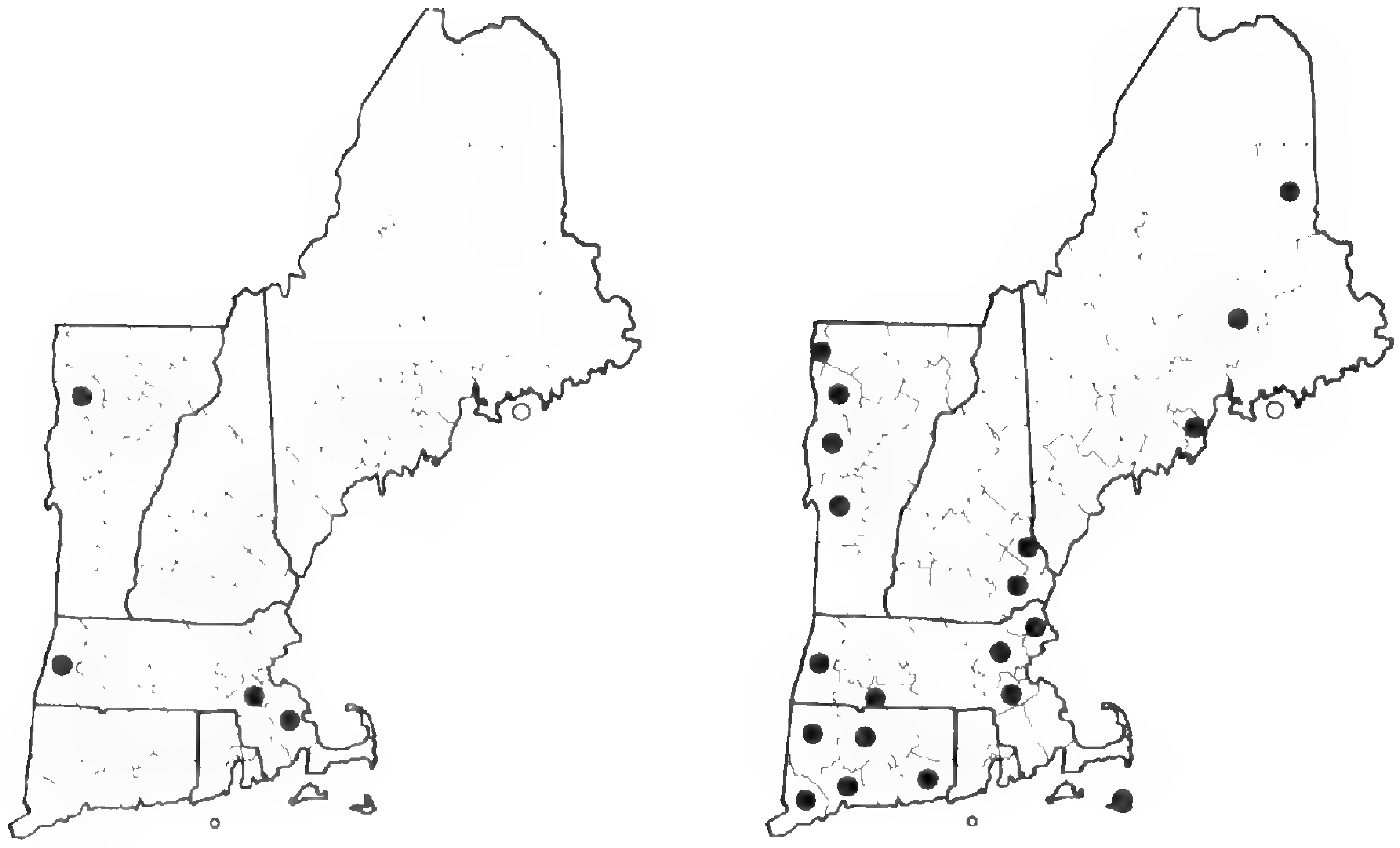
Triglochin gaspense

Triglochin maritima

Triglochin palustre

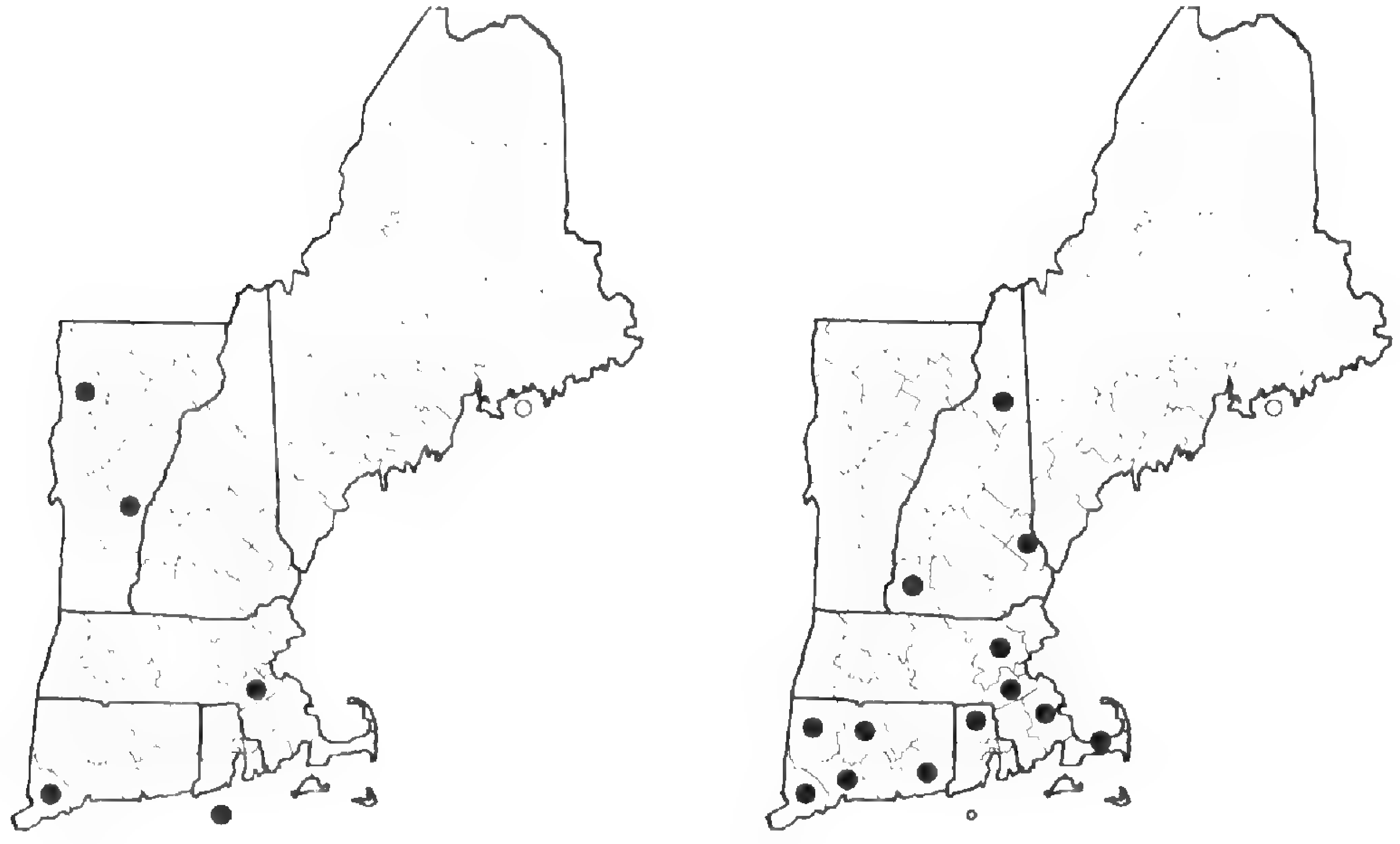
Lemna minor

Figure 29. Distribution maps for *Triglochin gaspense*, *T. maritima*, *T. palustre*, and *Lemna minor*.



Lemna perpusilla

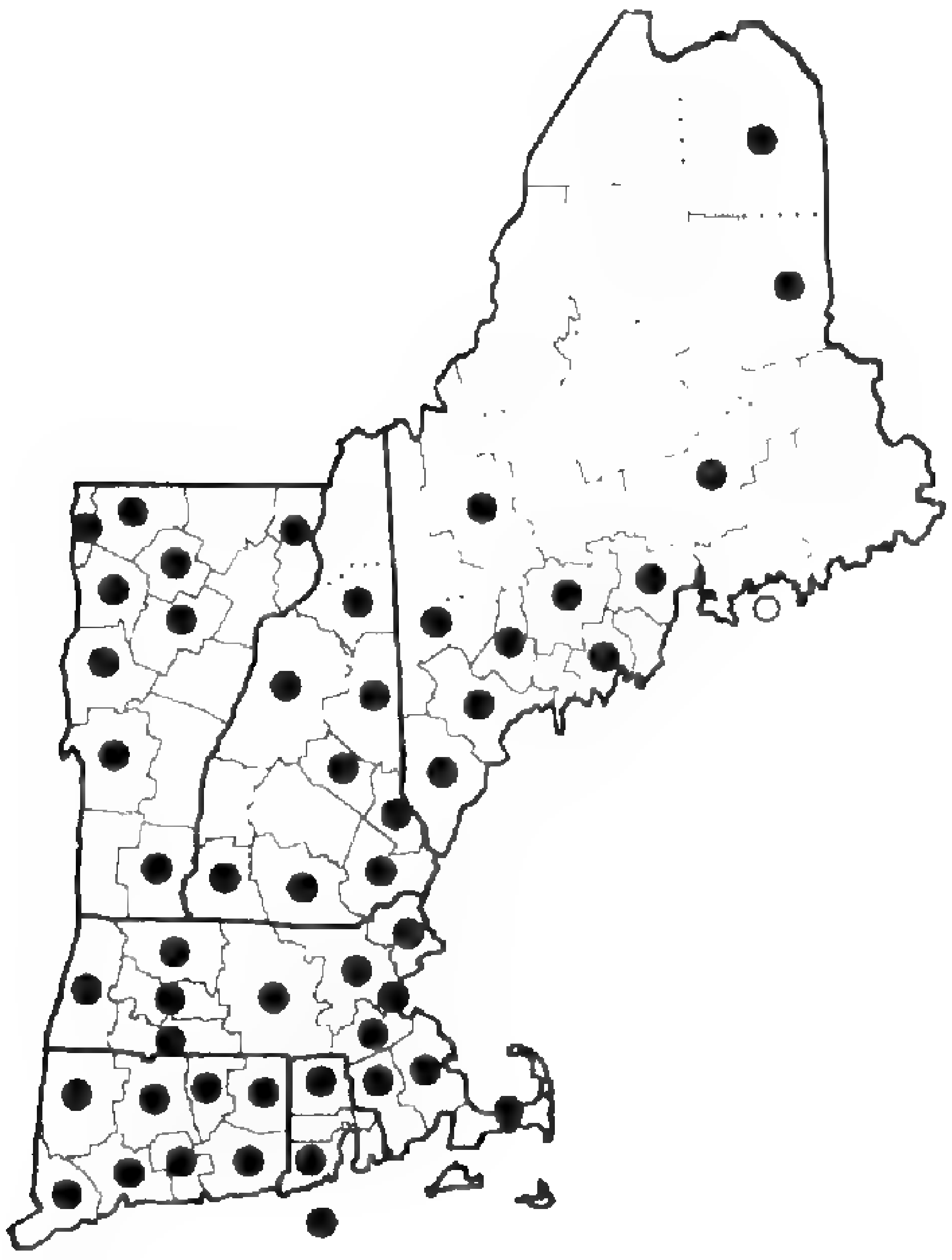
Lemna trisulca



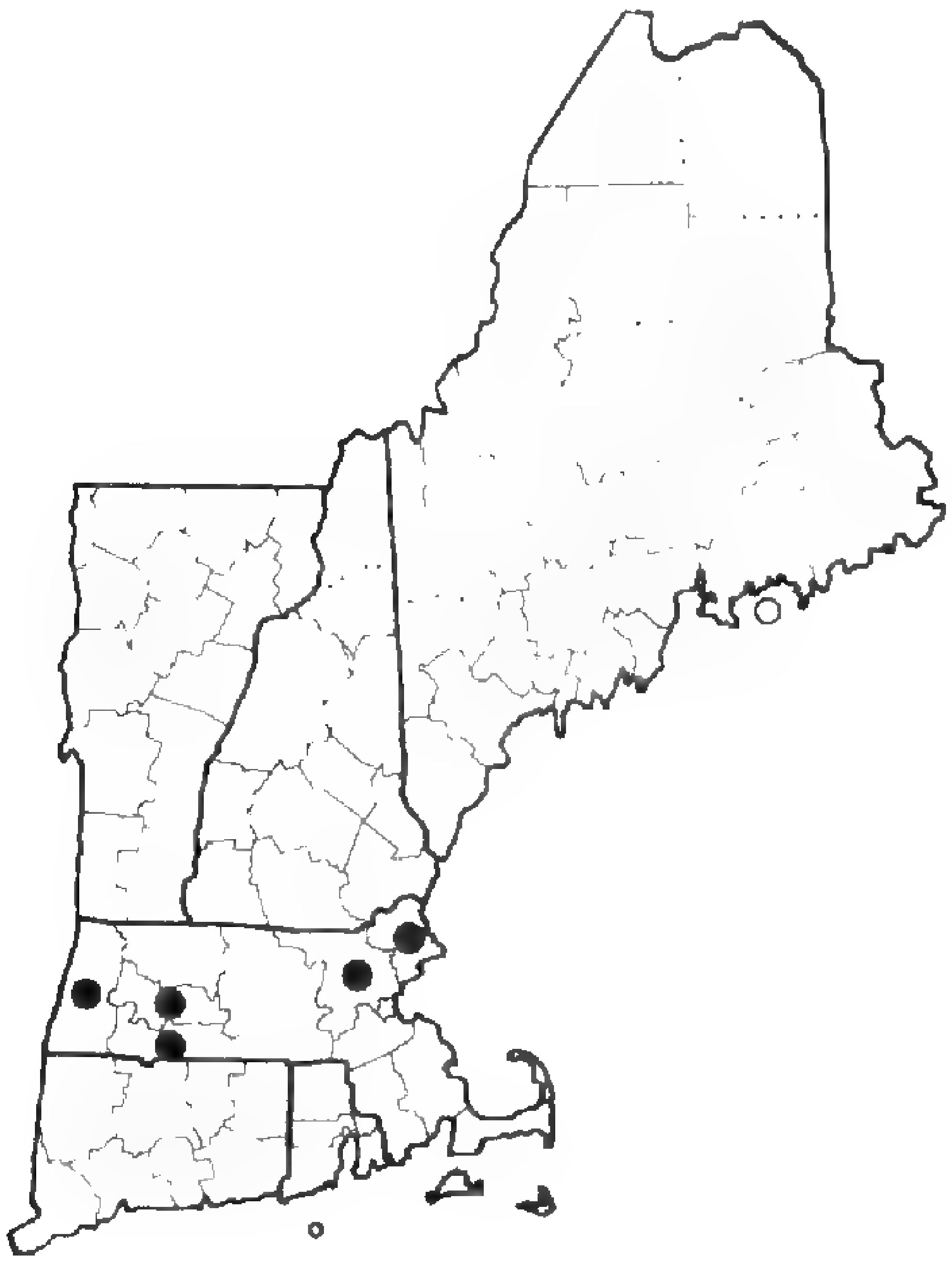
Lemna turionifera

Lemna valdiviana

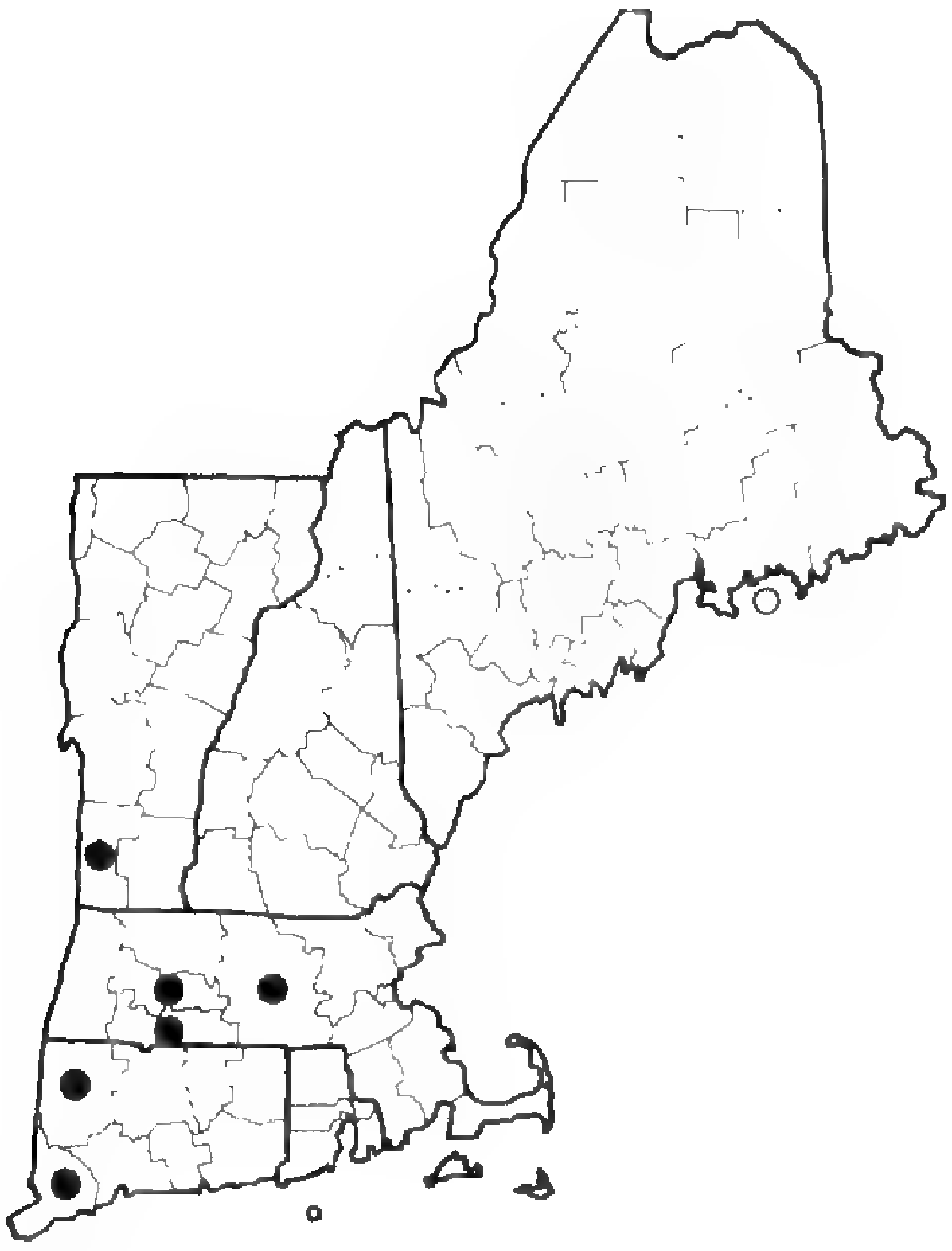
Figure 30. Distribution maps for *Lemna perpusilla*, *L. trisulca*, *L. turionifera*, and *L. valdiviana*.



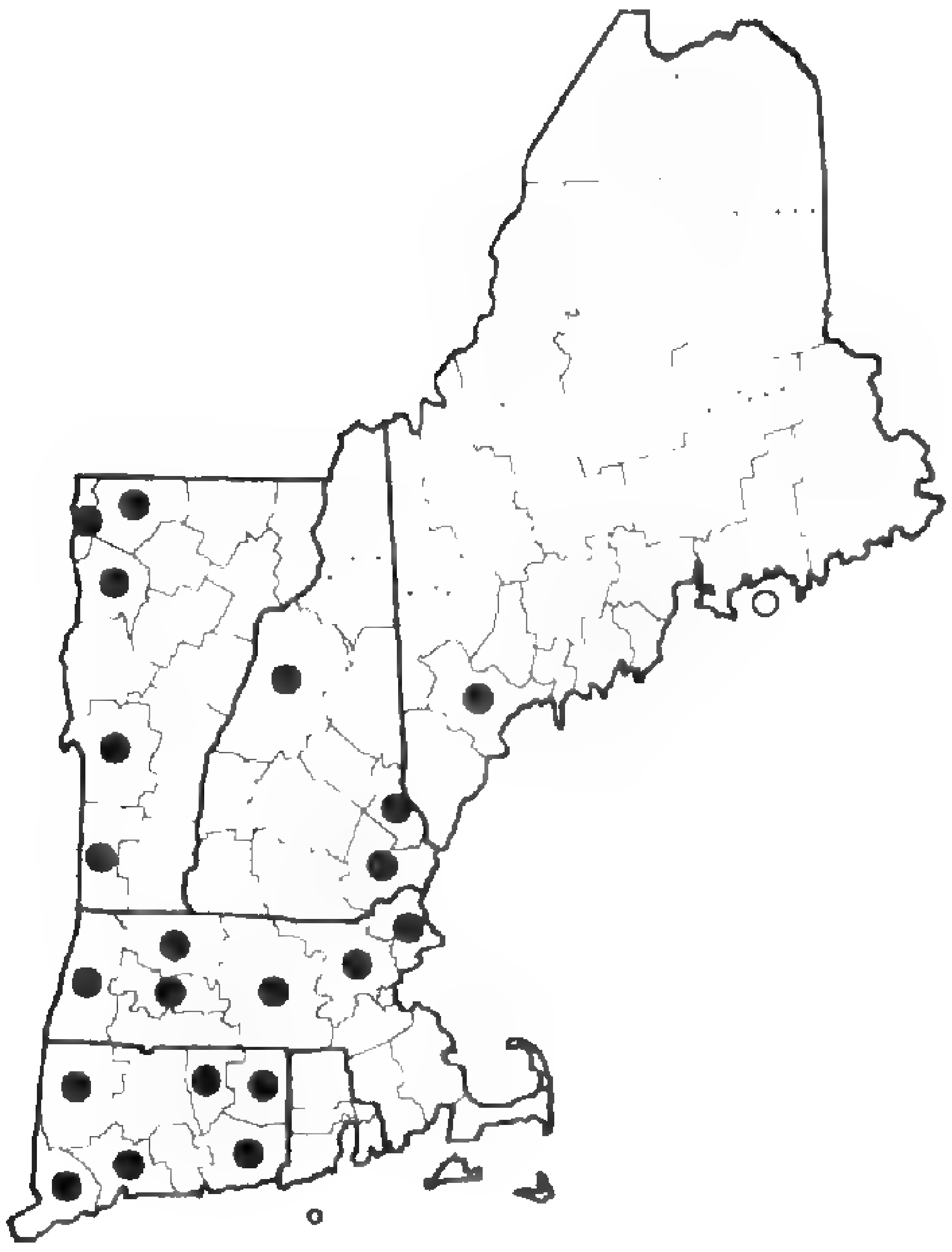
Spirodela polyrrhiza



Wolffia borealis

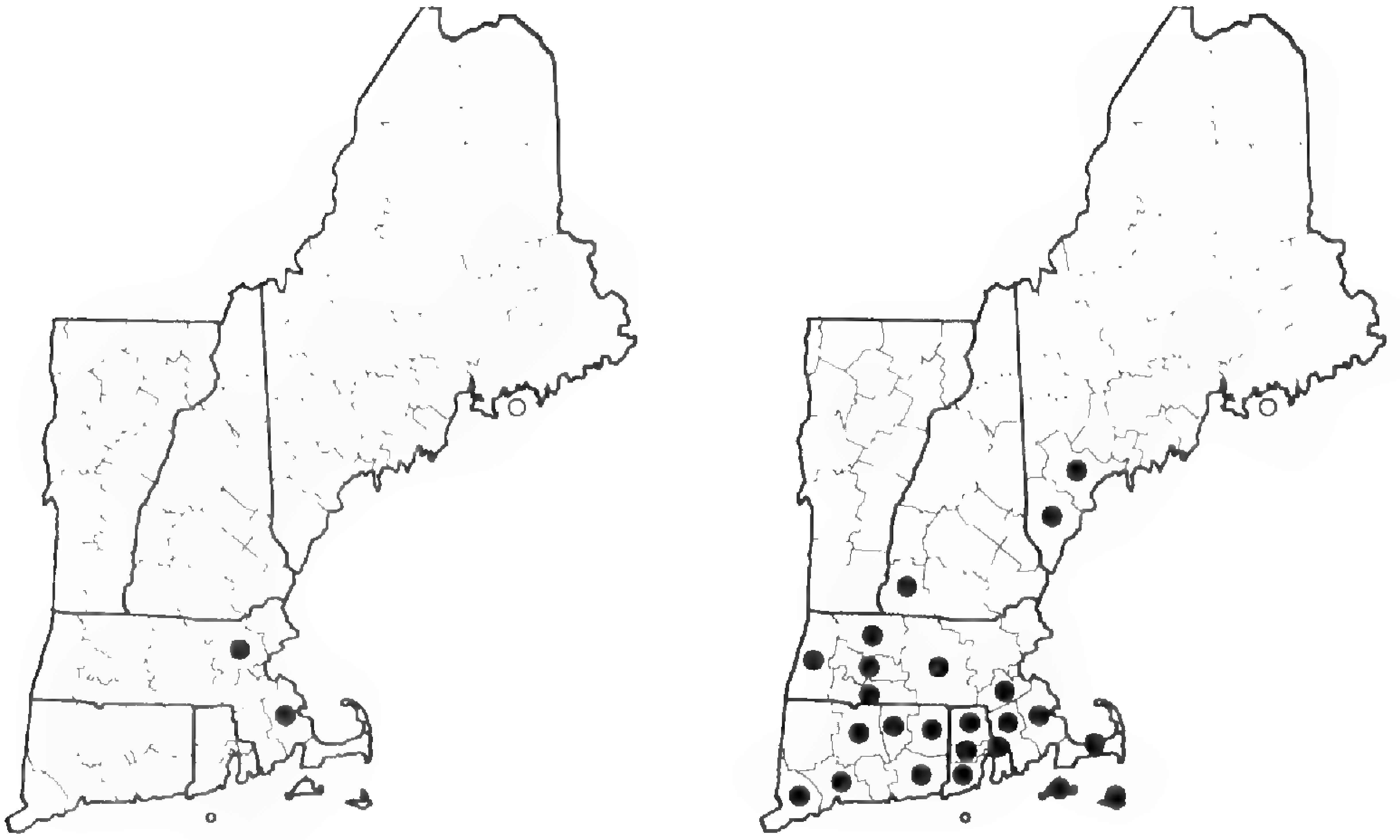


WOLFFIA BRASILIENSIS

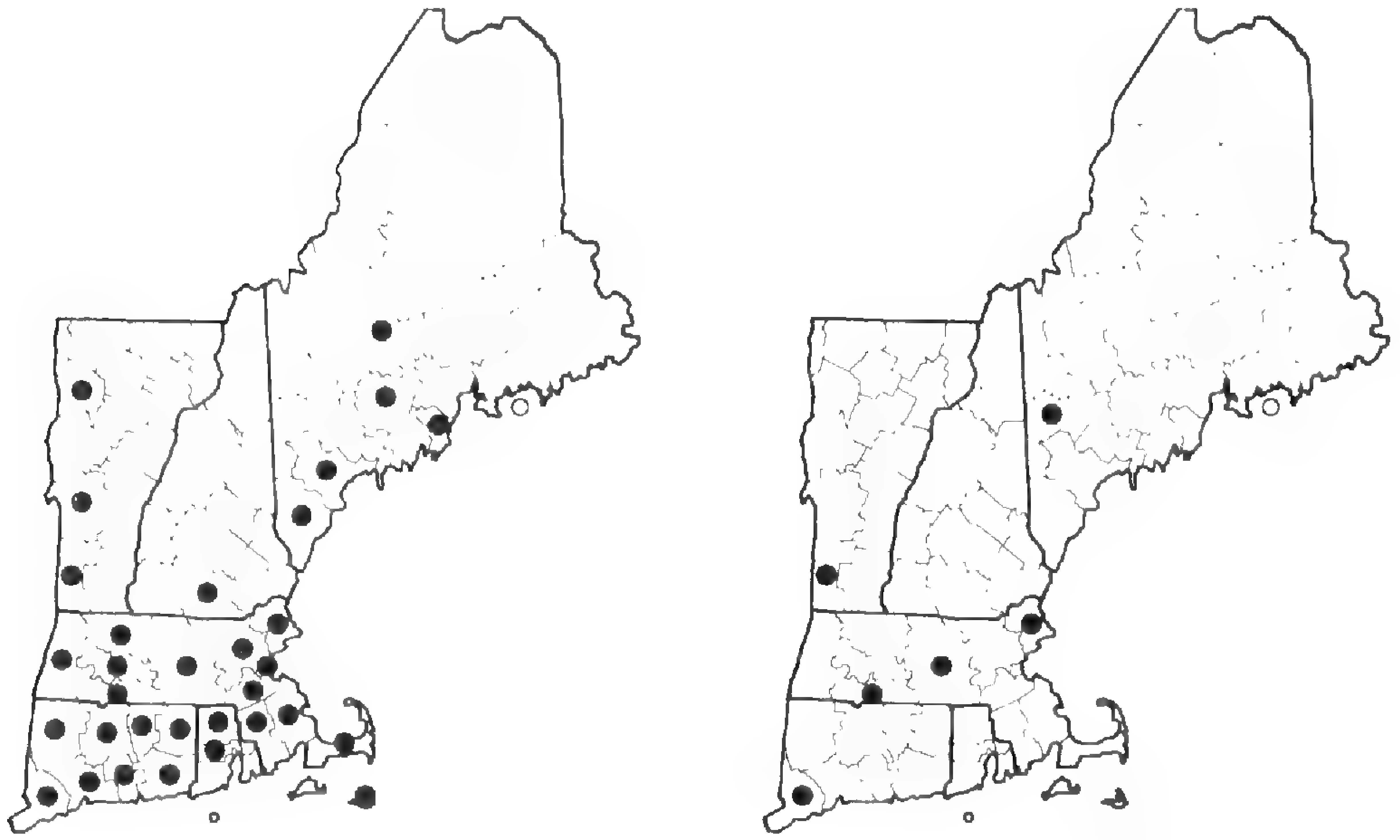


Wolffia columbiana

Figure 31. Distribution maps for *Spirodela polyrrhiza, Wolffia borealis, W. BRASILIENSIS,* and *W. columbiana.*

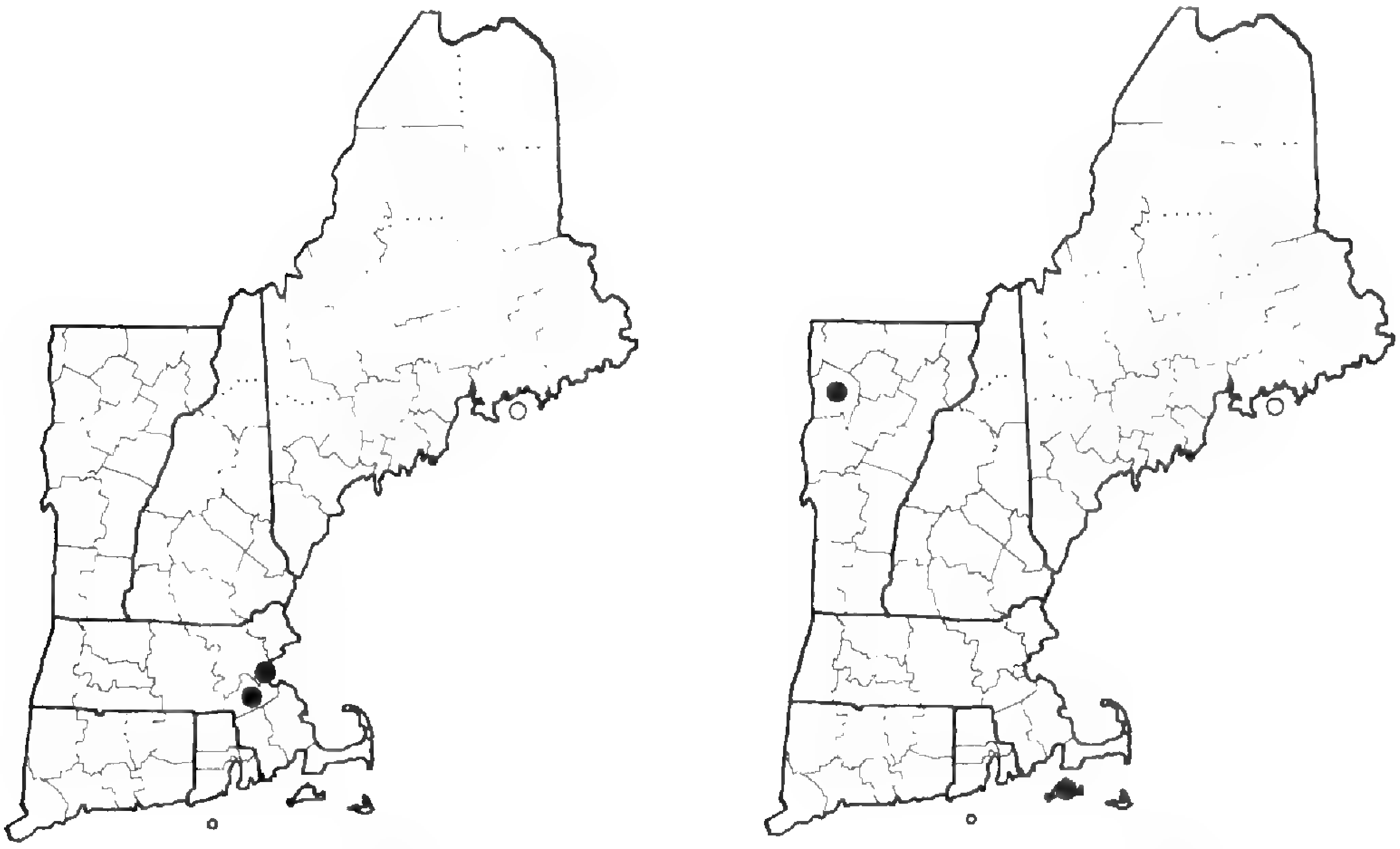


Wolffiella gladiata *Aletris farinosa*



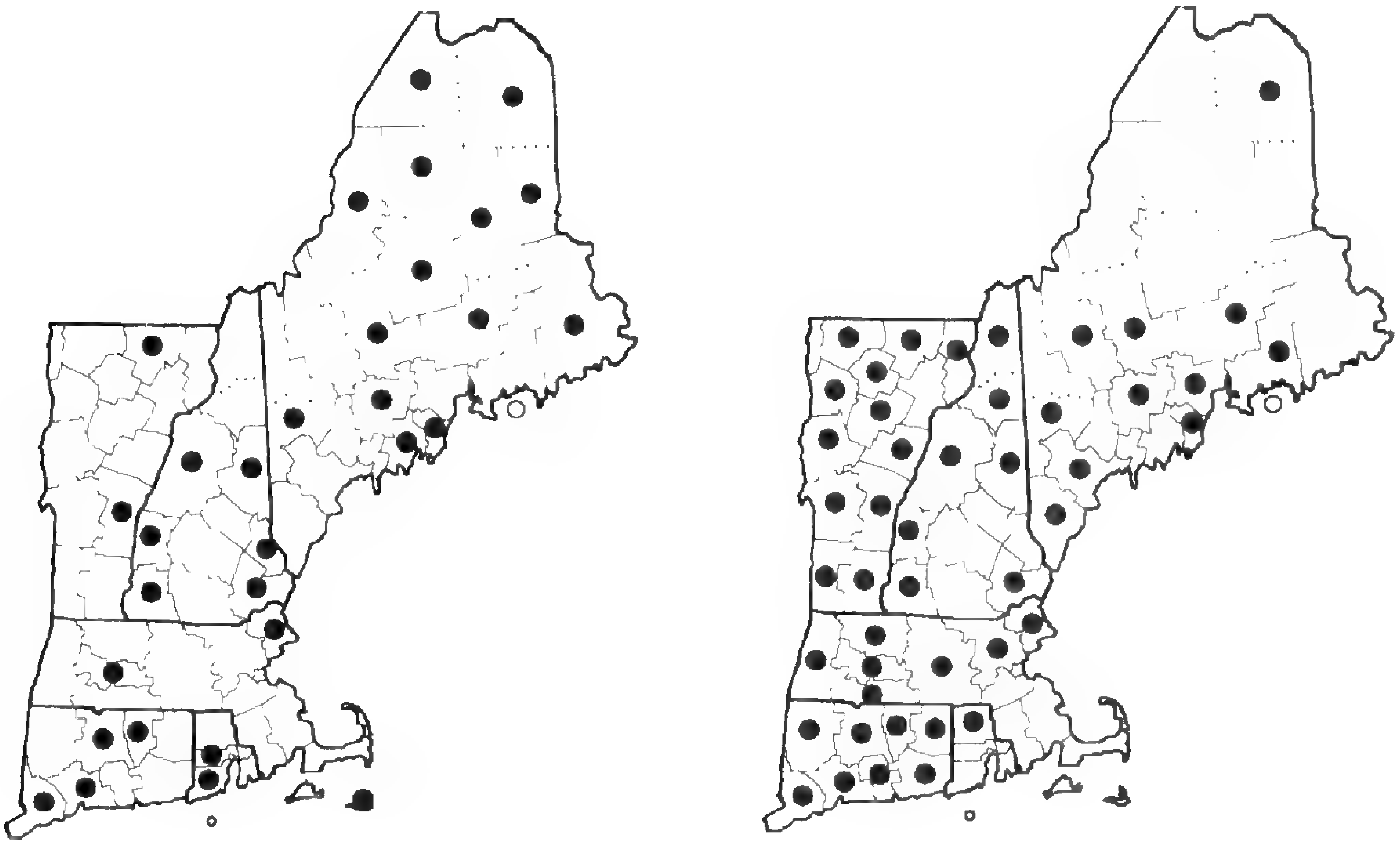
Allium canadense var. *canadense* *ALLIUM CEPA*

Figure 32. Distribution maps for *Wolffiella gladiata, Aletris farinosa, Allium canadense* var. *canadense,* and *A. CEPA.*



ALLIUM OLERACEUM

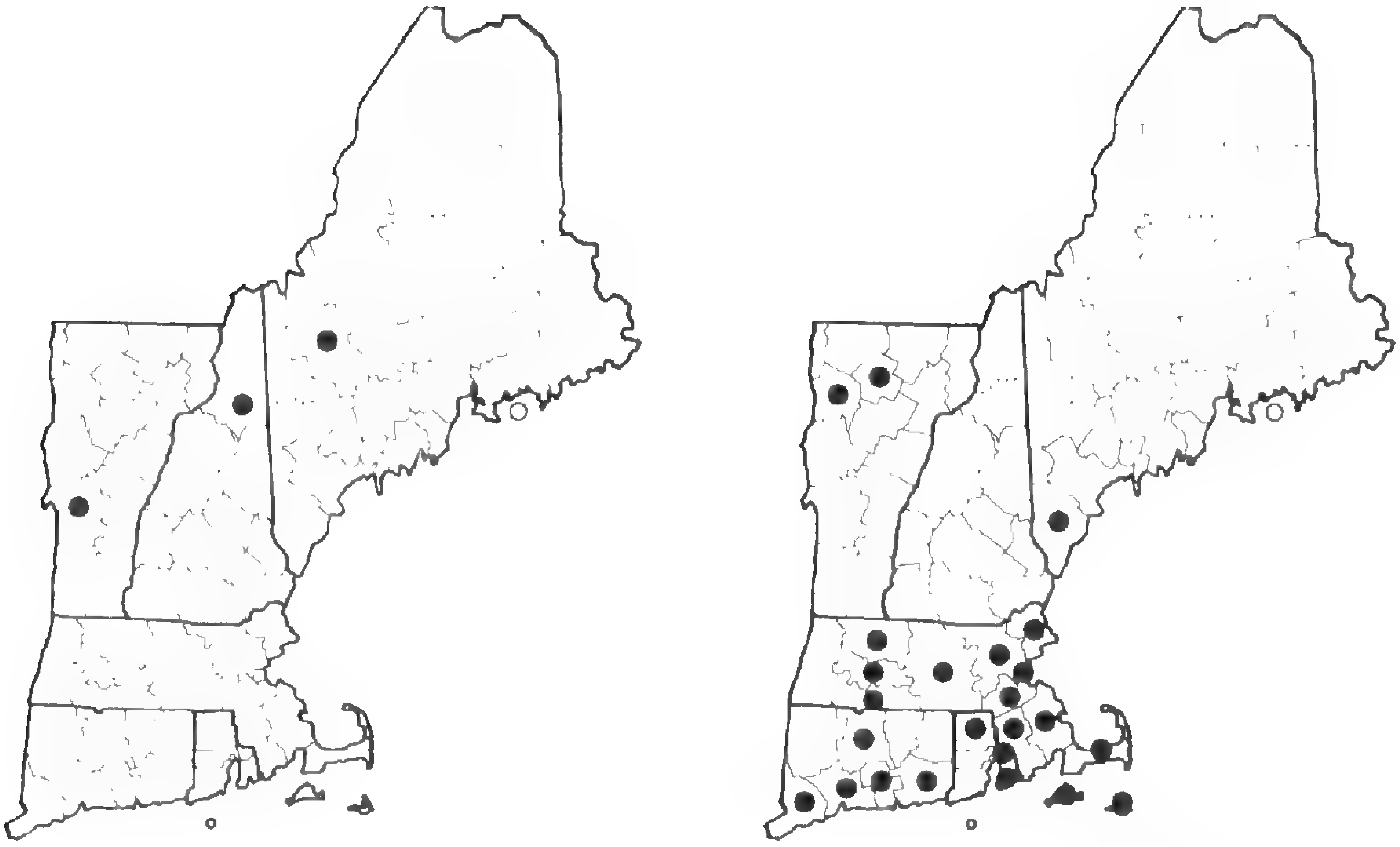
ALLIUM SATIVUM



Allium schoenoprasum

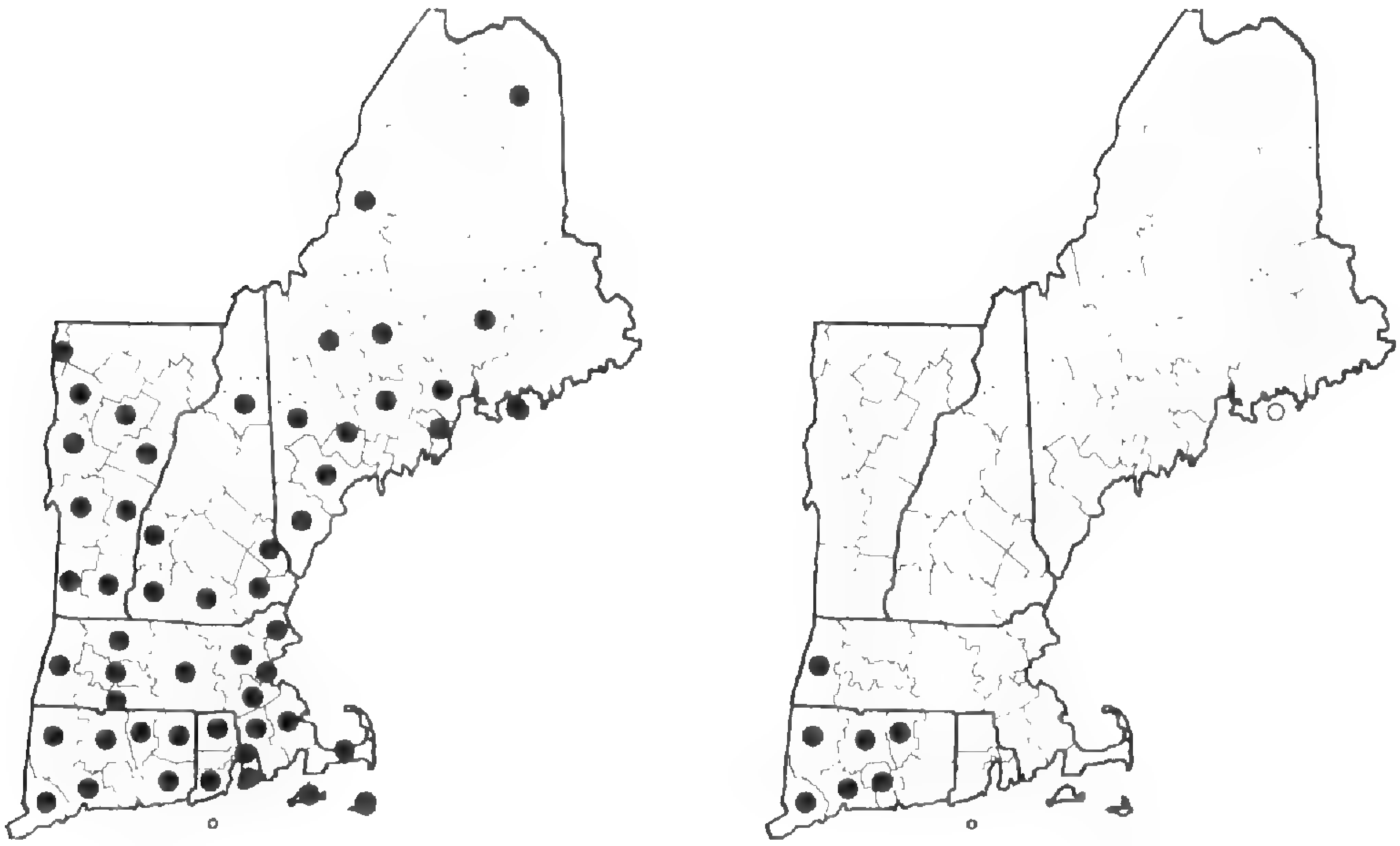
Allium tricoccum
var. *tricoccum*

Figure 33. Distribution maps for *ALLIUM OLERACEUM, A. SATIVUM, A. schoenoprasum,* and *A. tricoccum* var. *tricoccum.*



Allium tricoccum
var. *burdickii*

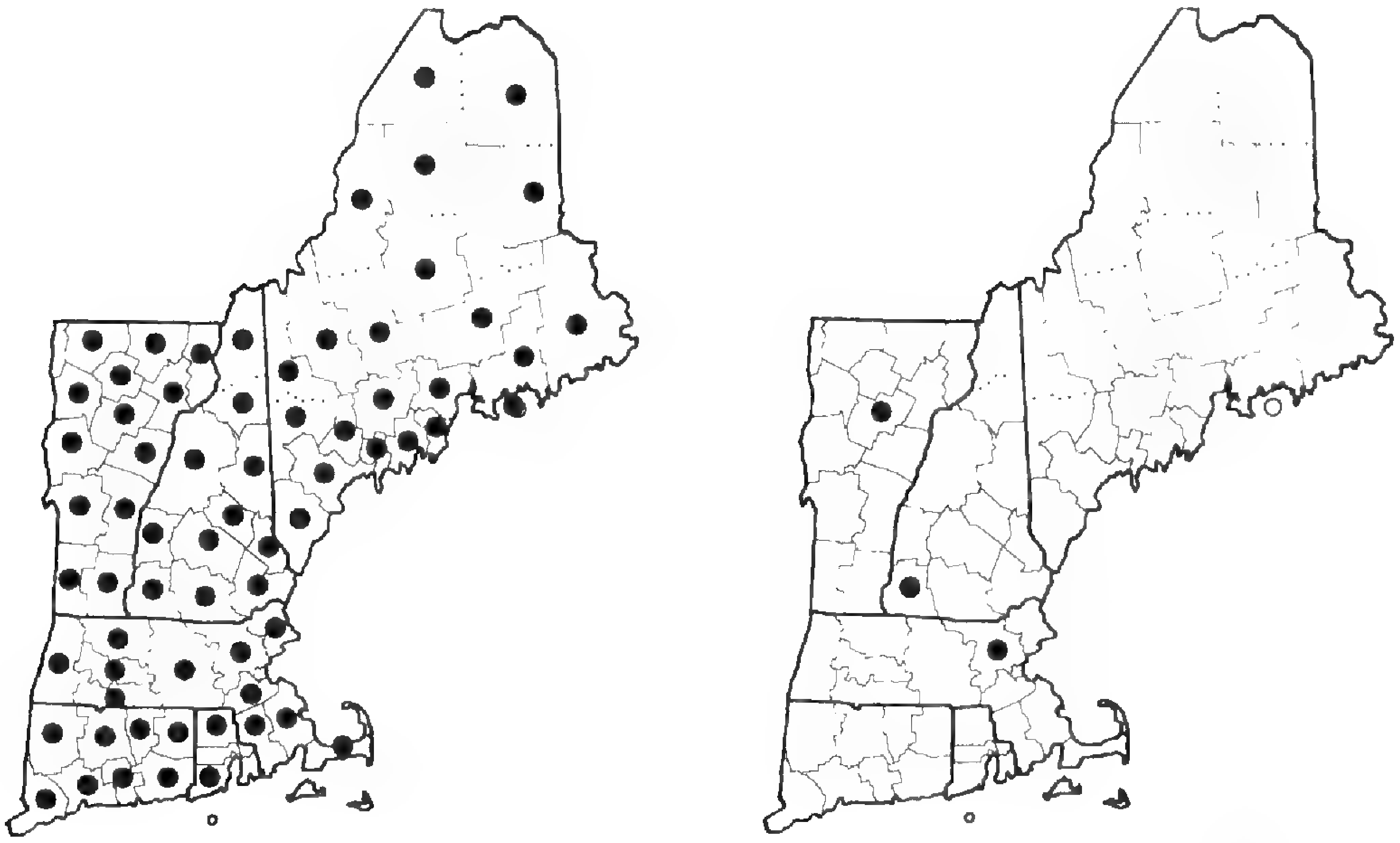
ALLIUM VINEALE



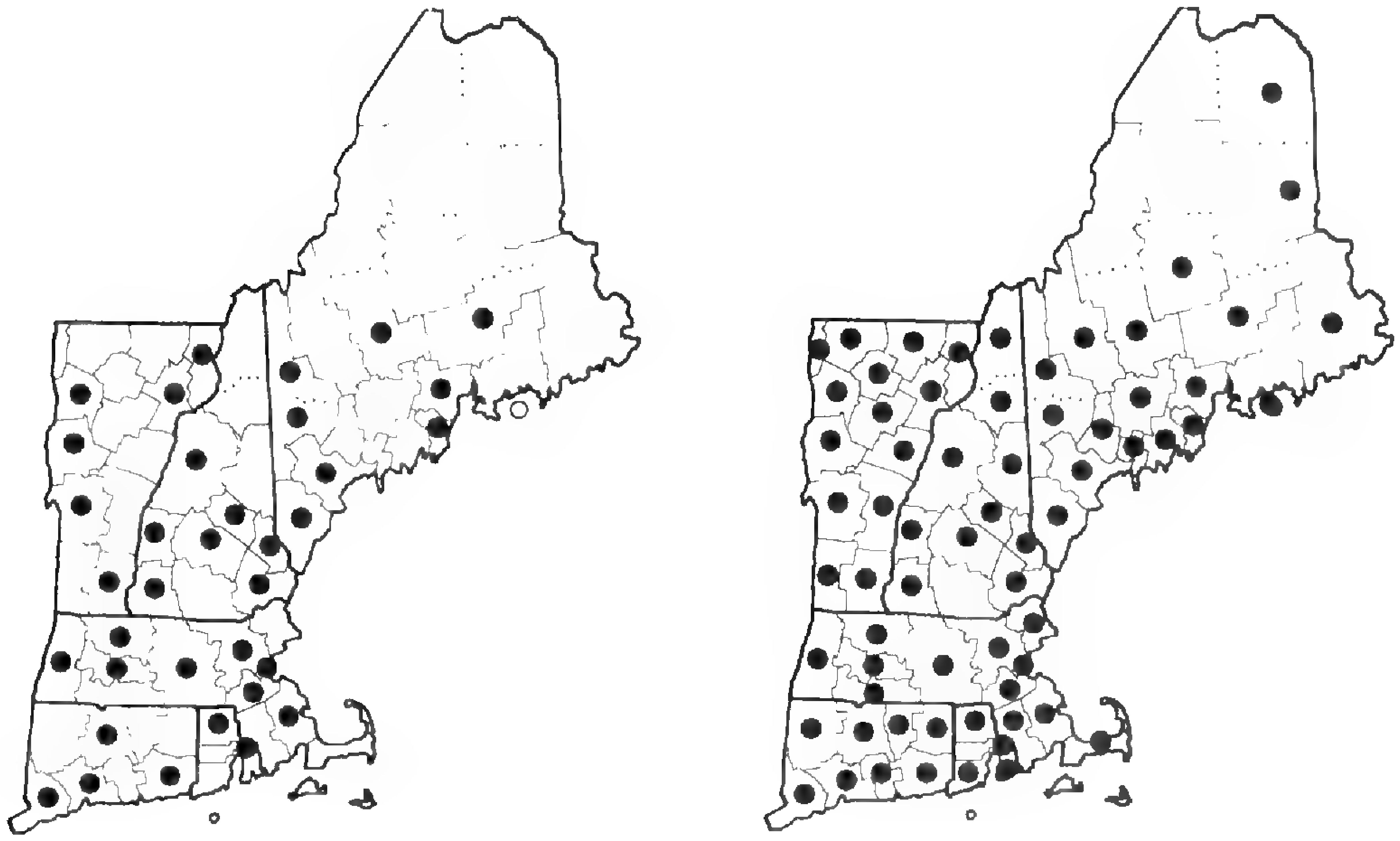
ASPARAGUS OFFICINALIS

Chamaelirium luteum

Figure 34. Distribution maps for *Allium tricoccum* var. *burdickii*, *A. VINEALE, ASPARAGUS OFFICINALIS,* and *Chamaelirium luteum.*



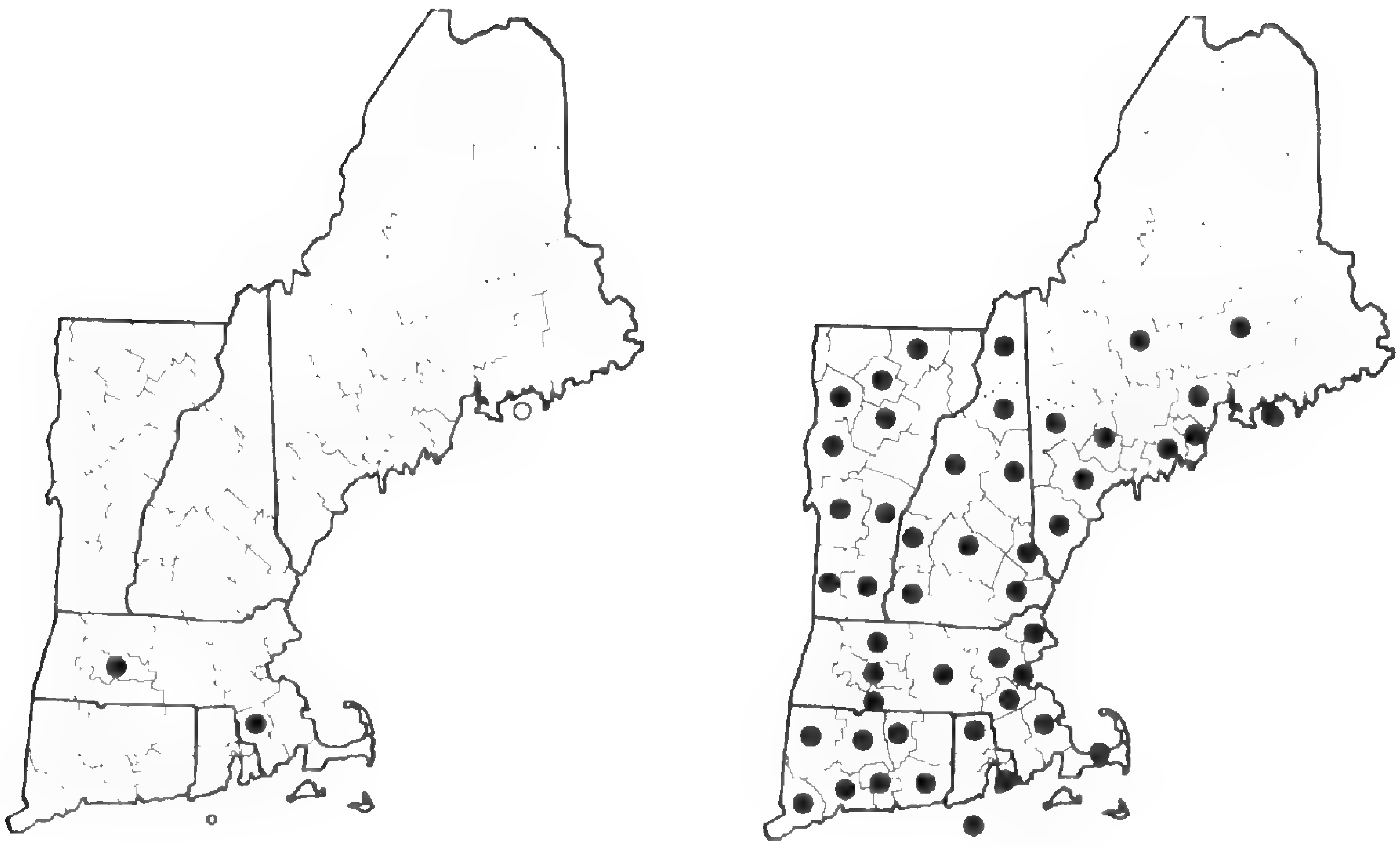
Clintonia borealis *COLCHICUM AUTUMNALE*



CONVALLARIA MAJALIS
var. *MAJALIS*

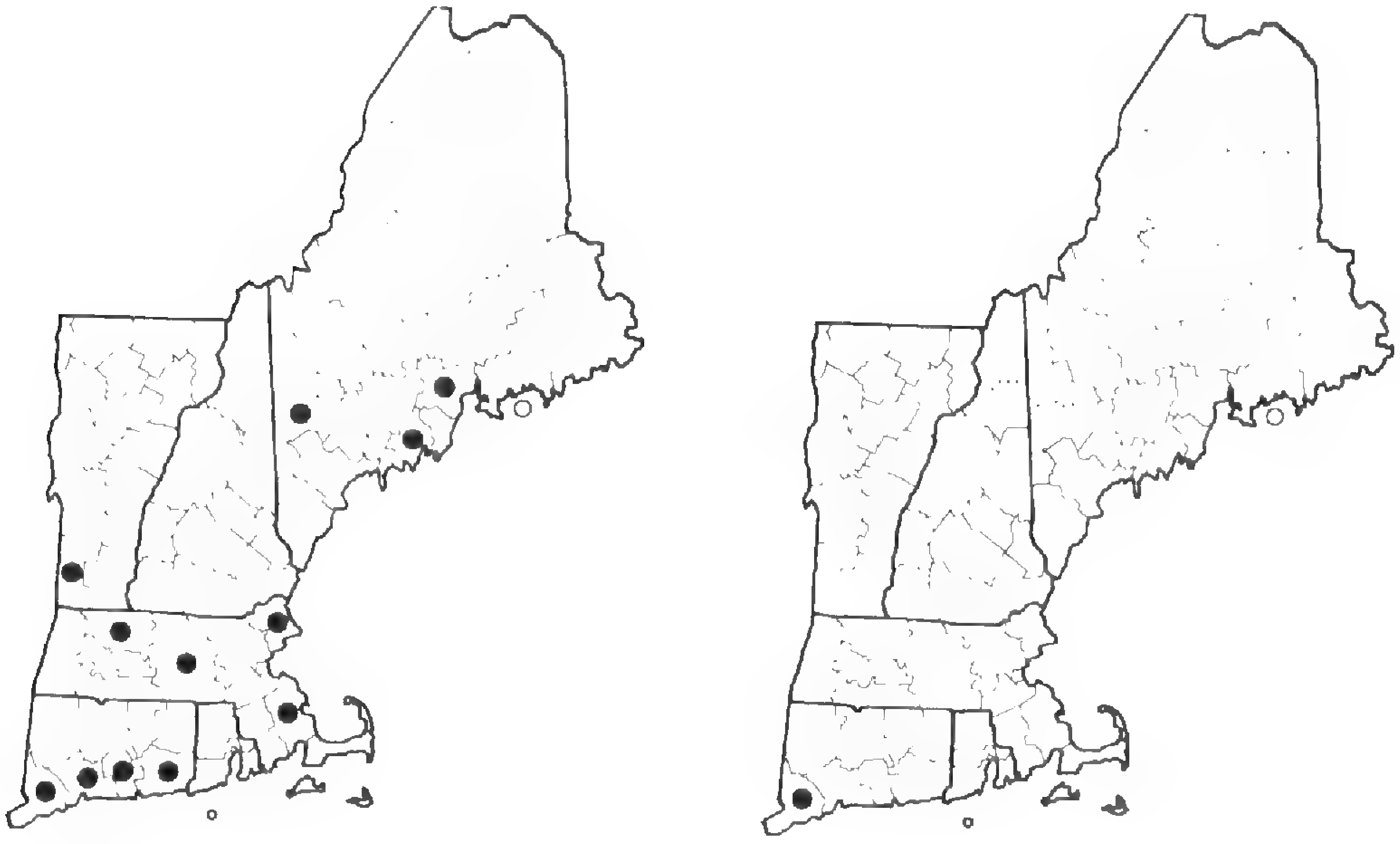
Erythronium americanum

Figure 35. Distribution maps for *Clintonia borealis, COLCHICUM AUTUMNALE, CONVALLARIA MAJALIS* var. *MAJALIS*, and *Erythronium americanum.*



GALANTHUS NIVALIS
subsp. *NIVALIS*

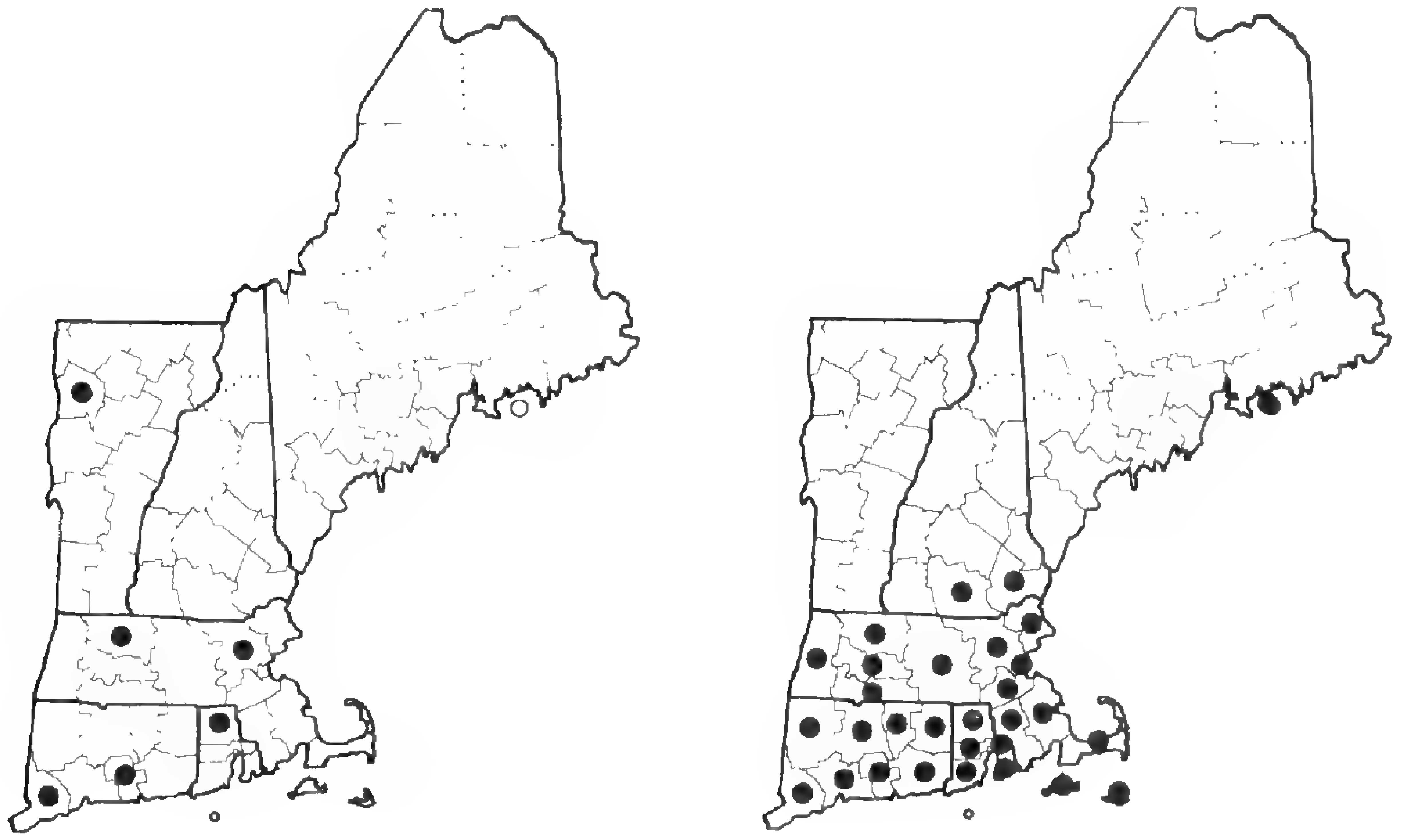
HEMEROCALLIS FULVA



HEMEROCALLIS LILIOASPHODELUS

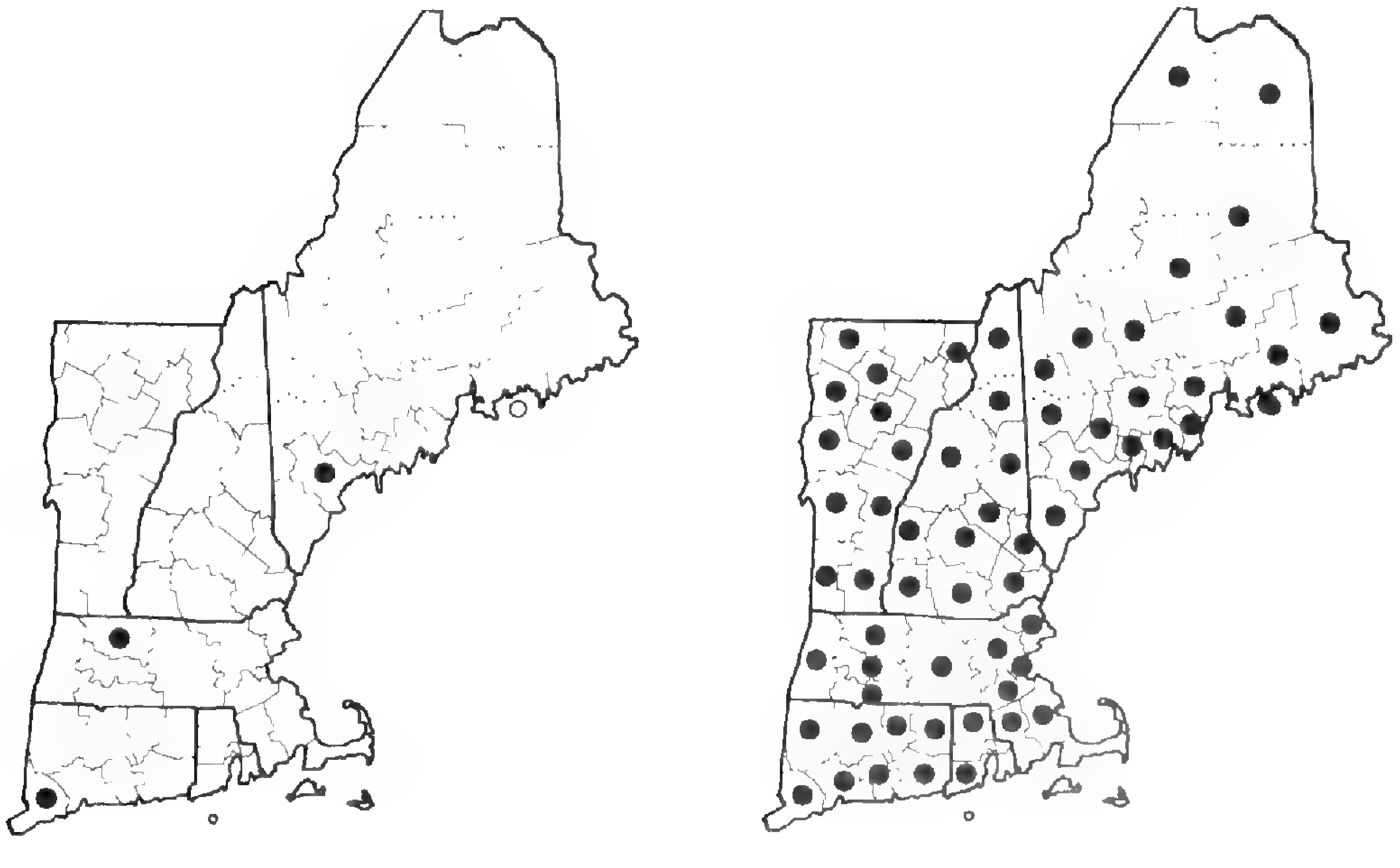
HOSTA LANCIFOLIA

Figure 36. Distribution maps for *GALANTHUS NIVALIS* subsp. *NIVALIS*, *HEMEROCALLIS FULVA*, *H. LILIOASPHODELUS*, and *HOSTA LANCIFOLIA*.



HOSTA VENTRICOSA

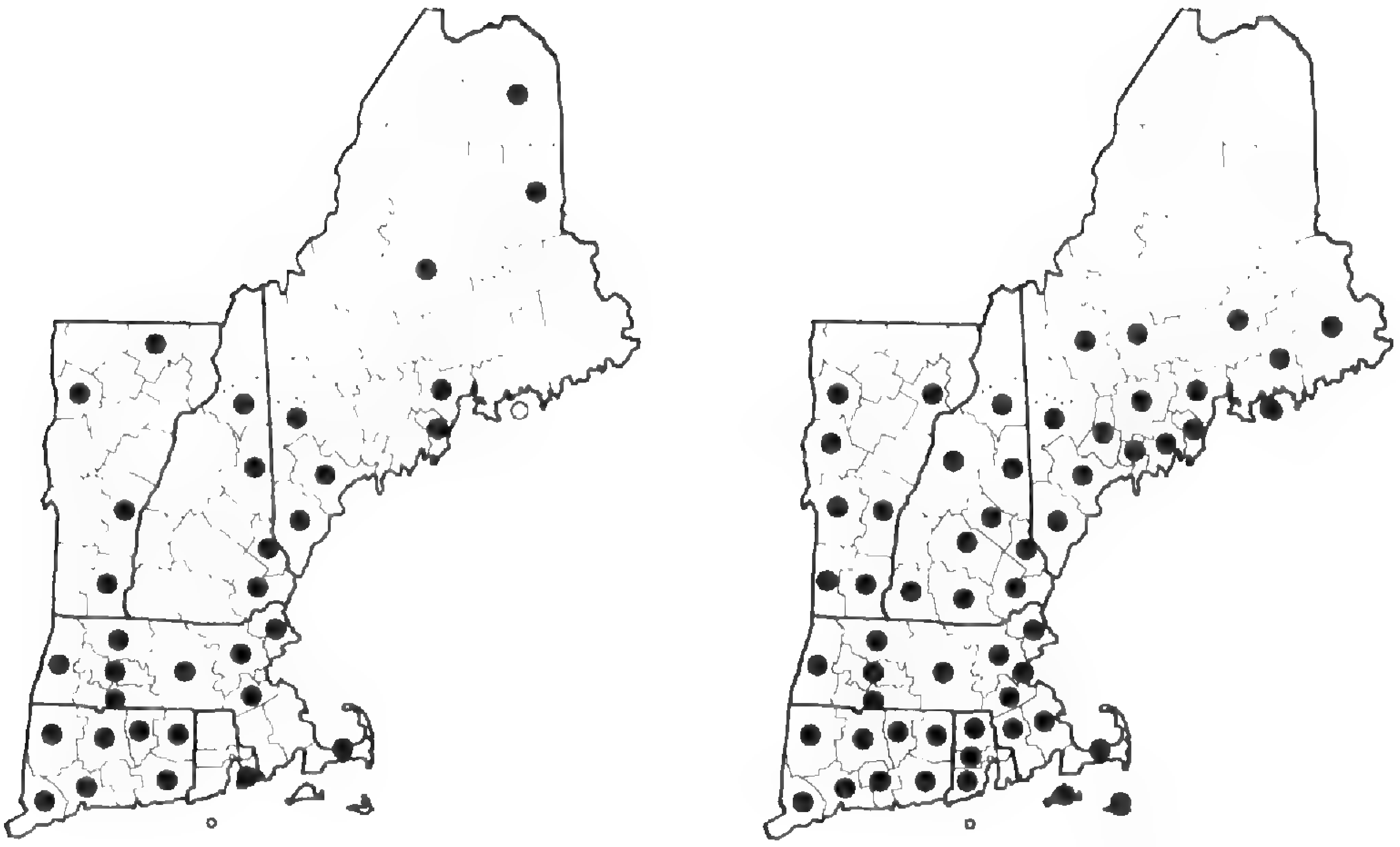
Hypoxis hirsuta



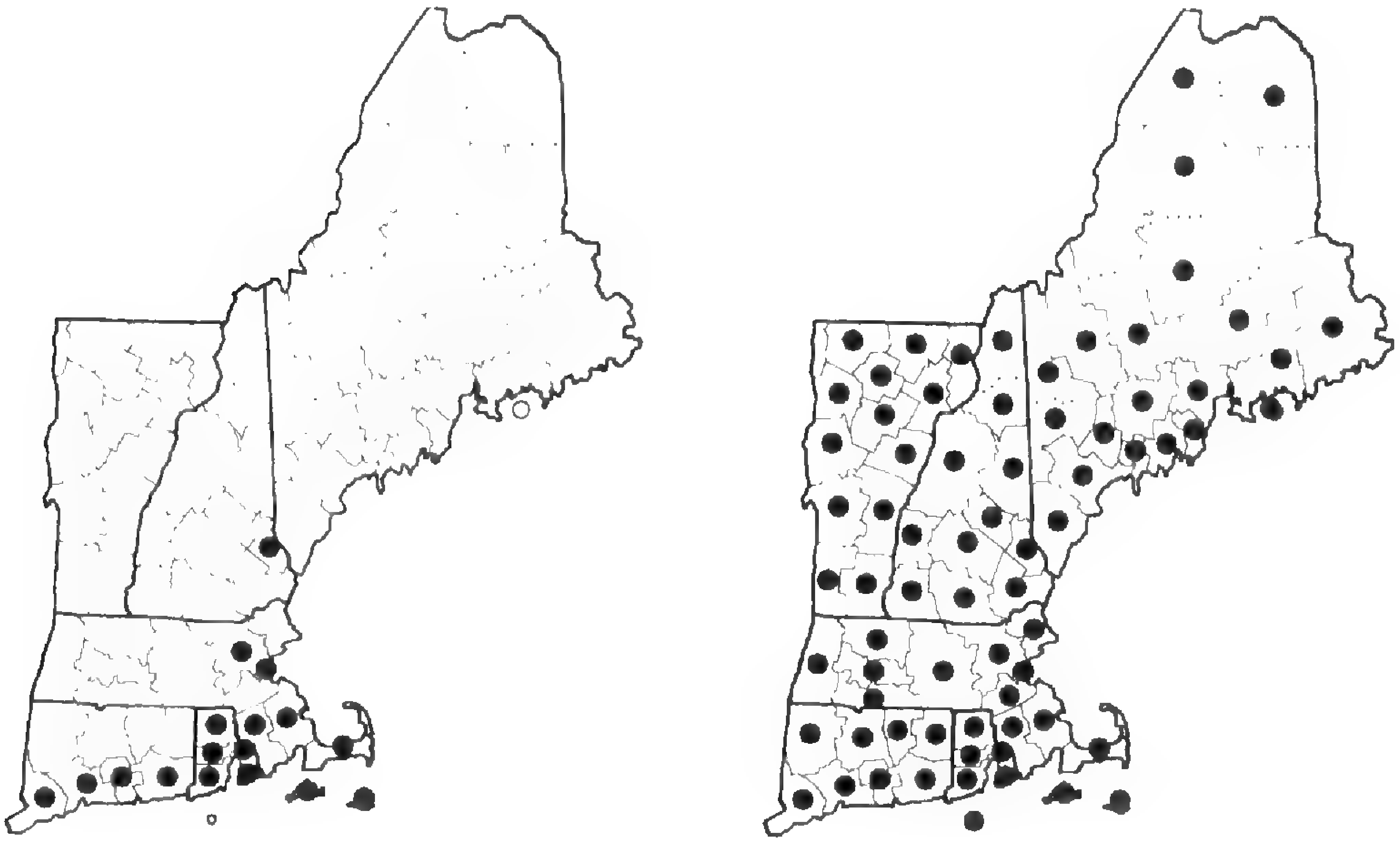
LEUCOJUM AESTIVUM

Lilium canadense

Figure 37. Distribution maps for *HOSTA VENTRICOSA*, *Hypoxis hirsuta*, *LEUCOJUM AESTIVUM*, and *Lilium canadense*.

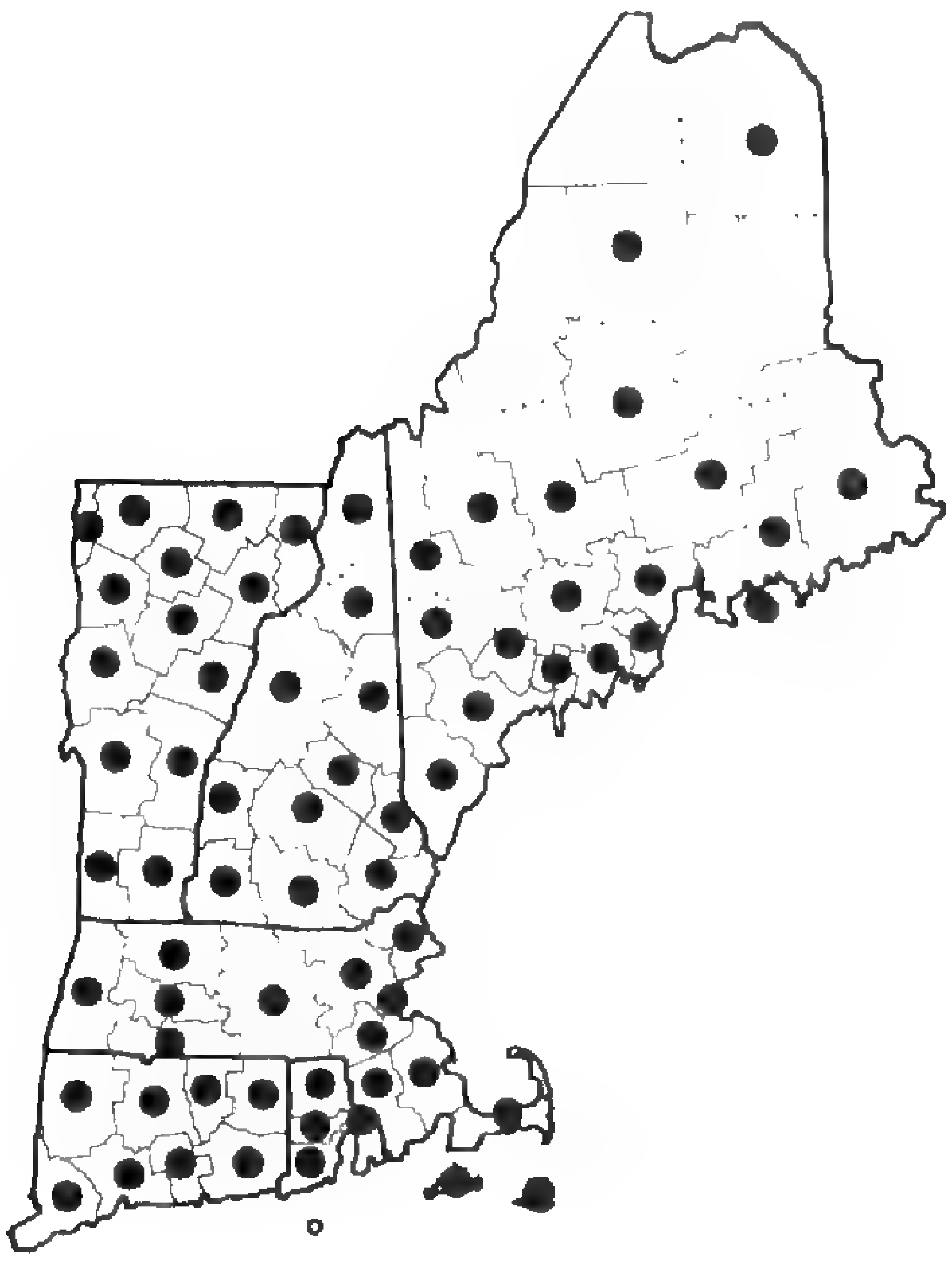


LILIUM LANCIFOLIUM *Lilium philadelphicum*

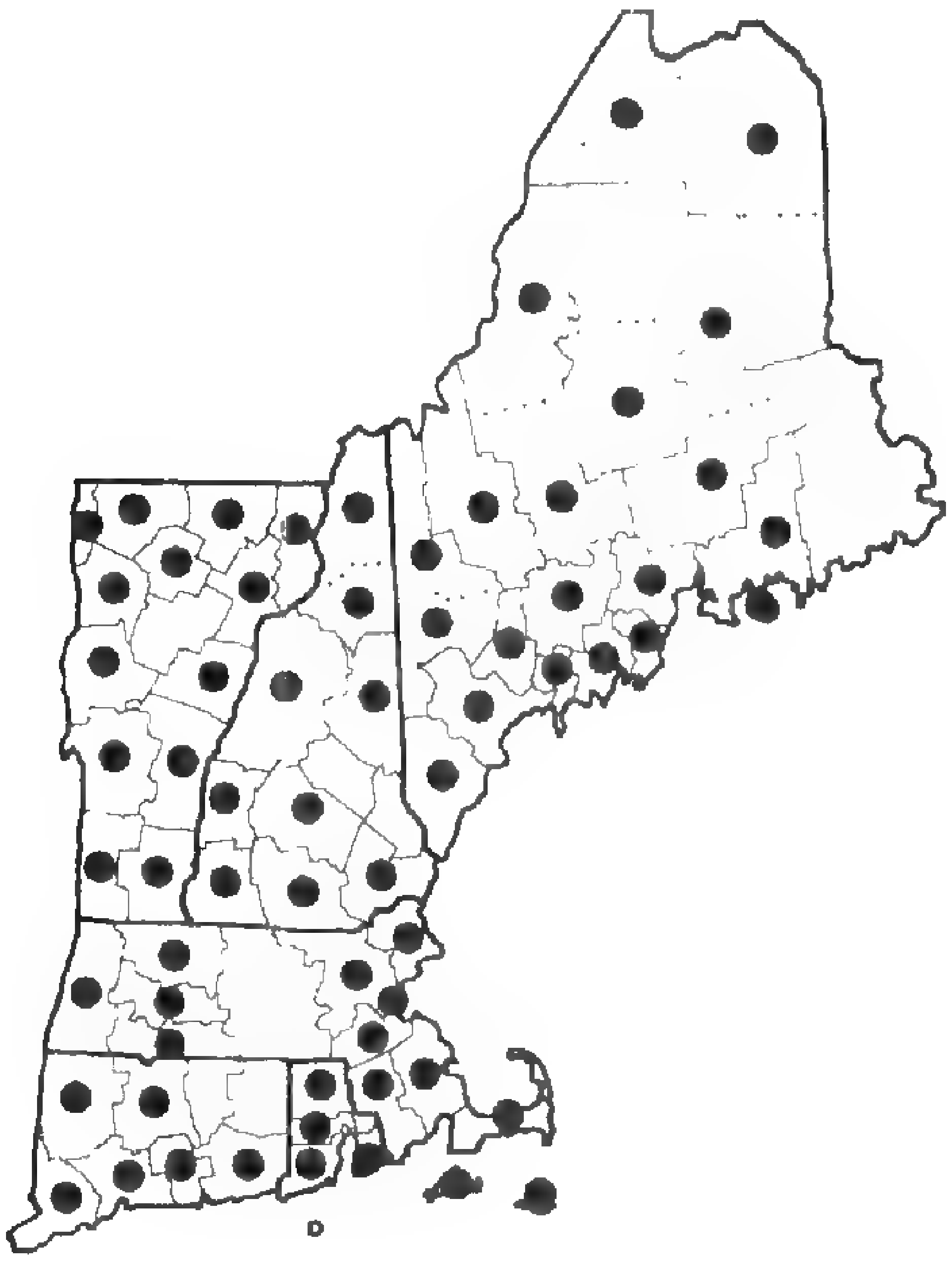


Lilium superbum *Maianthemum canadense*

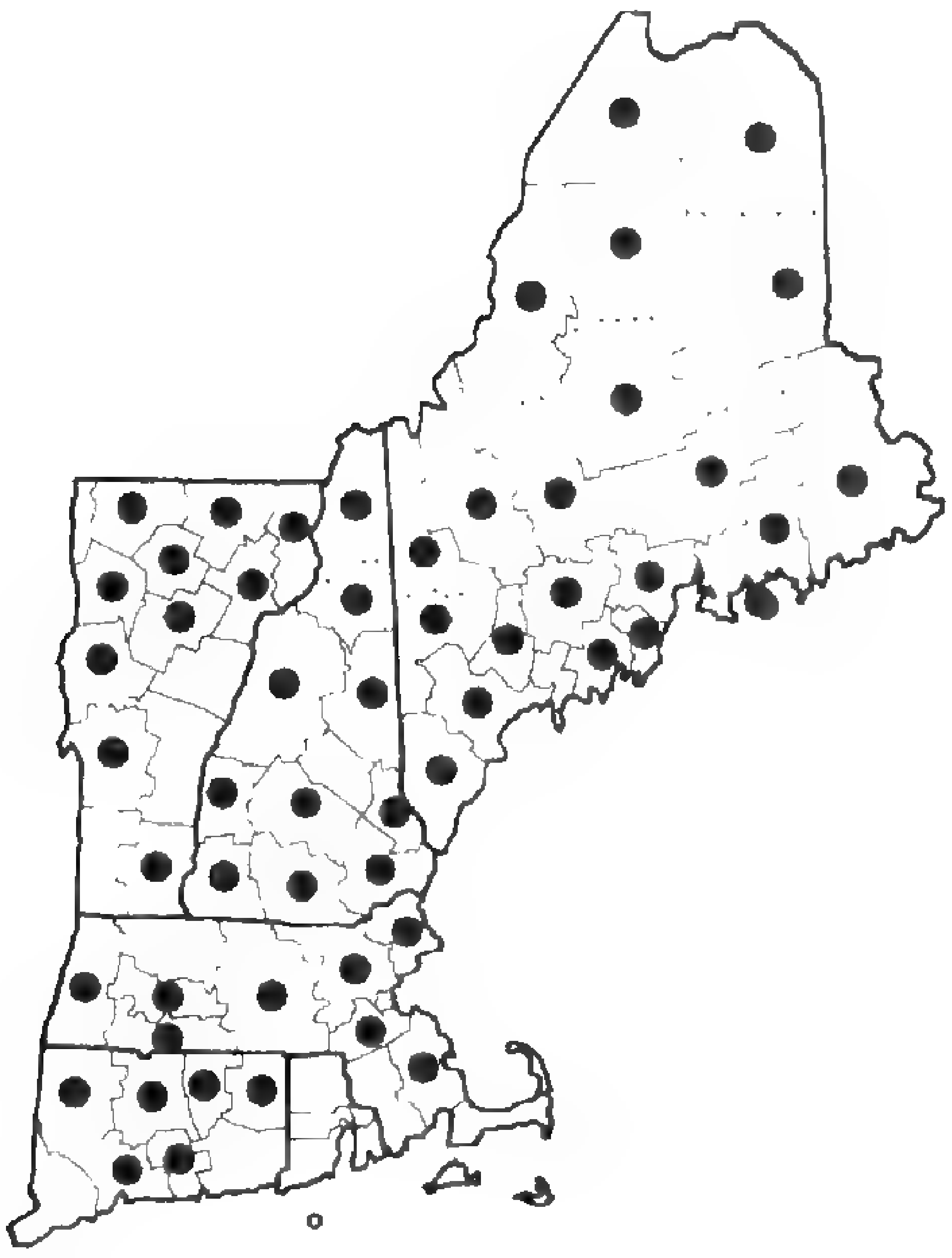
Figure 38. Distribution maps for *LILIUM LANCIFOLIUM*, *L. philadelphicum*, *L. superbum*, and *Maianthemum canadense*.



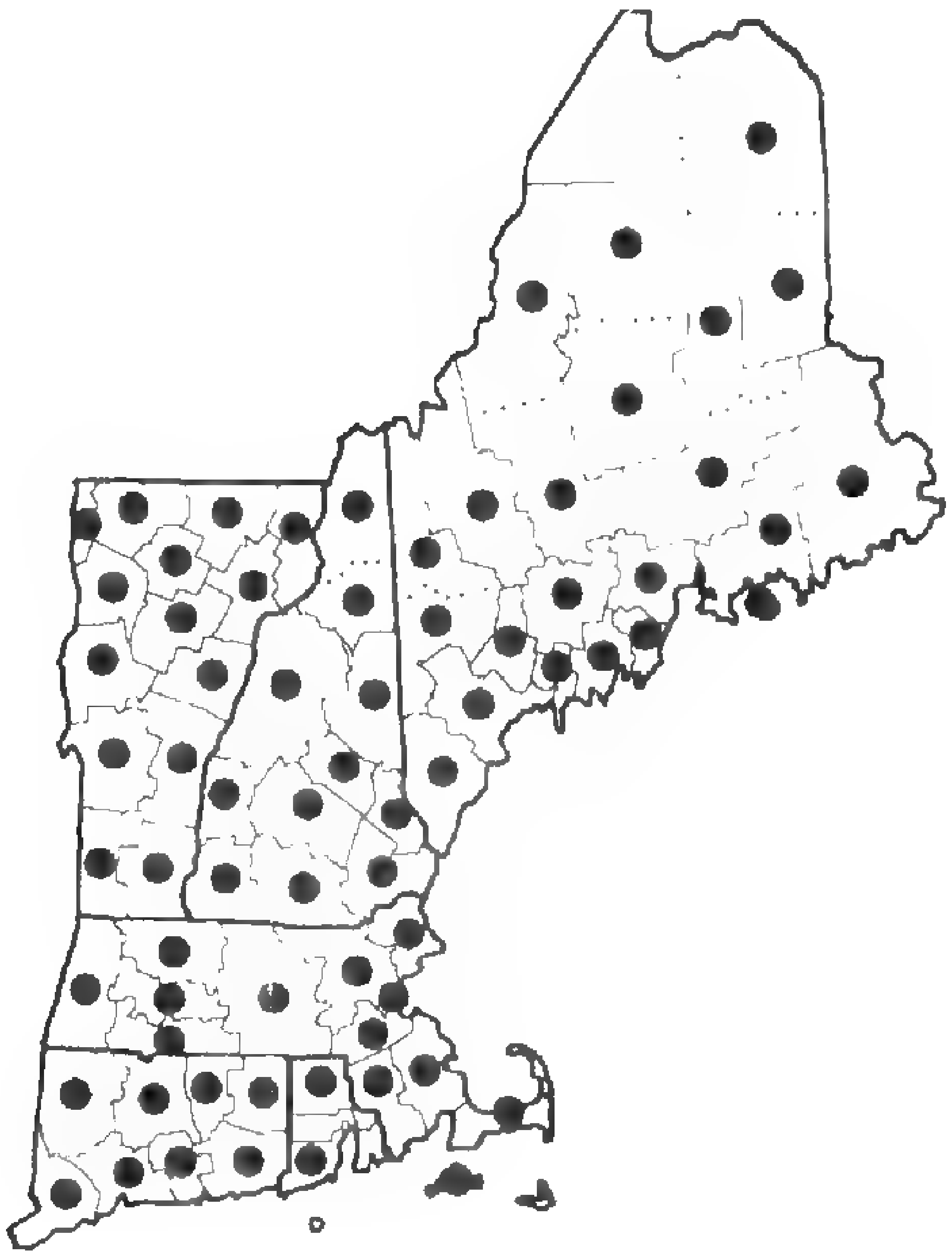
Maianthemum racemosum
subsp. *racemosum*



Maianthemum stellatum

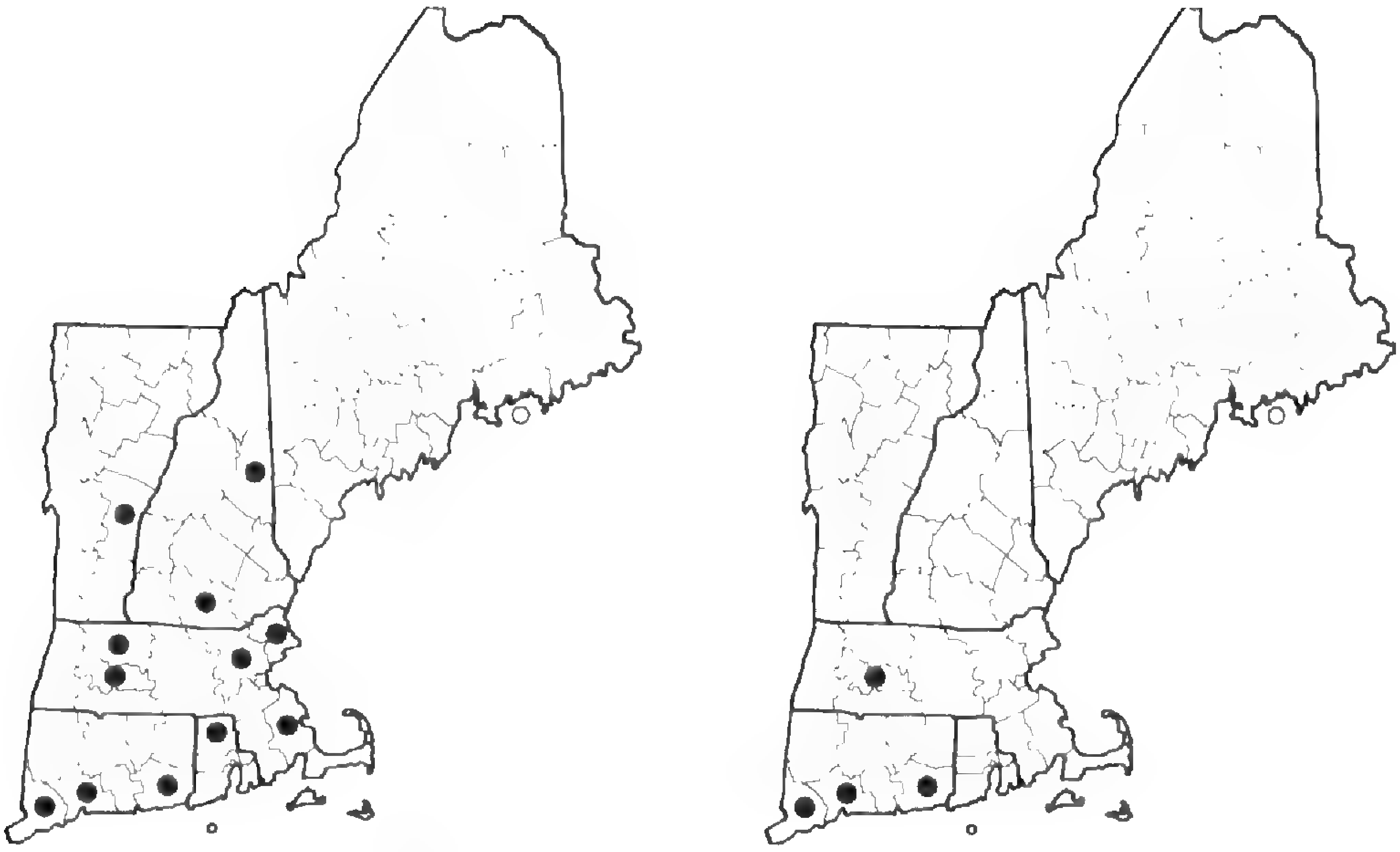


Maianthemum trifolium



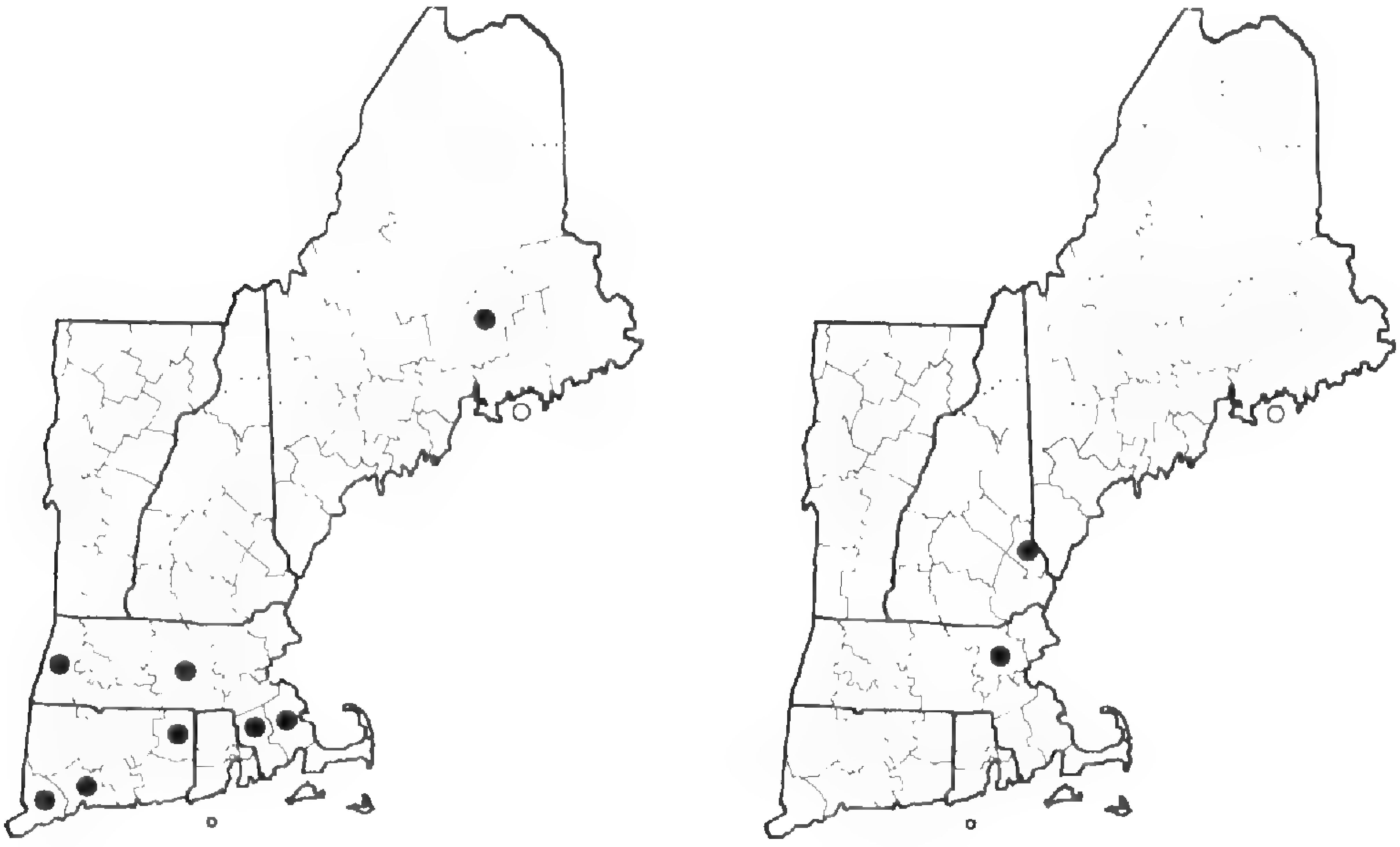
Medeola virginiana

Figure 39. Distribution maps for *Maianthemum racemosum* subsp. *racemosum*, *M. stellatum*, *M. trifolium*, and *Medeola virginiana*.



MUSCARI BOTRYOIDES

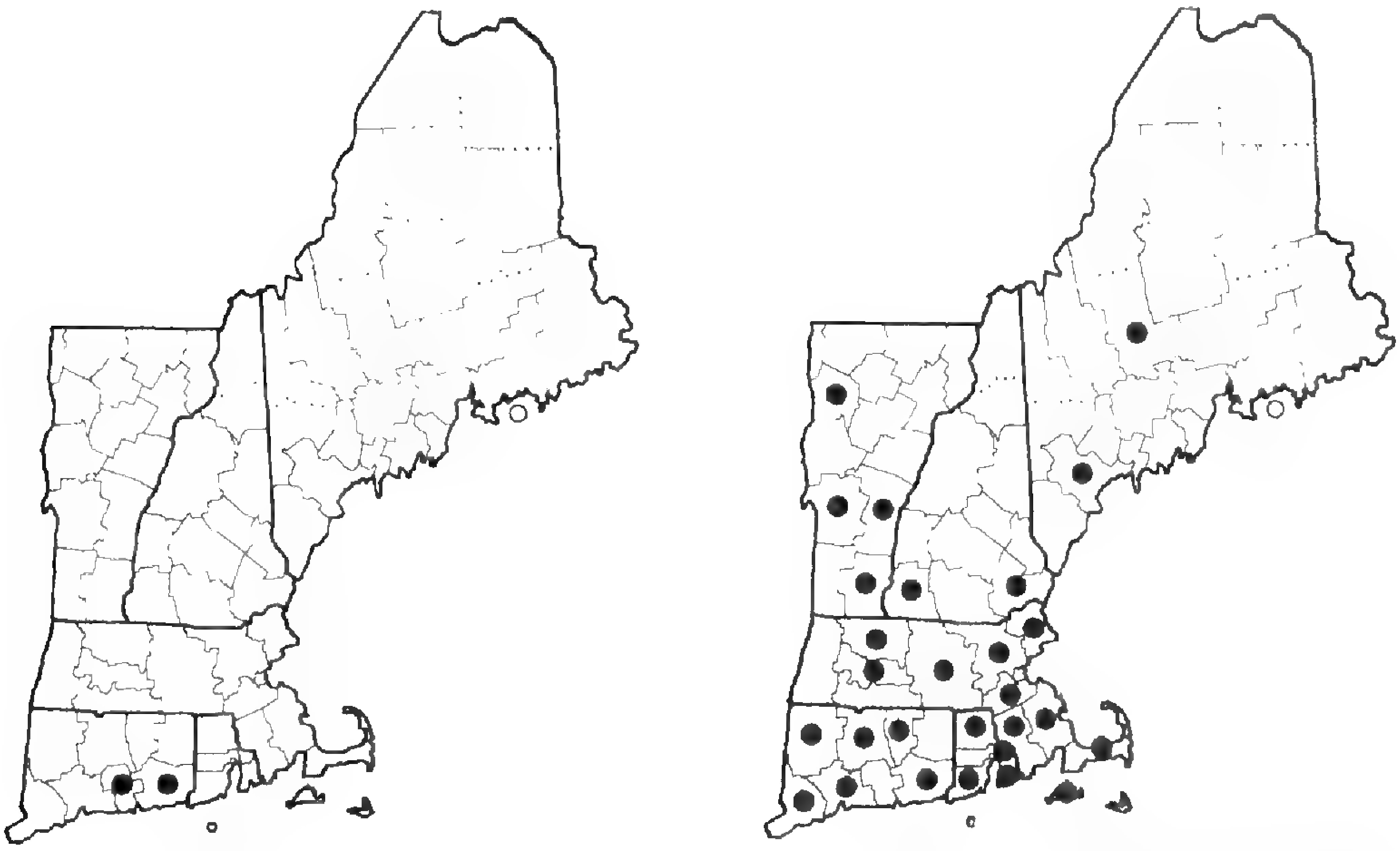
MUSCARI NEGLECTUM



NARCISSUS POETICUS

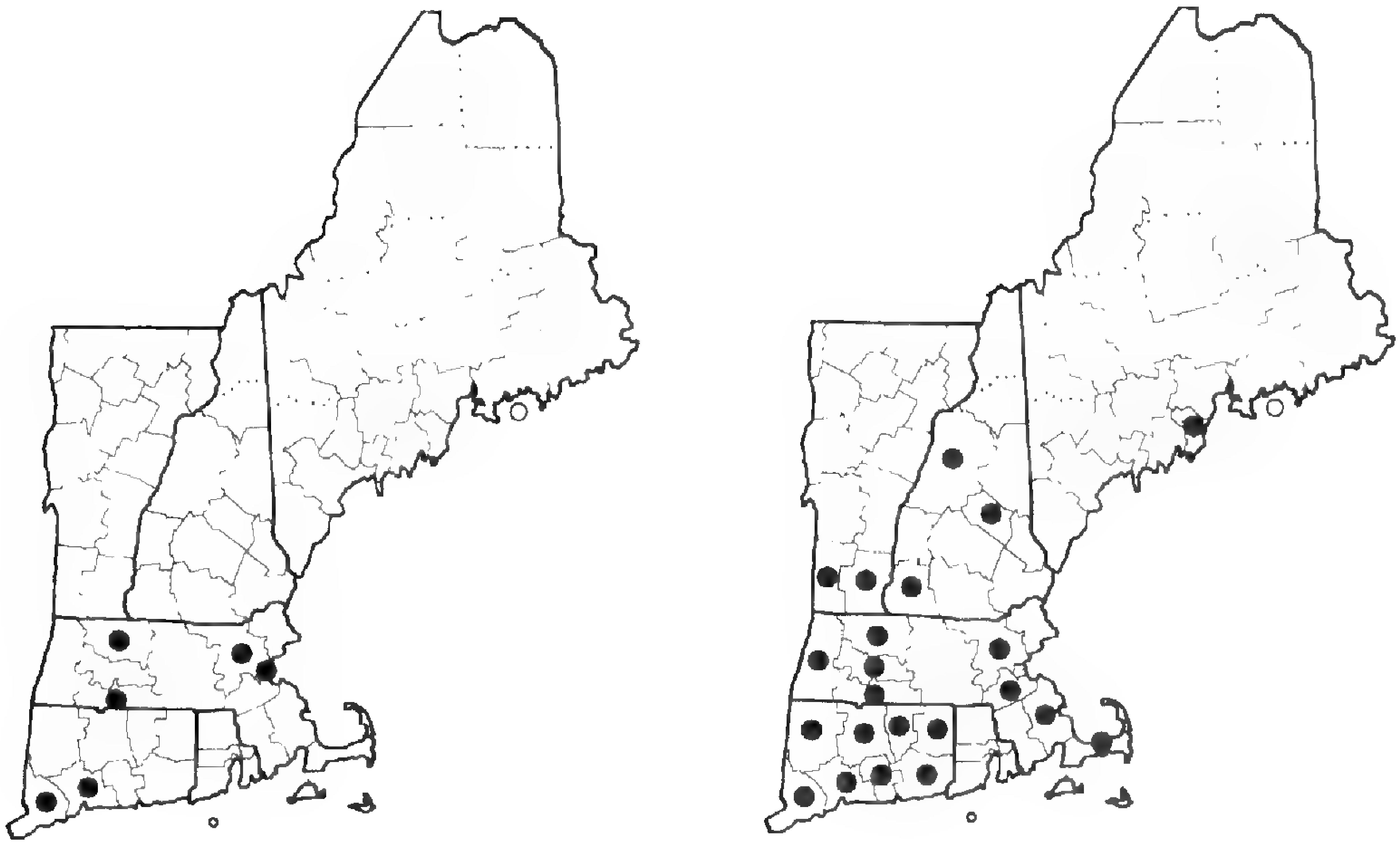
NARCISSUS PSEUDONARCISSUS

Figure 40. Distribution maps for *MUSCARI BOTRYOIDES*, *M. NEGLECTUM*, *NARCISSUS POETICUS*, and *N. PSEUDONARCISSUS*.



ORNITHOGALUM NUTANS

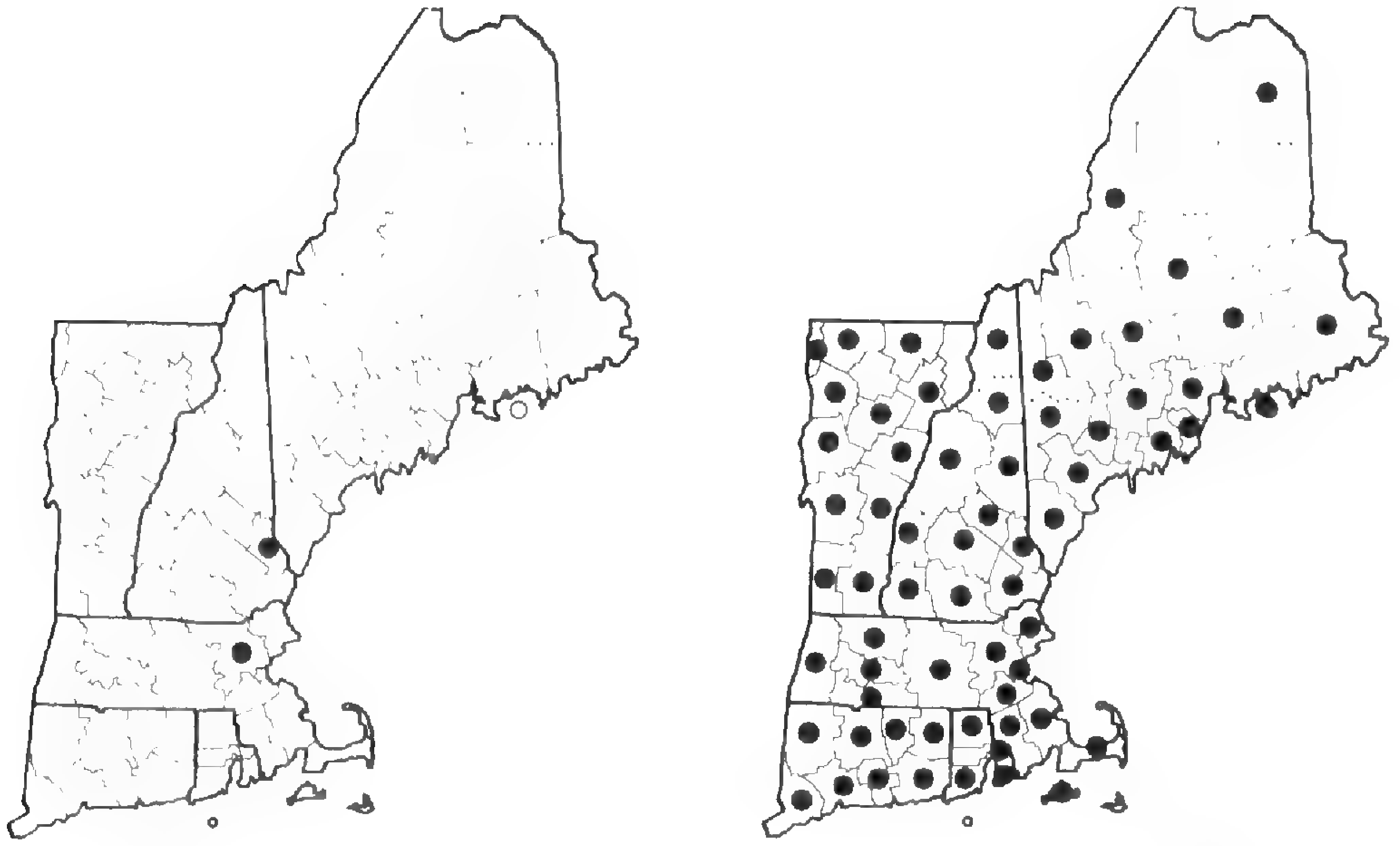
ORNITHOGALUM UMBELLATUM



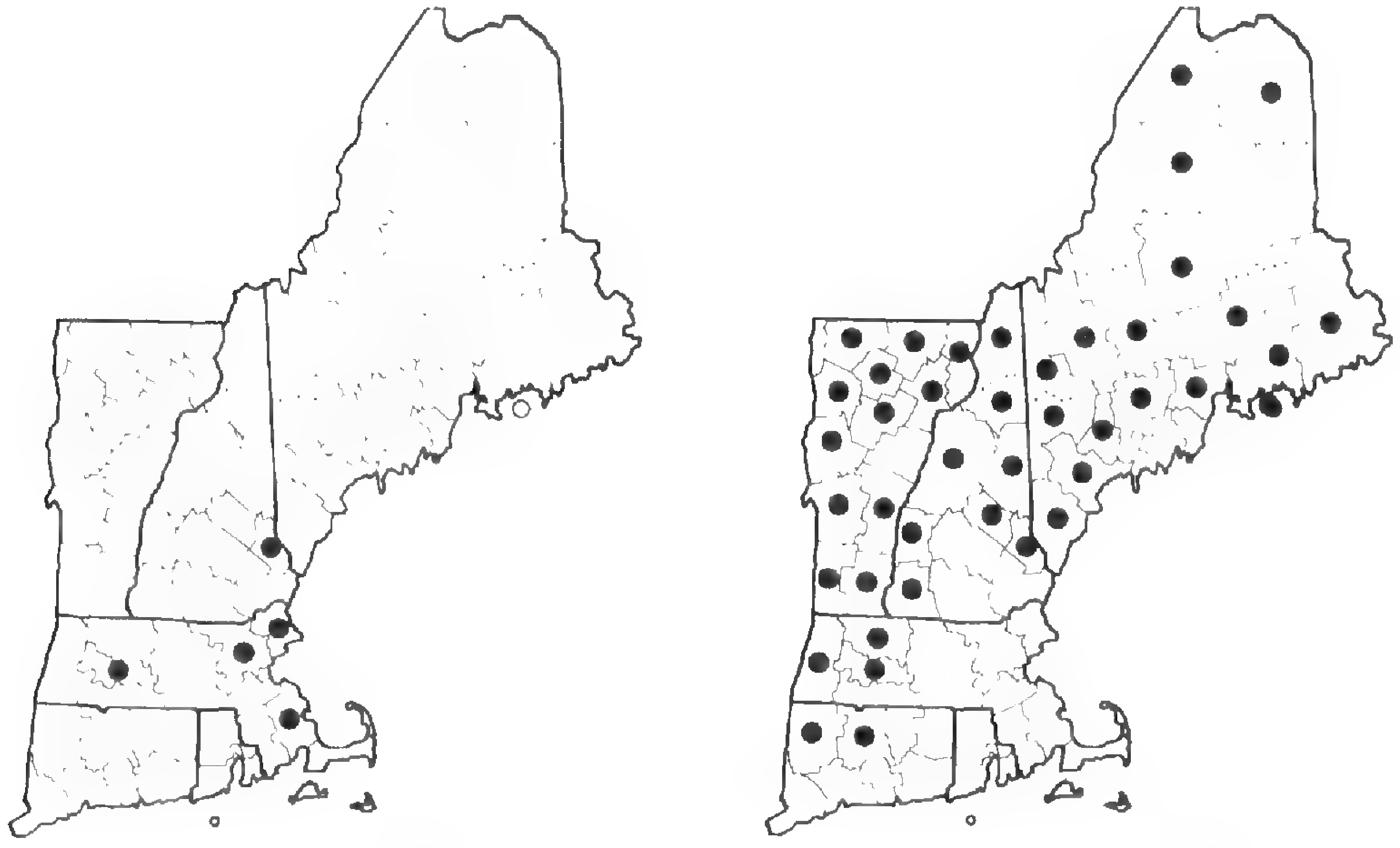
Polygonatum biflorum
var. *biflorum*

Polygonatum biflorum
var. *commutatum*

Figure 41. Distribution maps for *ORNITHOGALUM NUTANS*, *O. UMBELLATUM*, *Polygonatum biflorum* var. *biflorum*, and *P. biflorum* var. *commutatum*.

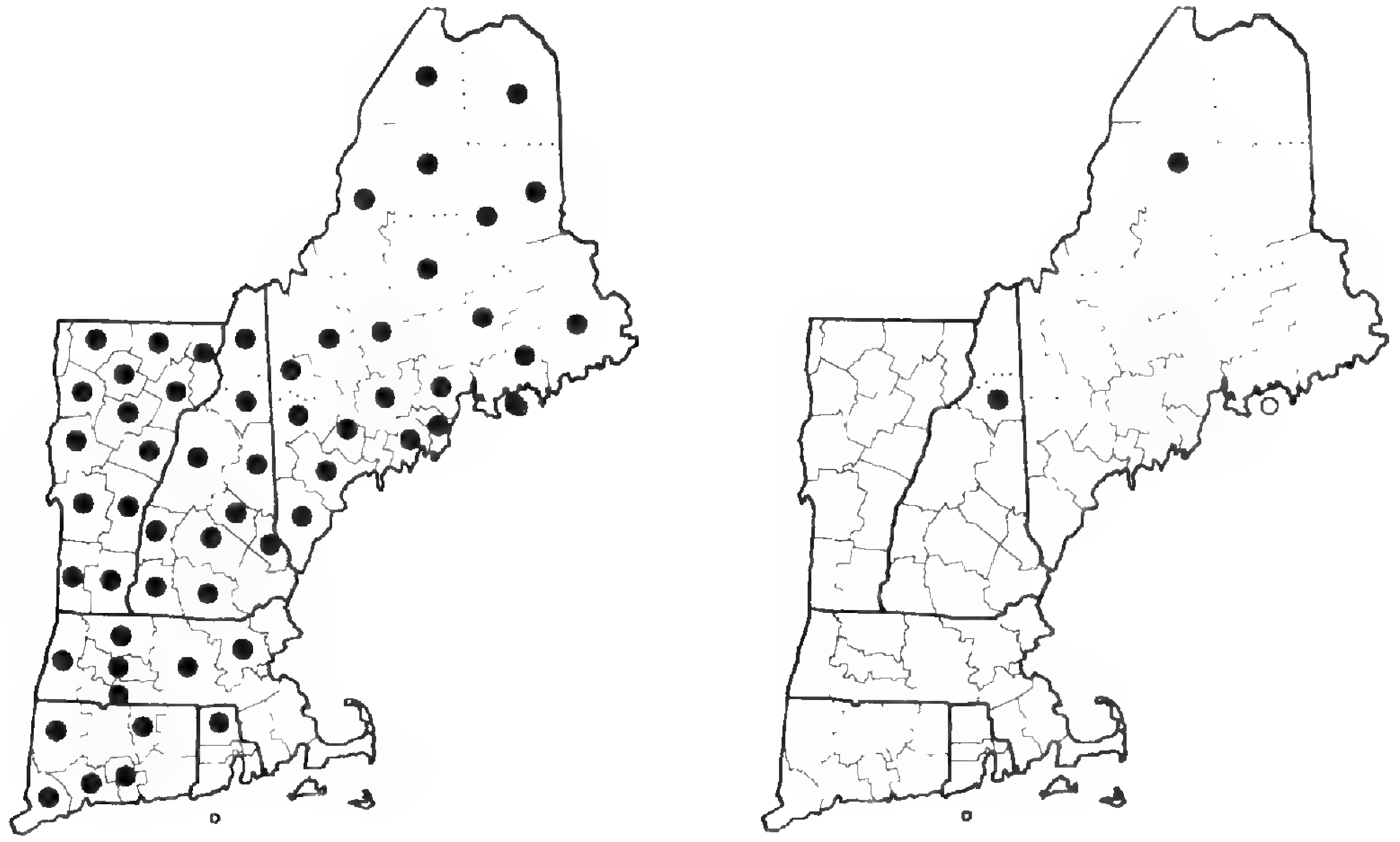


POLYGONATUM LATIFOLIUM *Polygonatum pubescens*

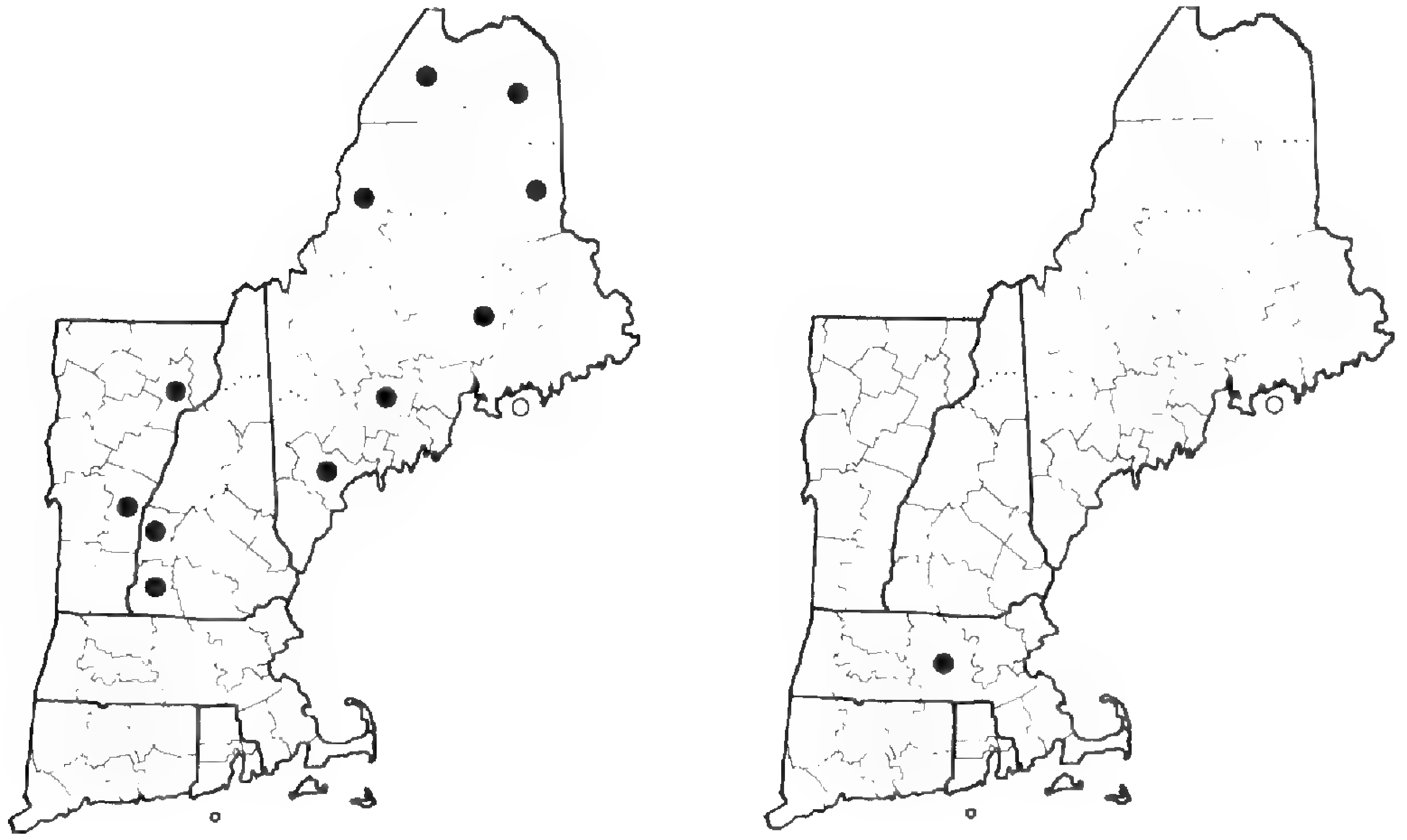


SCILLA SIBERICA *Streptopus amplexifolius*

Figure 42. Distribution maps for *POLYGONATUM LATIFOLIUM*, *P. pubescens*, *SCILLA SIBERICA*, and *Streptopus amplexifolius*.

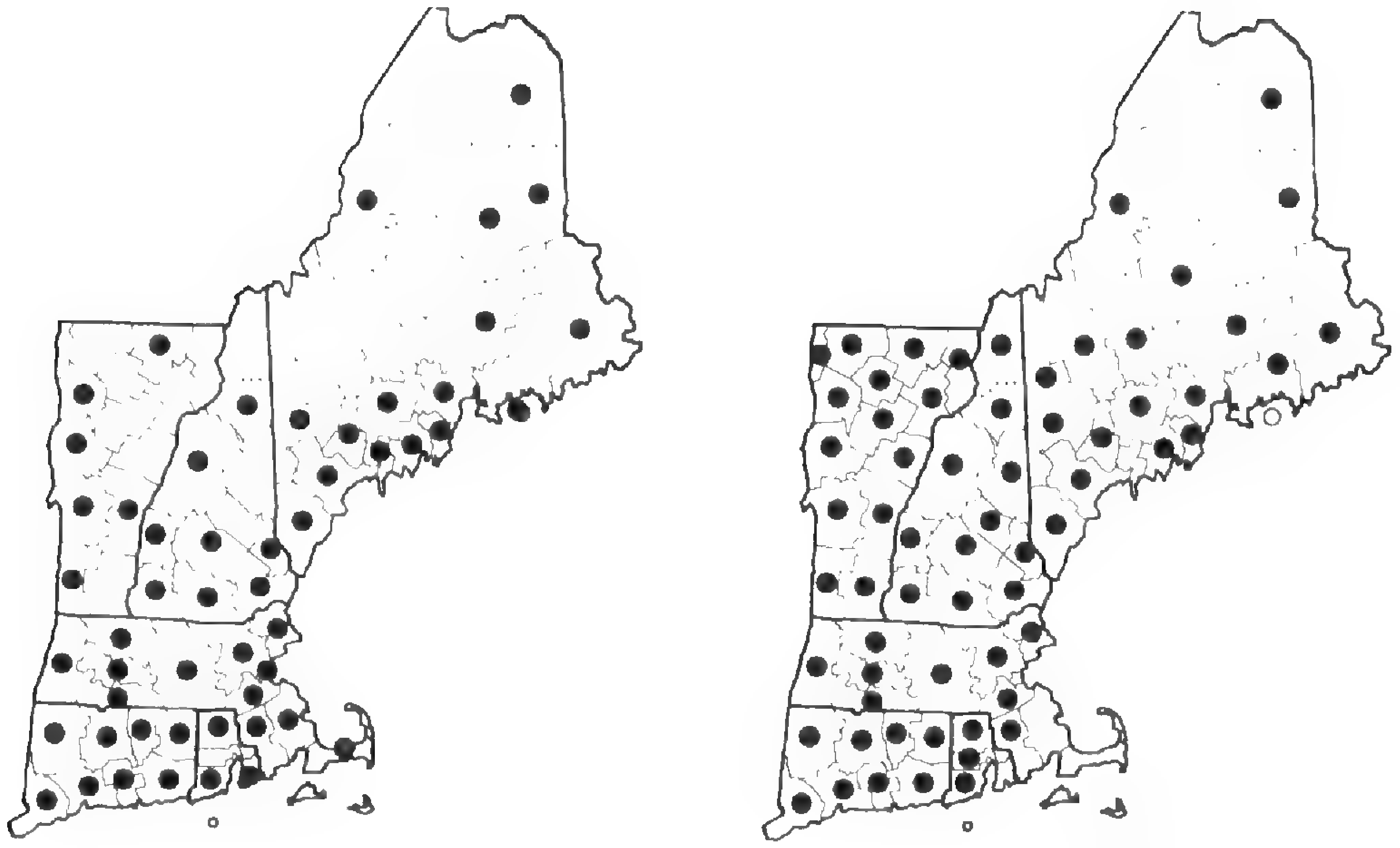


Streptopus lanceolatus *Streptopus* X *oreopolus*



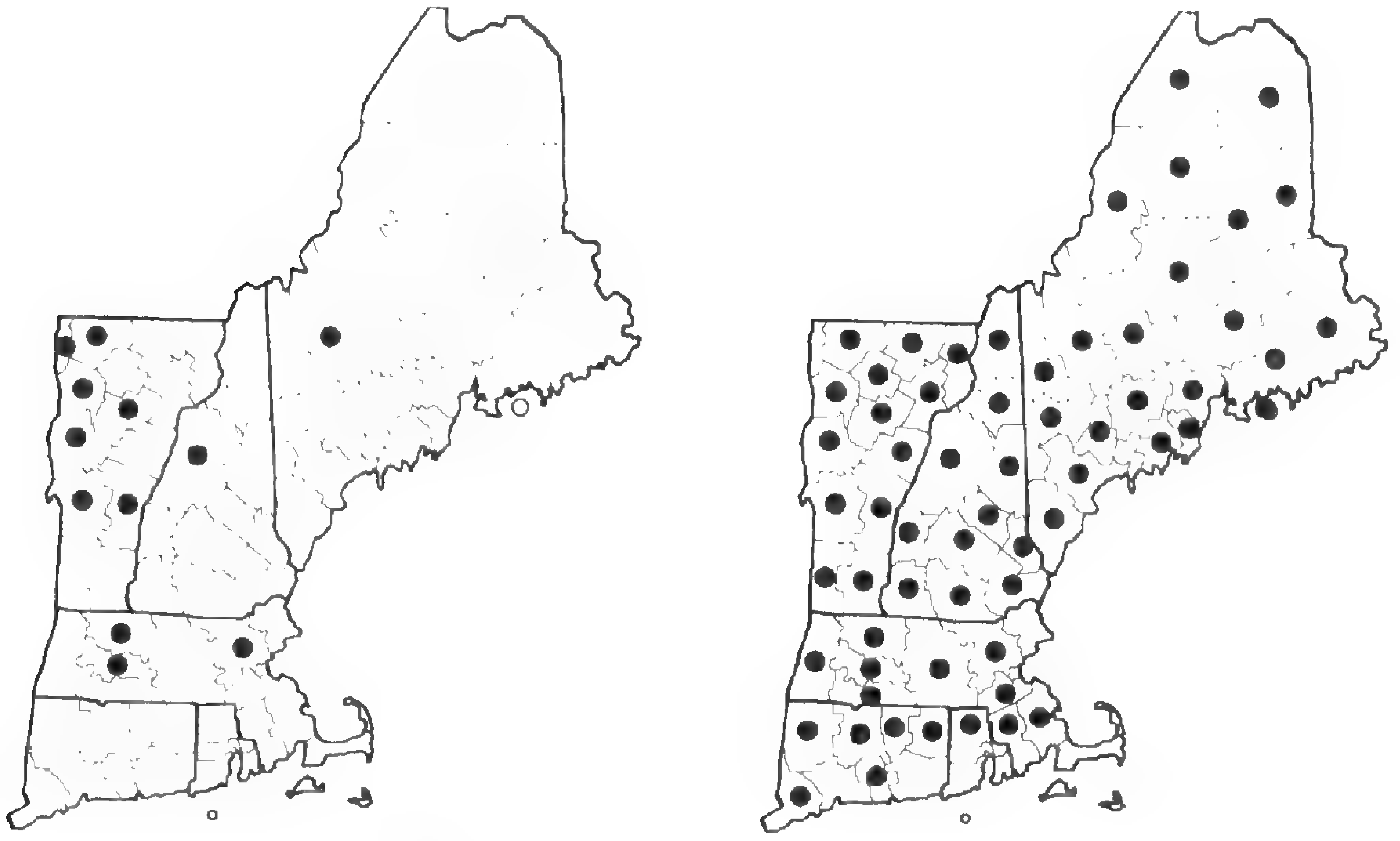
Tofieldia glutinosa *TRICYRTIS HIRTA*

Figure 43. Distribution maps for *Streptopus lanceolatus*, *S.* X *oreopolus*, *Tofieldia glutinosa*, and *TRICYRTIS HIRTA*.



Trillium cernuum

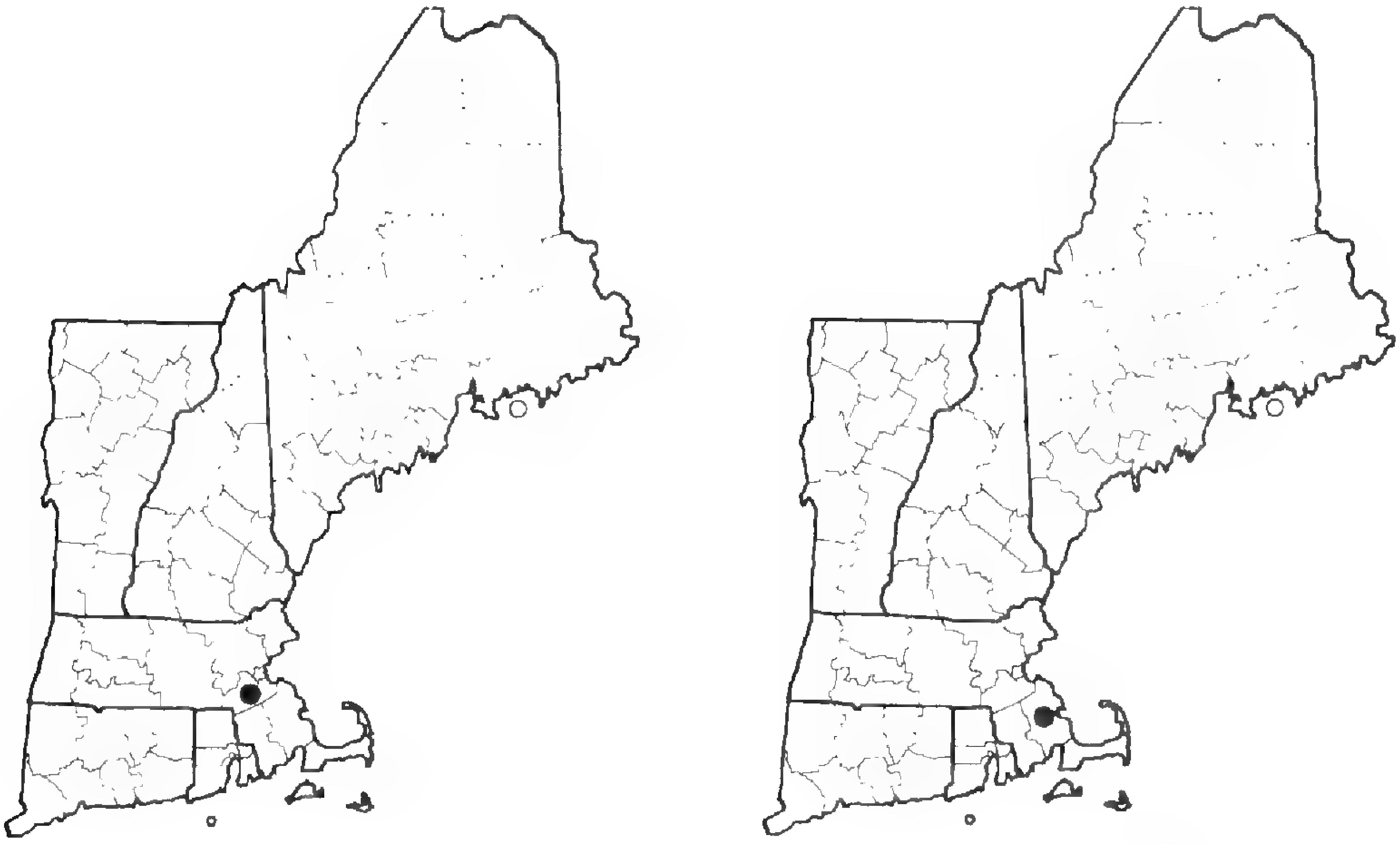
Trillium erectum



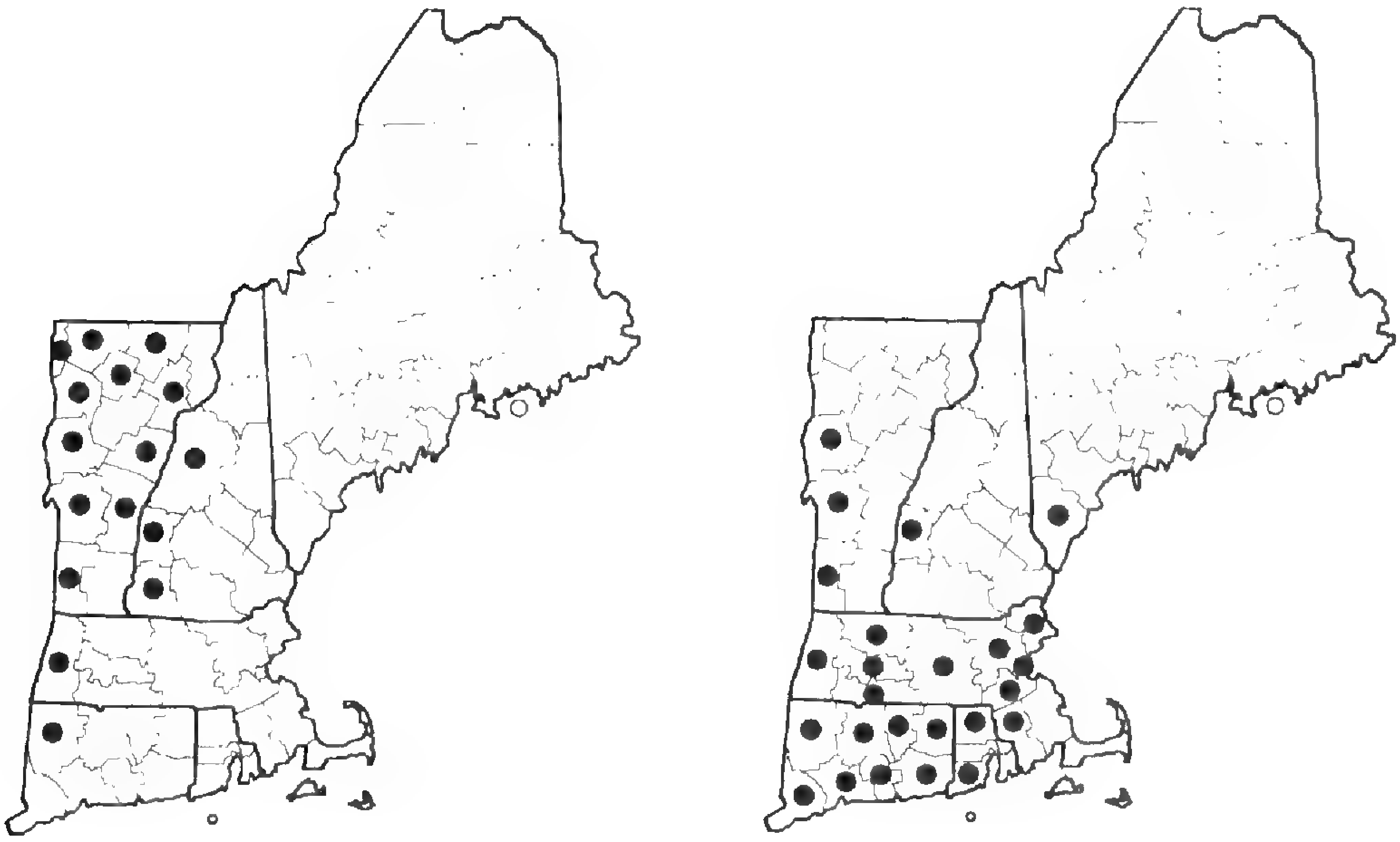
Trillium grandiflorum

Trillium undulatum

Figure 44. Distribution maps for *Trillium cernuum, T. erectum, T. grandiflorum,* and *T. undulatum.*

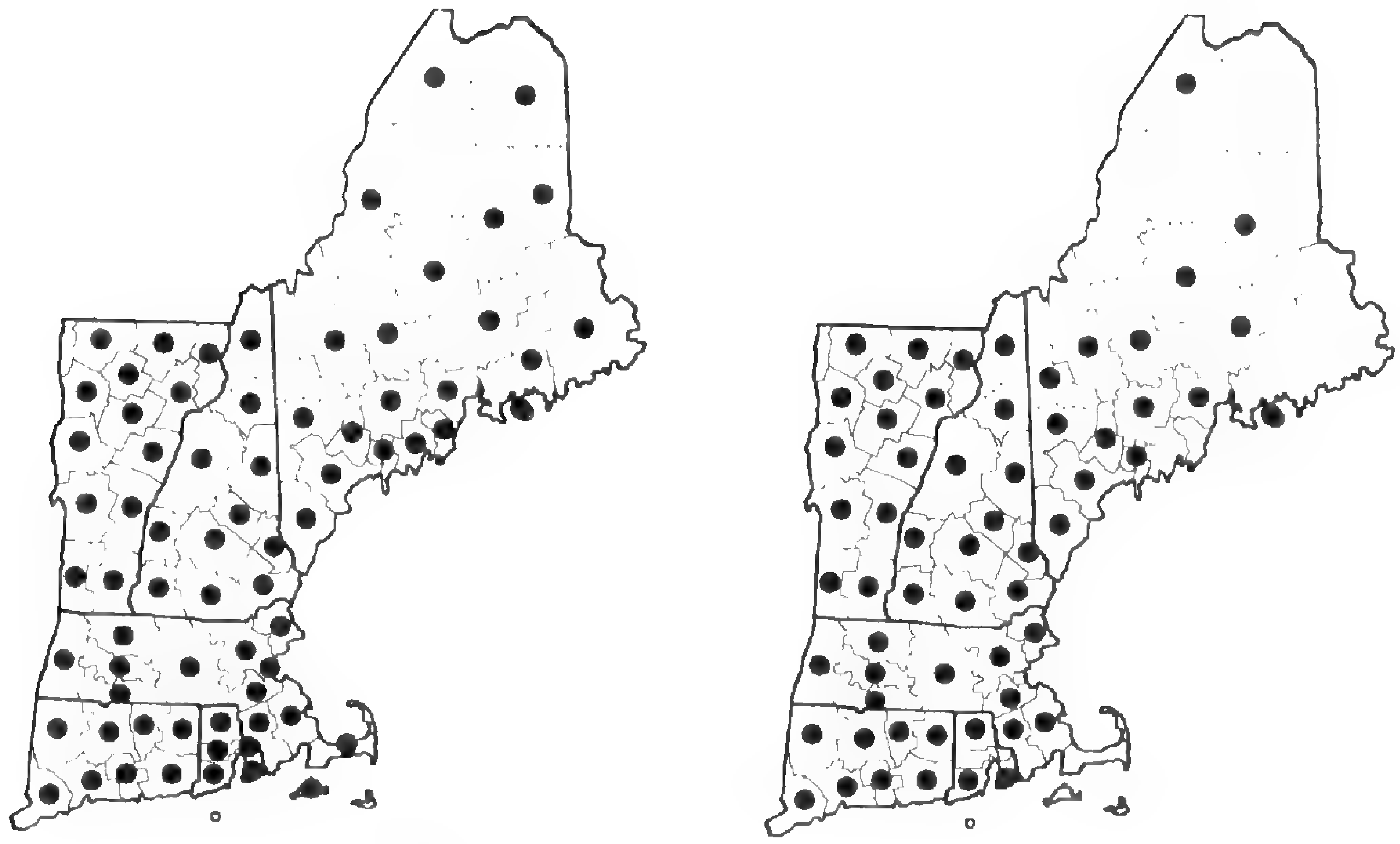


TULIPA GESNERIA *TULIPA SYLVESTRIS*



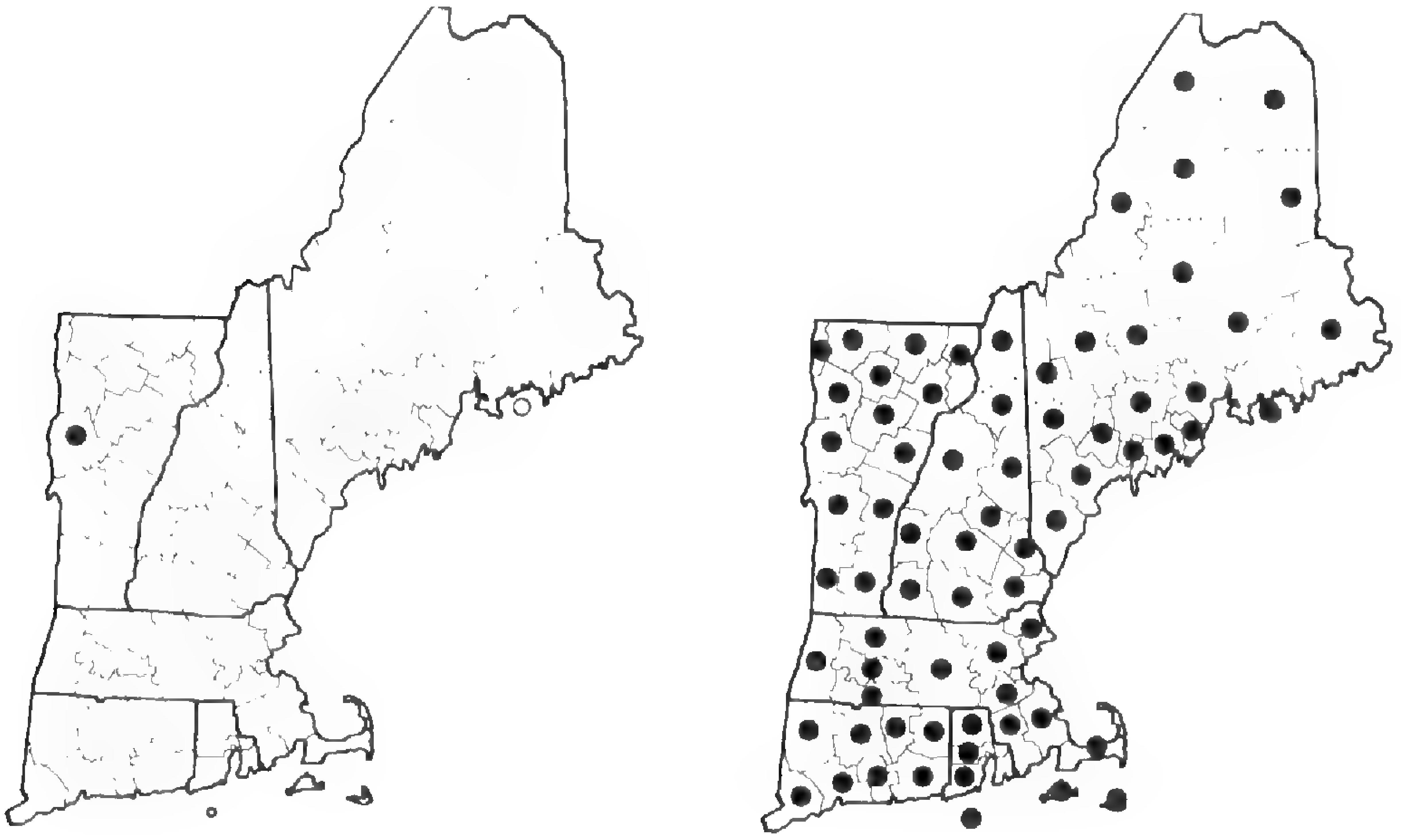
Uvularia grandiflora *Uvularia perfoliata*

Figure 45. Distribution maps for *TULIPA GESNERIA*, *T. SYLVESTRIS*, *Uvularia grandiflora*, and *U. perfoliata*.



Uvularia sessilifolia

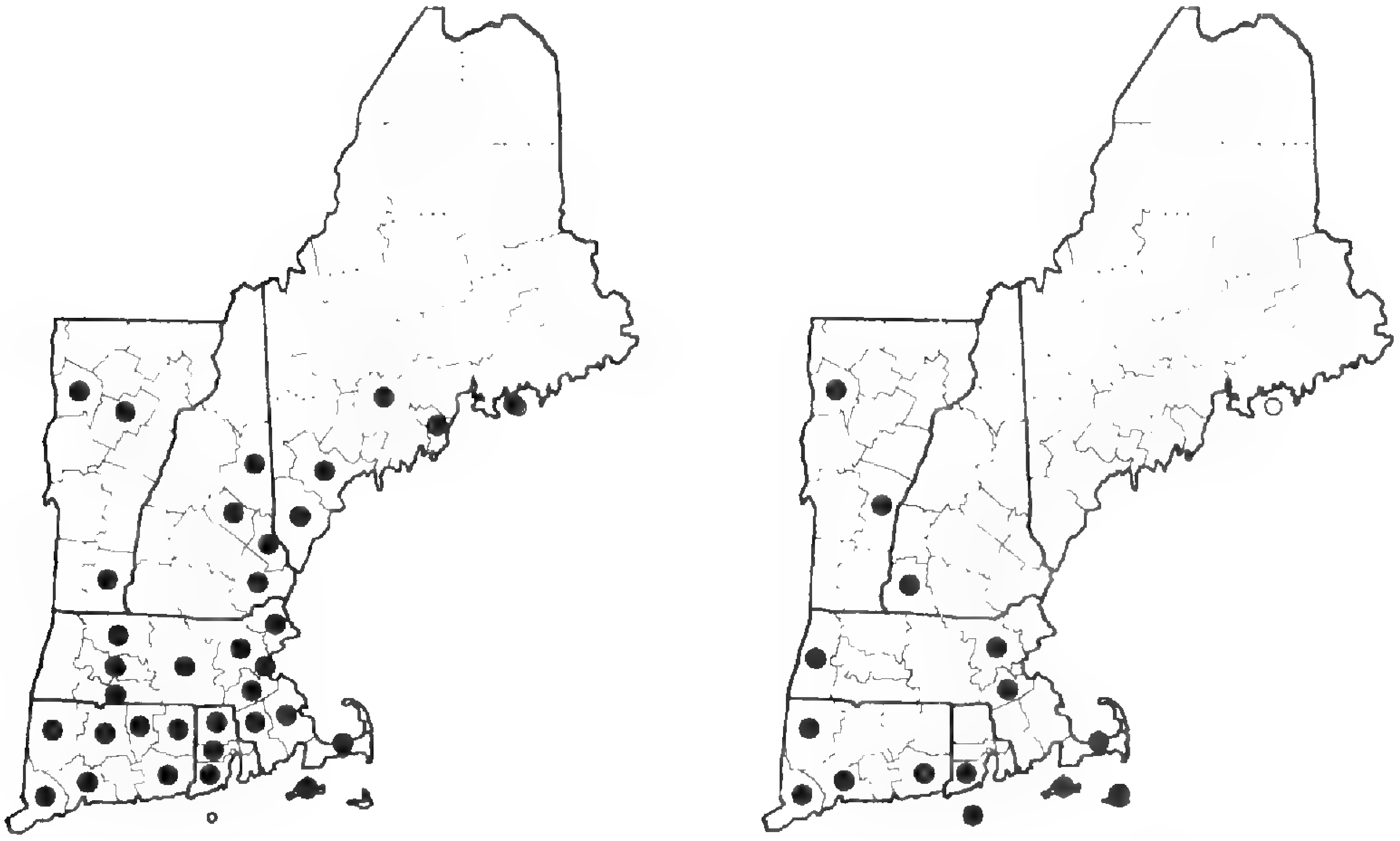
Veratrum viride



Zigadenus elegans var. *glaucus*

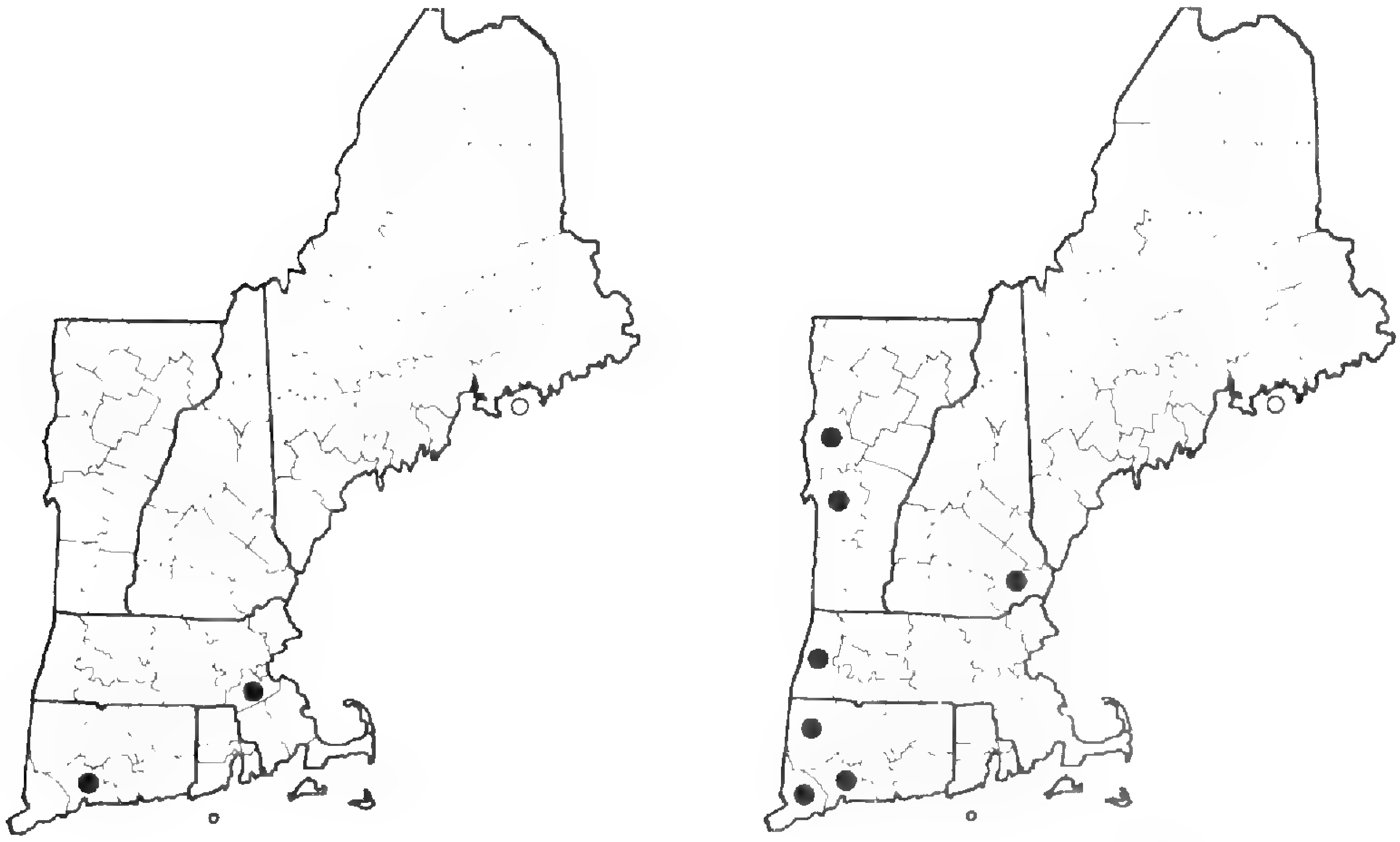
Najas flexilis

Figure 46. Distribution maps for *Uvularia sessilifolia, Veratrum viride, Zigadenus elegans* var. *glaucus*, and *Najas flexilis*.



Najas gracillima

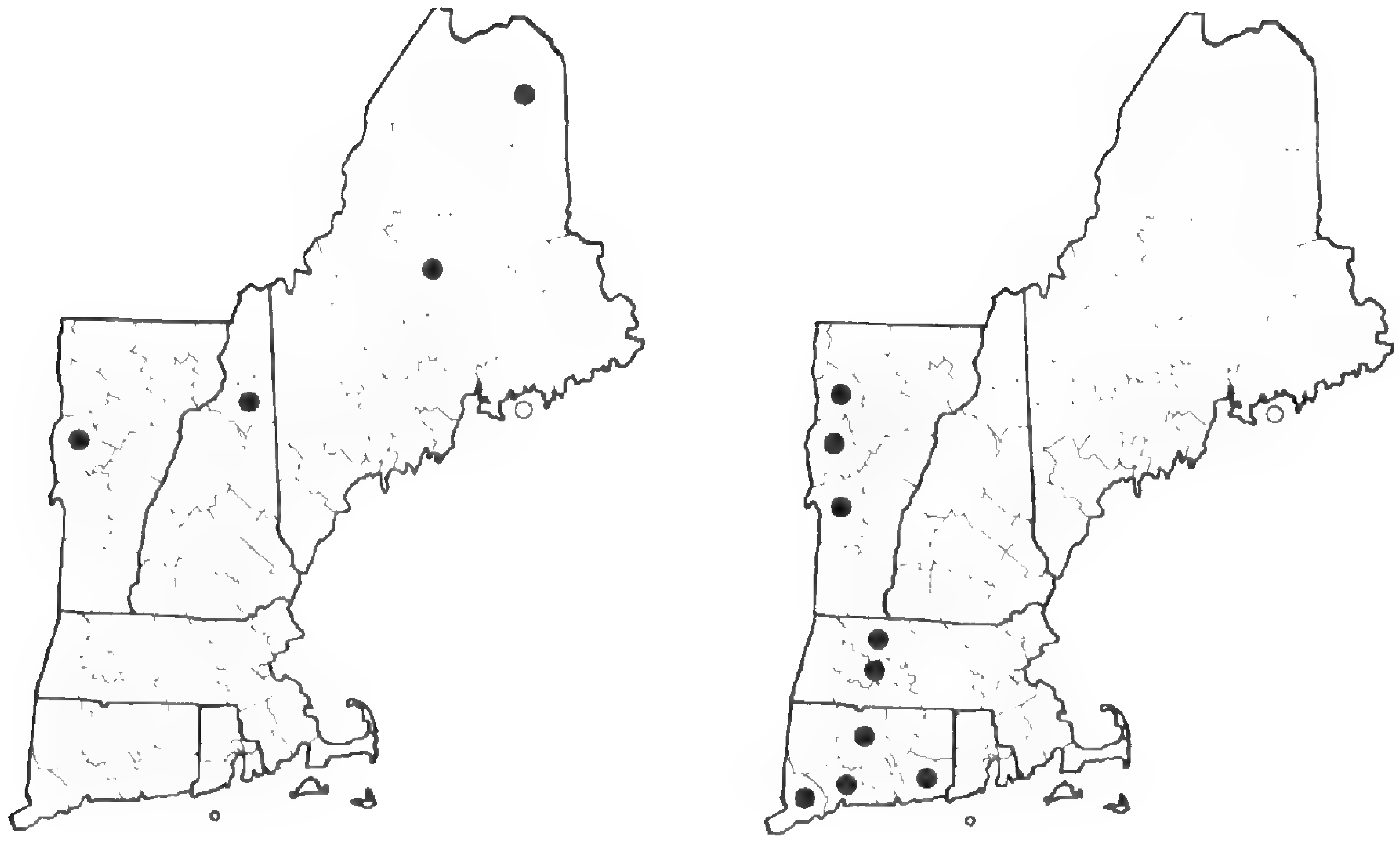
Najas guadalupensis subsp. *guadalupensis*



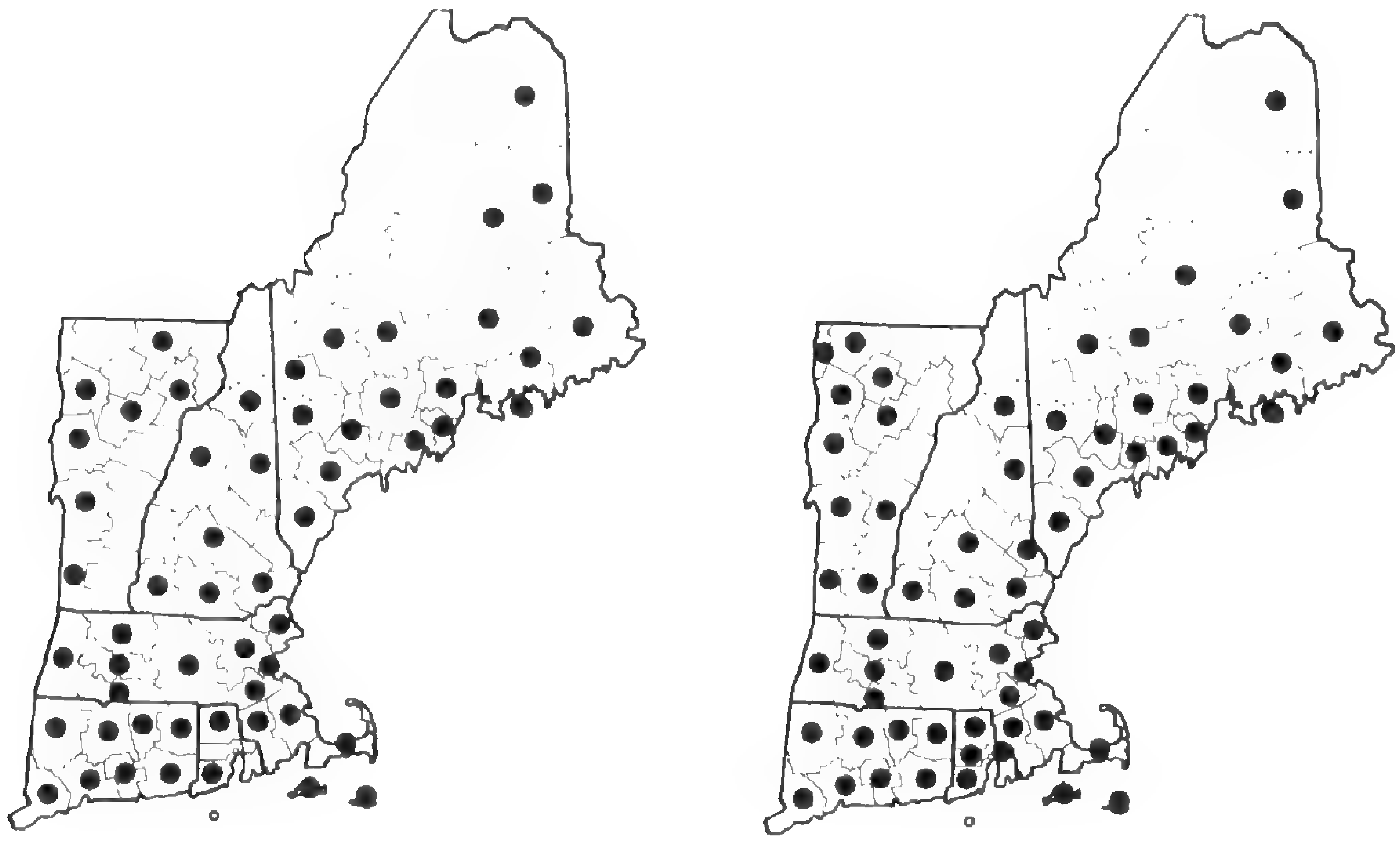
Najas guadalupensis subsp. *olivacea*

NAJAS MINOR

Figure 47. Distribution maps for *Najas gracillima, N. guadalupensis* subsp. *guadalupensis, N. guadalupensis* subsp. *olivacea,* and *N. MINOR.*

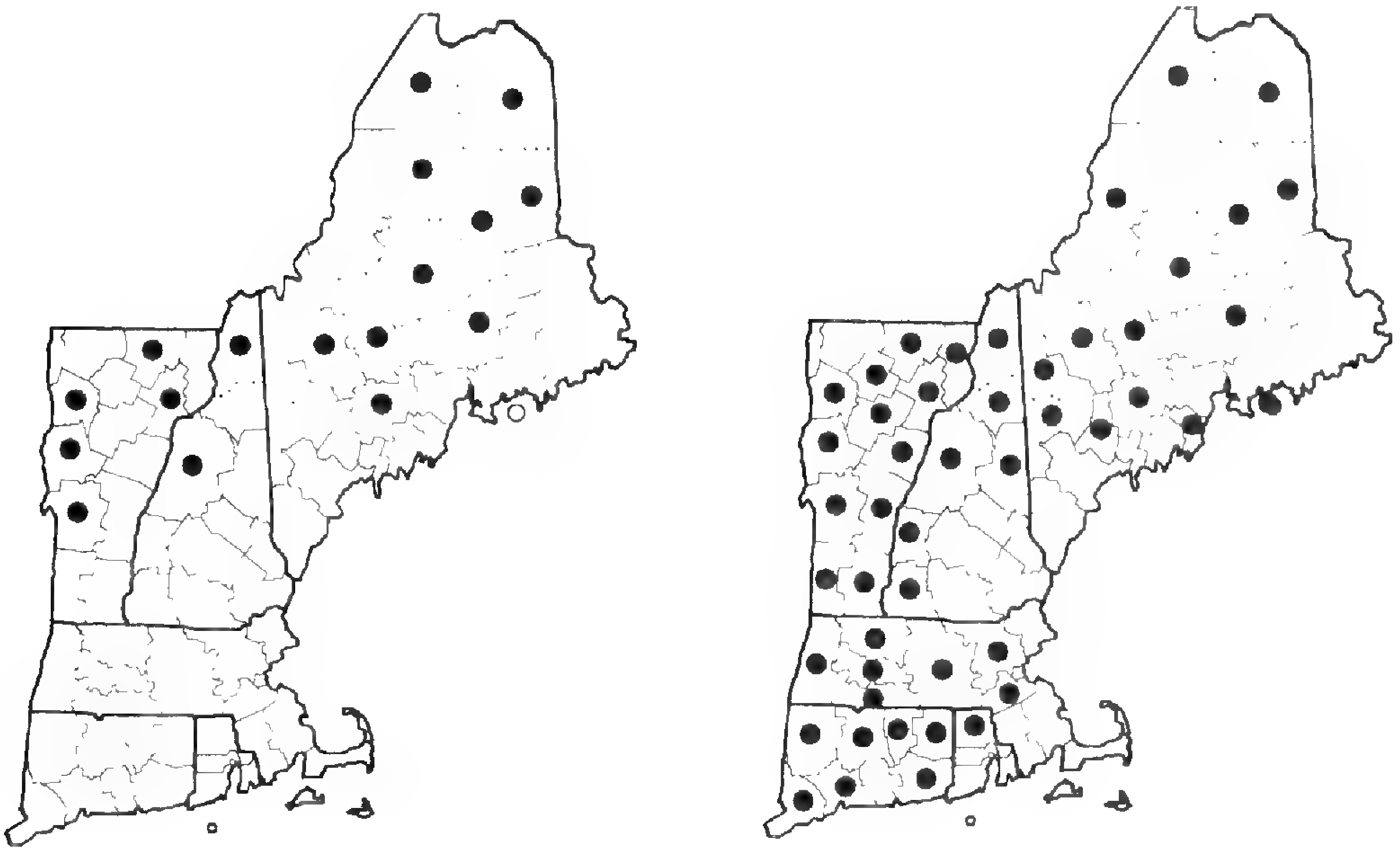


Amerorchis rotundifolia *Aplectrum hyemale*



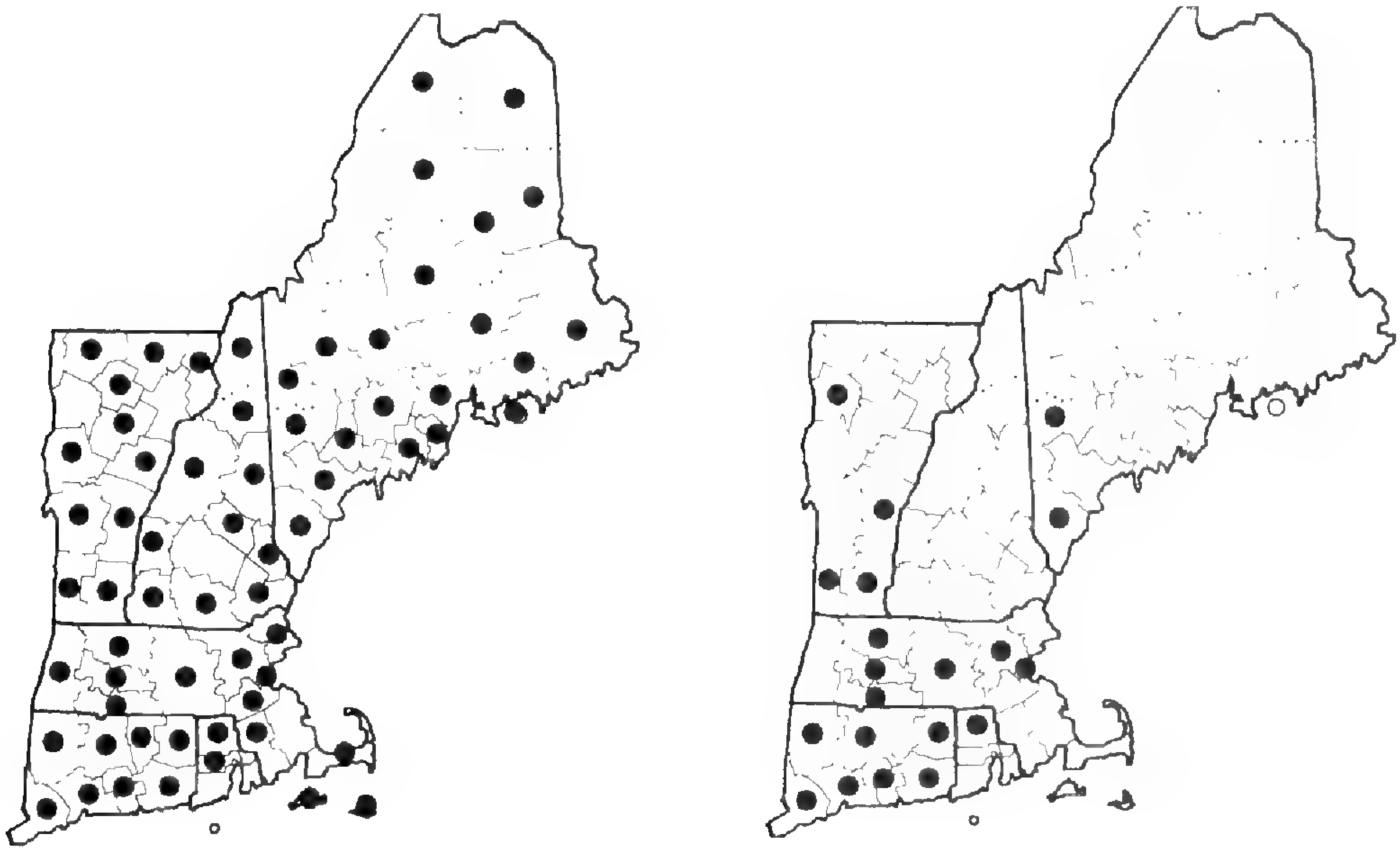
Arethusa bulbosa *Calopogon tuberosus*

Figure 48. Distribution maps for *Amerorchis rotundifolia, Aplectrum hyemale, Arethusa bulbosa,* and *Calopogon tuberosus.*



Calypso bulbosa
var. *americana*

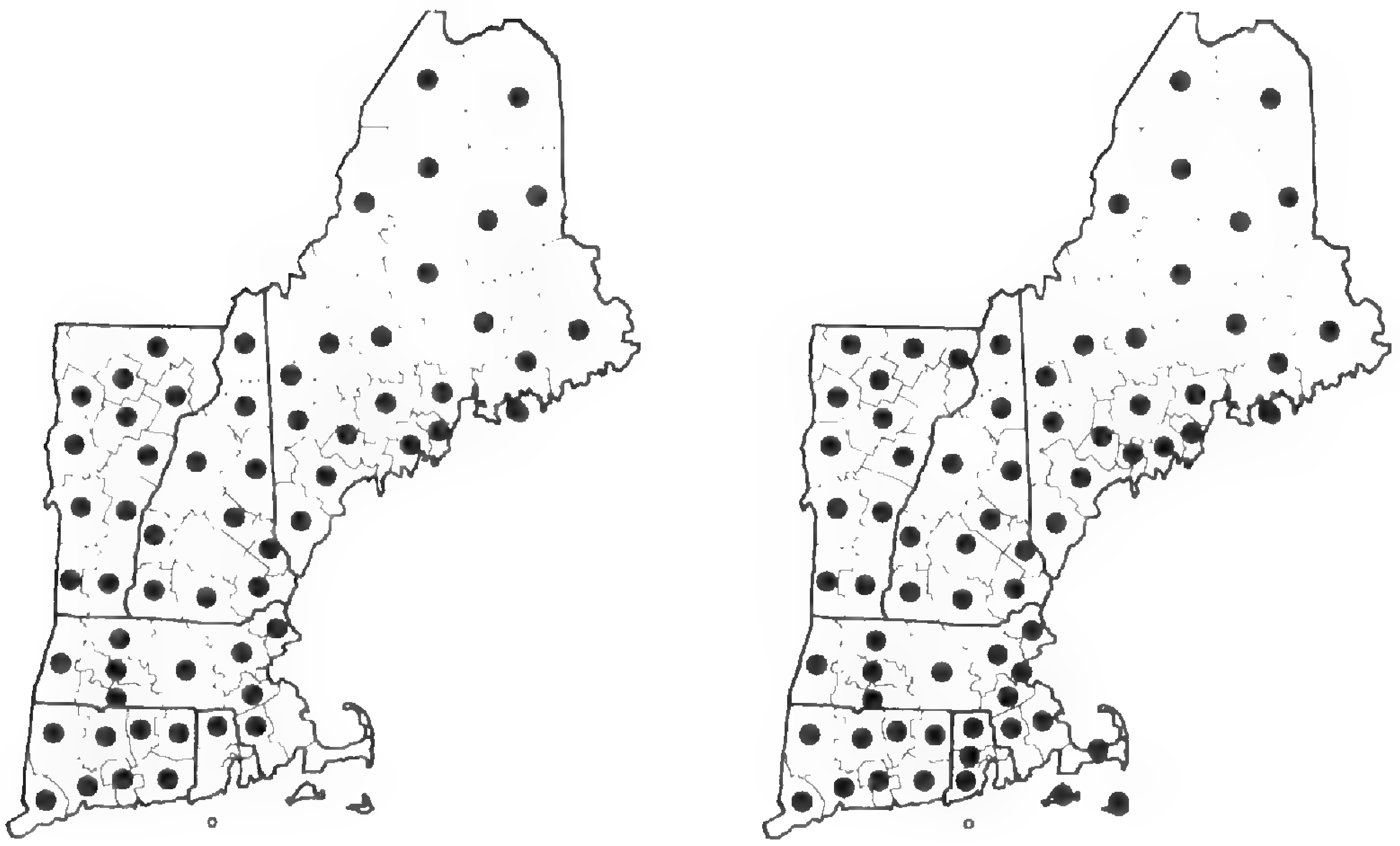
Coeloglossum viride
var. *virescens*



Corallorhiza maculata

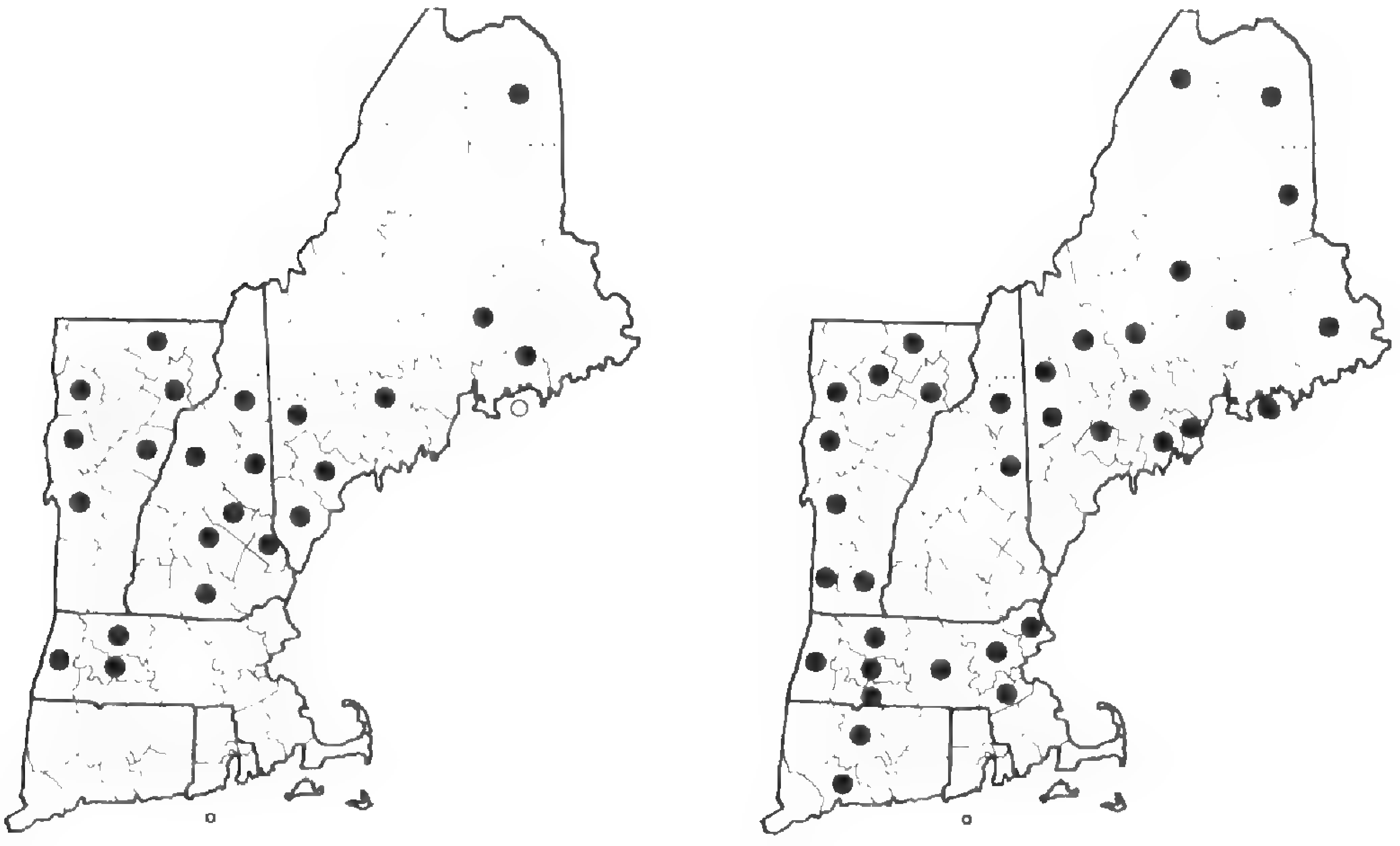
Corallorhiza odontorhiza

Figure 49. Distribution maps for *Calypso bulbosa* var. *americana*, *Coeloglossum viride* var. *virescens*, *Corallorhiza maculata*, and *C. odontorhiza*.



Corallorhiza trifida

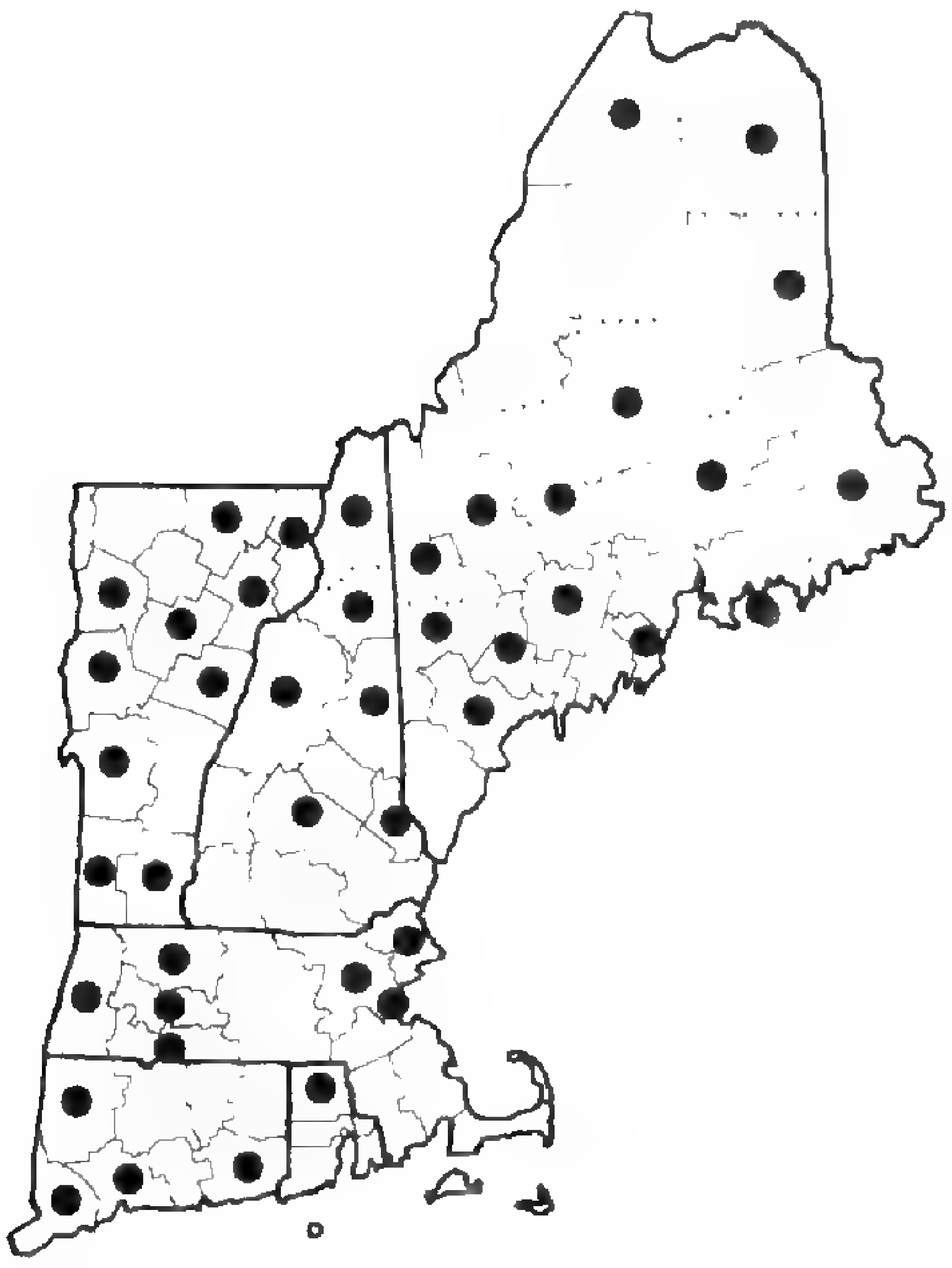
Cypripedium acaule



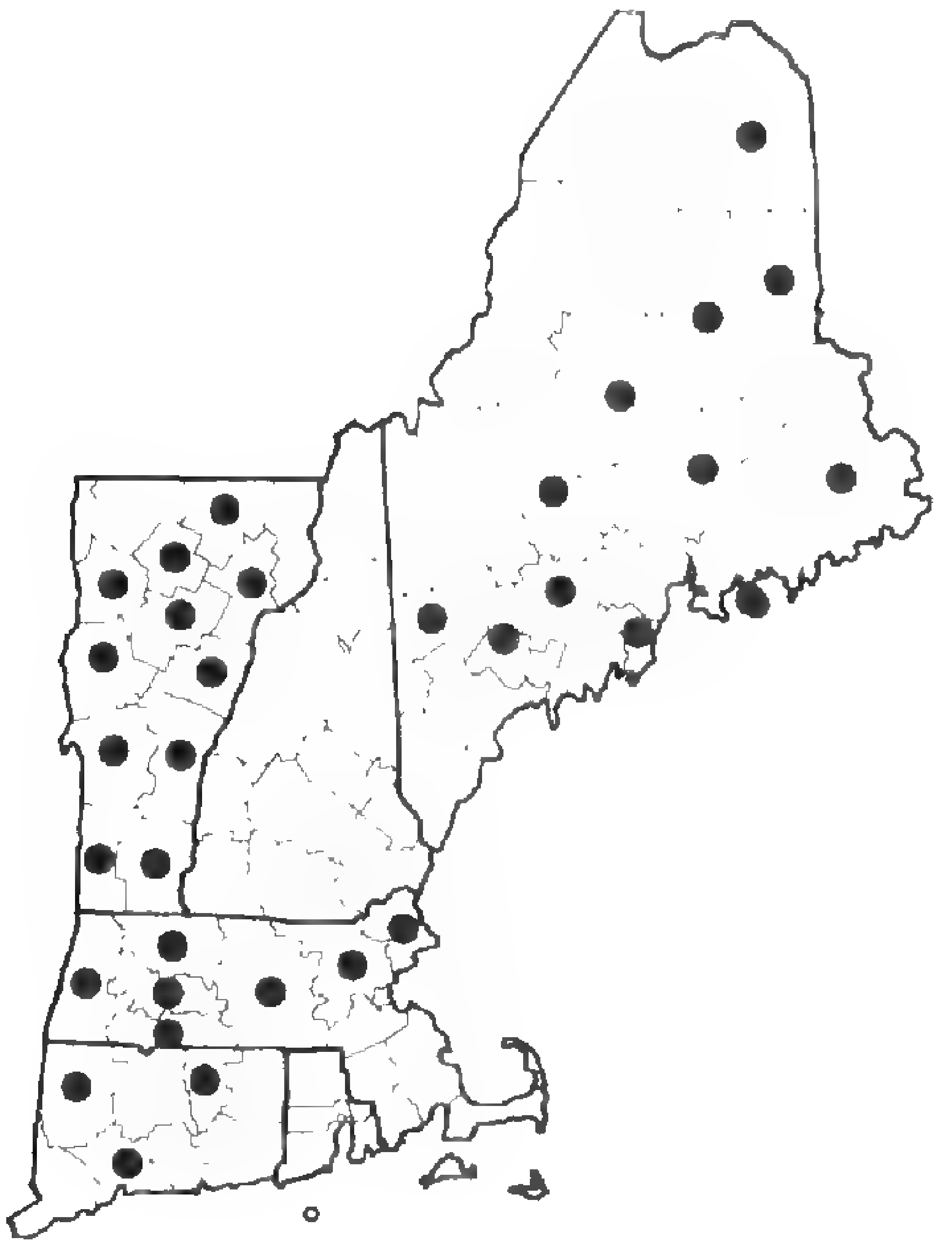
Cypripedium arietinum

Cypripedium parviflorum
var. *parviflorum*

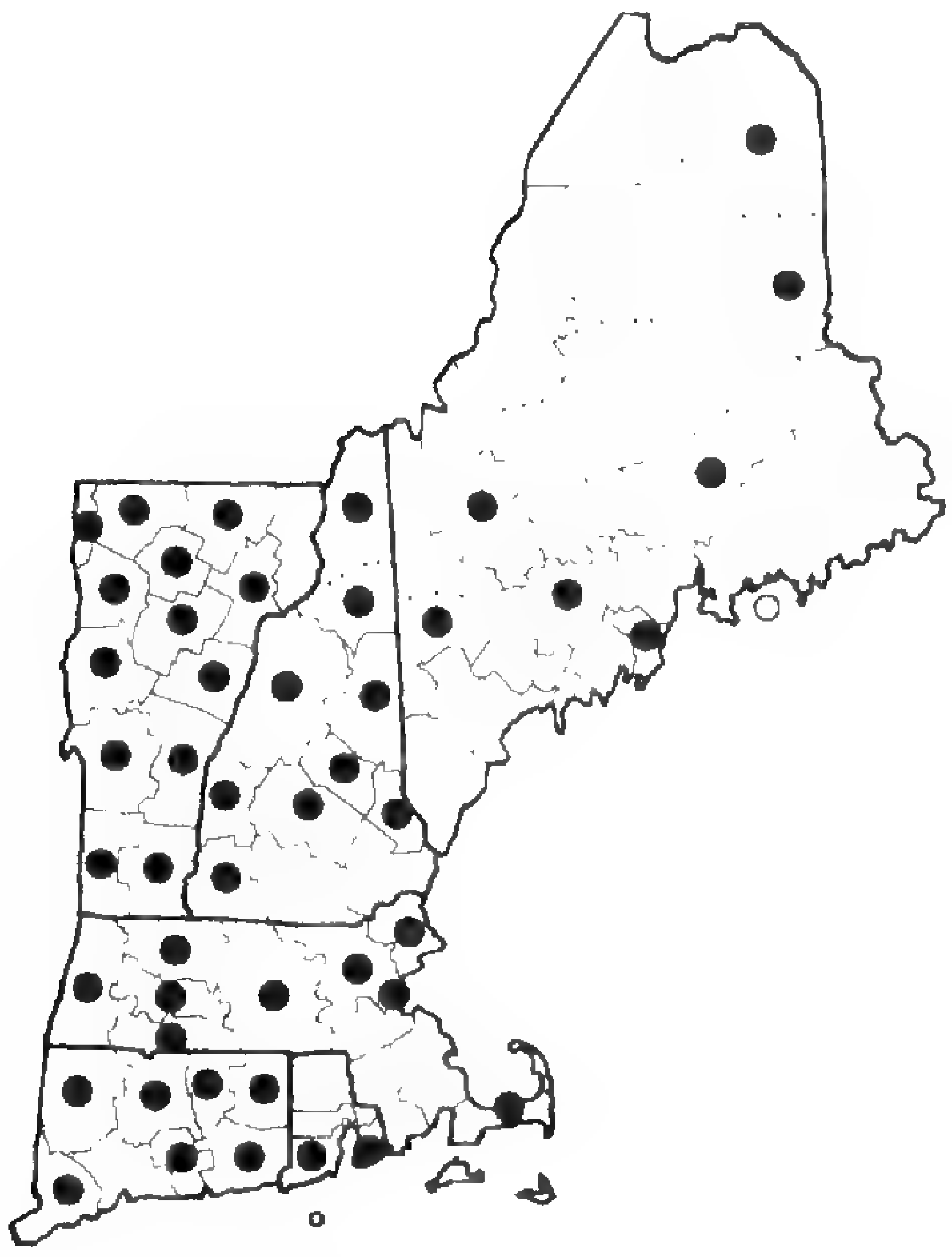
Figure 50. Distribution maps for *Corallorhiza trifida, Cypripedium acaule, C. arietinum,* and *C. parviflorum* var. *parviflorum.*



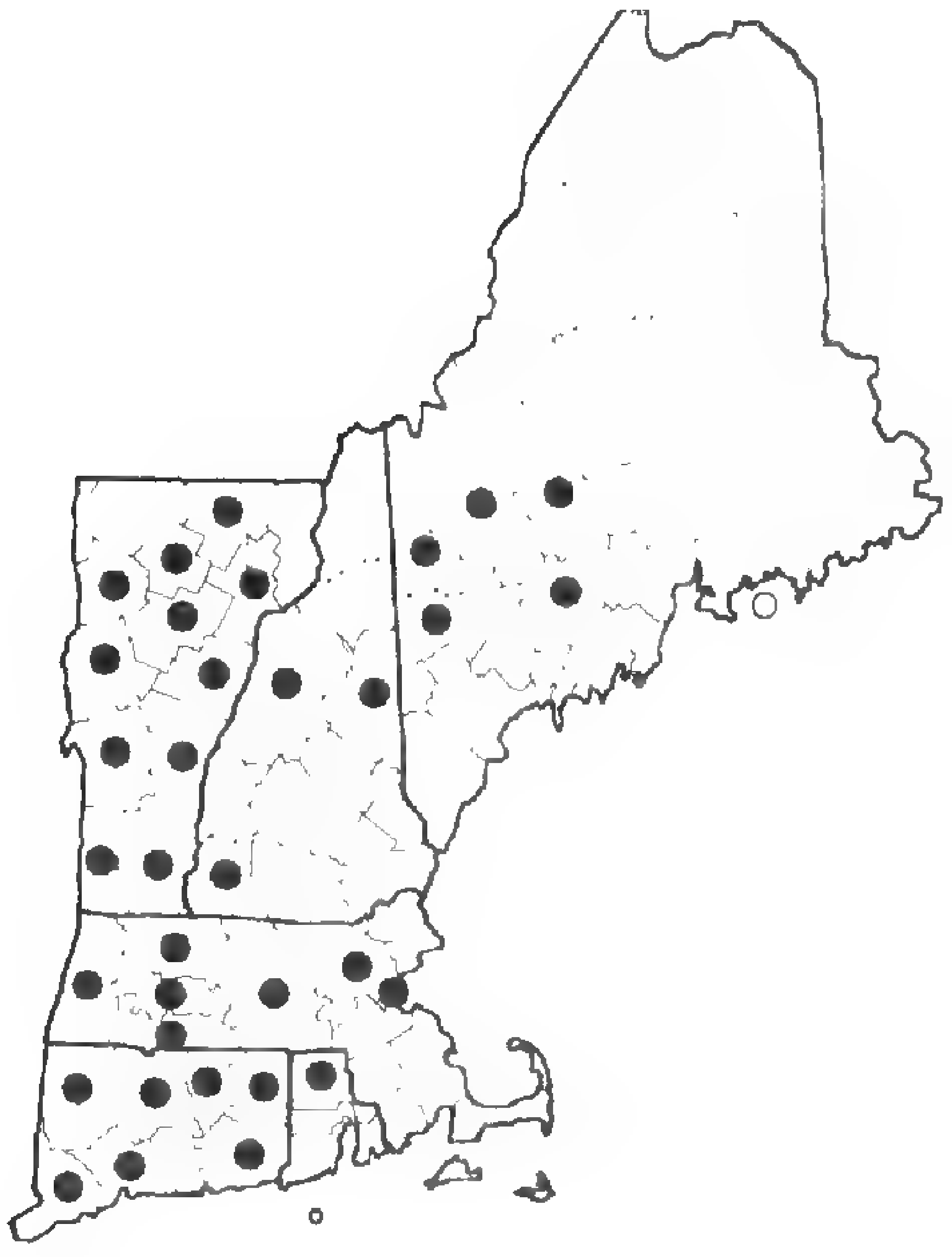
Cypripedium parviflorum
var. *pubescens*



Cypripedium reginae

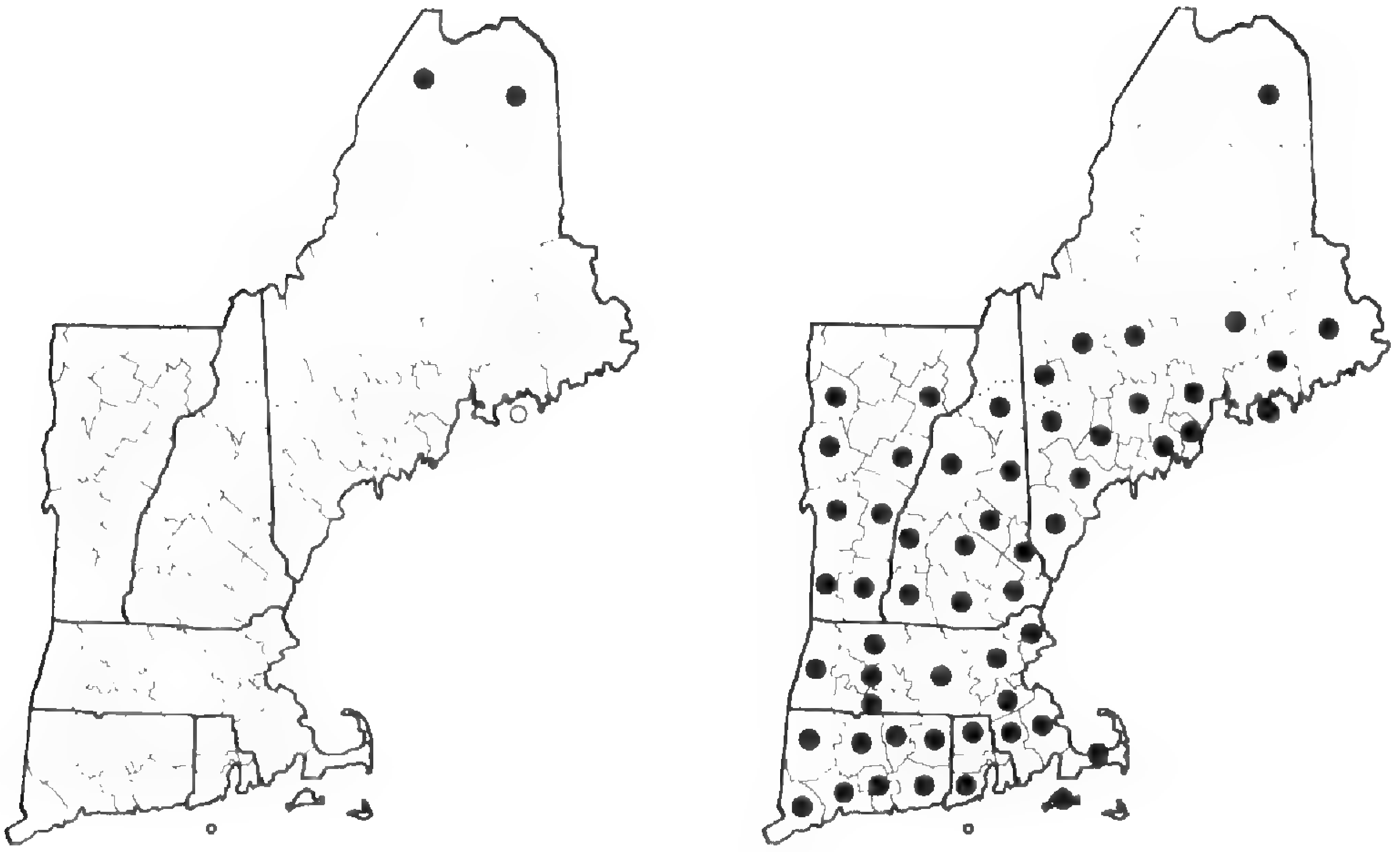


EPIPACTIS HELLEBORINE



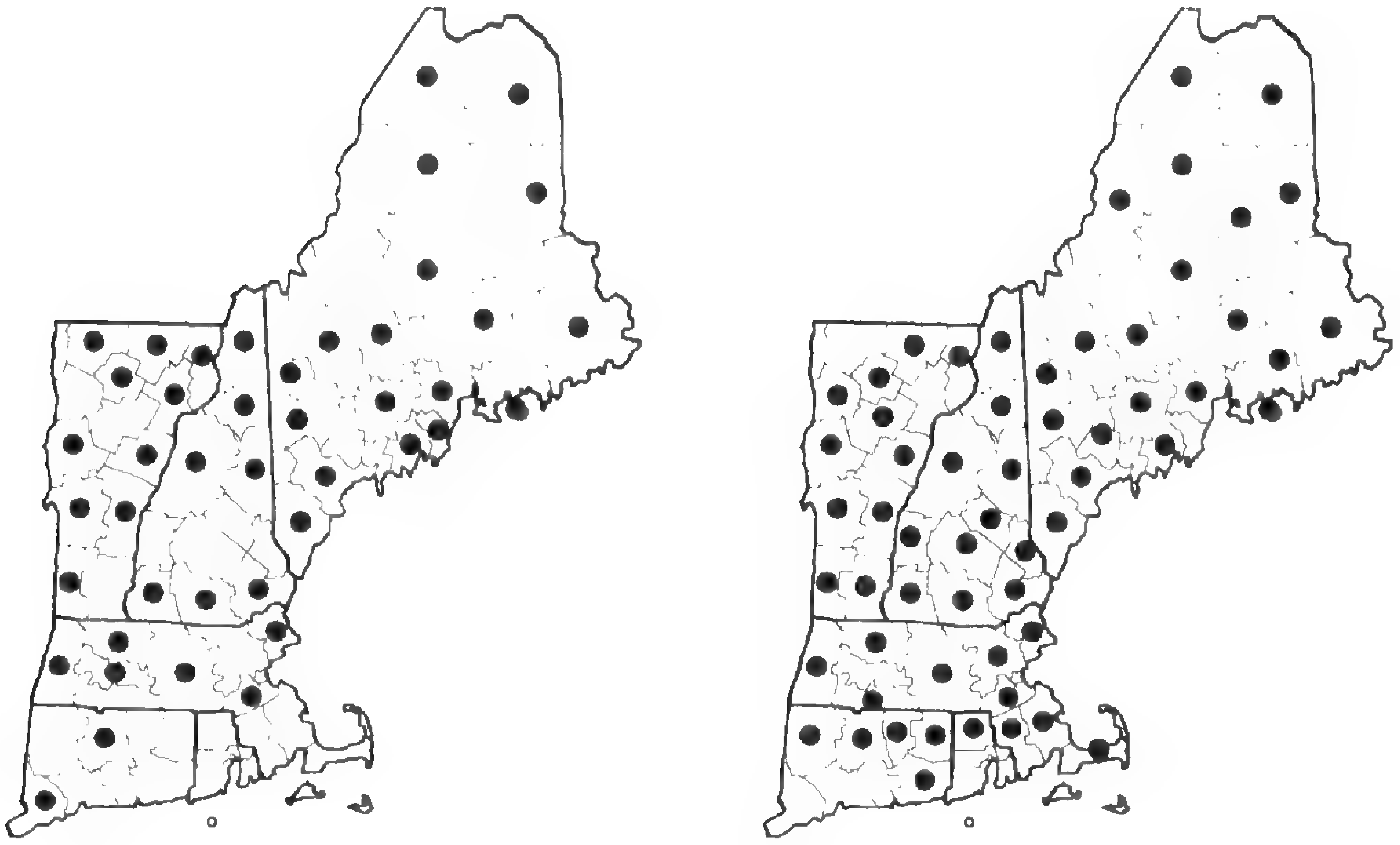
Galearis spectabilis

Figure 51. Distribution maps for *Cypripedium parviflorum* var. *pubescens*, *C. reginae*, *EPIPACTIS HELLEBORINE*, and *Galearis spectabilis*.



Goodyera oblongifolia

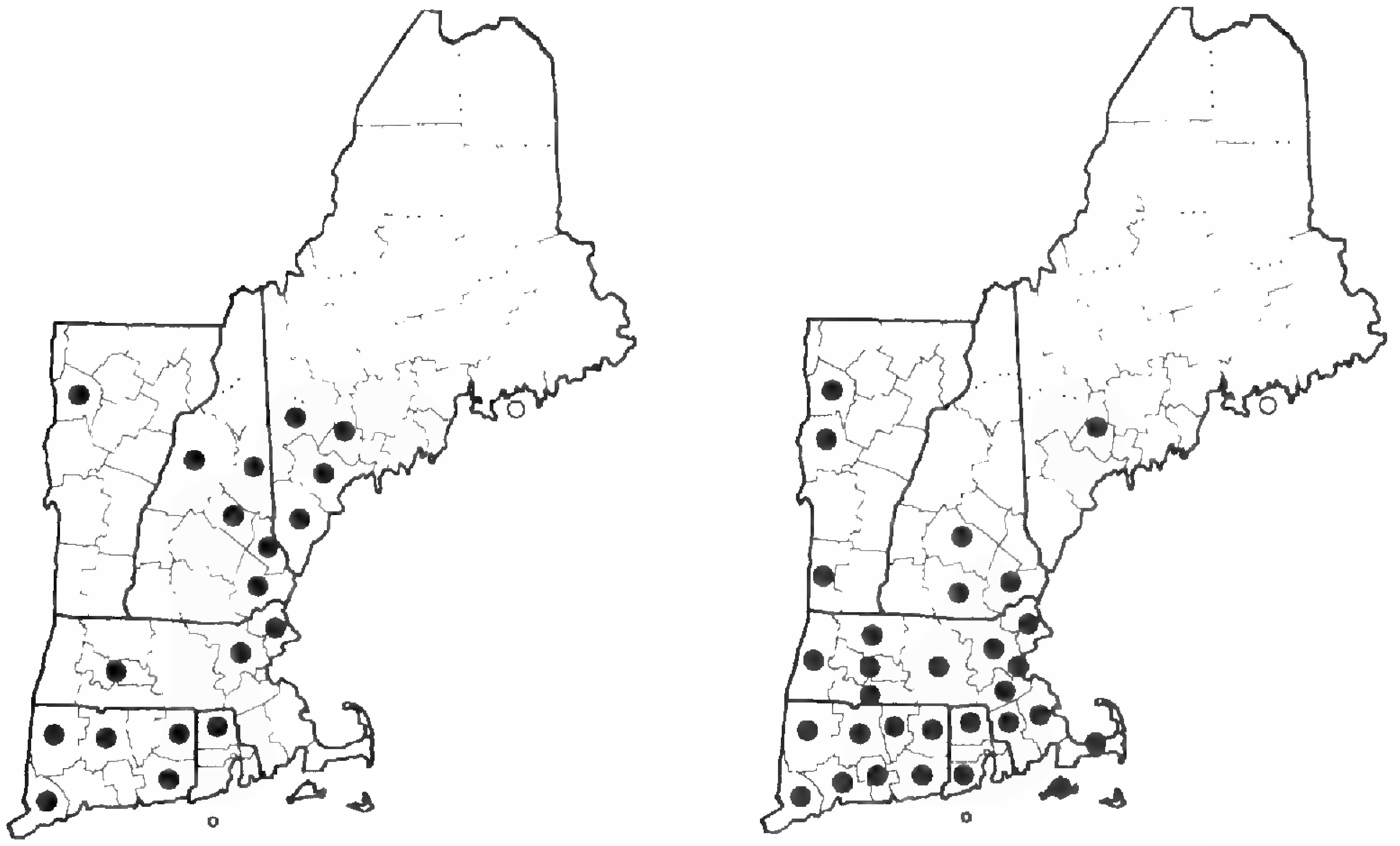
Goodyera pubescens



Goodyera repens
var. *ophioides*

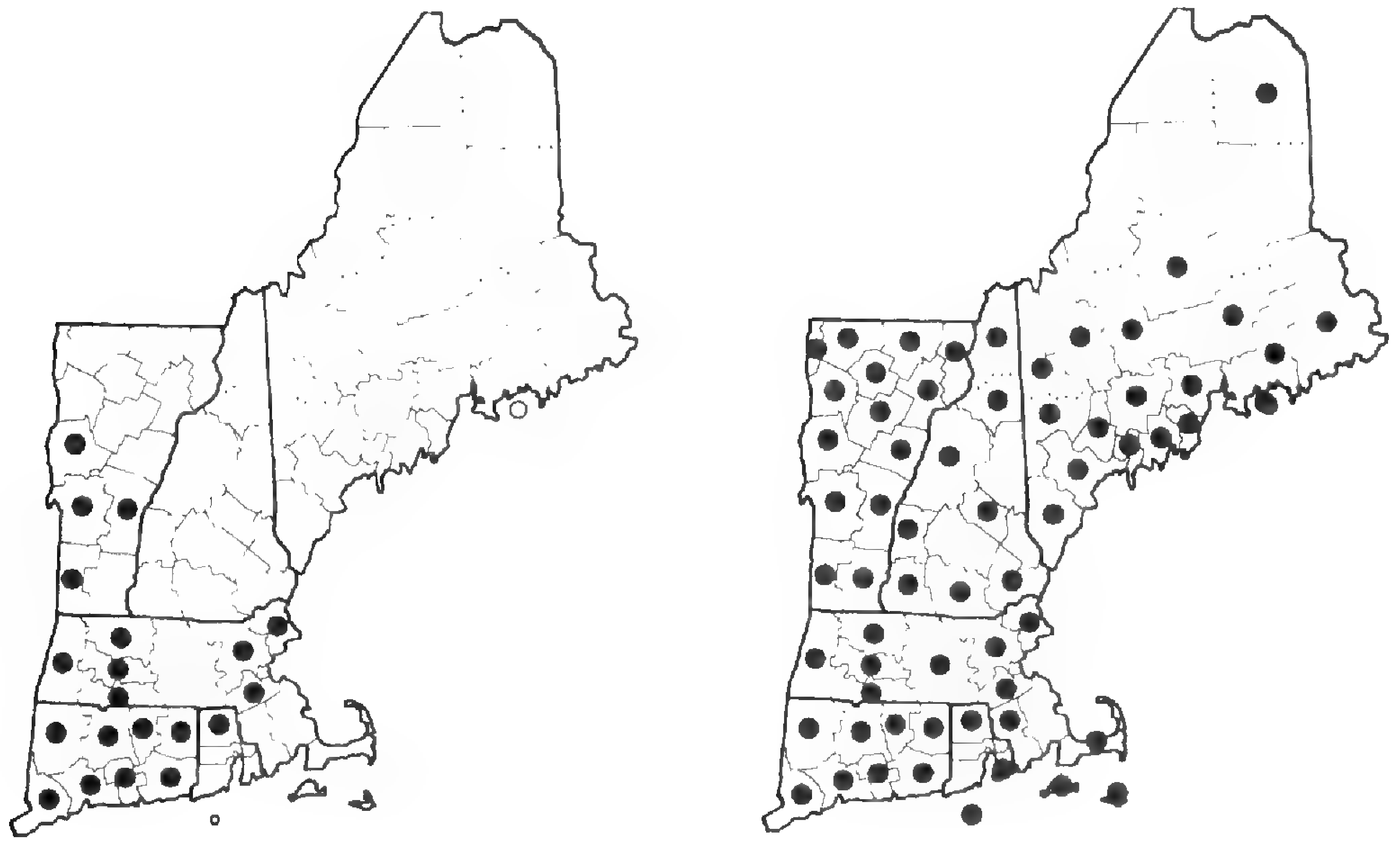
Goodyera X *tesselata*

Figure 52. Distribution maps for *Goodyera oblongifolia, G. pubescens, G. repens* var. *ophioides*, and *G.* X *tesselata*.



Isotria medeoloides

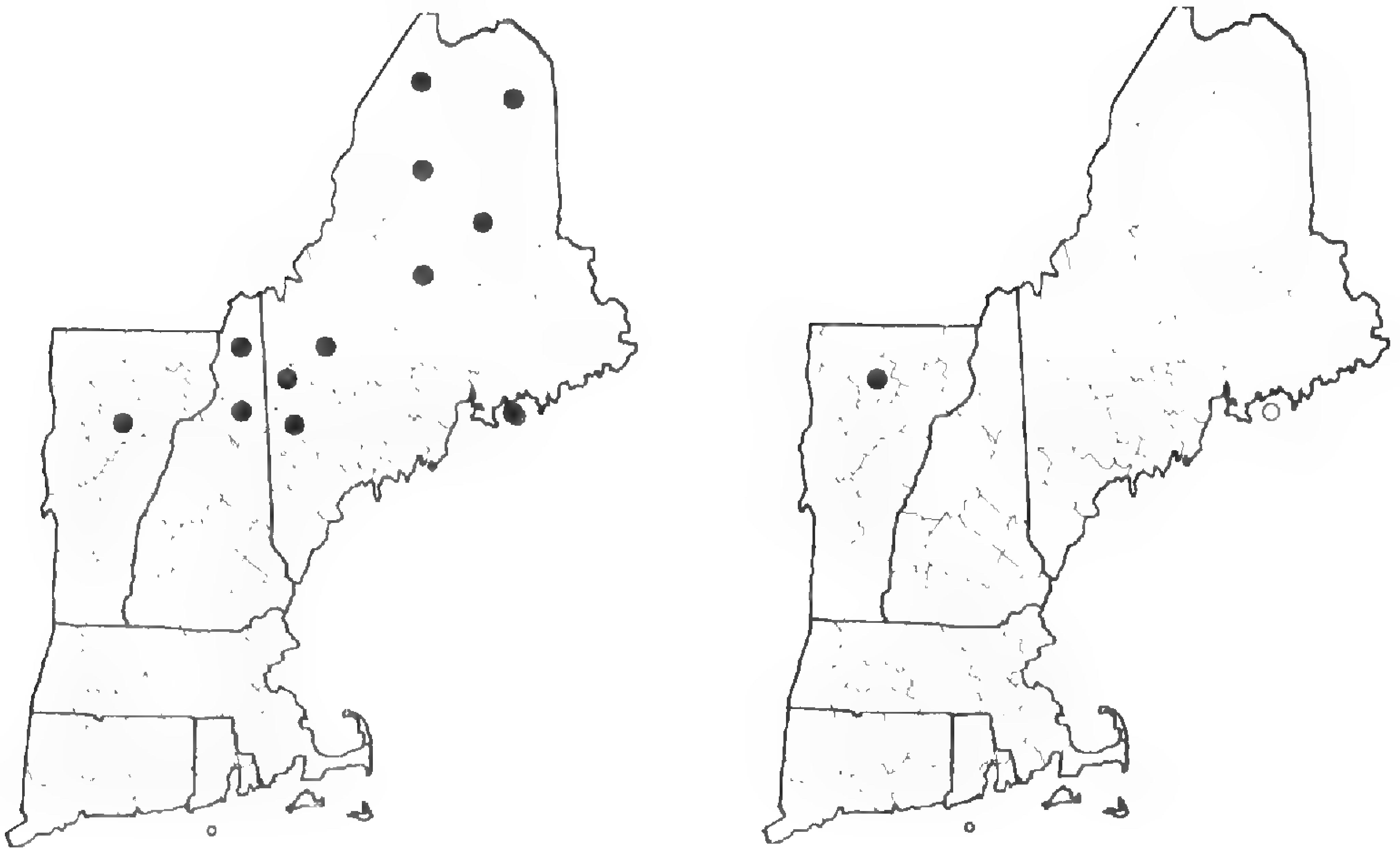
Isotria verticillata



Liparis liliifolia

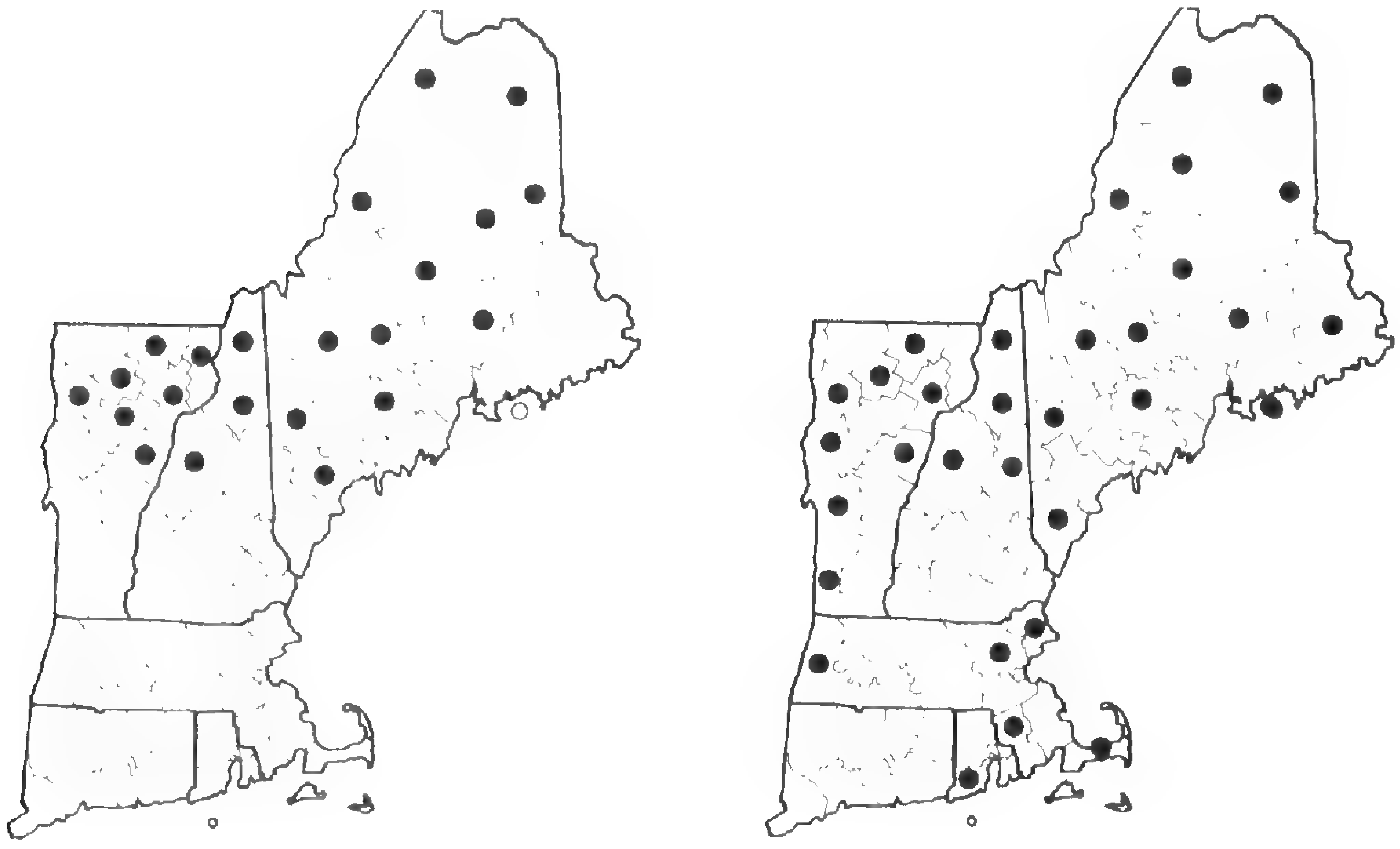
Liparis loeselii

Figure 53. Distribution maps for *Isotria medeoloides, I. verticillata, Liparis liliifolia,* and *L. loeselii.*



Listera auriculata

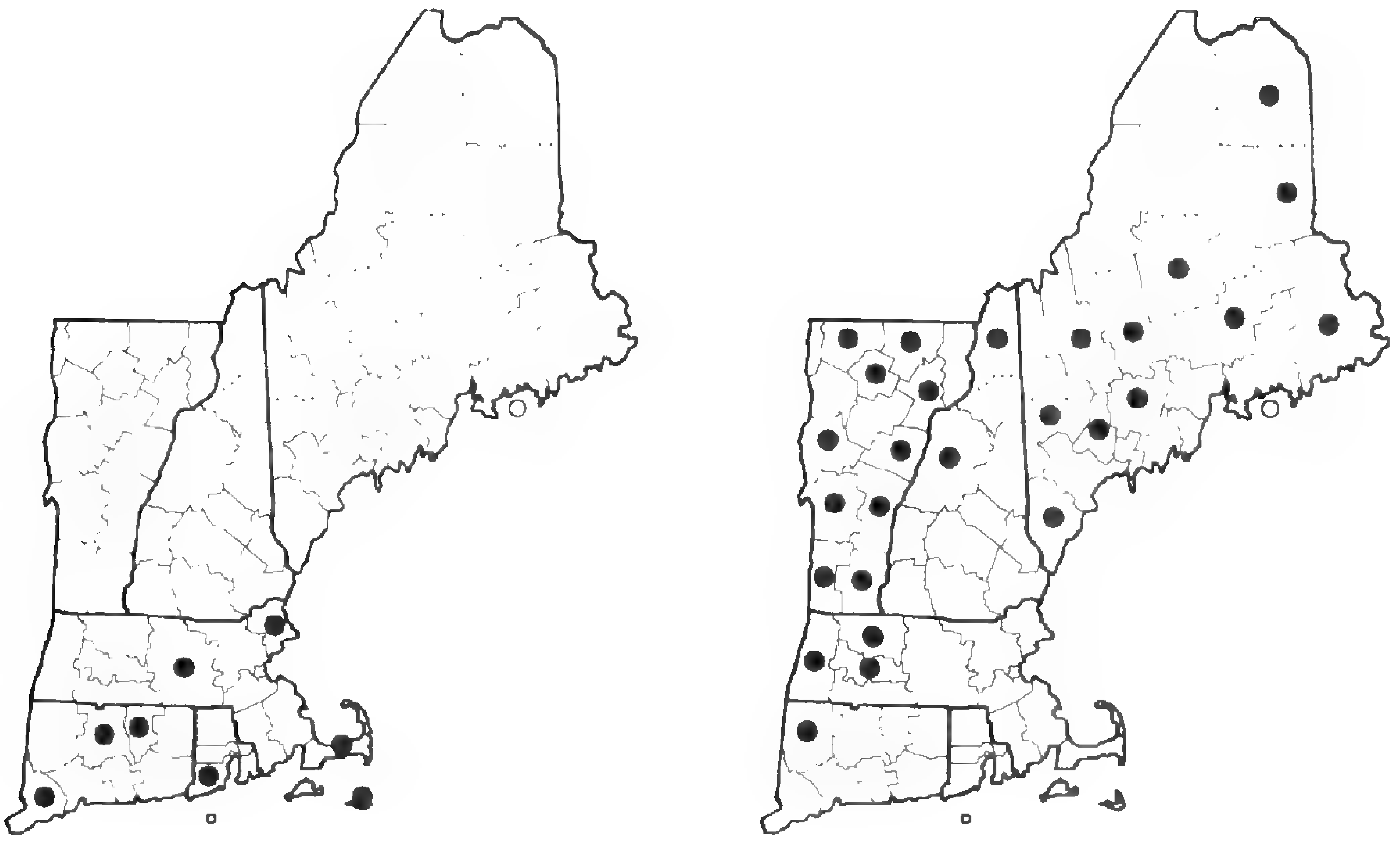
Listera australis



Listera convallarioides

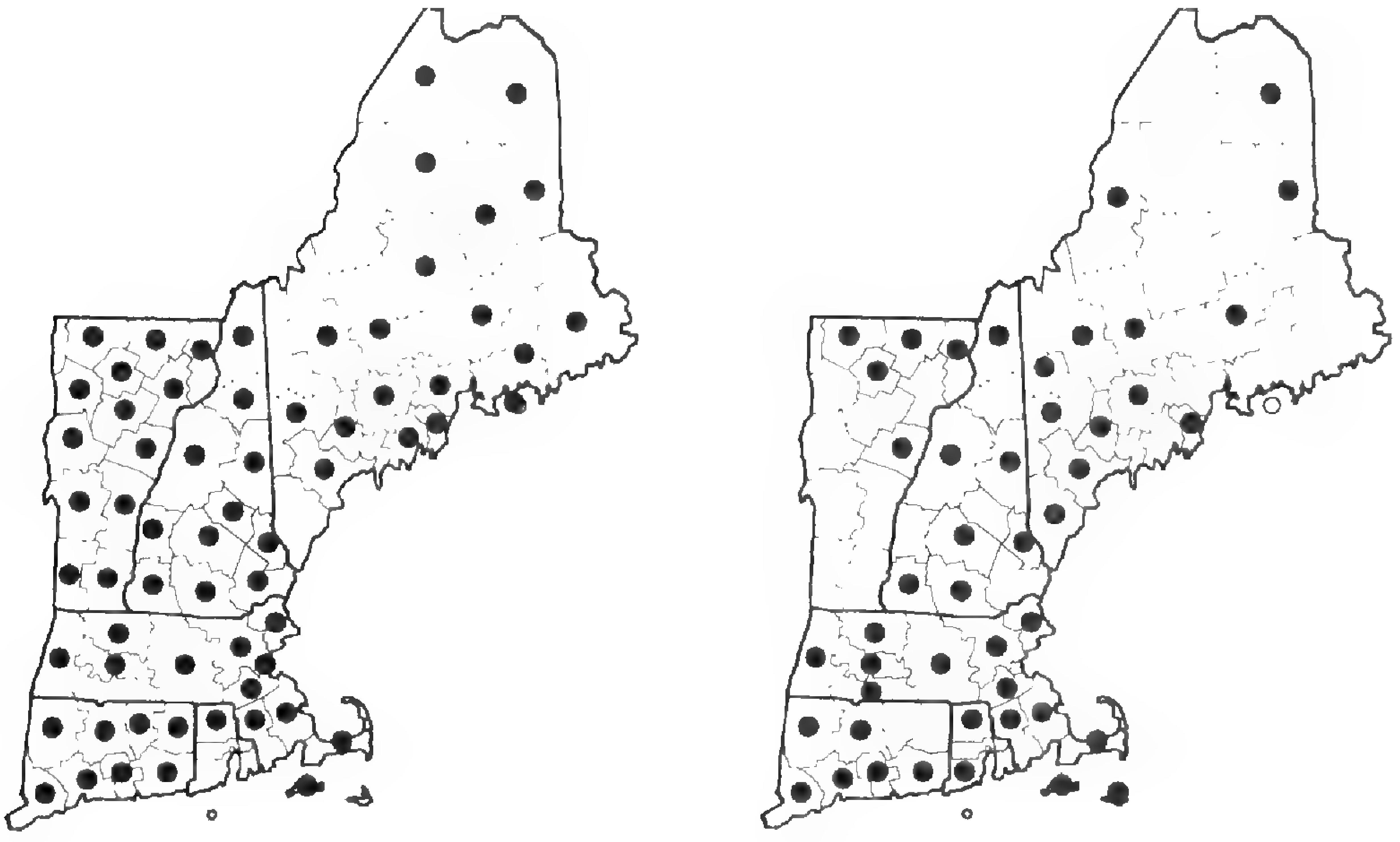
Listera cordata

Figure 54. Distribution maps for *Listera auriculata, L. australis, L. convallarioides,* and *L. cordata.*



Malaxis bayardii

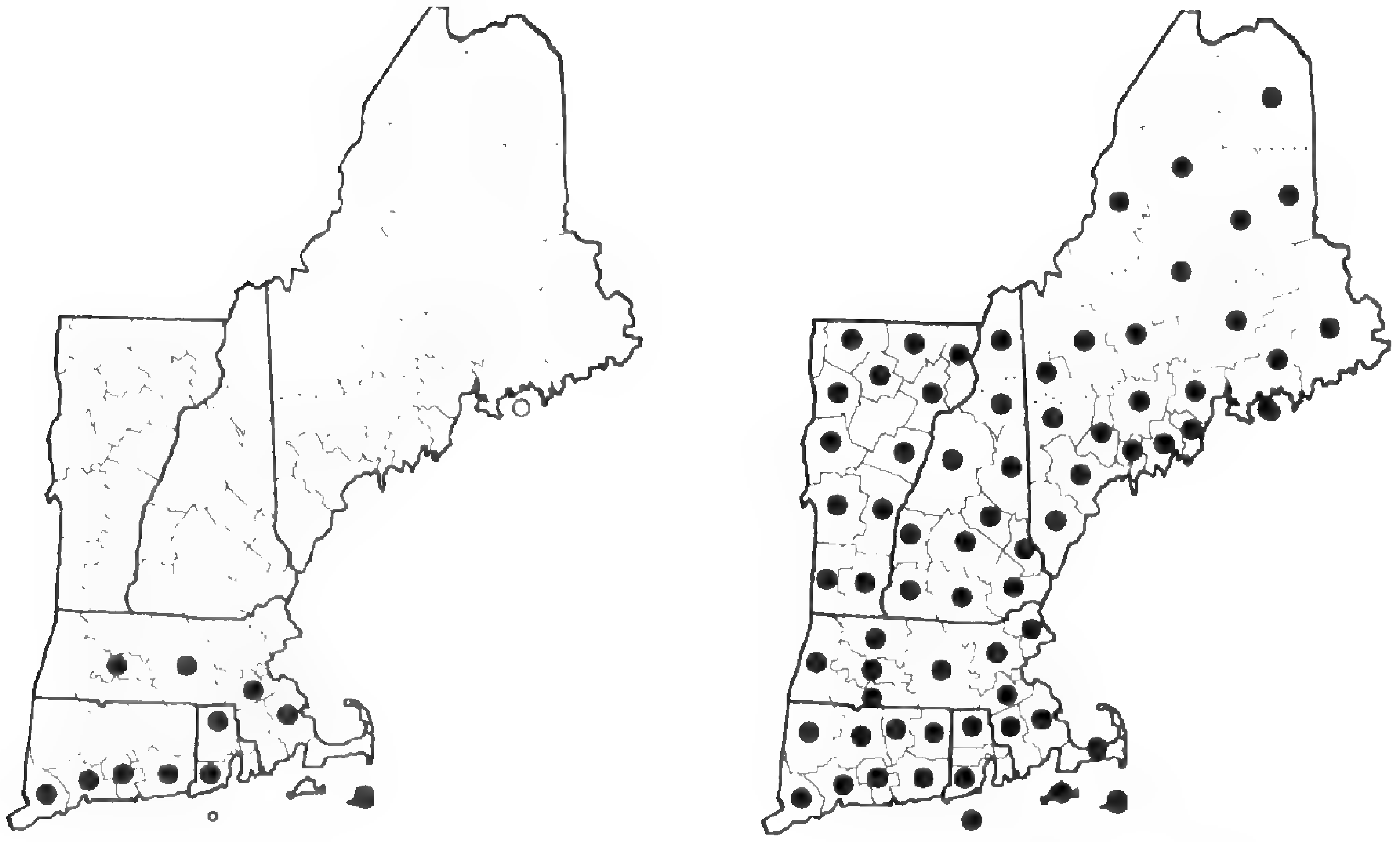
Malaxis monophyllos var. *brachypoda*



Malaxis unifolia

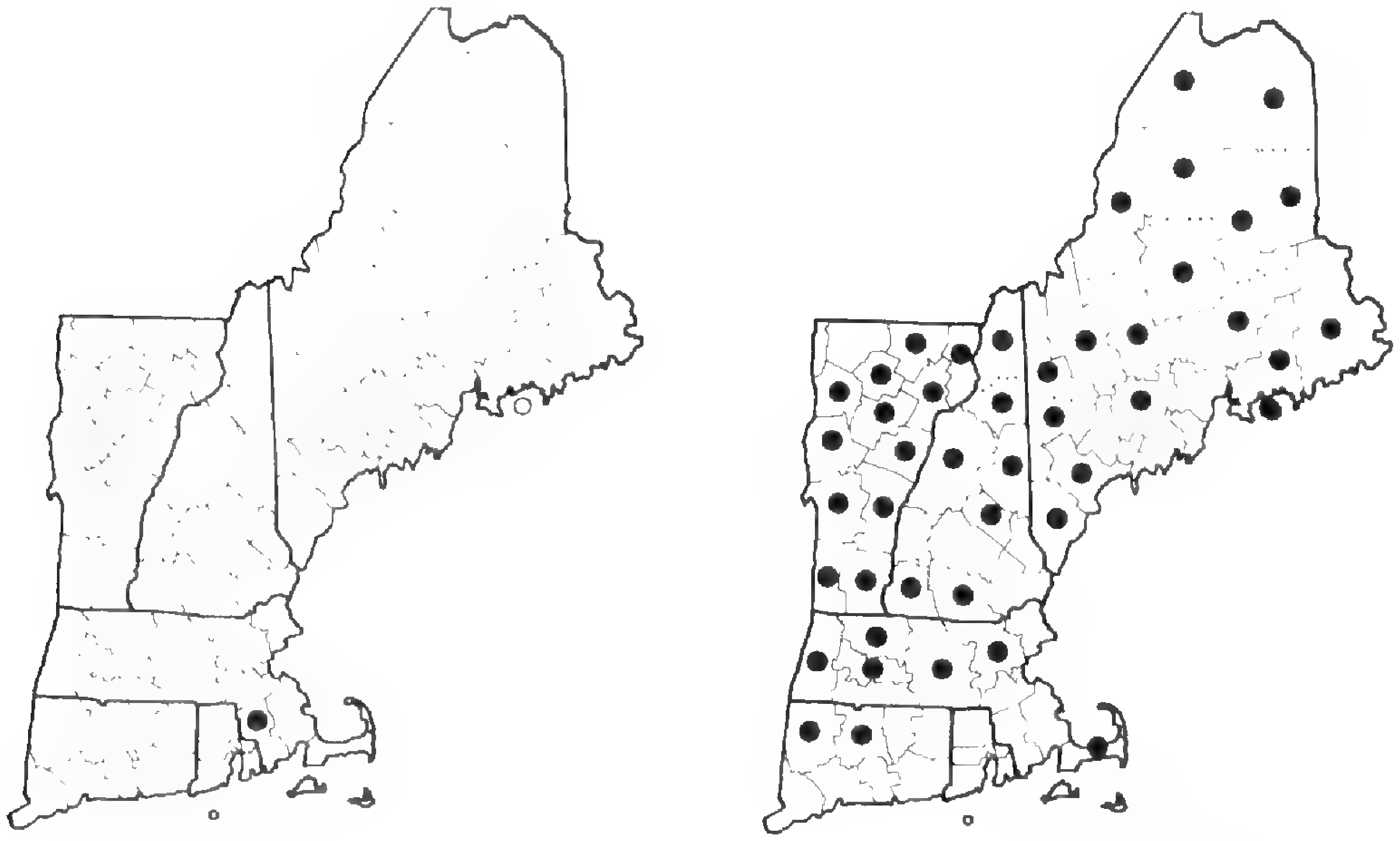
Platanthera blephariglottis var. *blephariglottis*

Figure 55. Distribution maps for *Malaxis bayardii, M. monophyllos* var. *brachypoda, M. unifolia,* and *Platanthera blephariglottis* var. *blephariglottis.*



Platanthera ciliaris

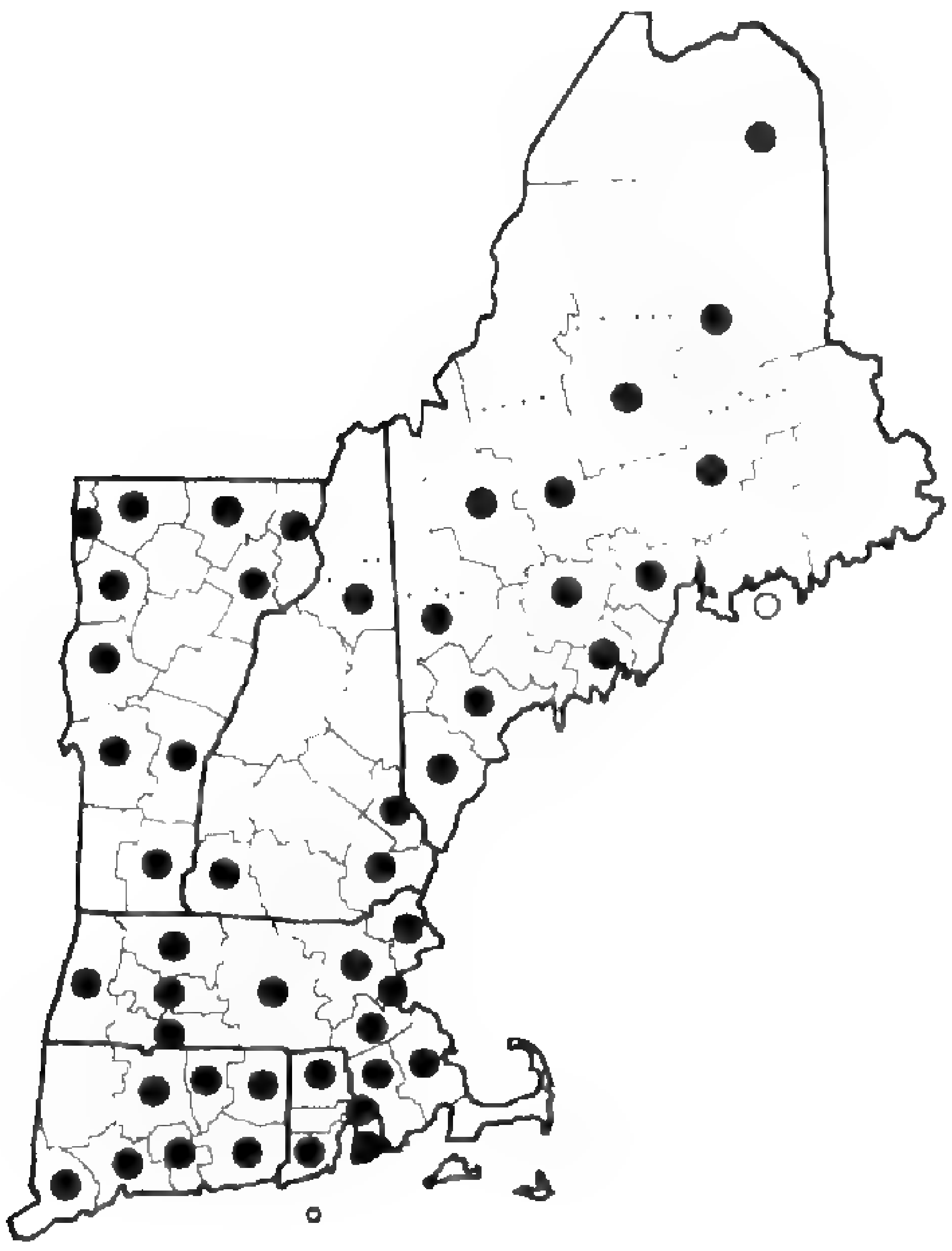
Platanthera clavellata



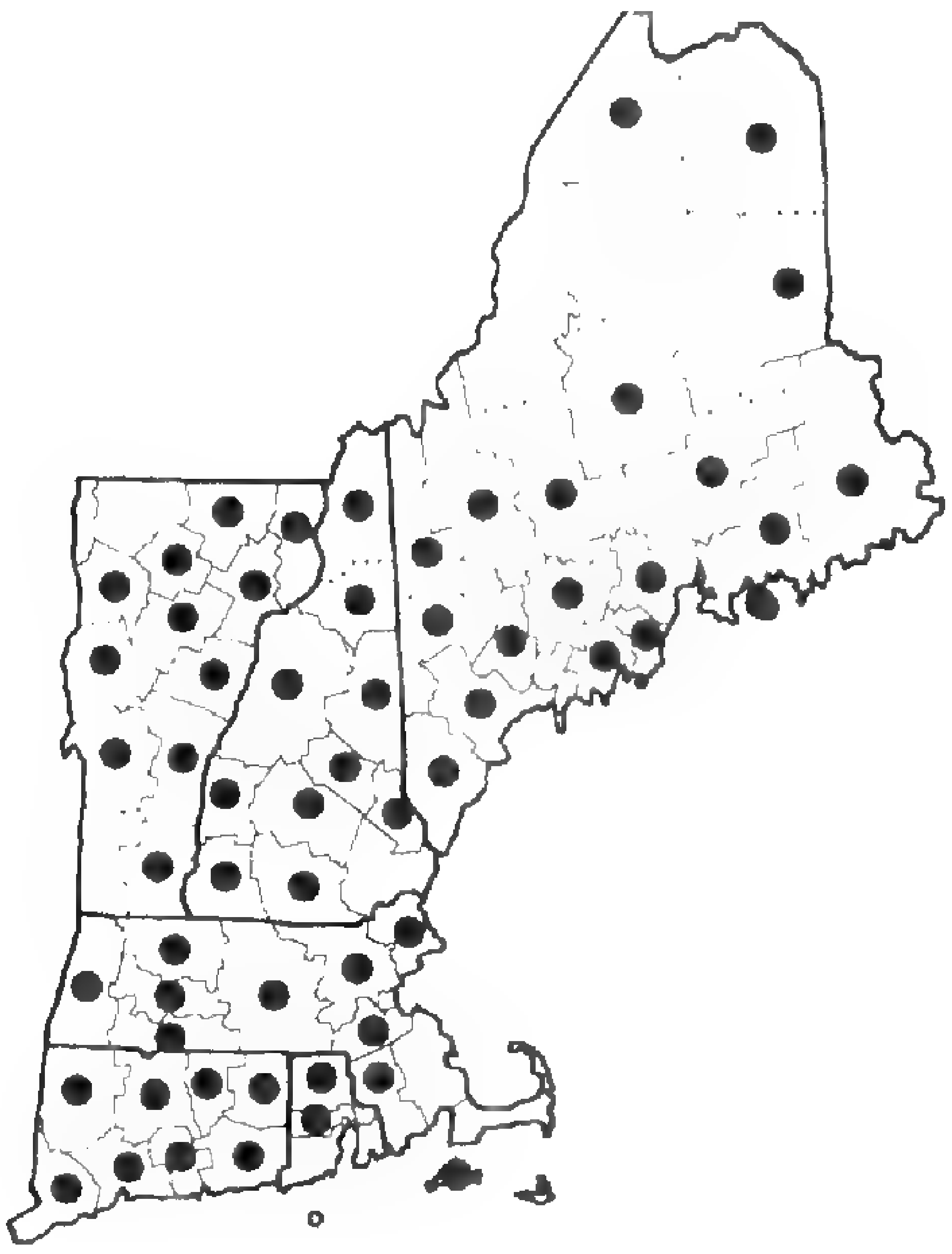
Platanthera cristata

Platanthera dilatata
var. *dilatata*

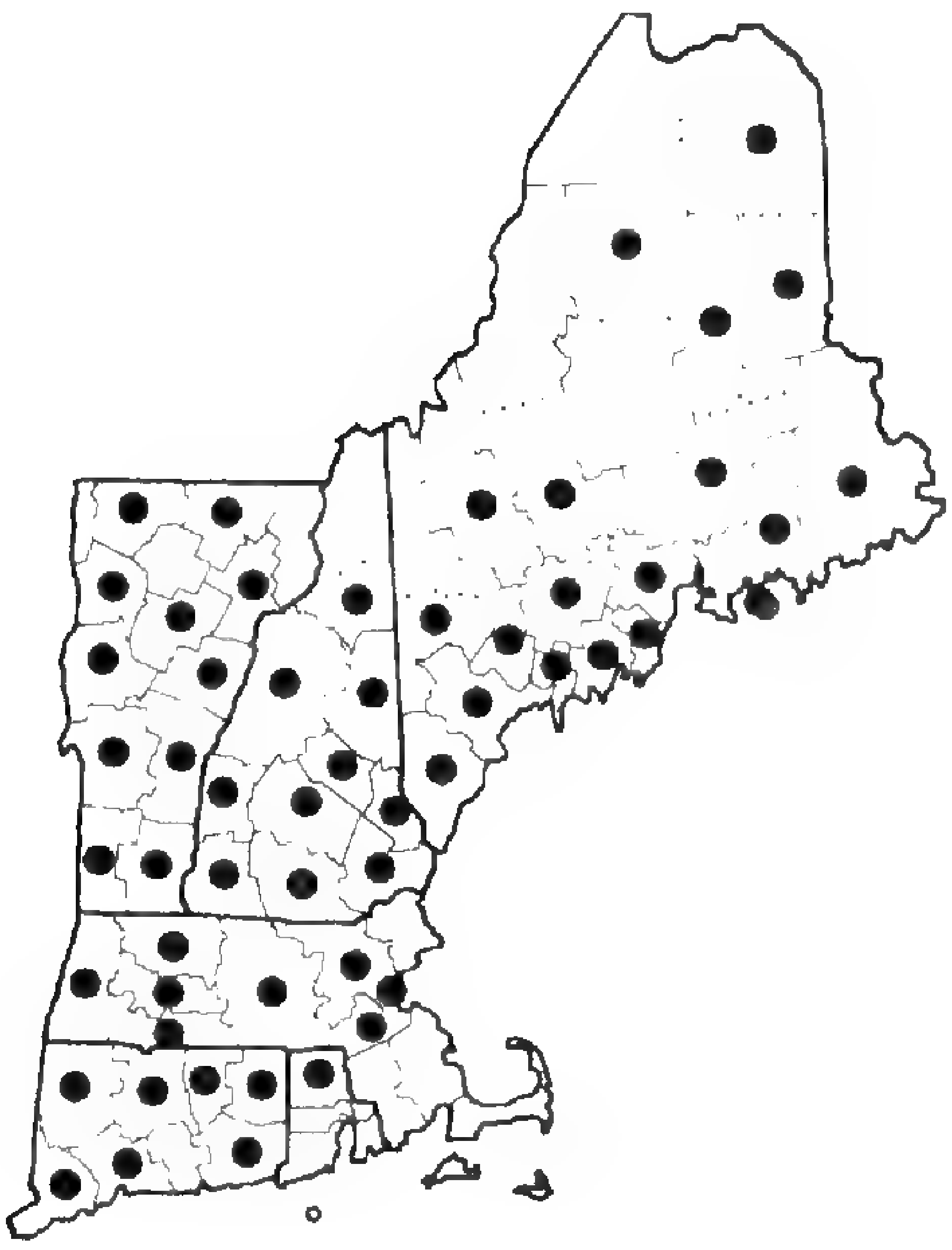
Figure 56. Distribution maps for *Platanthera ciliaris, P. clavellata, P. cristata,* and *P. dilatata* var. *dilatata.*



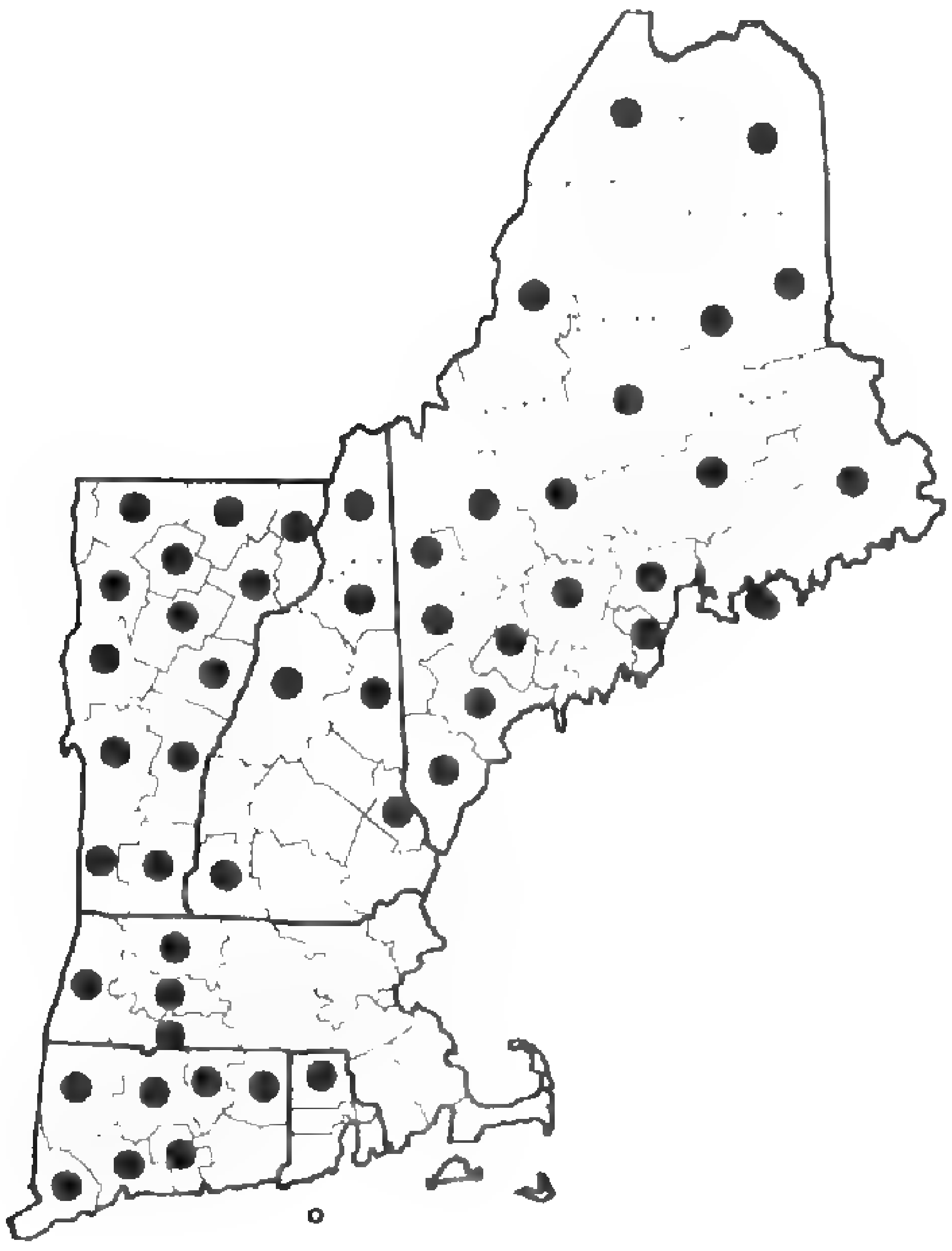
Platanthera flava
var. *herbiola*



Platanthera grandiflora

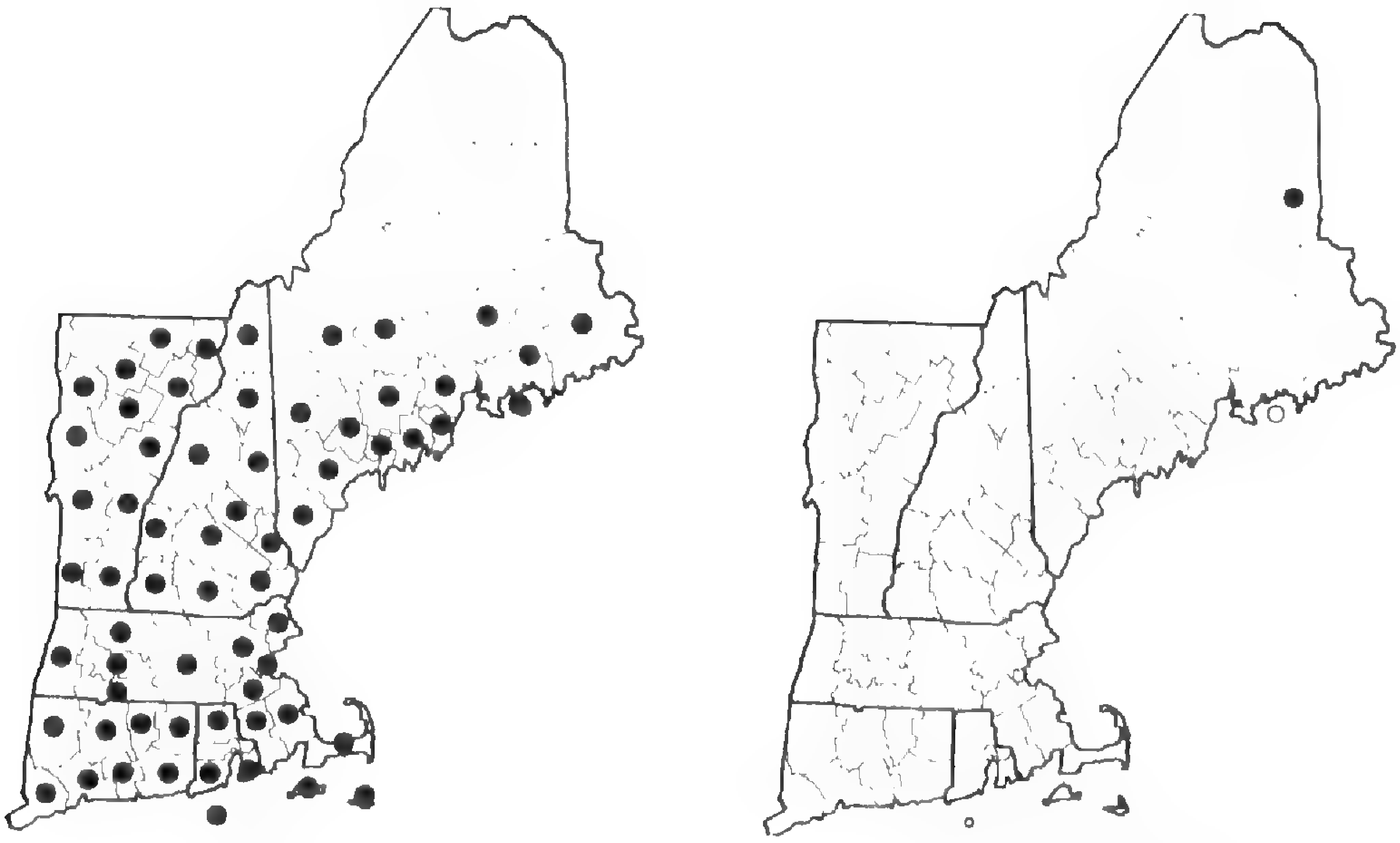


Platanthera hookeri



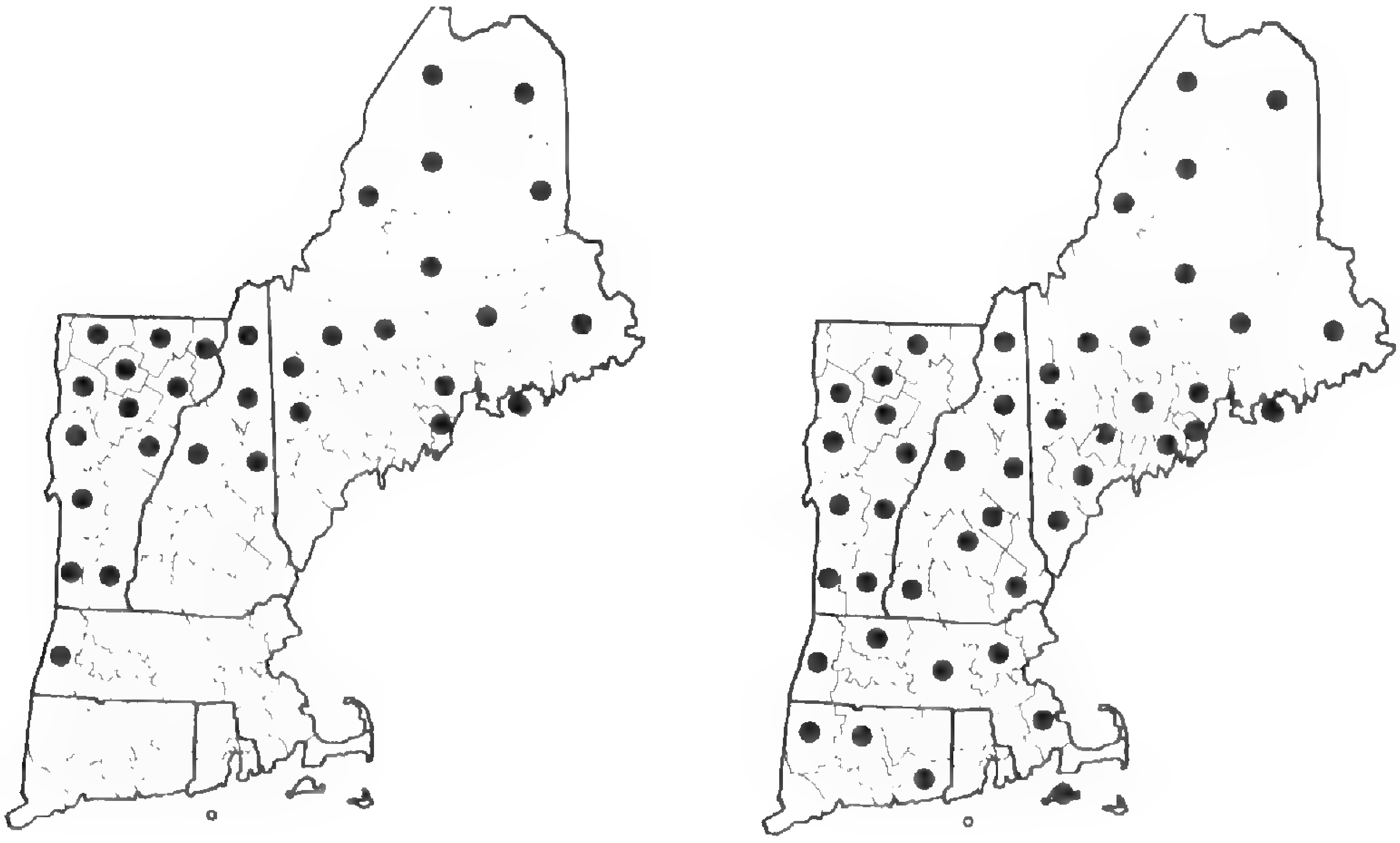
Platanthera hyperborea

Figure 57. Distribution maps for *Platanthera flava* var. *herbiola*, *P. grandiflora*, *P. hookeri*, and *P. hyperborea*.



Platanthera lacera

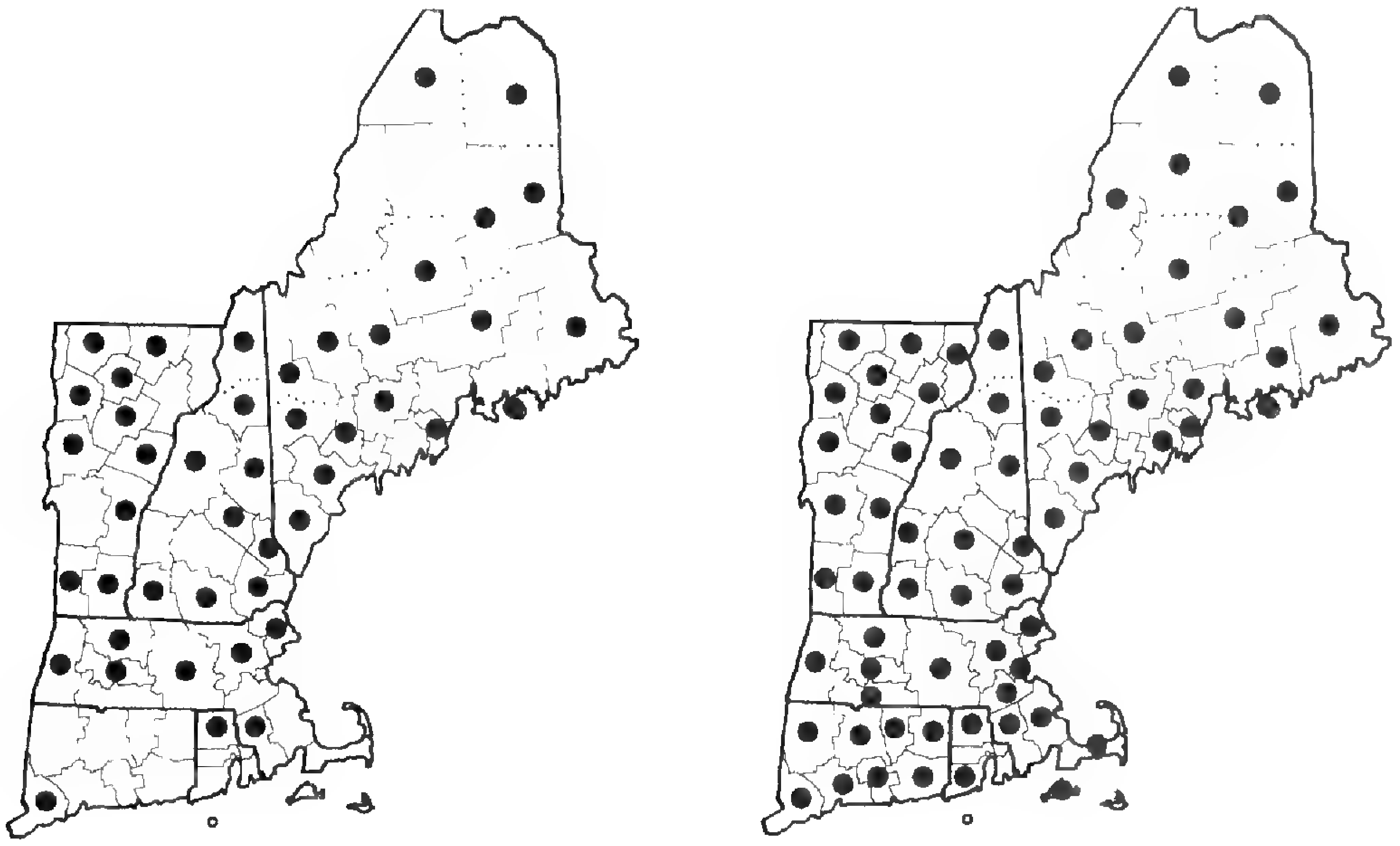
Platanthera leucophaea



Platanthera obtusata

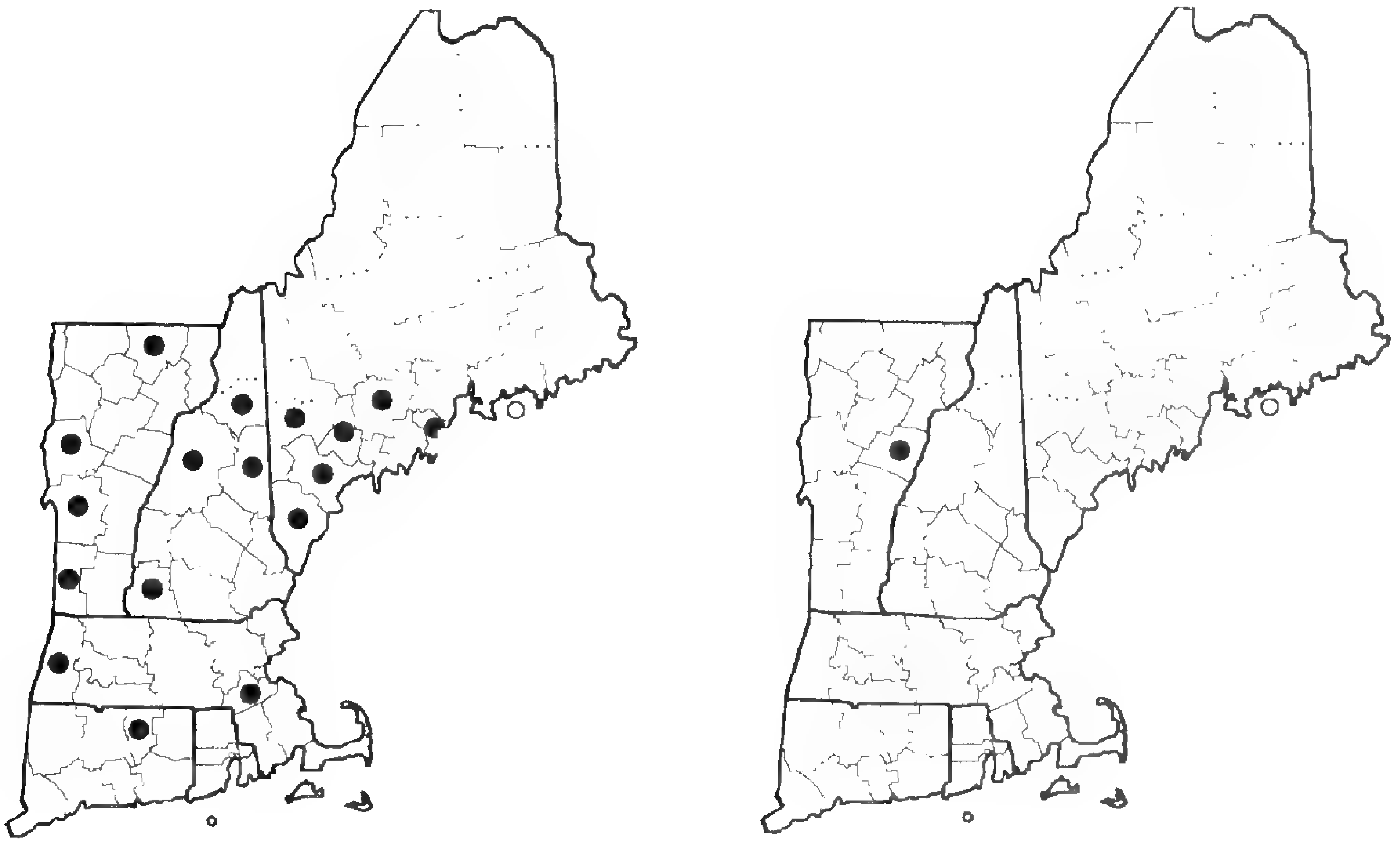
Platanthera orbiculata
var. *orbiculata*

Figure 58. Distribution maps for *Platanthera lacera, P. leucophaea, P. obtusata,* and *P. orbiculata* var. *orbiculata.*



Platanthera orbiculata
var. *macrophylla*

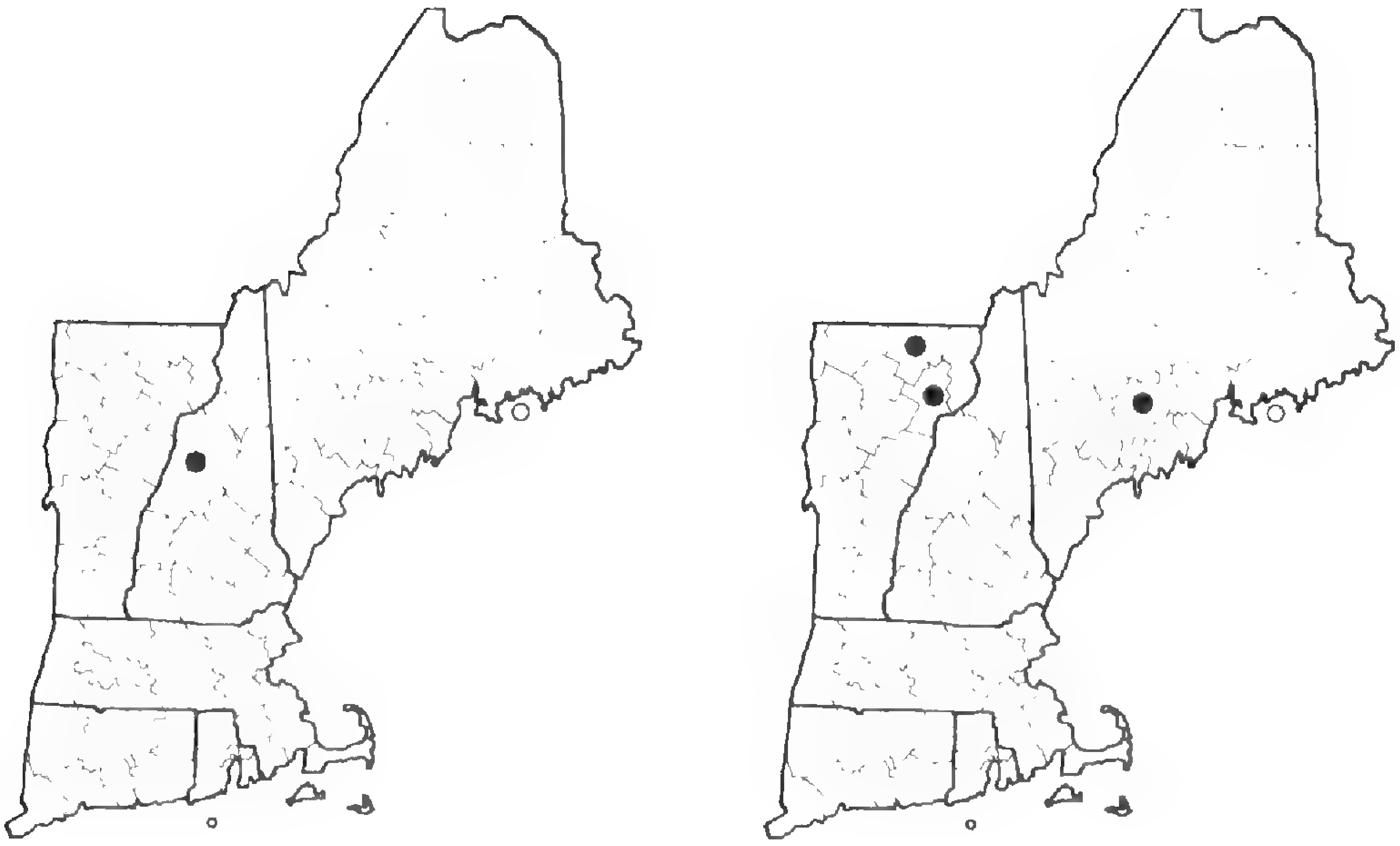
Platanthera psycodes



Platanthera X *andrewsii*

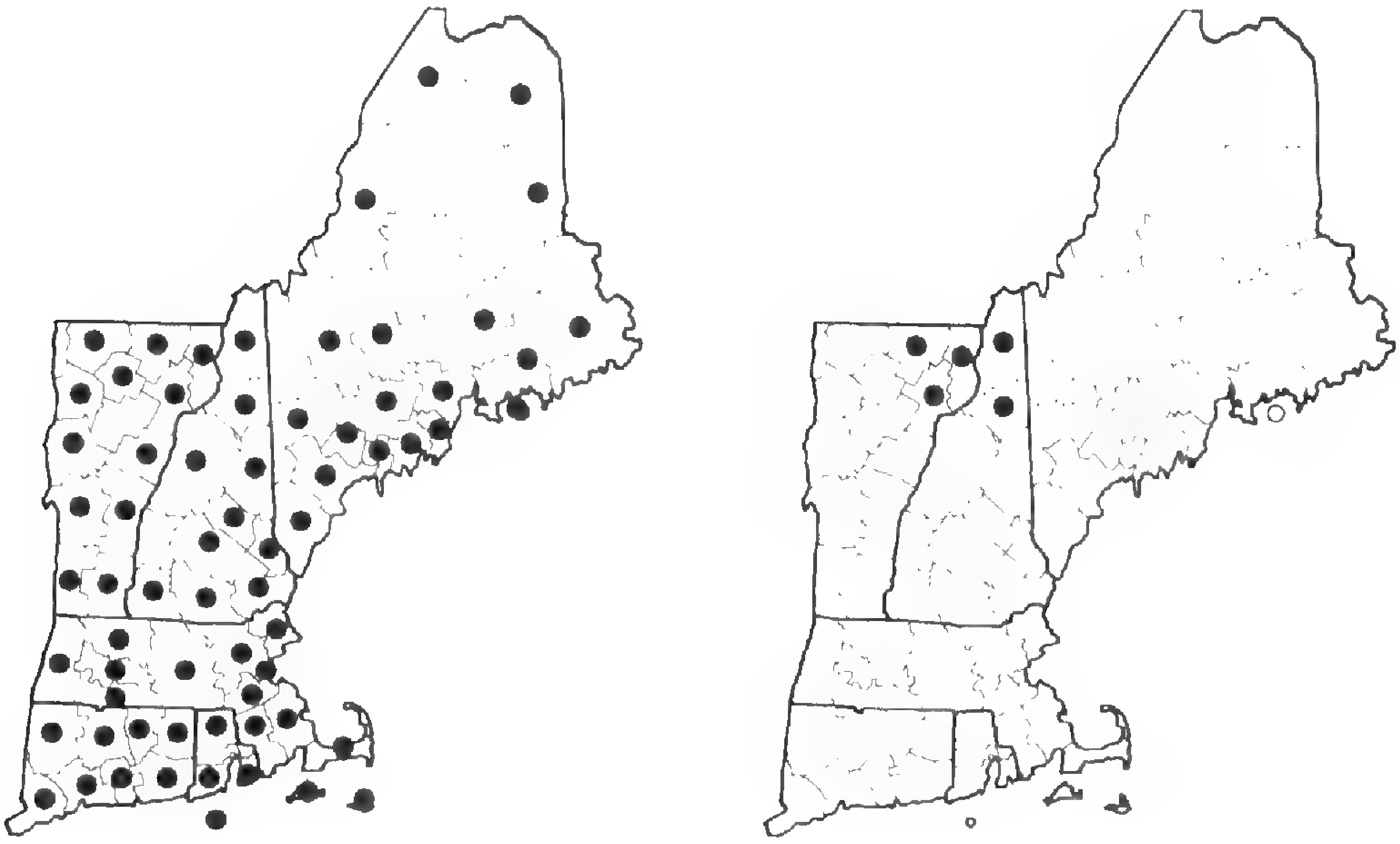
Platanthera grandiflora
X *P. hyperborea*

Figure 59. Distribution maps for *Platanthera orbiculata* var. *macrophylla*, *P. psycodes*, *P.* X *andrewsii*, and *P. grandiflora* X *P. hyperborea*.



Platanthera grandiflora
X *P. lacera*

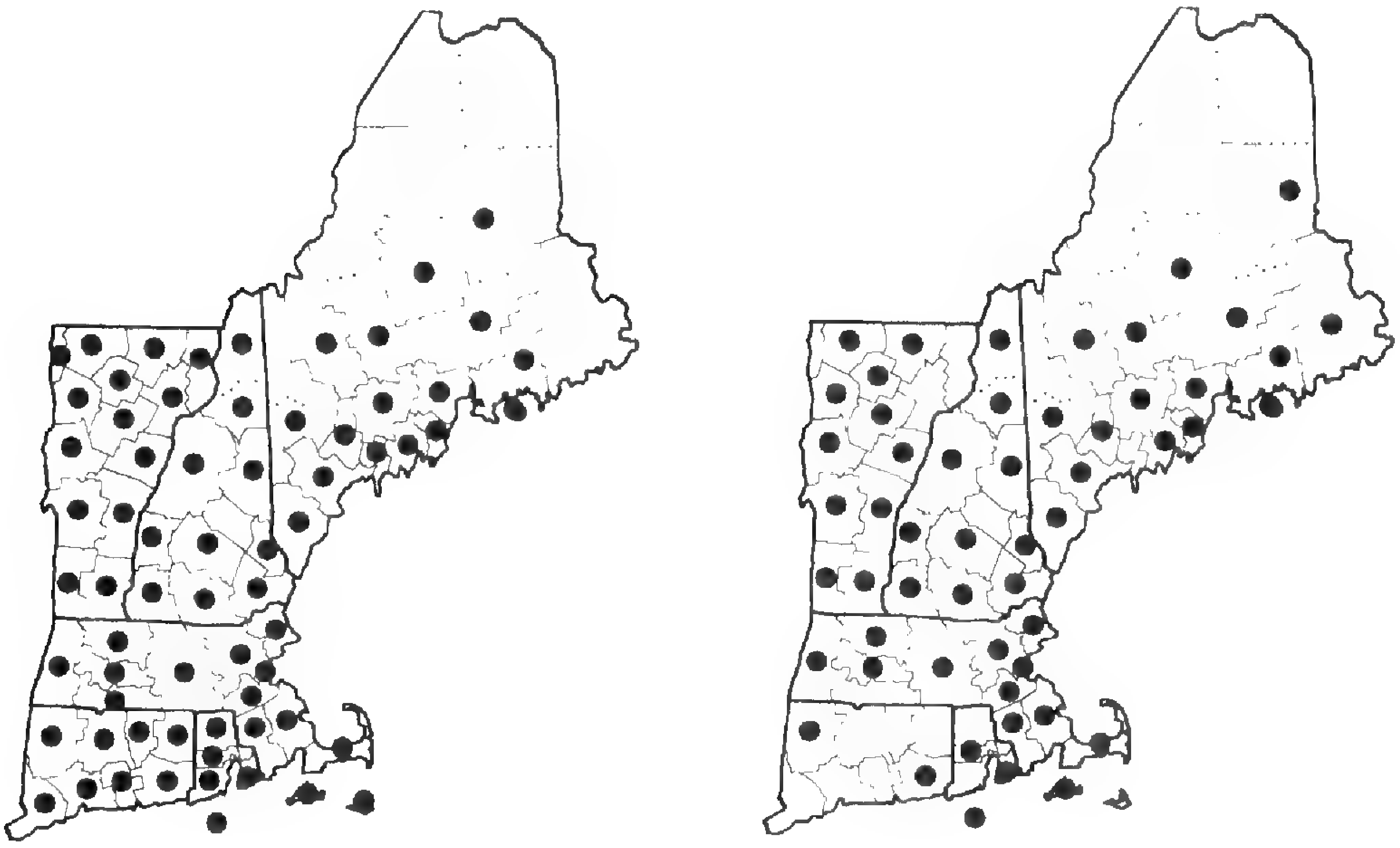
Platanthera X *media*



Pogonia ophioglossoides

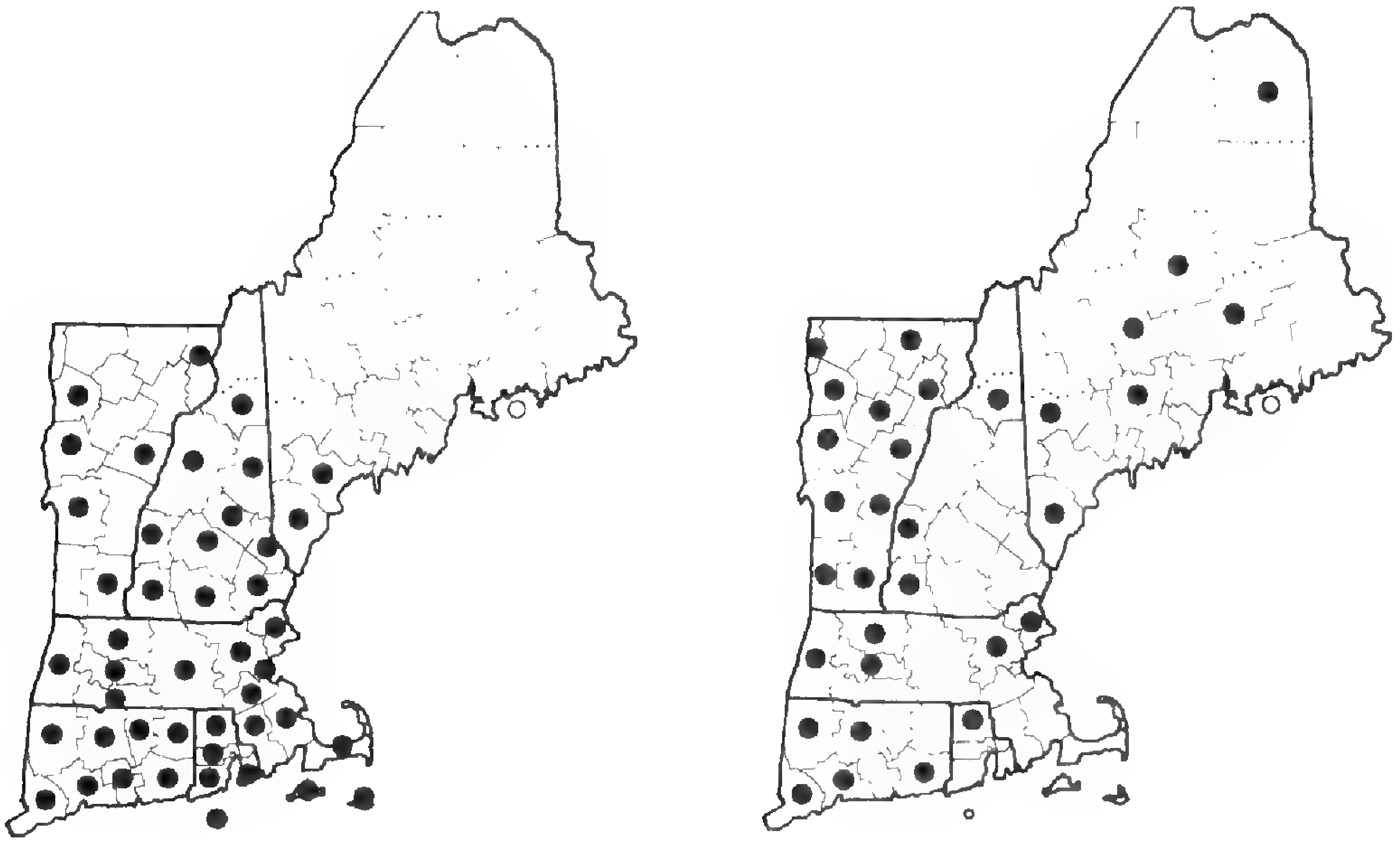
Spiranthes casei

Figure 60. Distribution maps for *Platanthera grandiflora* X *P. lacera*, *P.* X *media*, *Pogonia ophioglossoides*, and *Spiranthes casei*.



Spiranthes cernua

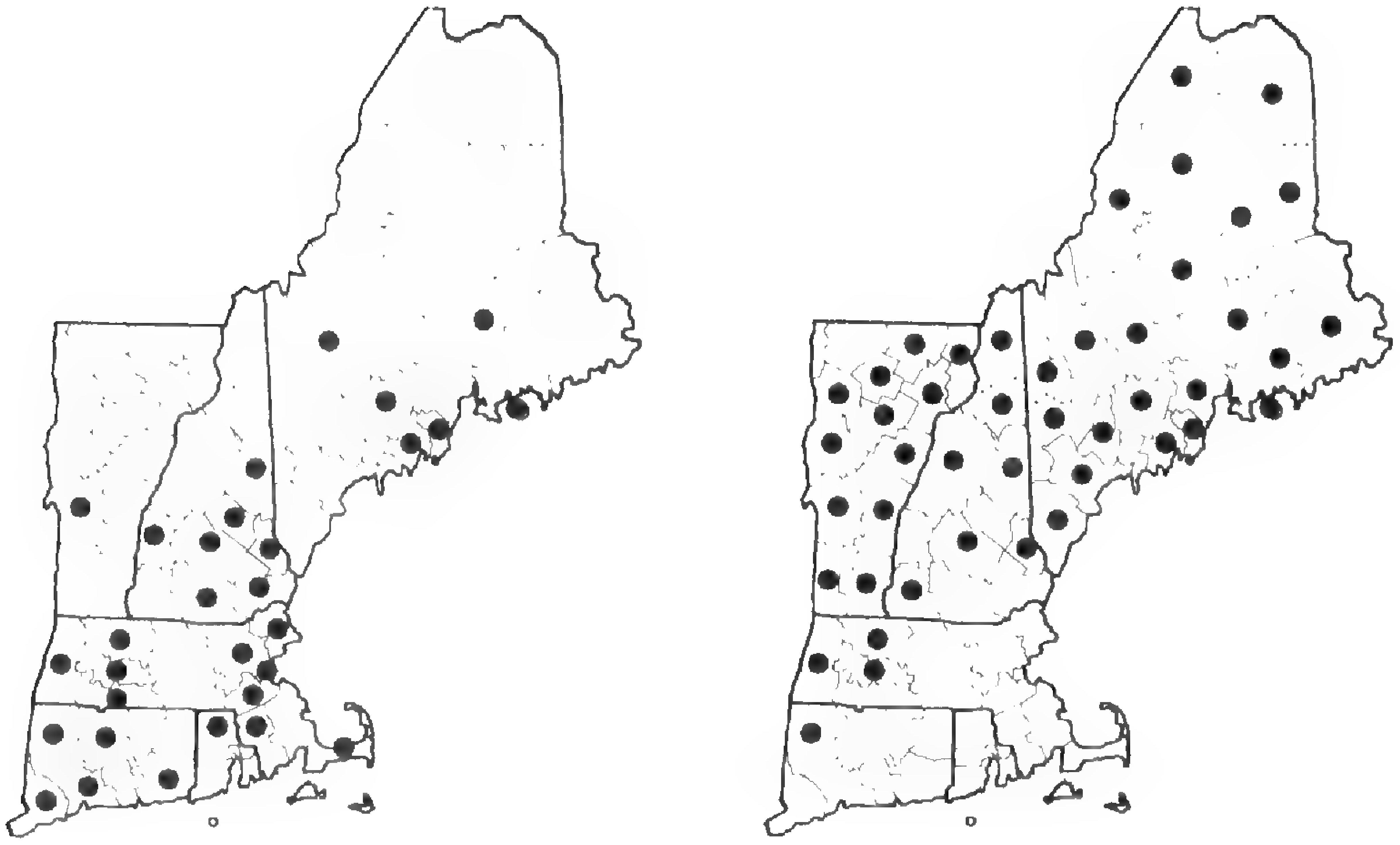
Spiranthes lacera
var. *lacera*



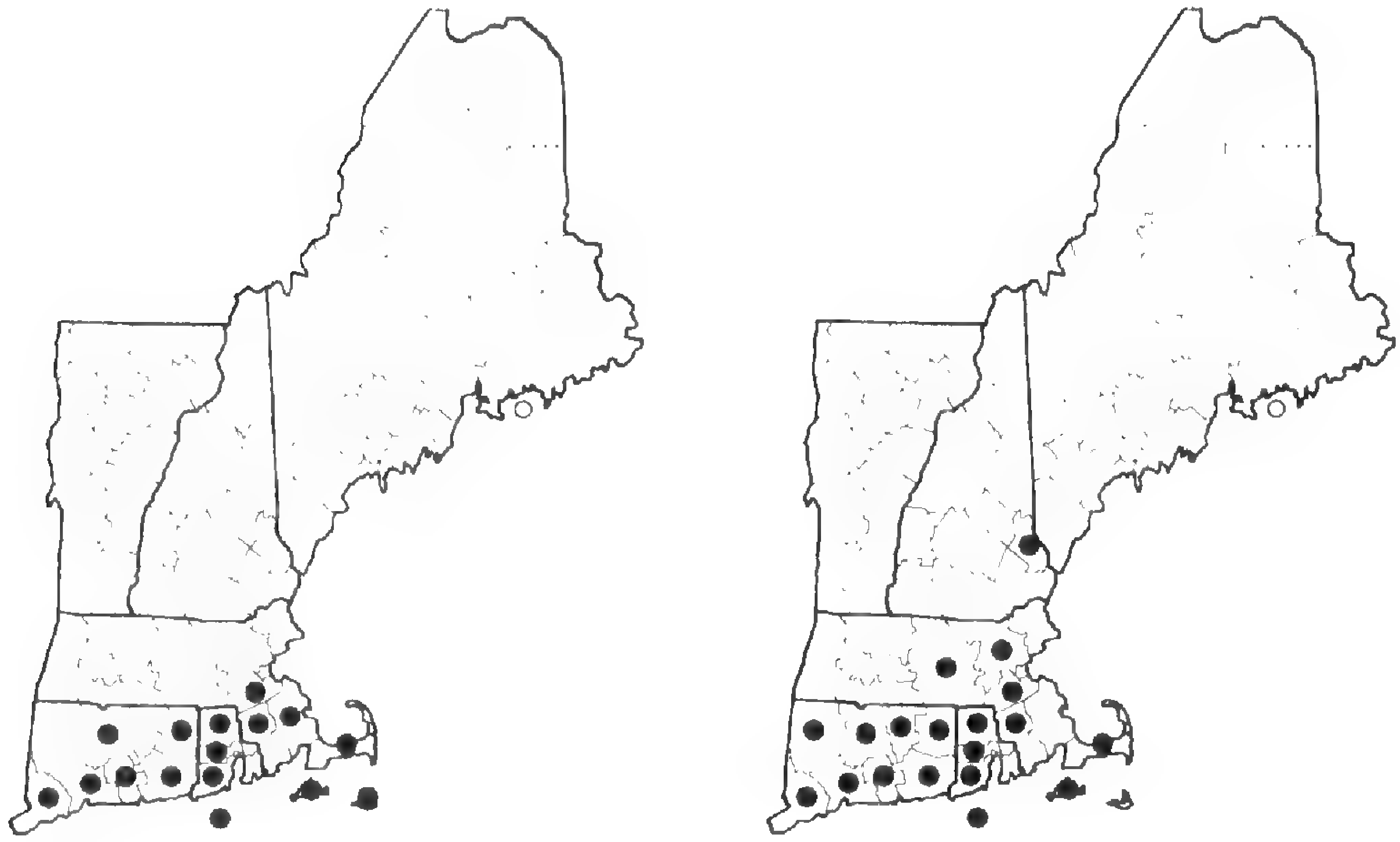
Spiranthes lacera
var. *gracilis*

Spiranthes lucida

Figure 61. Distribution maps for *Spiranthes cernua, S. lacera* var. *lacera, S. lacera* var. *gracilis,* and *S. lucida.*

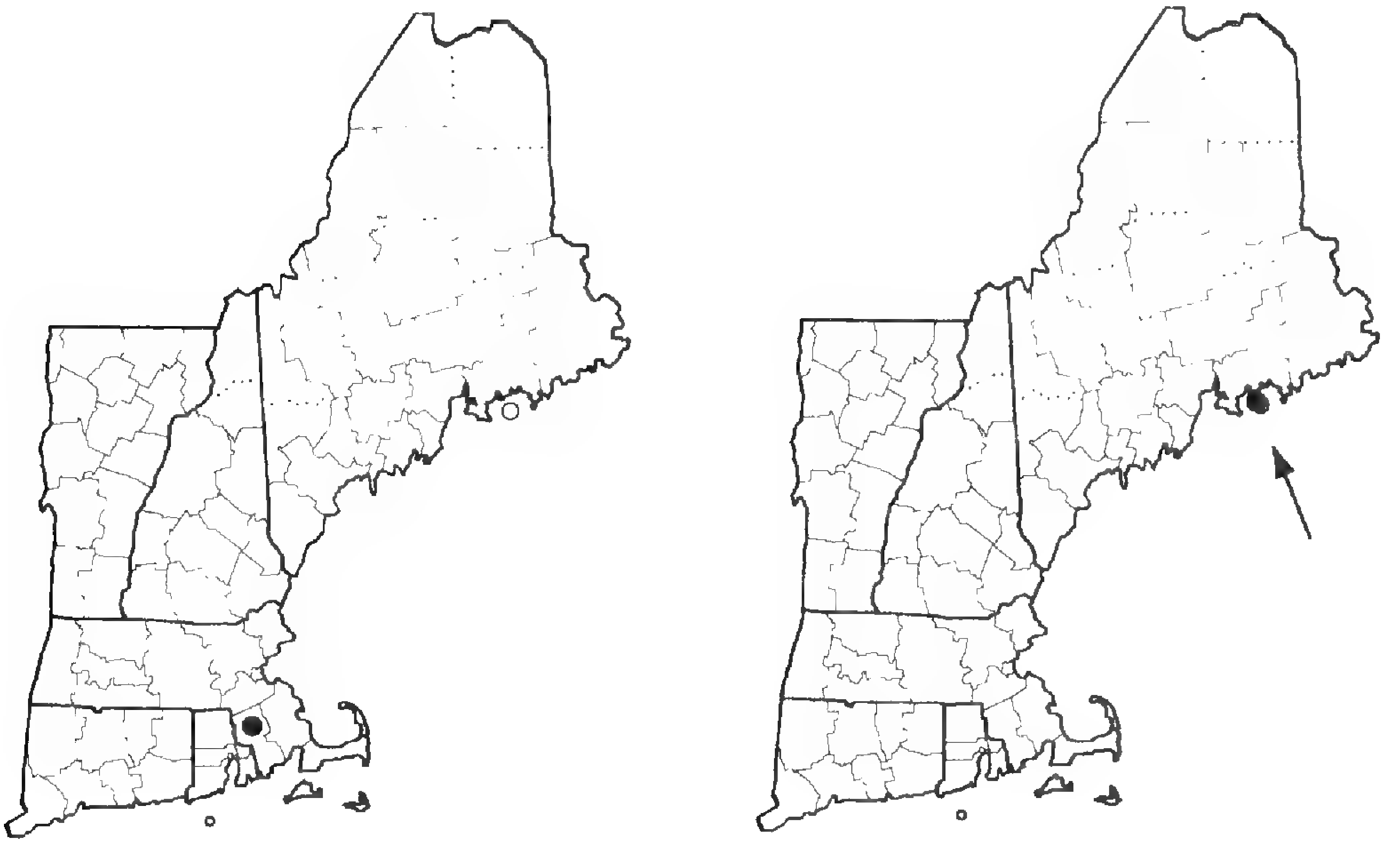


Spiranthes ochroleuca *Spiranthes romanzoffiana*



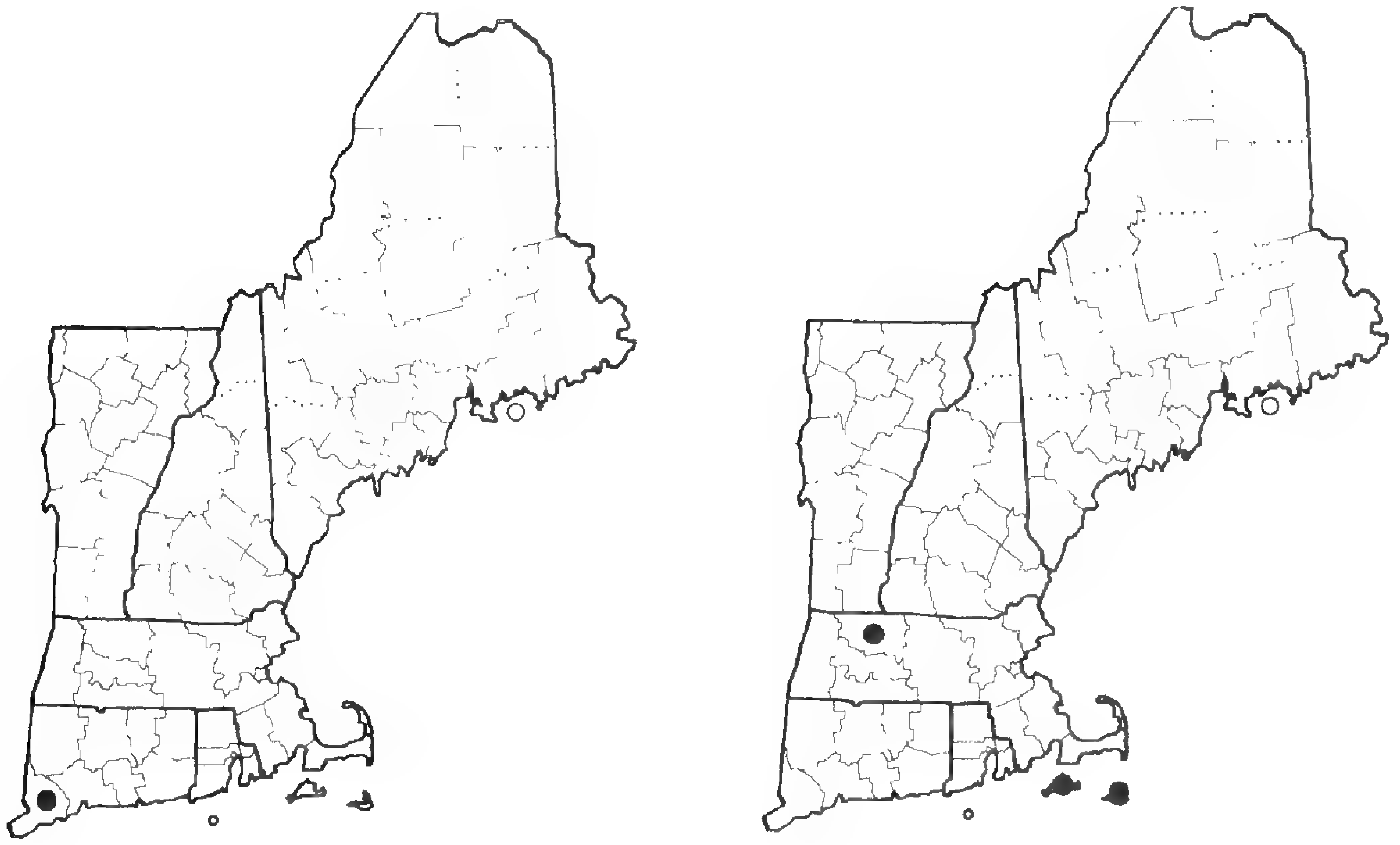
Spiranthes tuberosa *Spiranthes vernalis*

Figure 62. Distribution maps for *Spiranthes ochroleuca, S. romanzoffiana, S. tuberosa,* and *S. vernalis.*



Spiranthes X *intermedia*

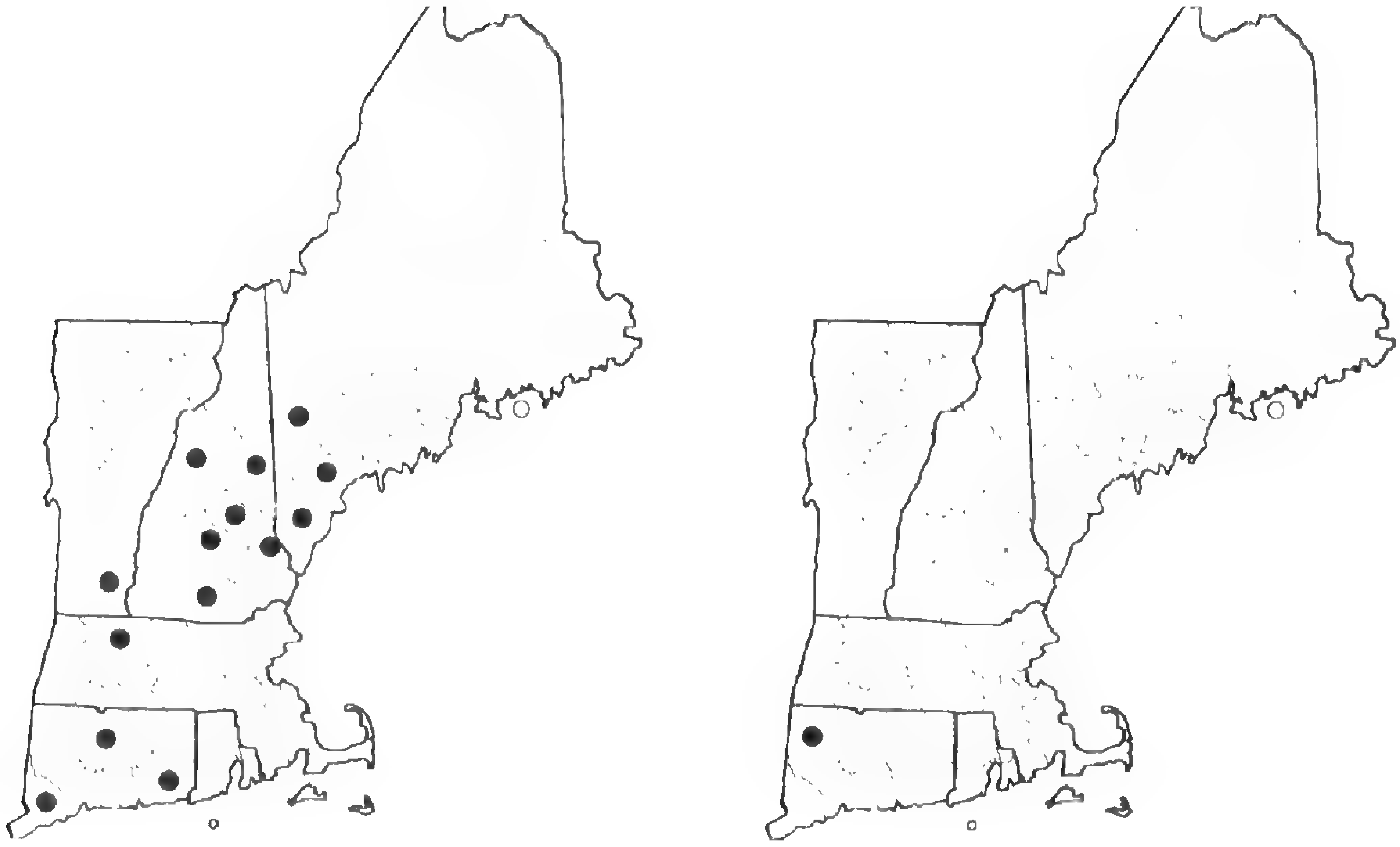
Spiranthes lacera var. *lacera*
X *S. romanzoffiana*



Spiranthes lacera var. *gracilis*
X *S. tuberosa*

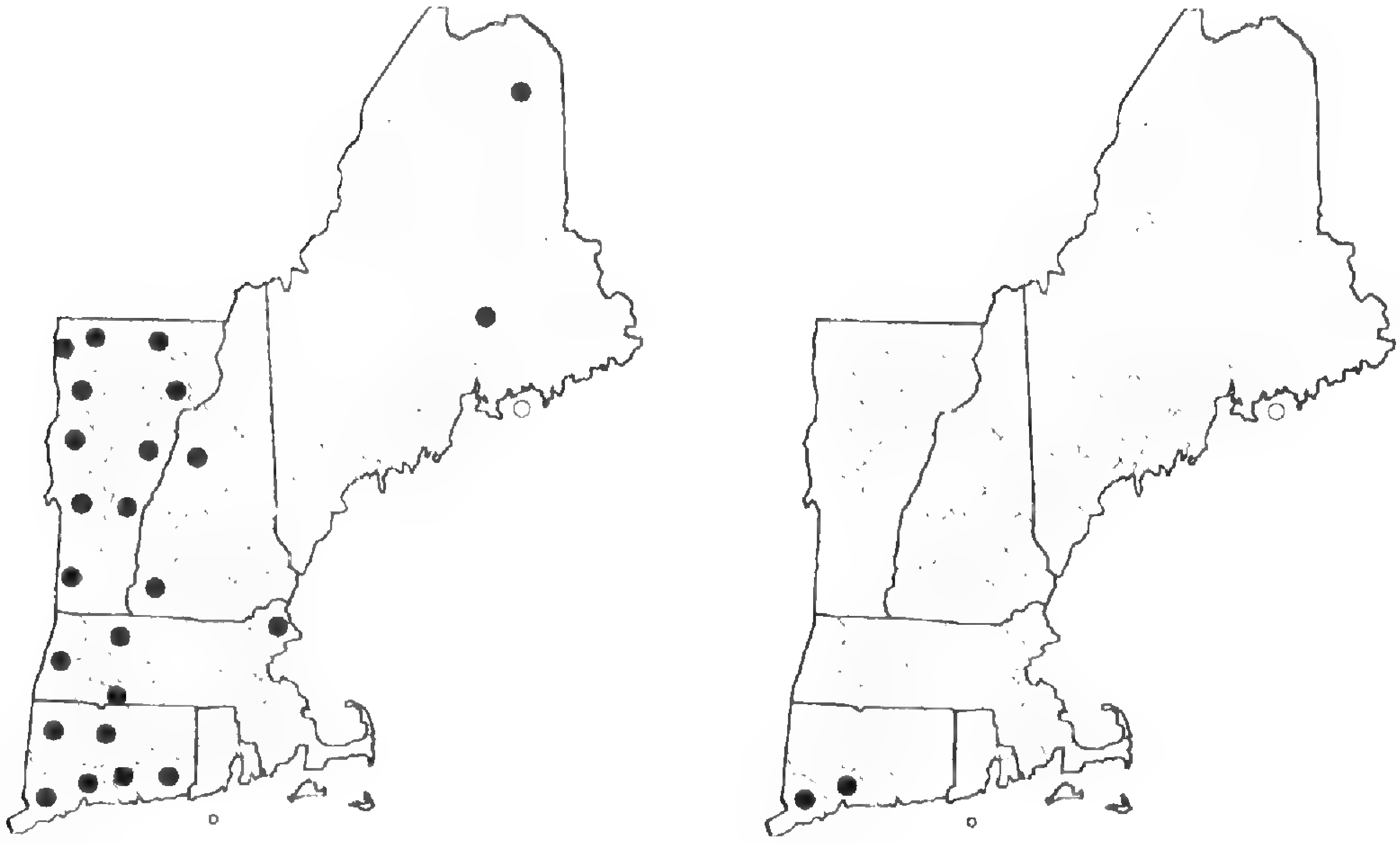
Tipularia discolor

Figure 63. Distribution maps for *Spiranthes* X *intermedia, S. lacera* var. *lacera* X *S. romanzoffiana, S. lacera* var. *gracilis* X *S. tuberosa,* and *Tipularia discolor.*



Triphora trianthophora
subsp. *trianthophora*

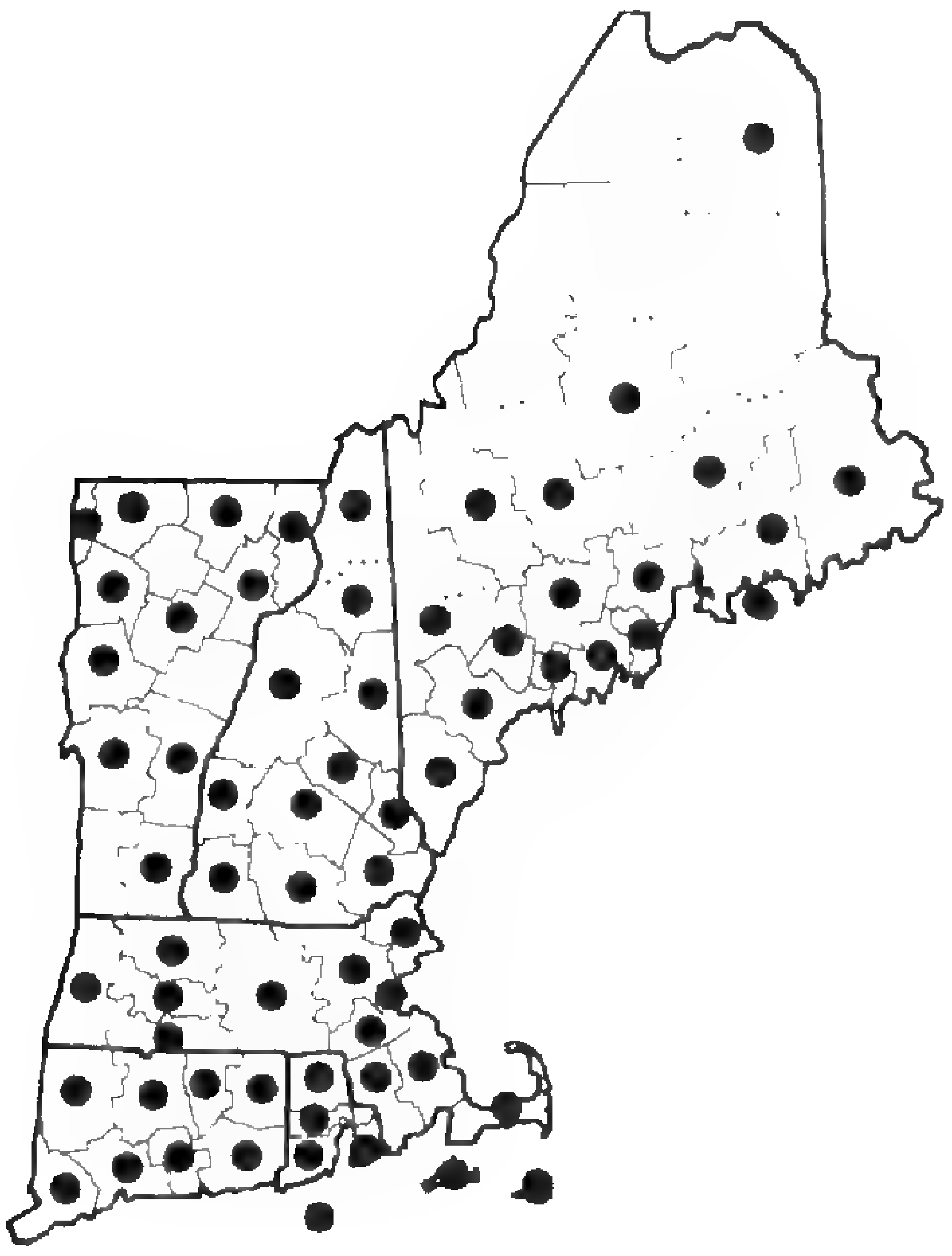
EICHHORNIA CRASSIPES



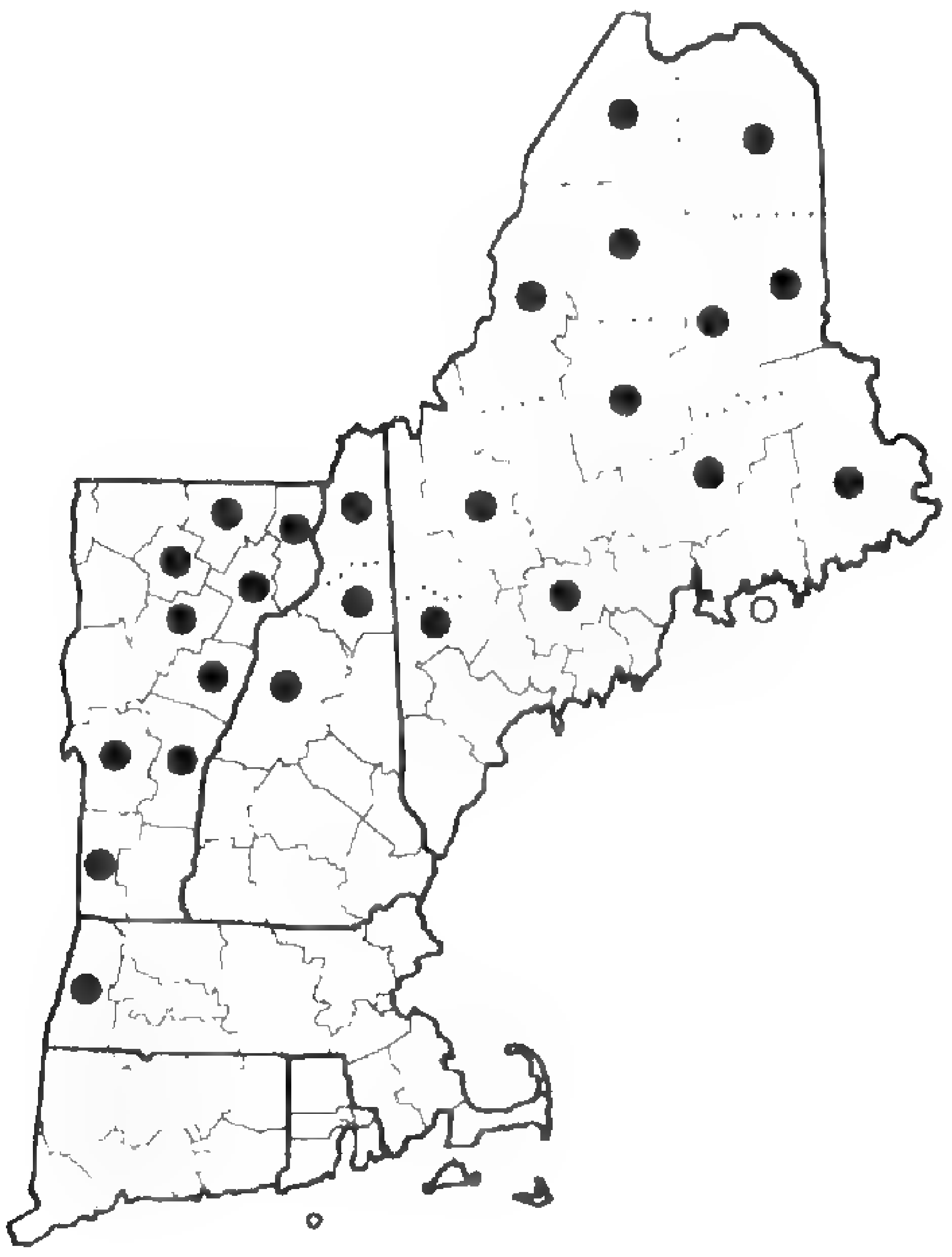
Heteranthera dubia

Heteranthera reniformis

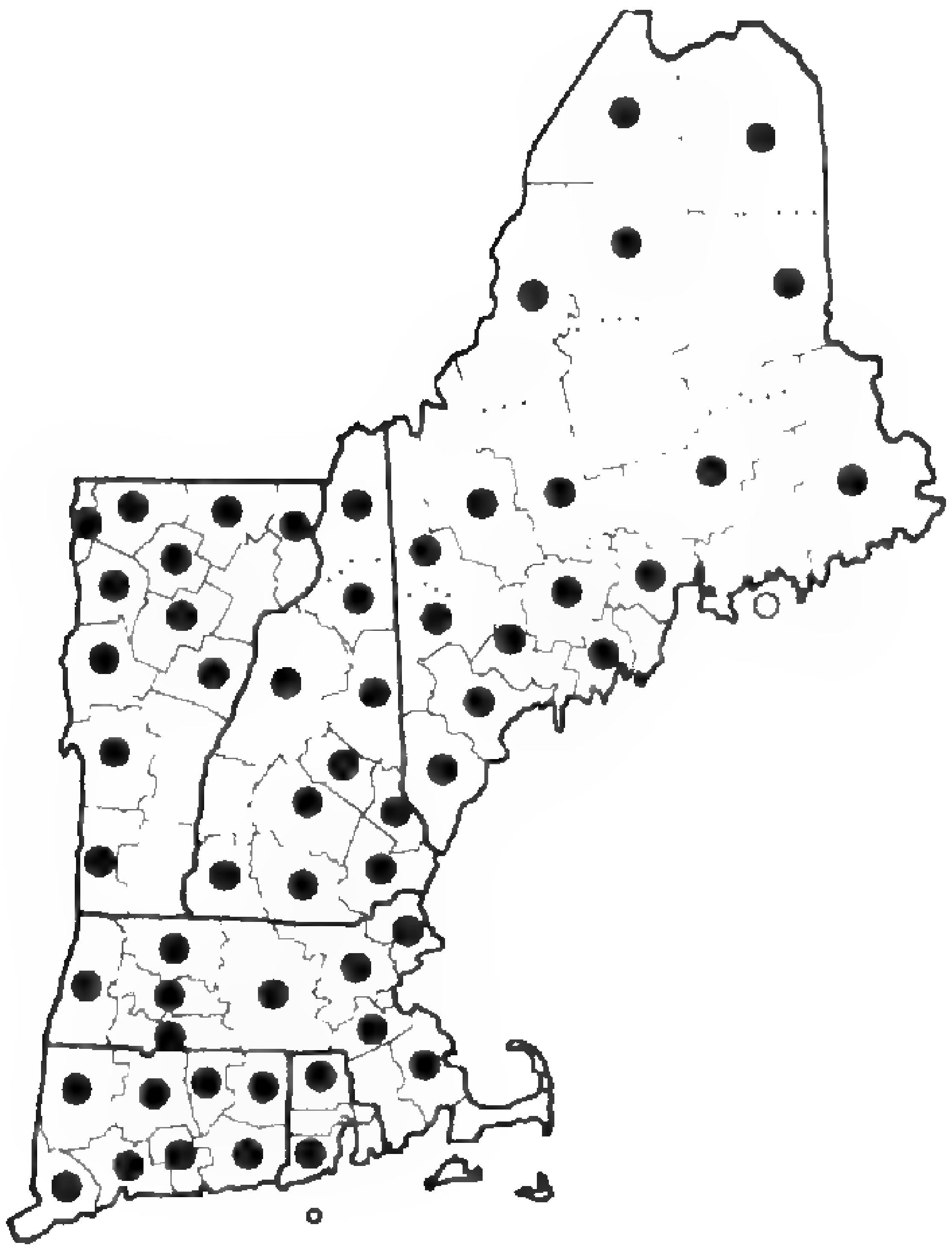
Figure 64. Distribution maps for *Triphora trianthophora* subsp. *trianthophora, EICHHORNIA CRASSIPES, Heteranthera dubia,* and *H. reniformis.*



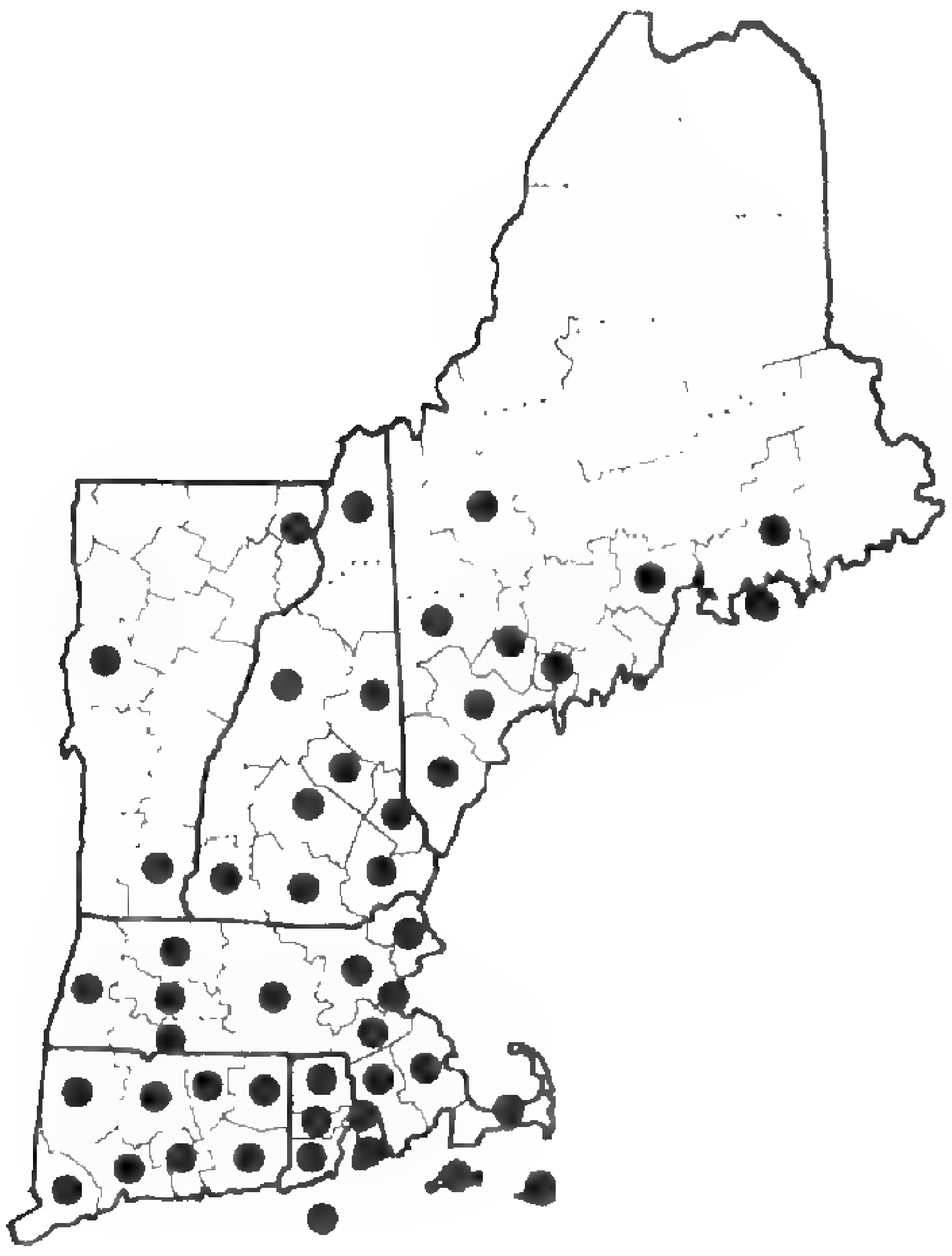
Pontederia cordata



Potamogeton alpinus

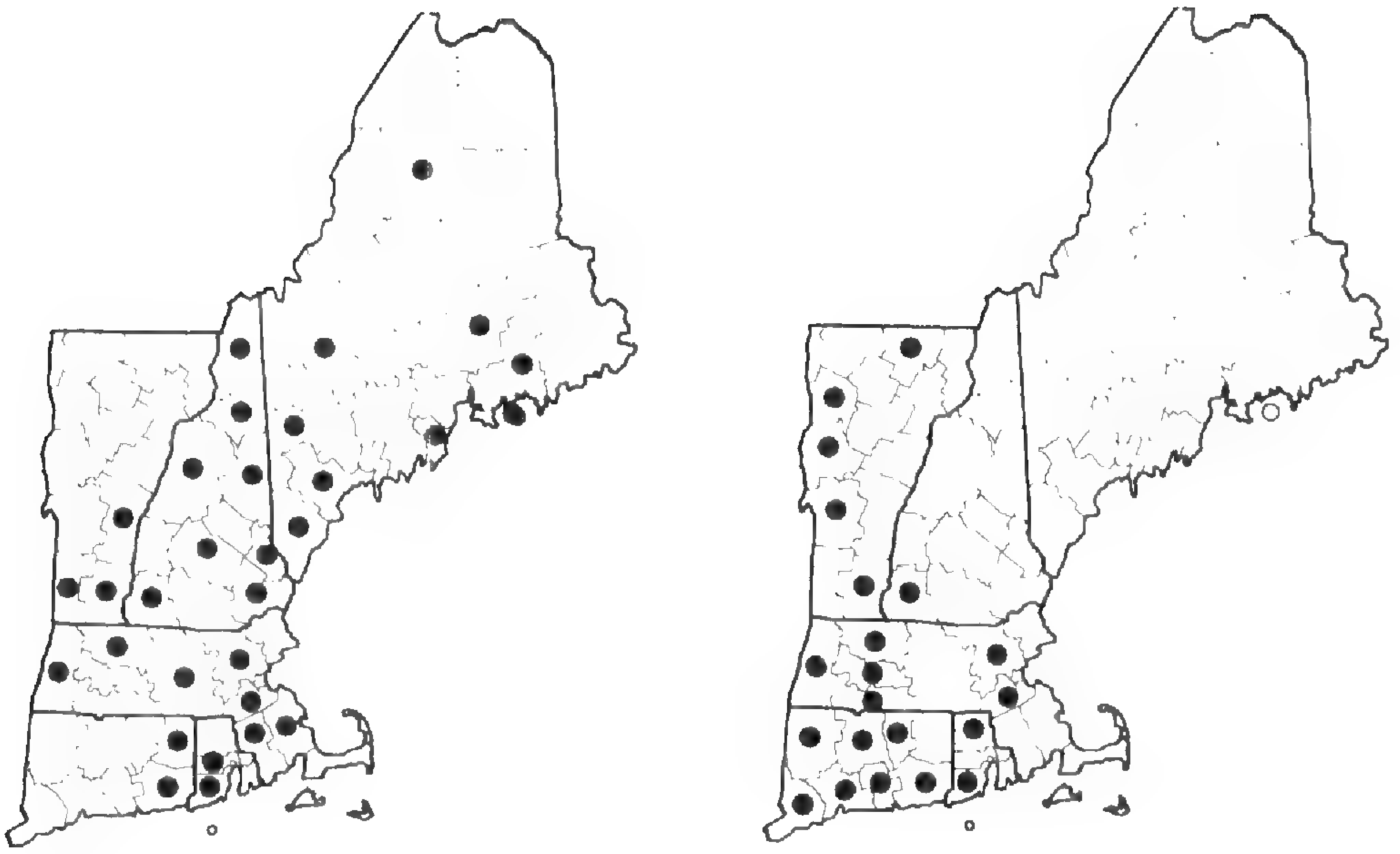


Potamogeton amplifolius



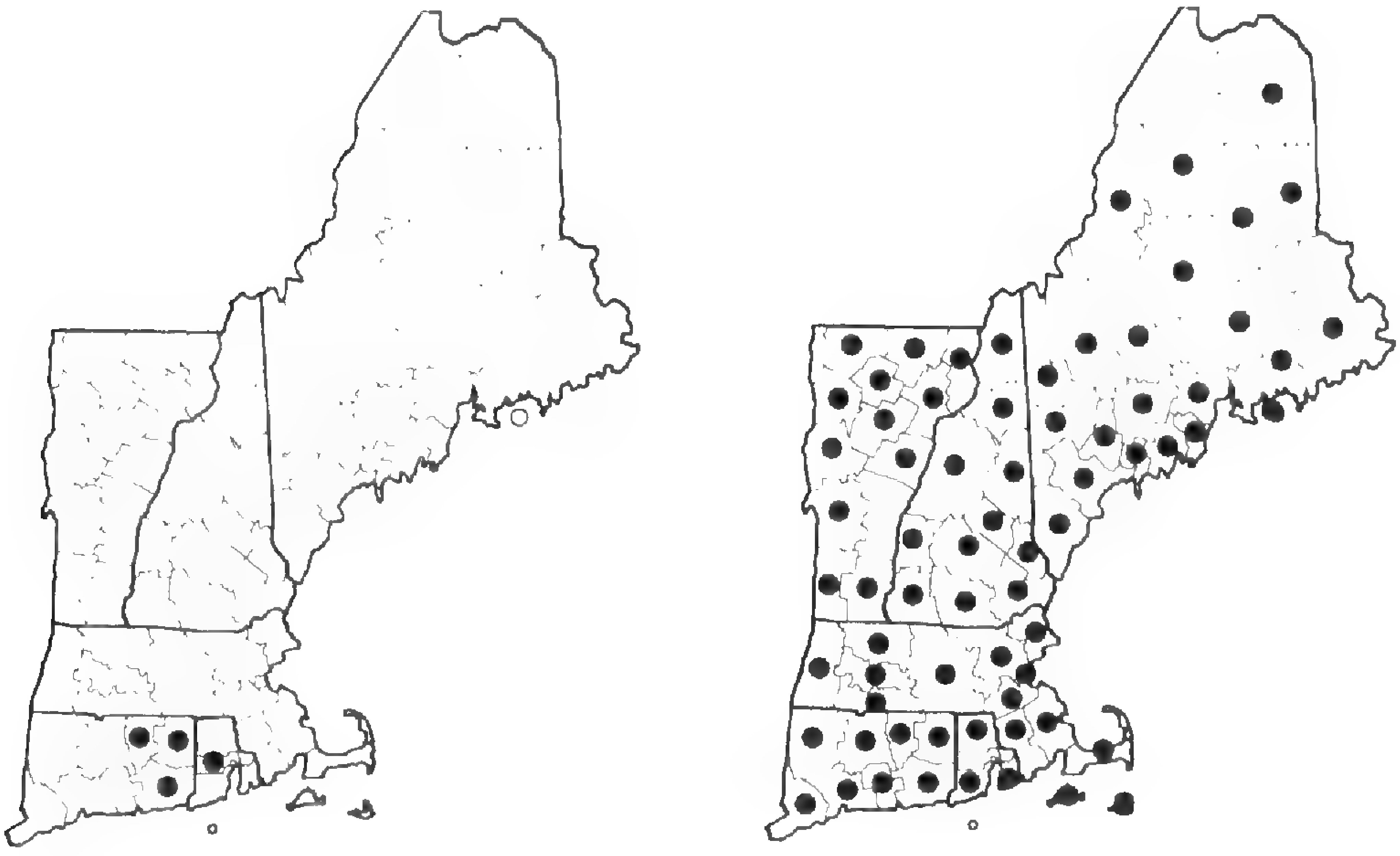
Potamogeton bicupulatus

Figure 65. Distribution maps for *Pontederia cordata, Potamogeton alpinus, P. amplifolius,* and *P. bicupulatus.*



Potamogeton confervoides

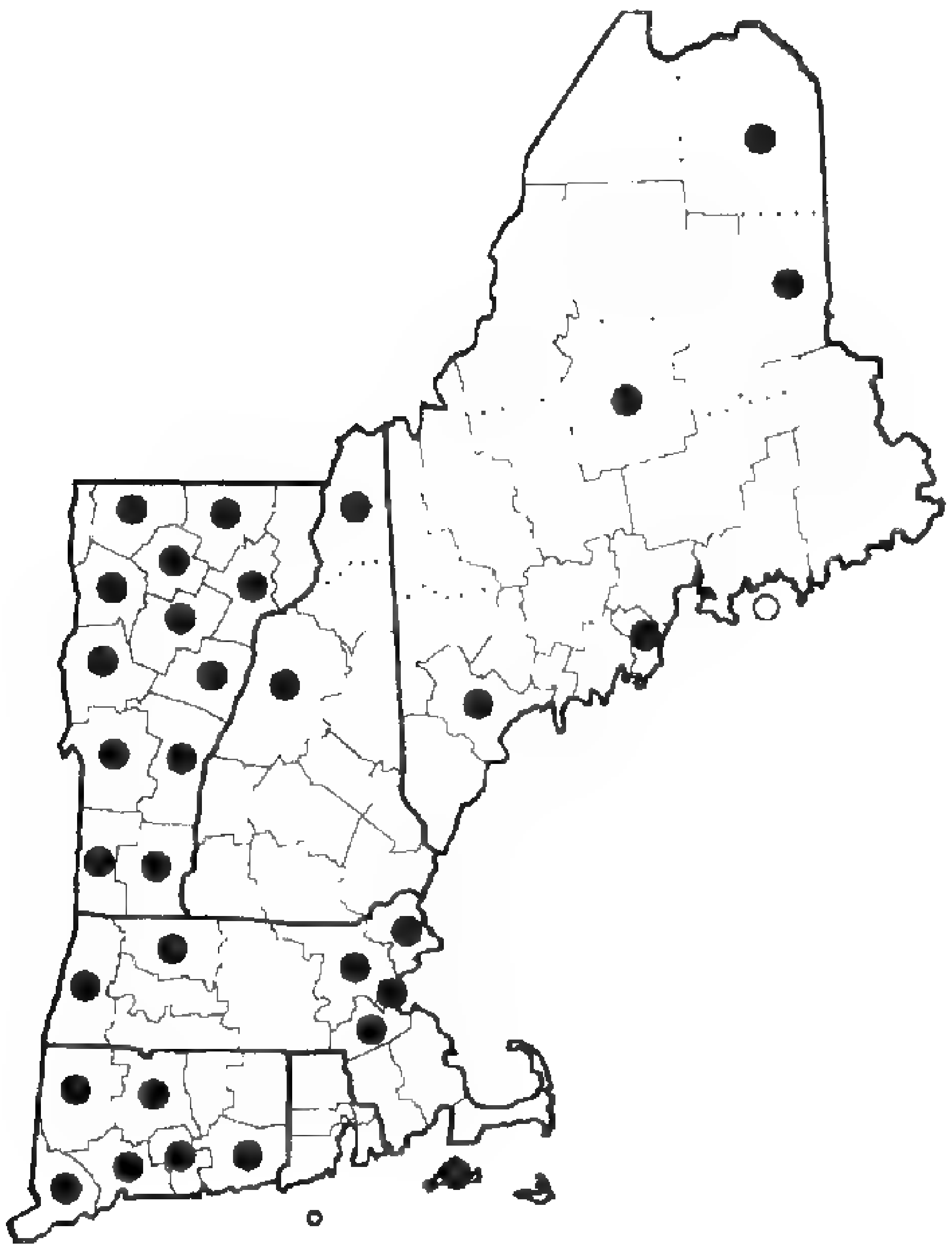
POTAMOGETON CRISPUS



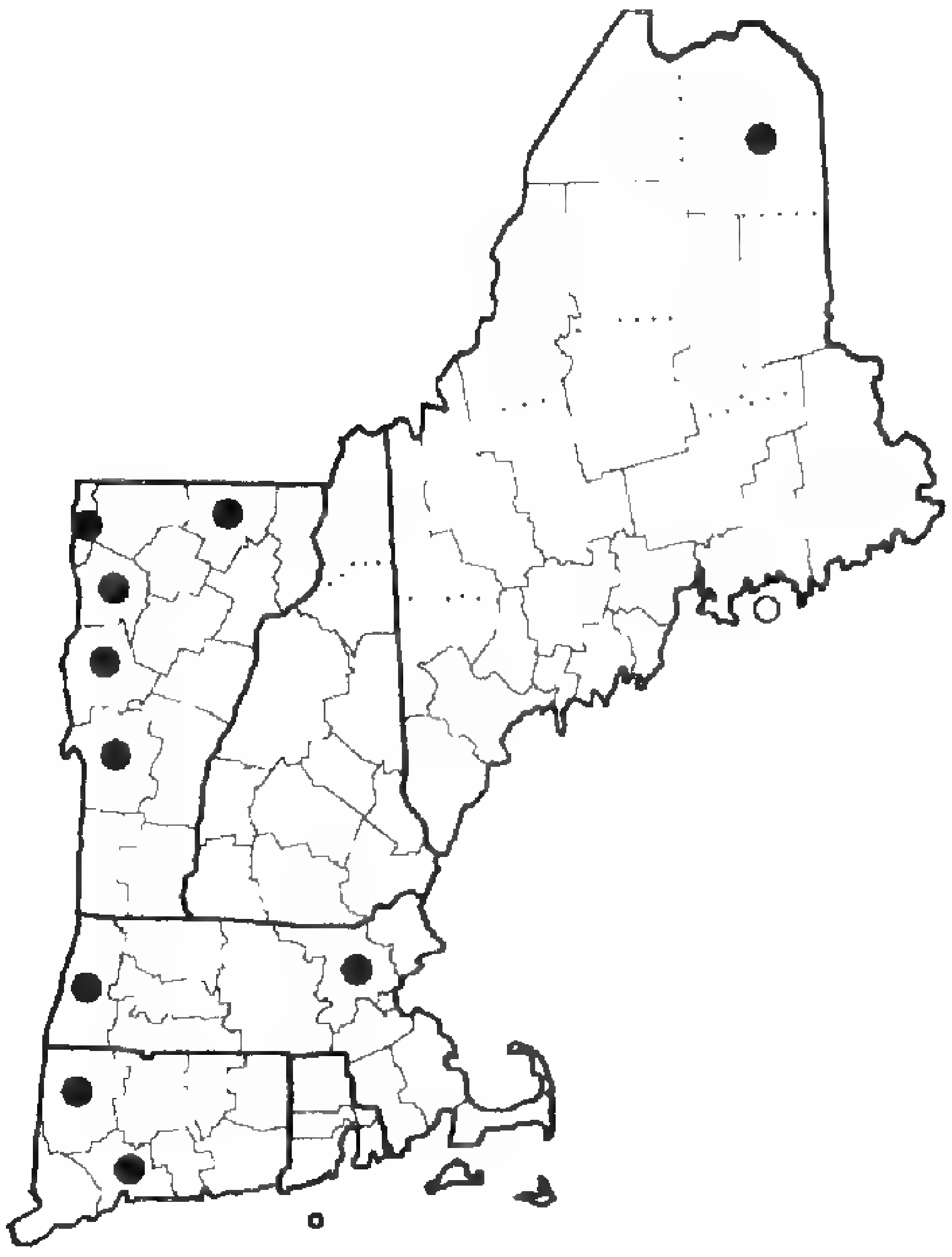
Potamogeton diversifolius

Potamogeton epihydrus

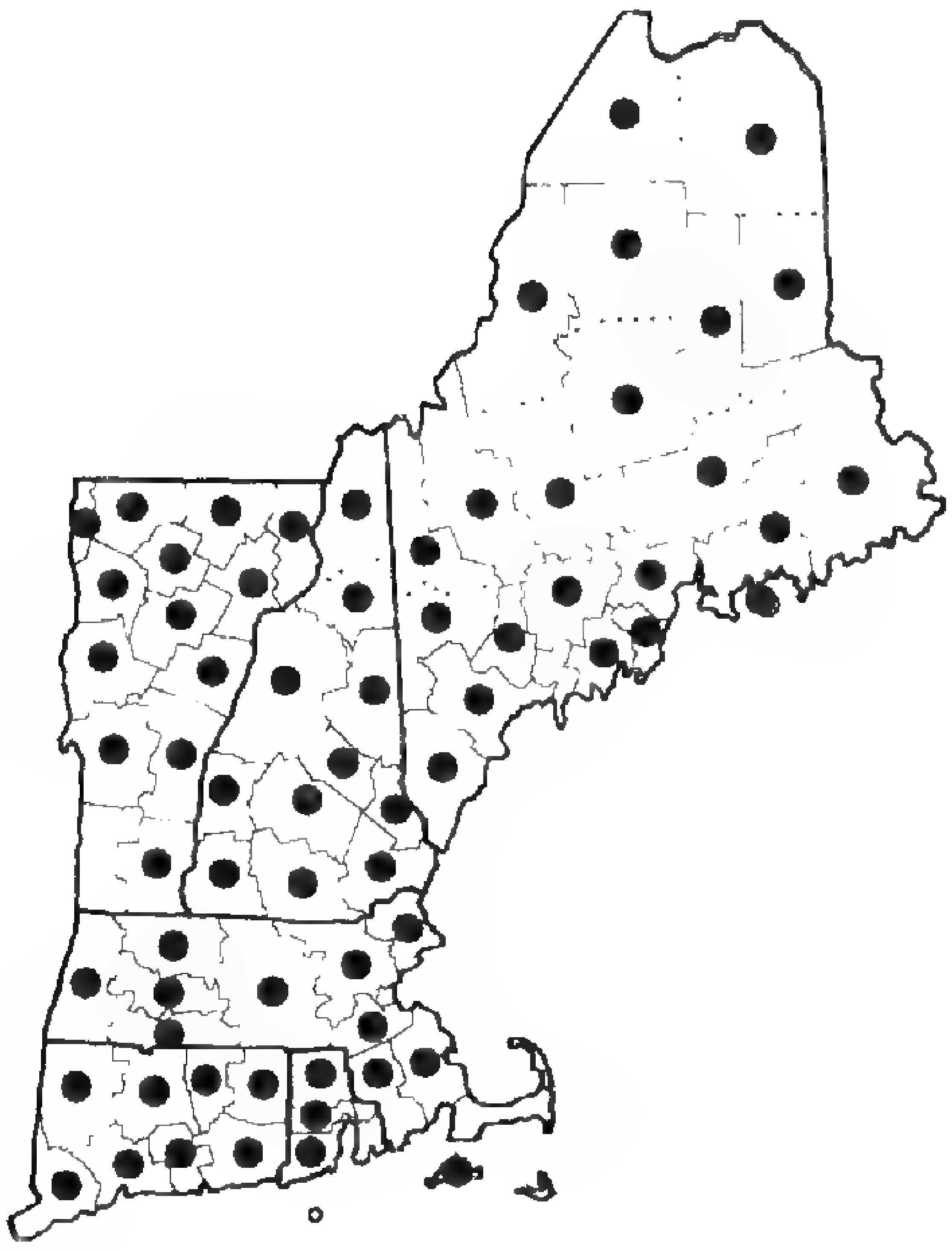
Figure 66. Distribution maps for *Potamogeton confervoides*, *P. CRISPUS*, *P. diversifolius*, and *P. epihydrus*.



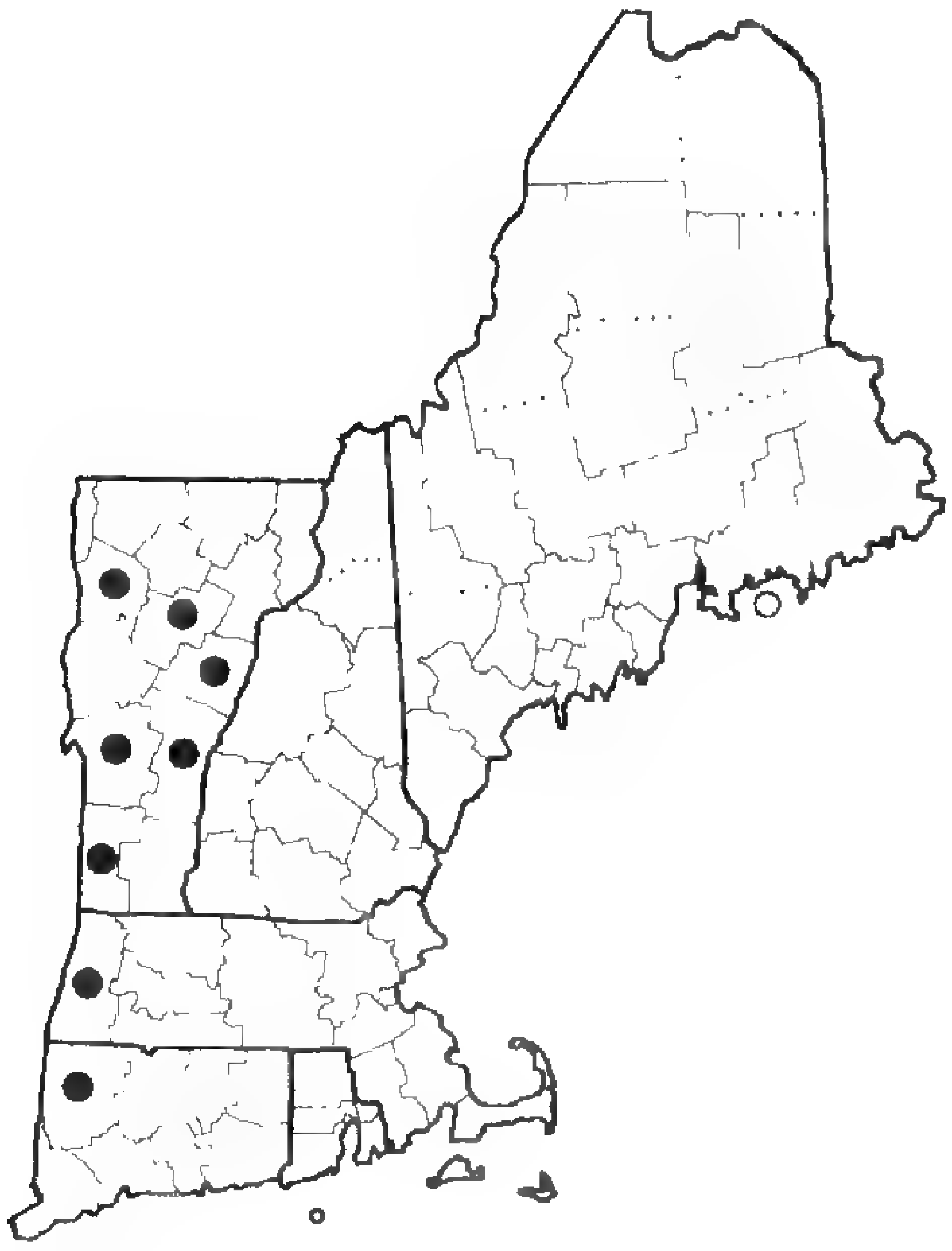
Potamogeton foliosus
subsp. *foliosus*



Potamogeton friesii

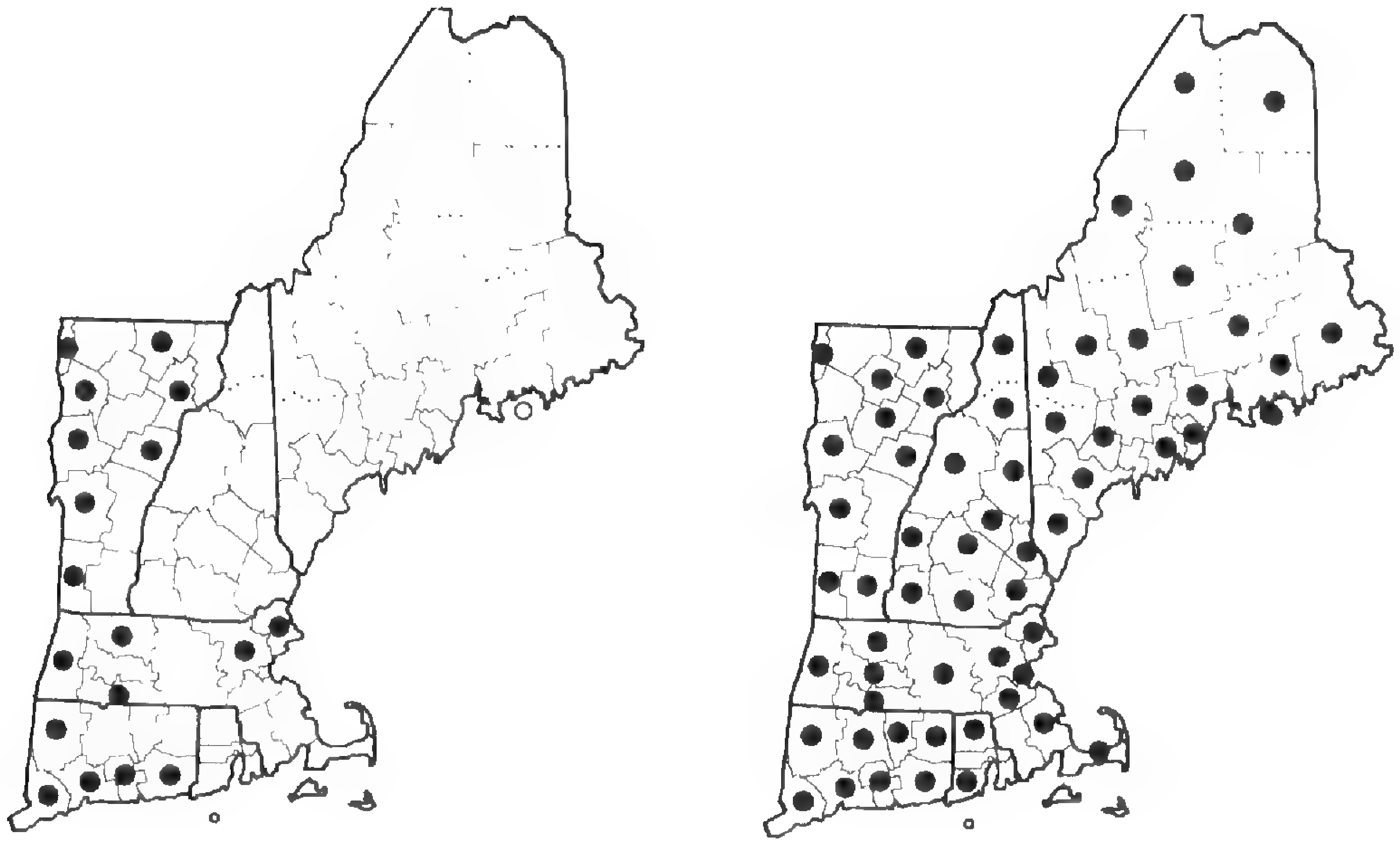


Potamogeton gramineus

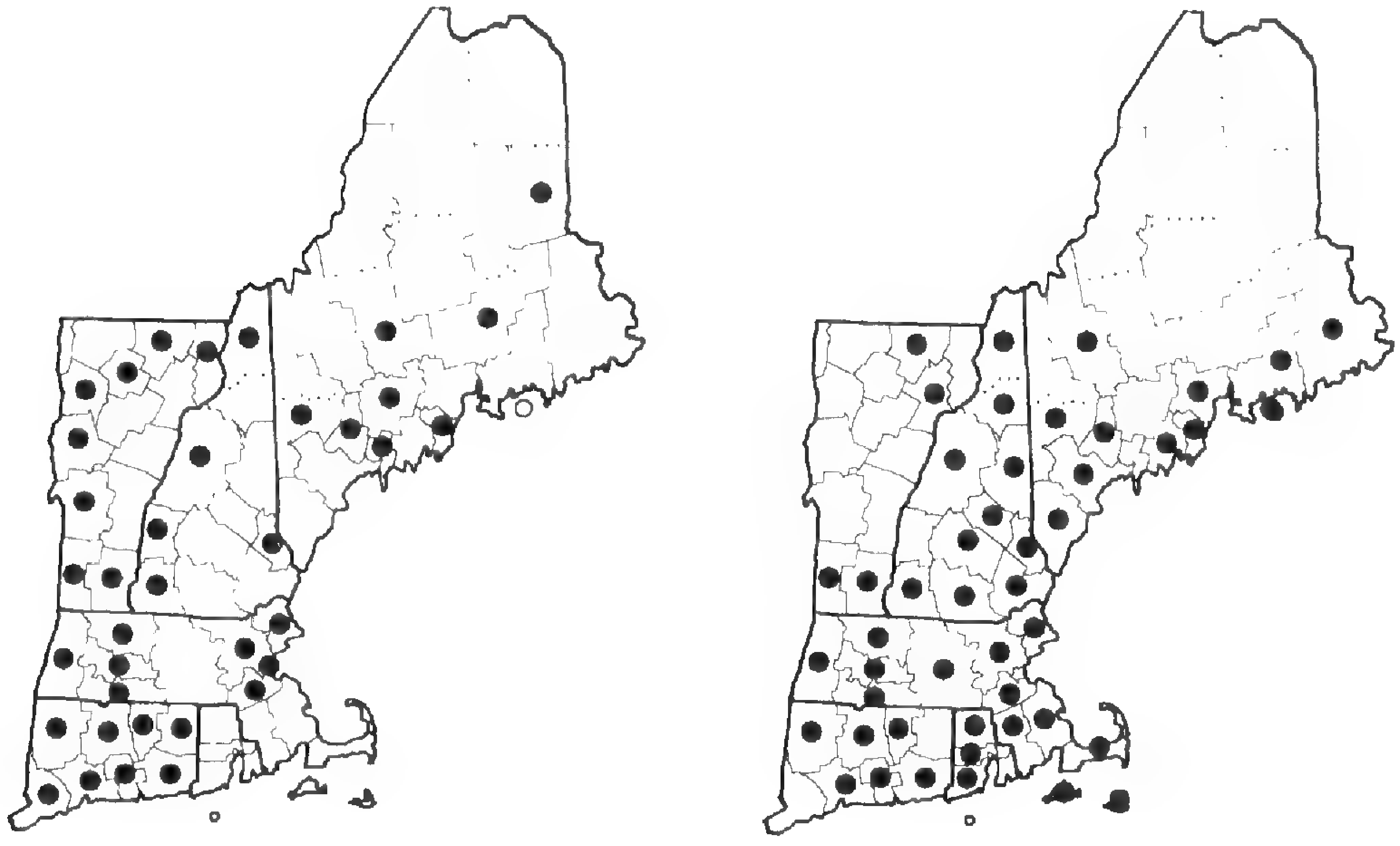


Potamogeton hillii

Figure 67. Distribution maps for *Potamogeton foliosus* subsp. *foliosus*, *P. friesii*, *P. gramineus*, and *P. hillii*.

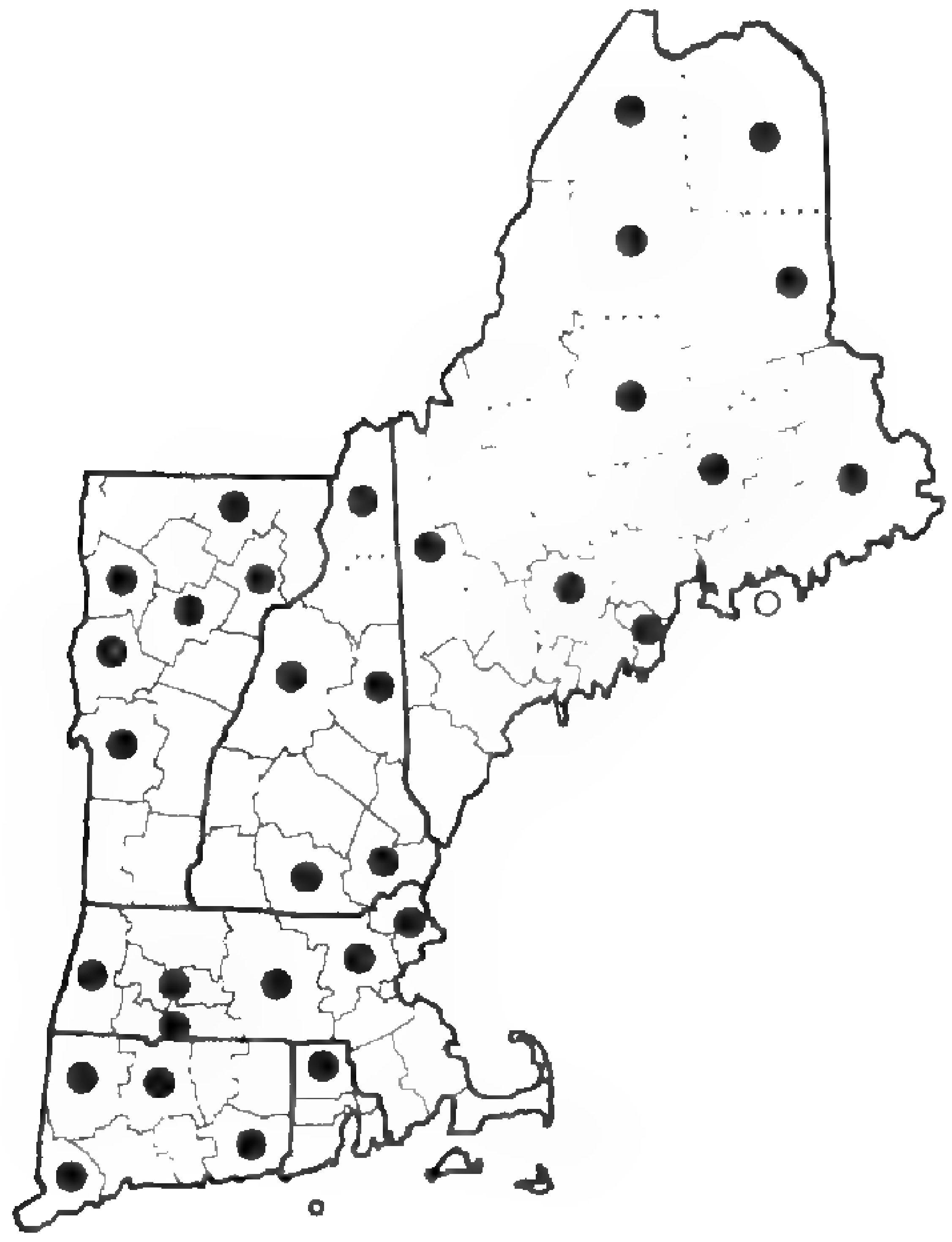


Potamogeton illinoensis *Potamogeton natans*

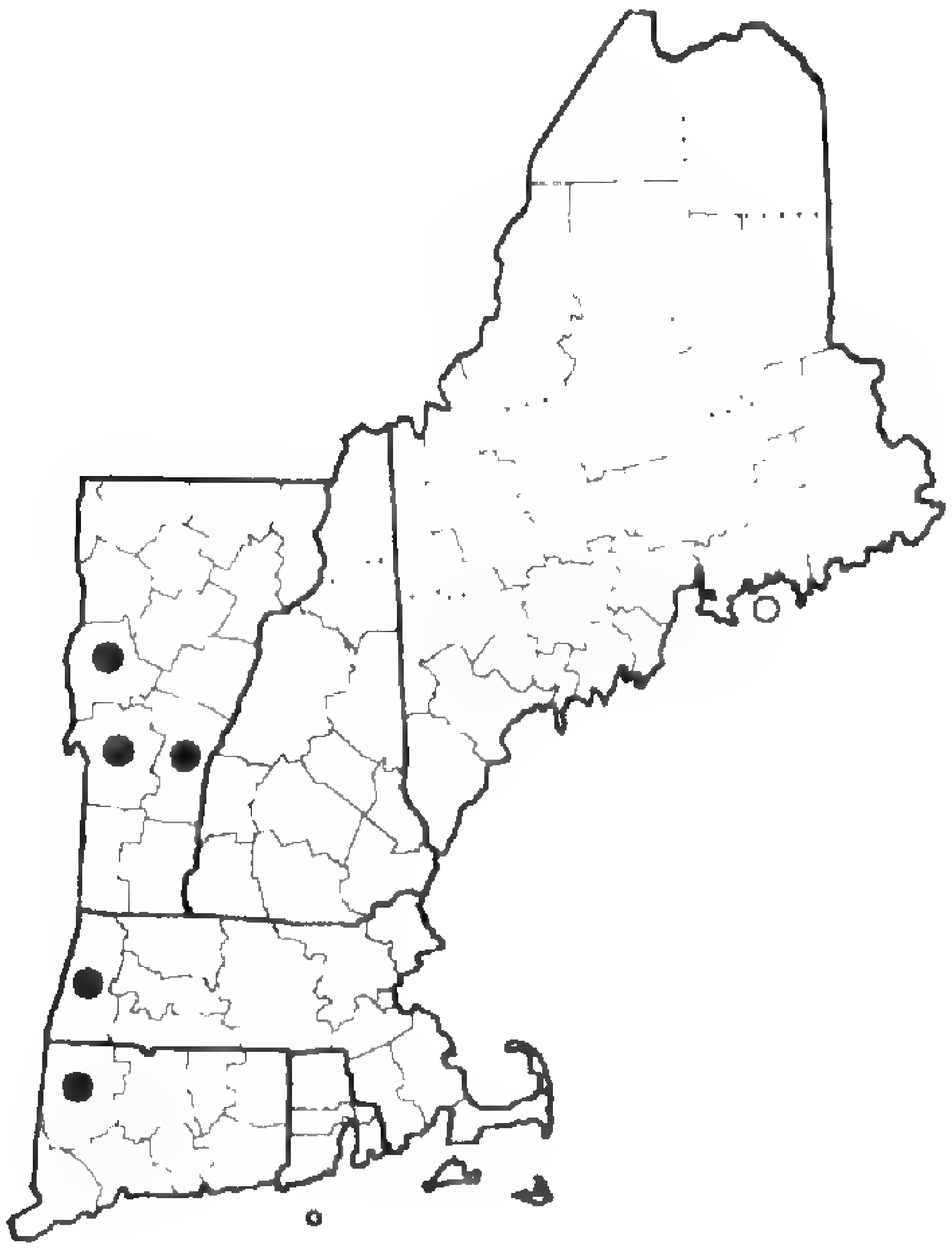


Potamogeton nodosus *Potamogeton oakesianus*

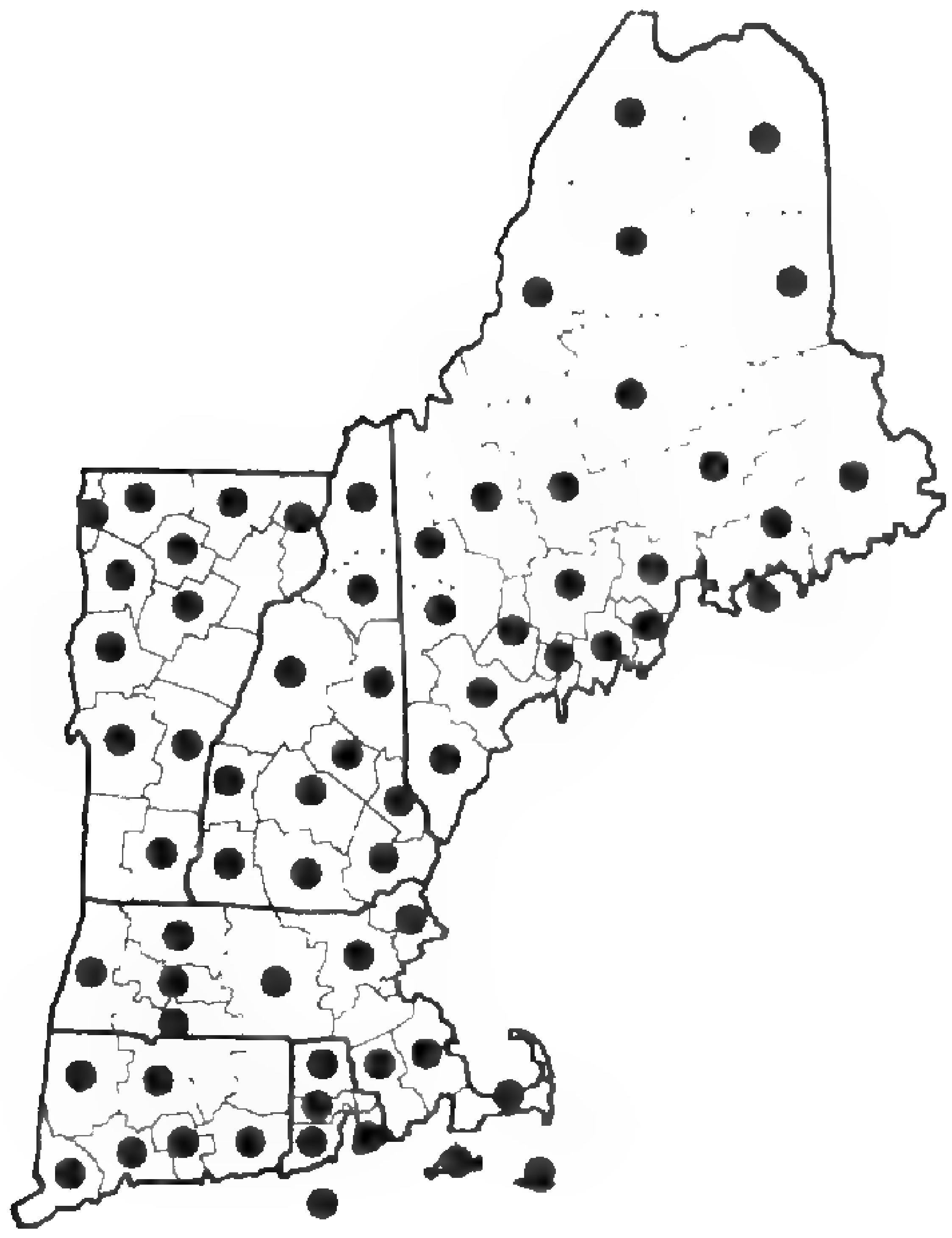
Figure 68. Distribution maps for *Potamogeton illinoensis*, *P. natans*, *P. nodosus*, and *P. oakesianus*.



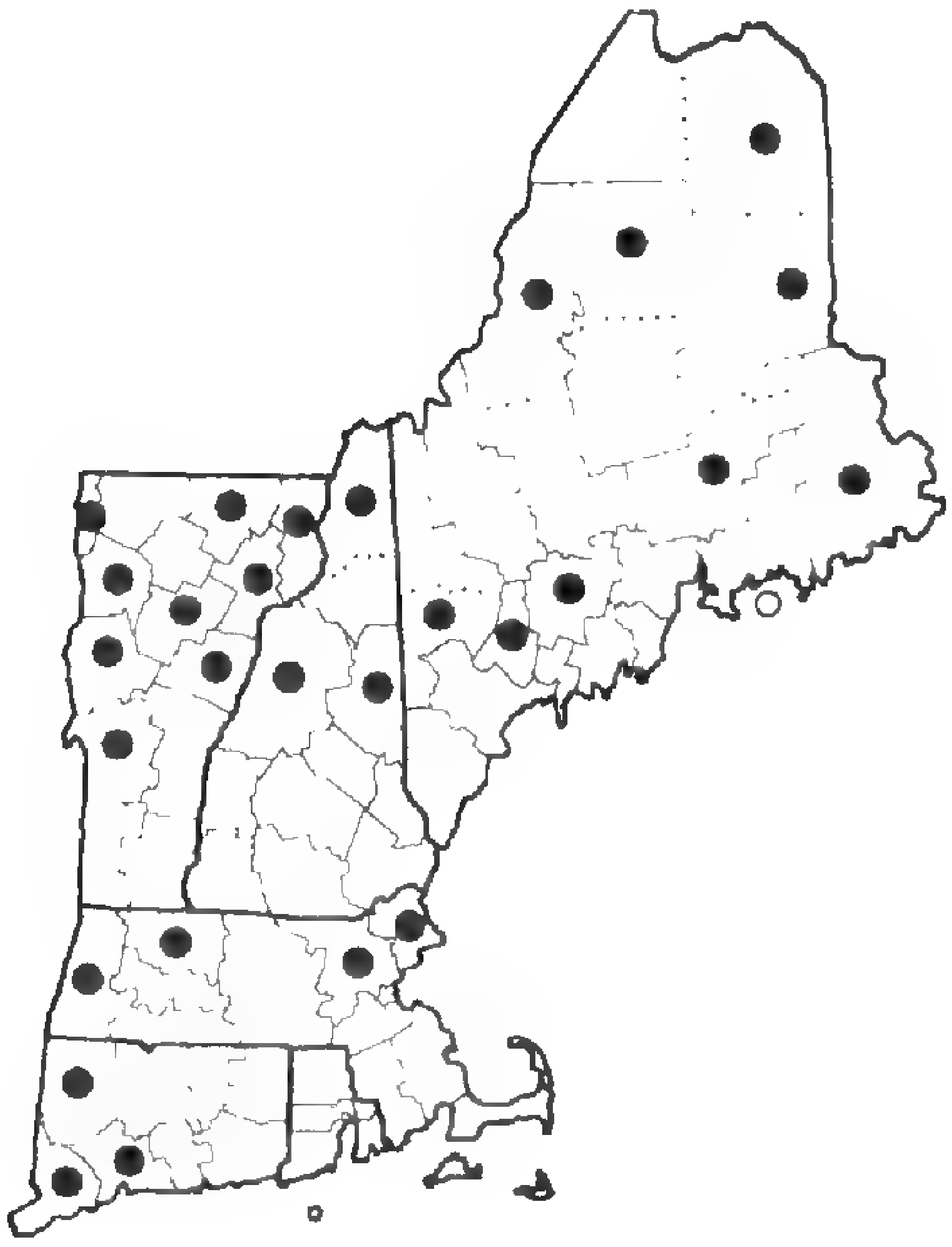
Potamogeton obtusifolius



Potamogeton ogdenii

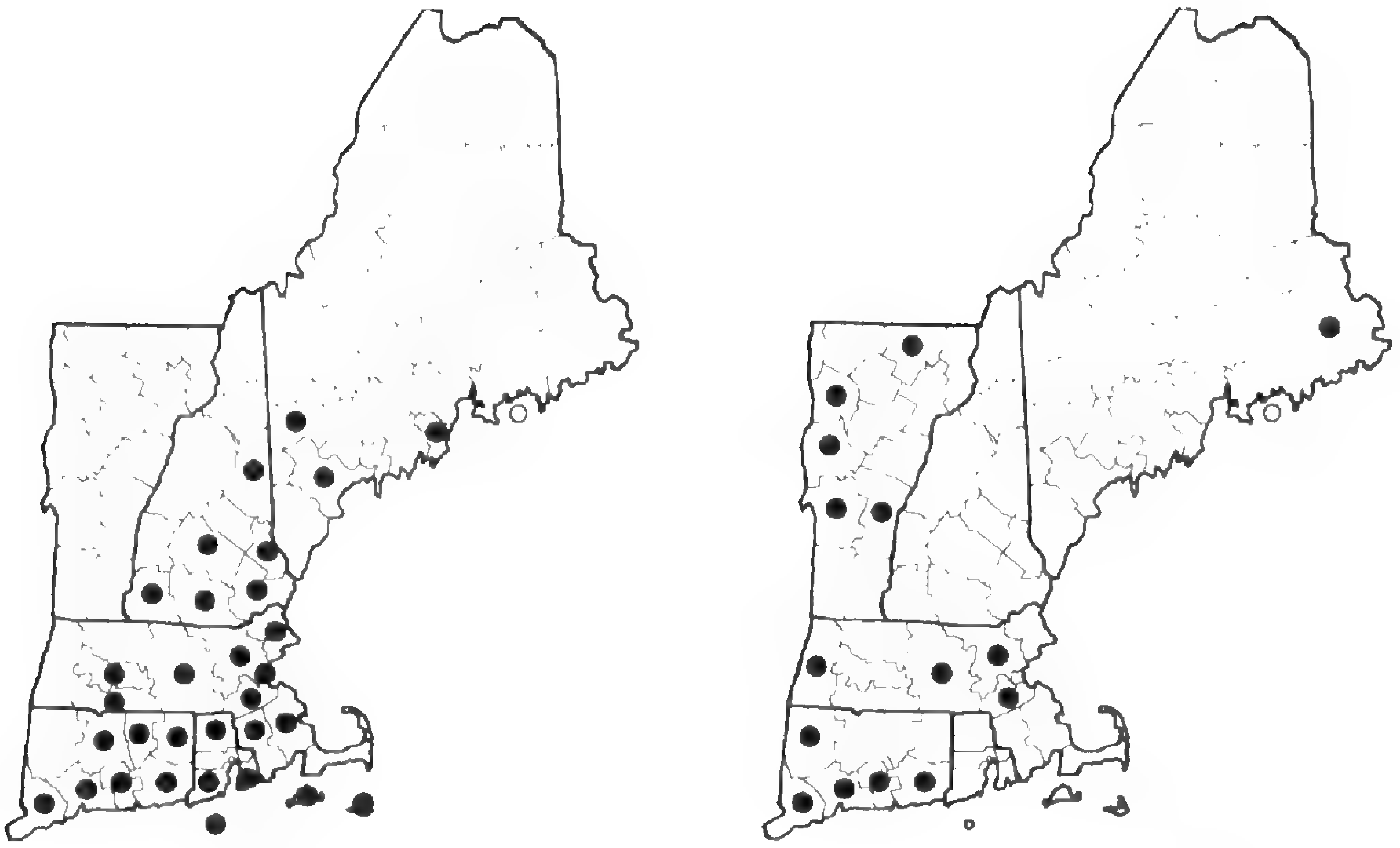


Potamogeton perfoliatus



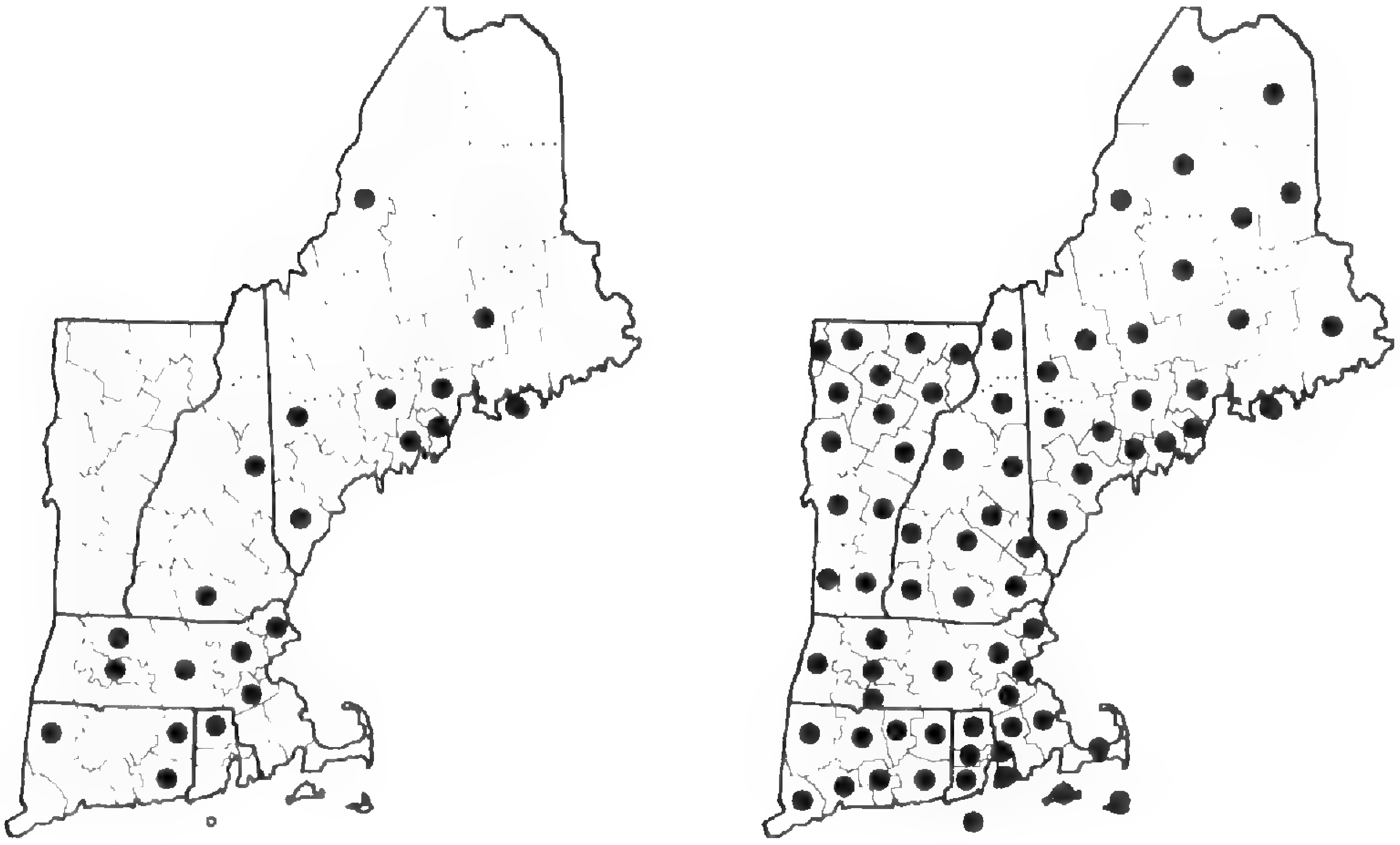
Potamogeton praelongus

Figure 69. Distribution maps for *Potamogeton obtusifolius*, *P. ogdenii*, *P. perfoliatus*, and *P. praelongus*.



Potamogeton pulcher

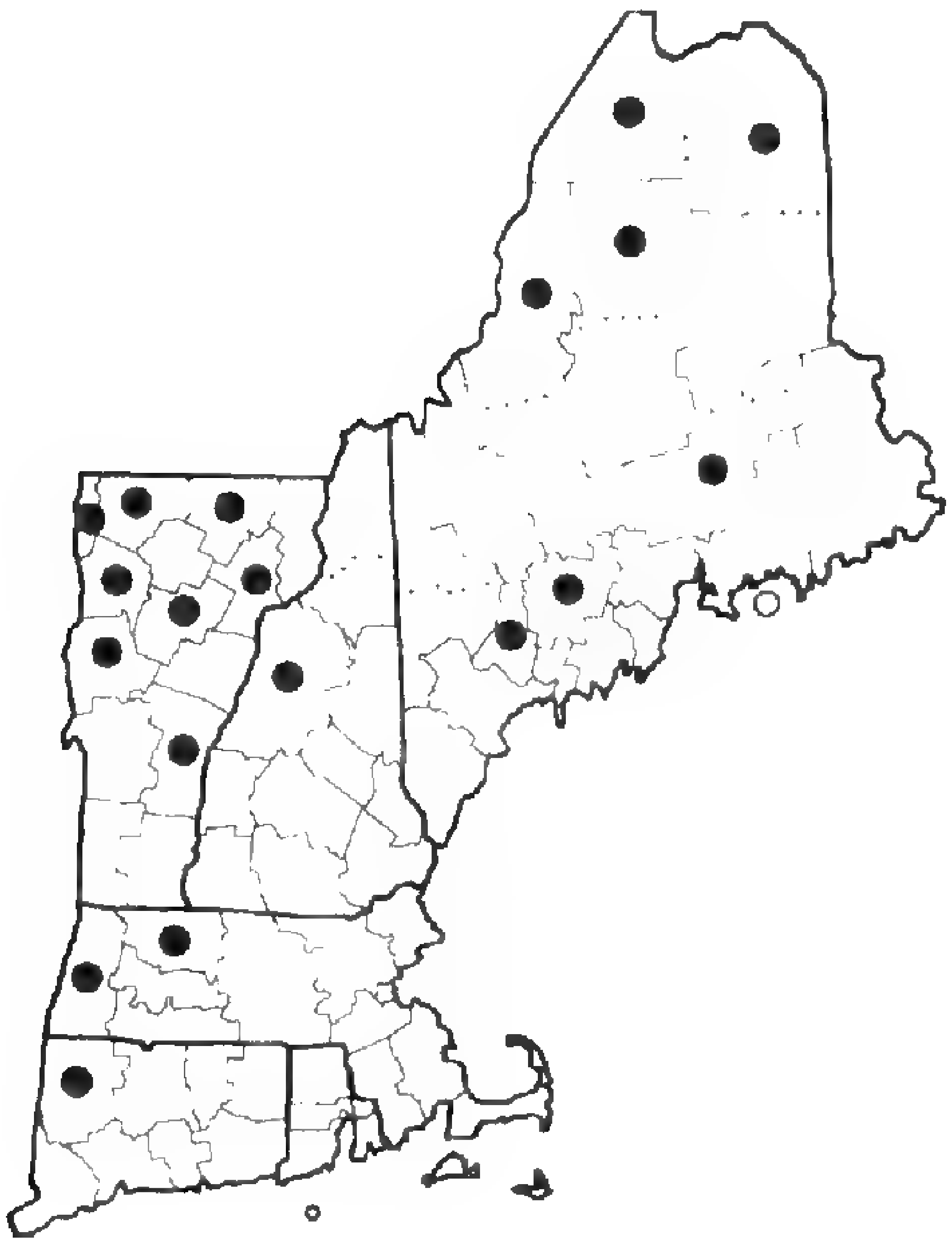
Potamogeton pusillus subsp. *pusillus*



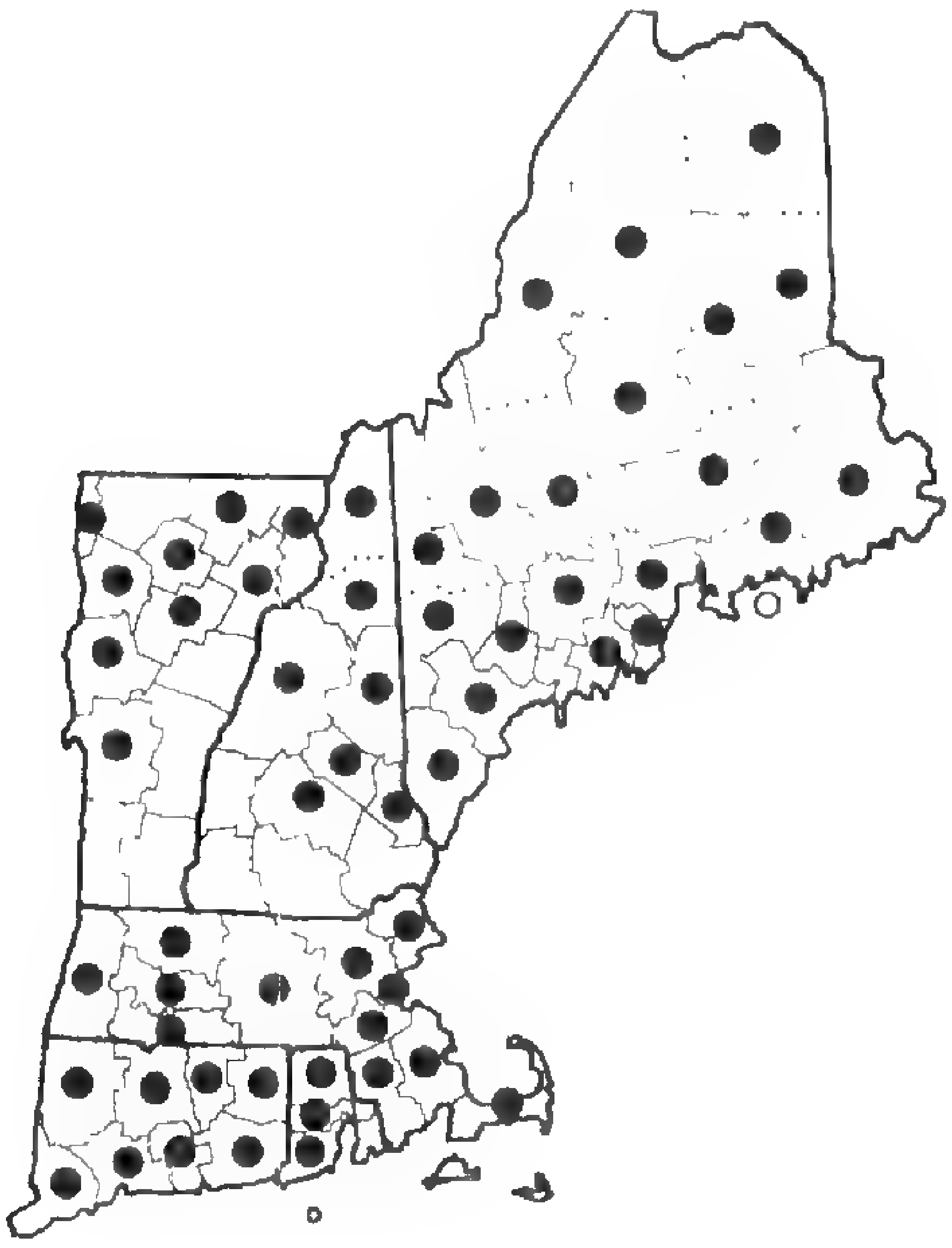
Potamogeton pusillus subsp. *gemmiparus*

Potamogeton pusillus subsp. *tenuissimus*

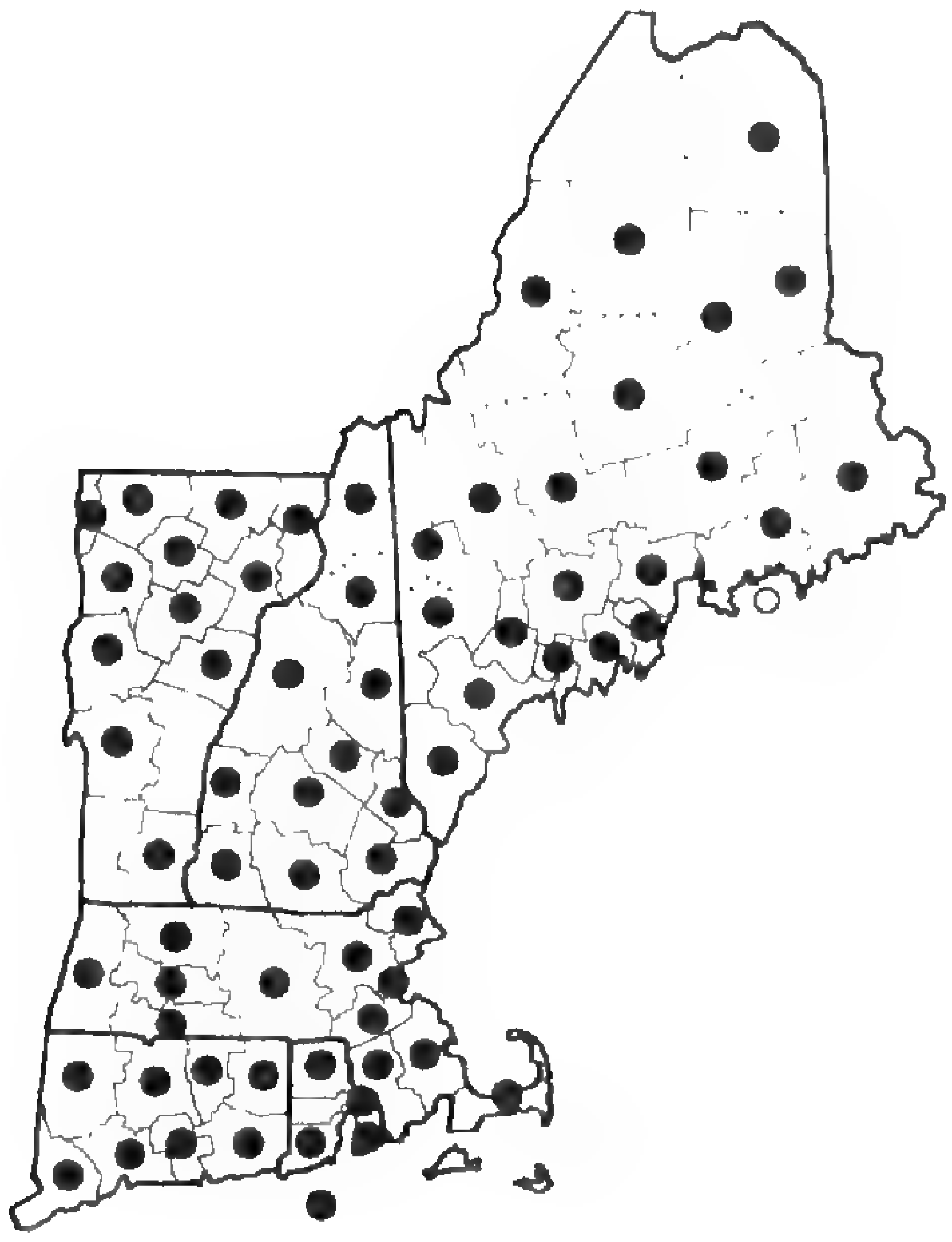
Figure 70. Distribution maps for *Potamogeton pulcher, P. pusillus* subsp. *pusillus, P. pusillus* subsp. *gemmiparus,* and *P. pusillus* subsp. *tenuissimus.*



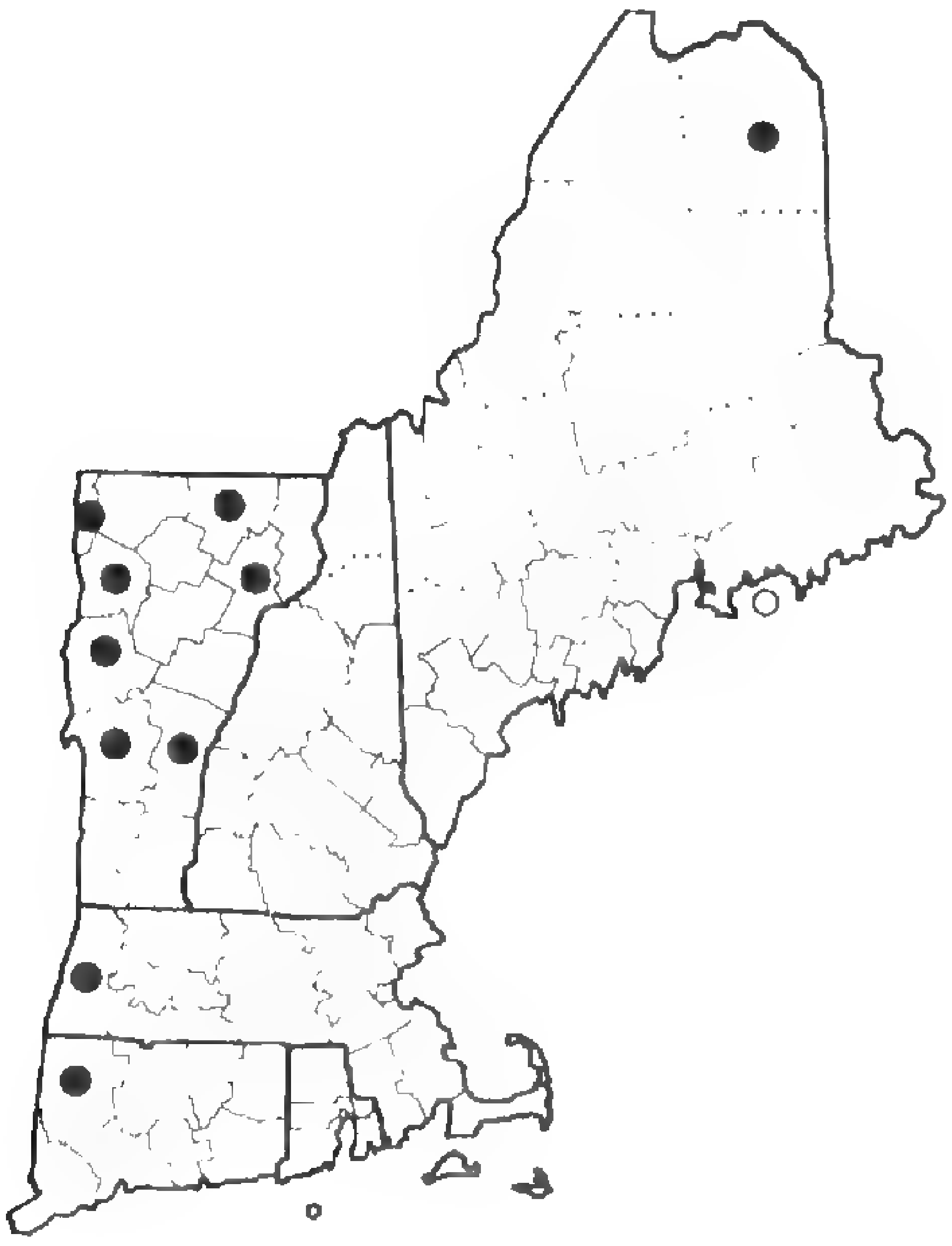
Potamogeton richardsonii



Potamogeton robbinsii

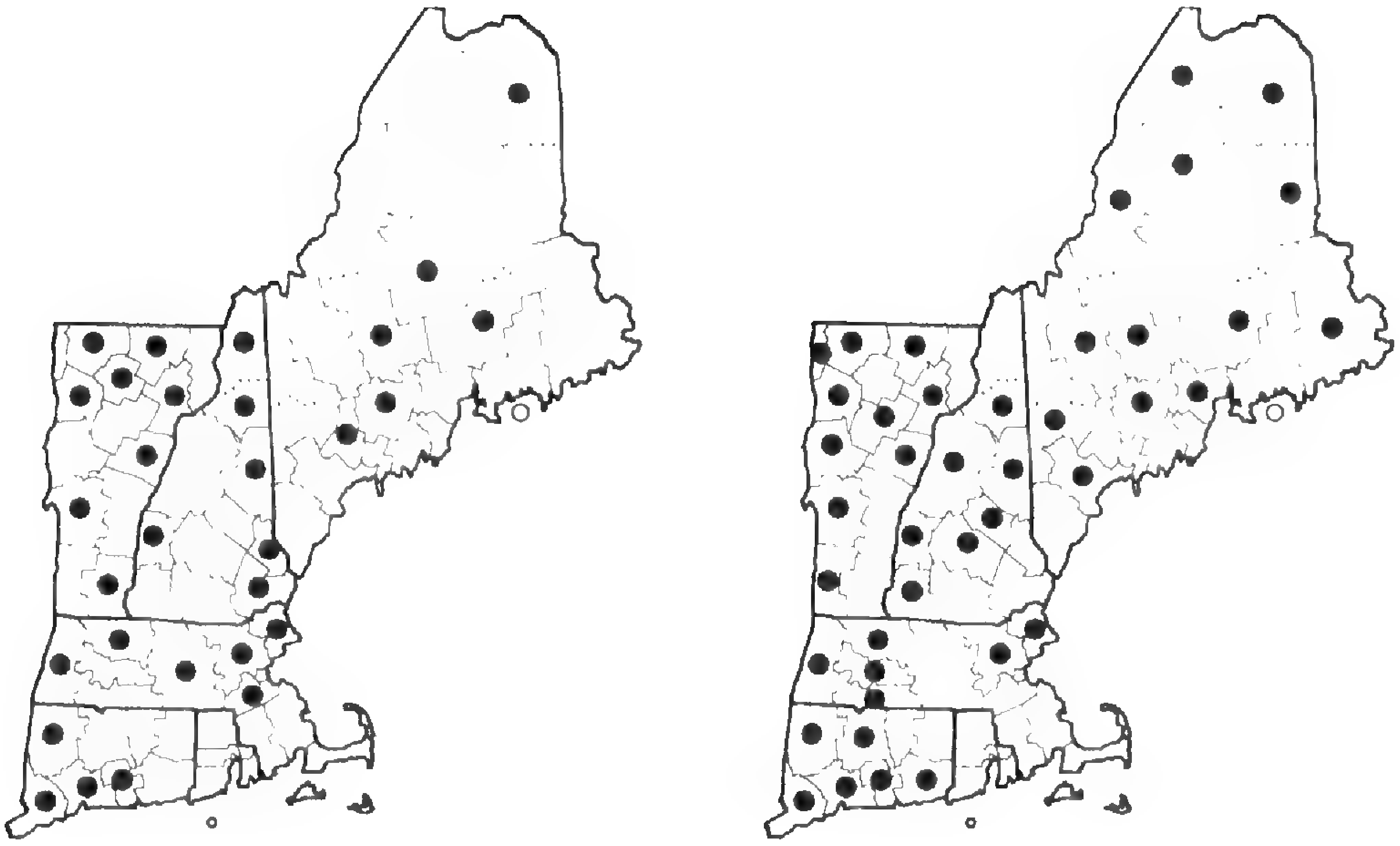


Potamogeton spirillus



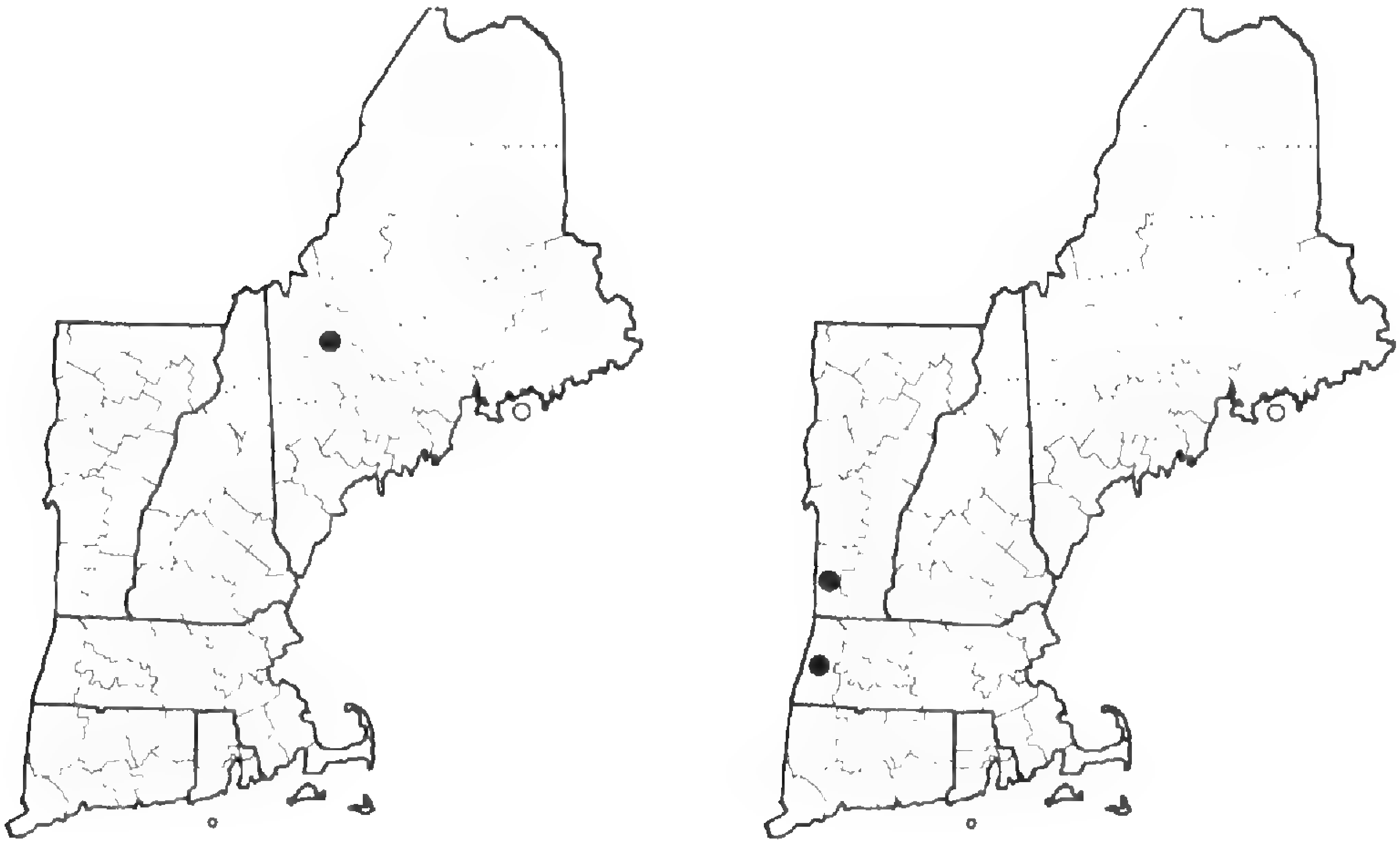
Potamogeton strictifolius

Figure 71. Distribution maps for *Potamogeton richardsonii, P. robbinsii, P. spirillus,* and *P. strictifolius.*



Potamogeton vaseyi

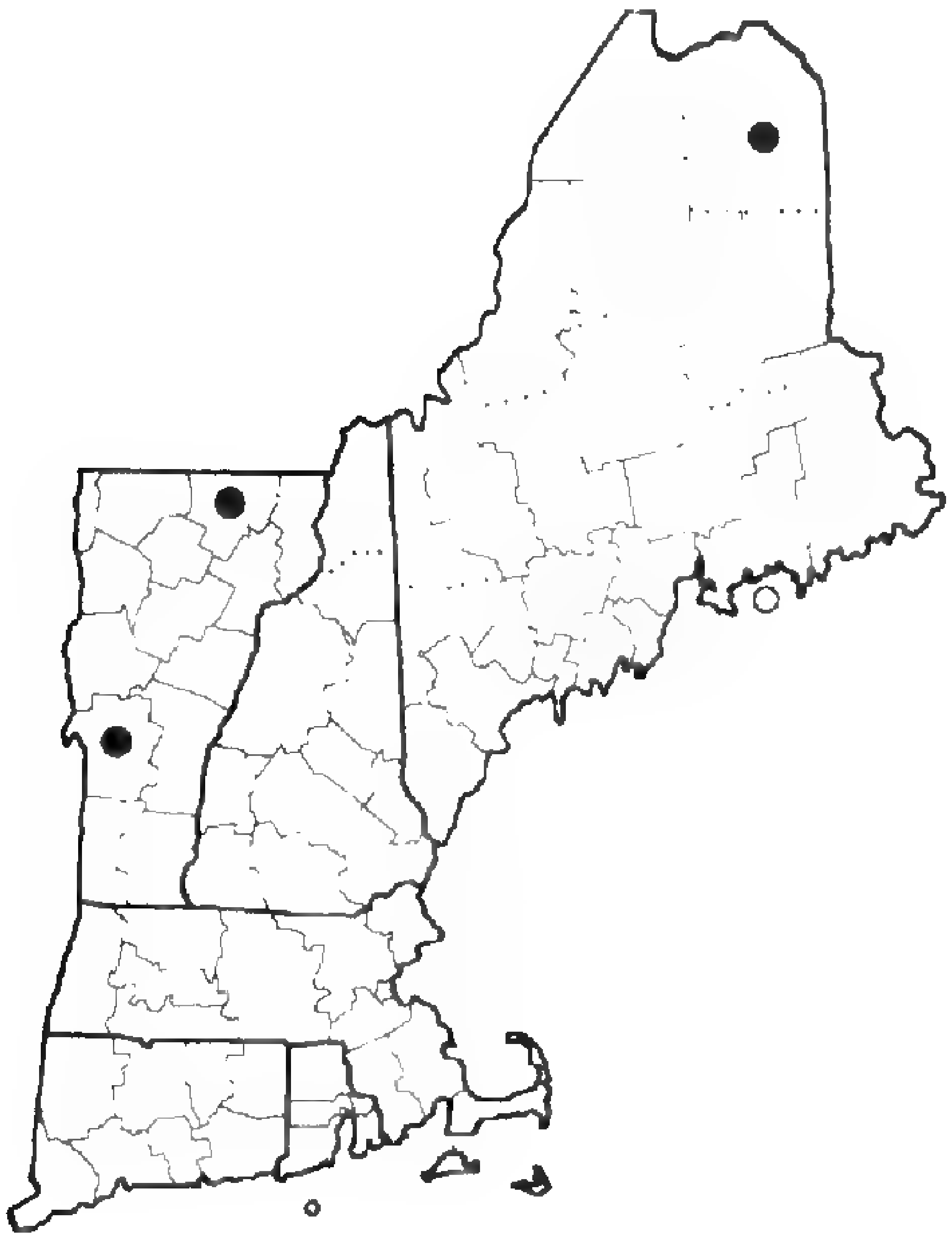
Potamogeton zosteriformis



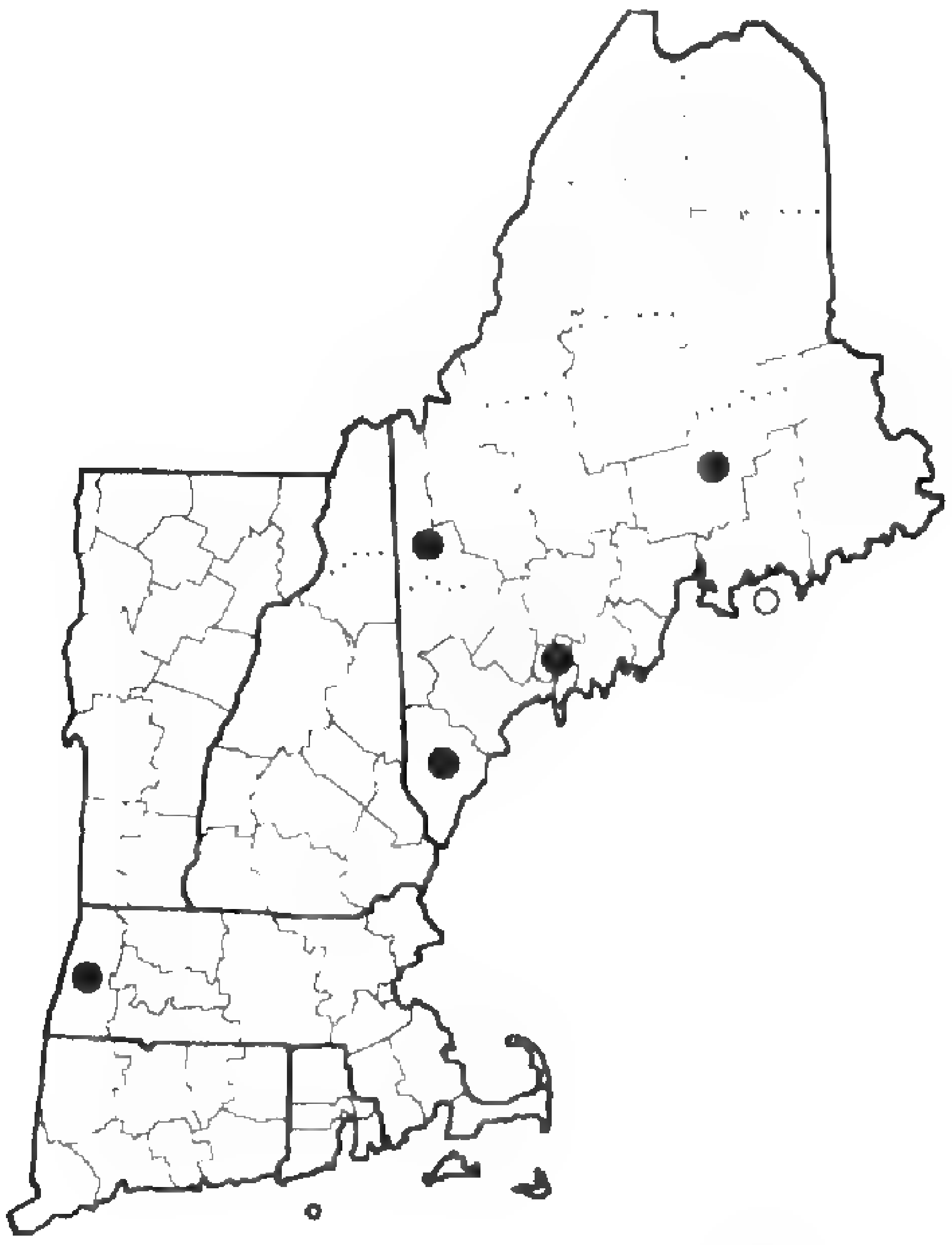
Potamogeton alpinus
X *P. epihydrus*

Potamogeton amplifolius
X *P. illinoensis*

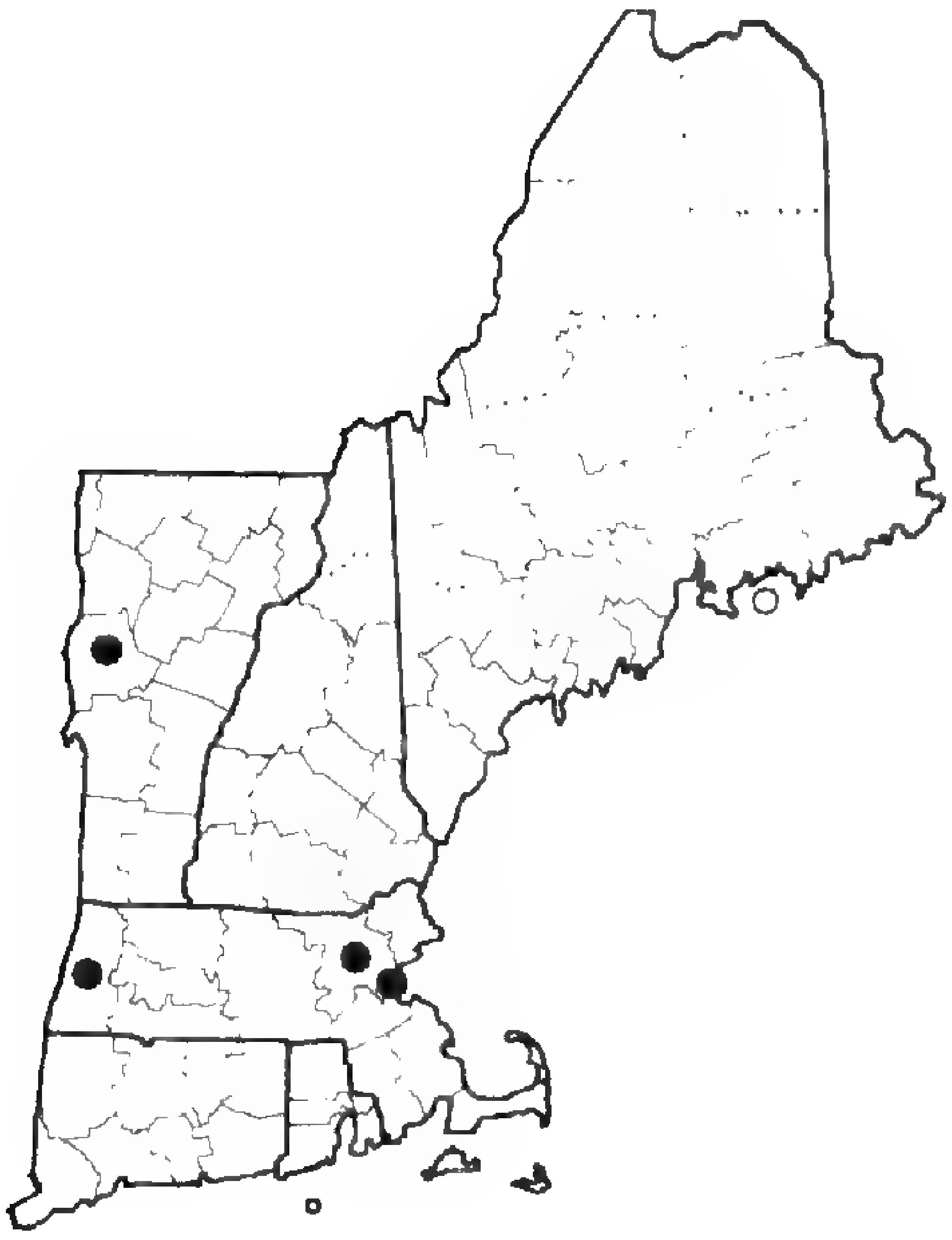
Figure 72. Distribution maps for *Potamogeton vaseyi*, *P. zosteriformis*, *P. alpinus* X *P. epihydrus*, and *P. amplifolius* X *P. illinoensis*.



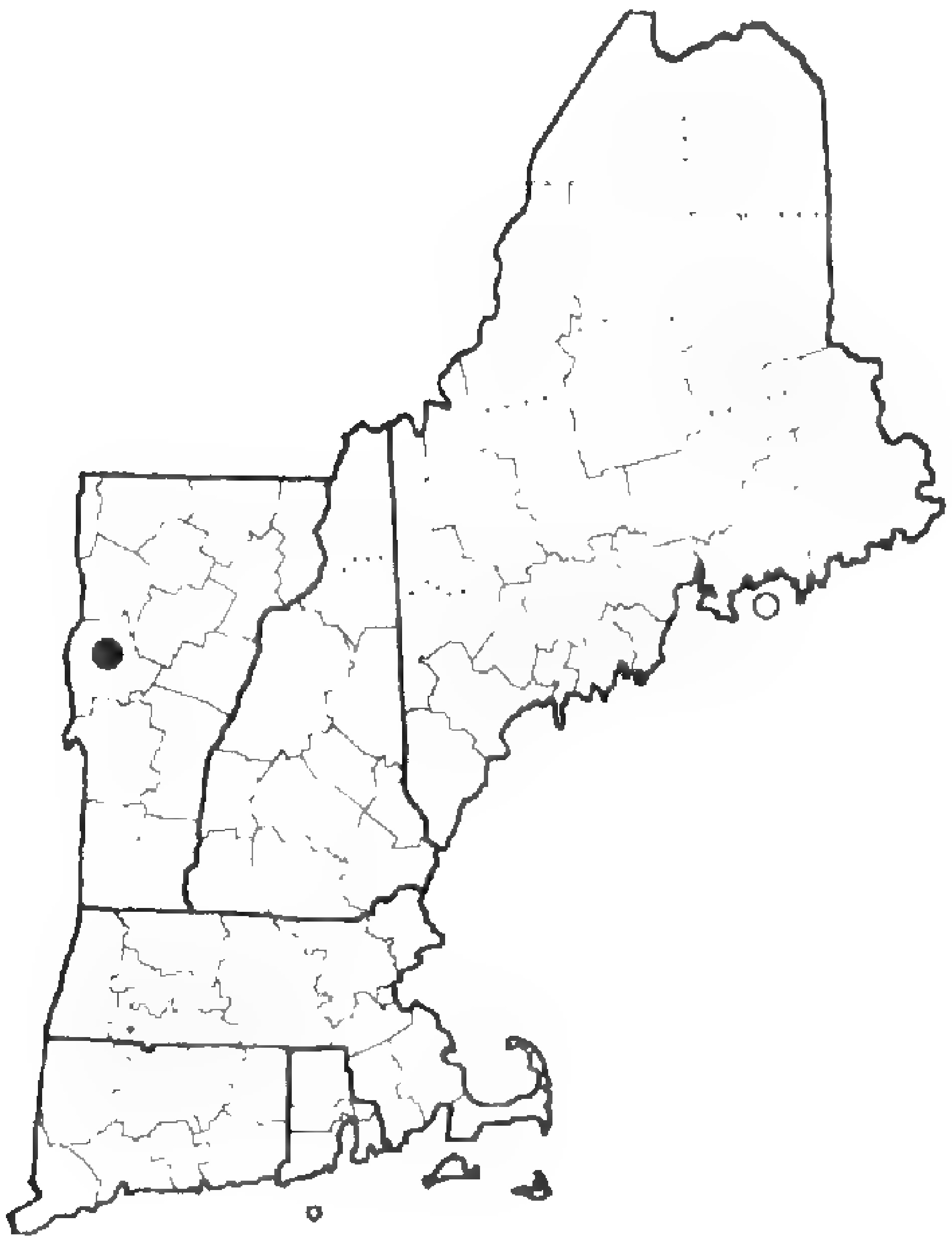
Potamogeton amplifolius X *P. praelongus*



Potamogeton X *argutulus*

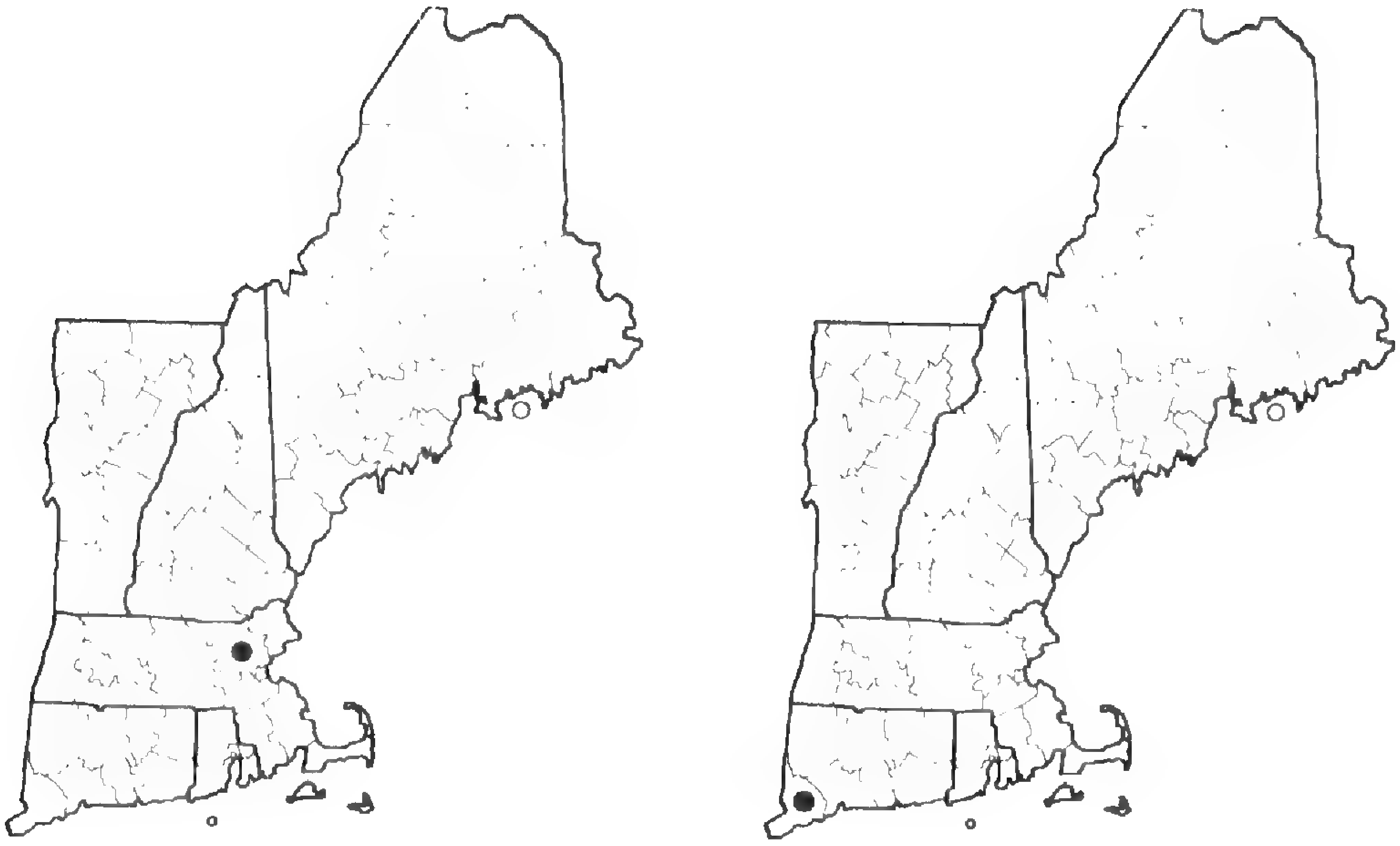


Potamogeton X *faxonii*



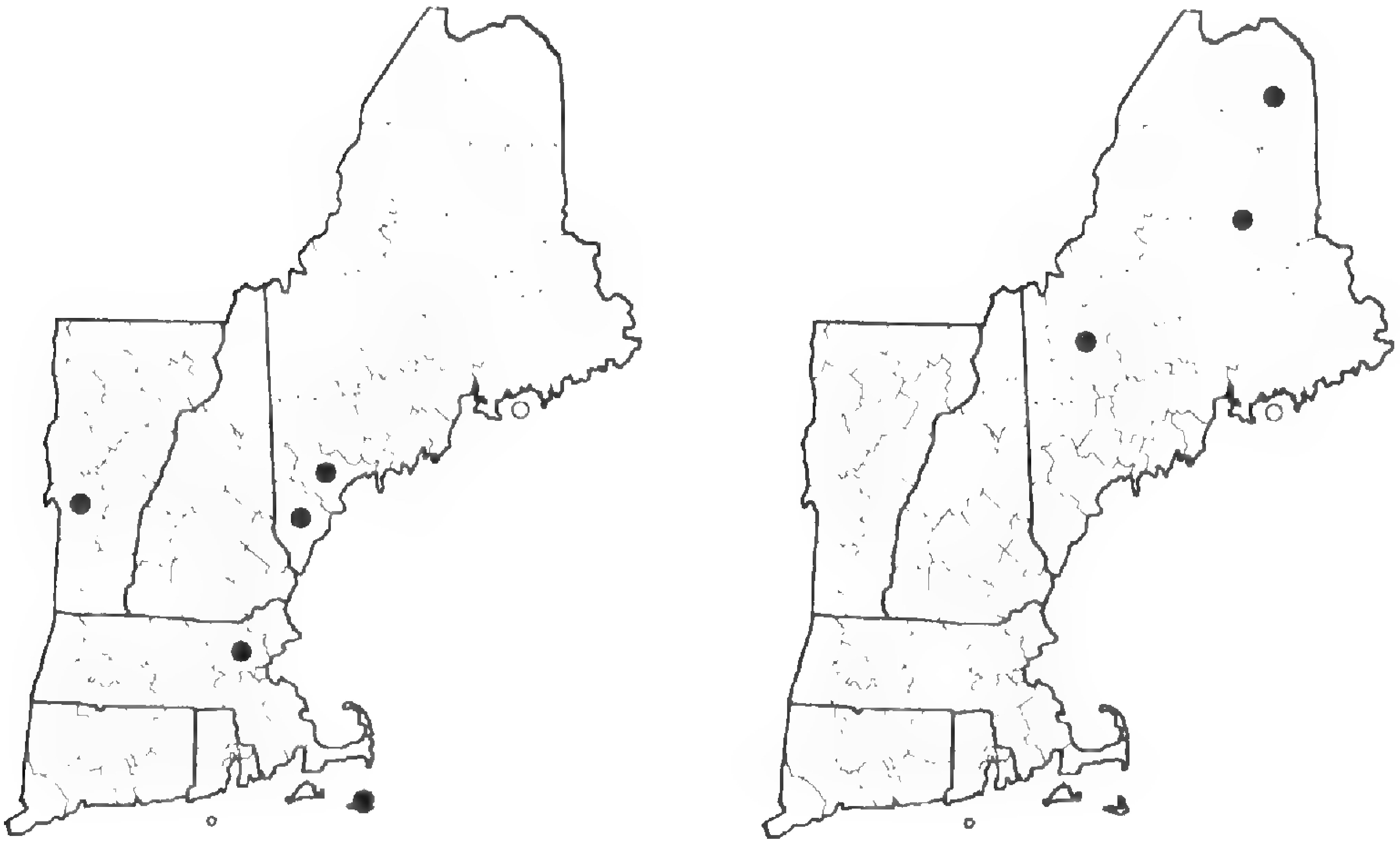
Potamogeton X *haynesii*

Figure 73. Distribution maps for *Potamogeton amplifolius* X *P. praelongus*, *P.* X *argutulus*, *P.* X *faxonii*, and *P.* X *haynesii*.



Potamogeton illinoensis X *P. perfoliatus*

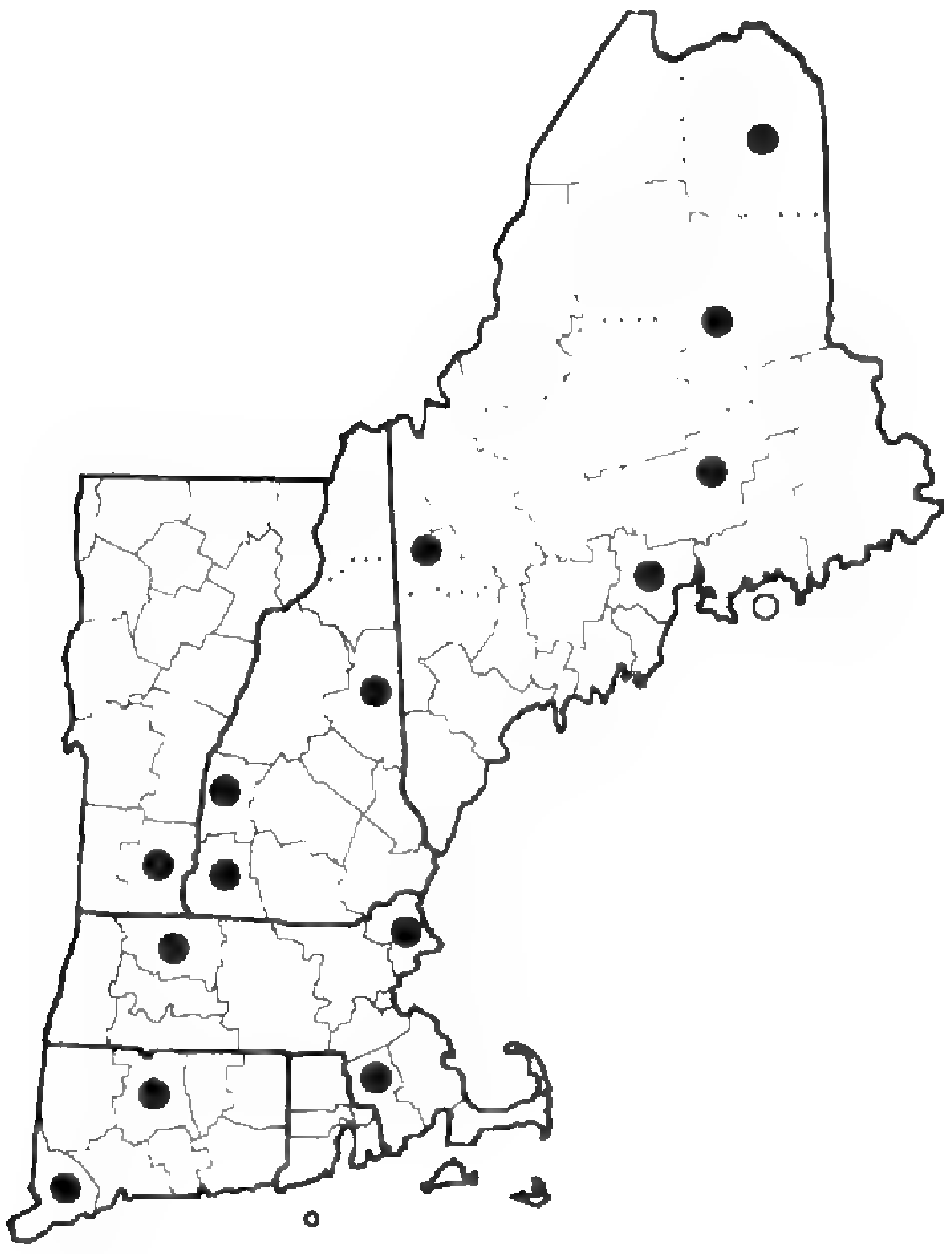
Potamogeton illinoensis X *P. richardsonii*



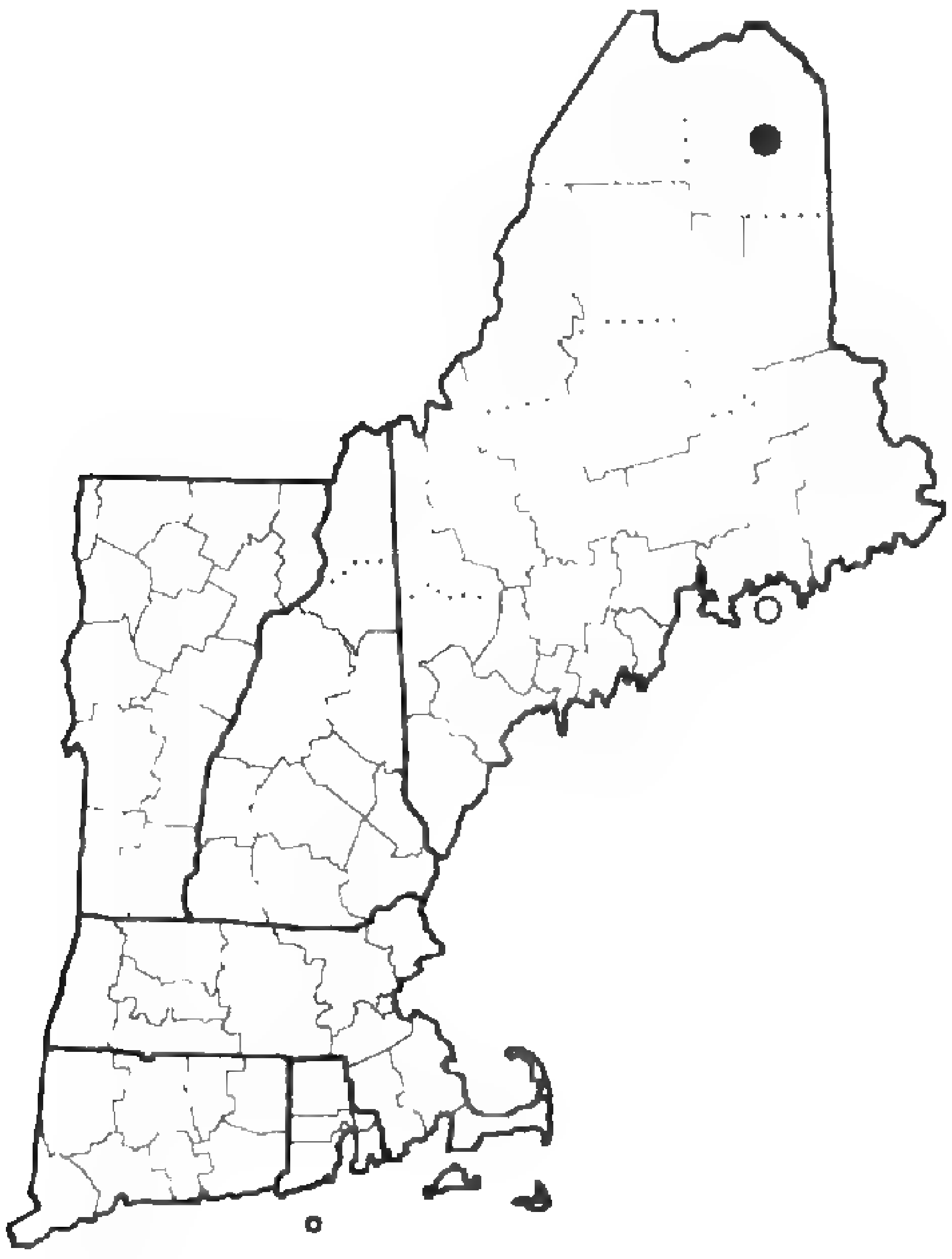
Potamogeton X *mysticus*

Potamogeton X *nericius*

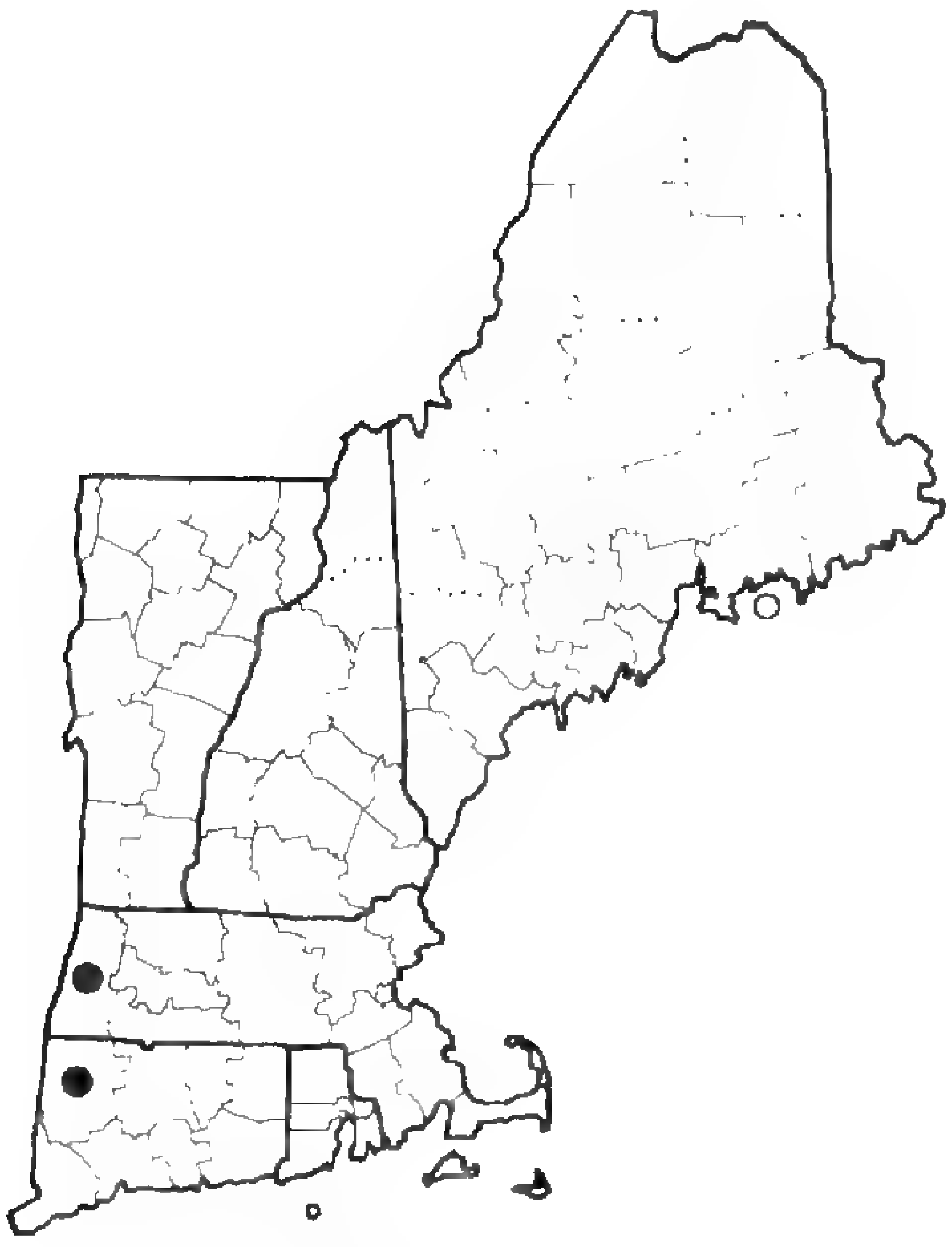
Figure 74. Distribution maps for *Potamogeton illinoensis* X *P. perfoliatus*, *P. illinoensis* X *P. richardsonii*, *P.* X *mysticus*, and *P.* X *nericius*.



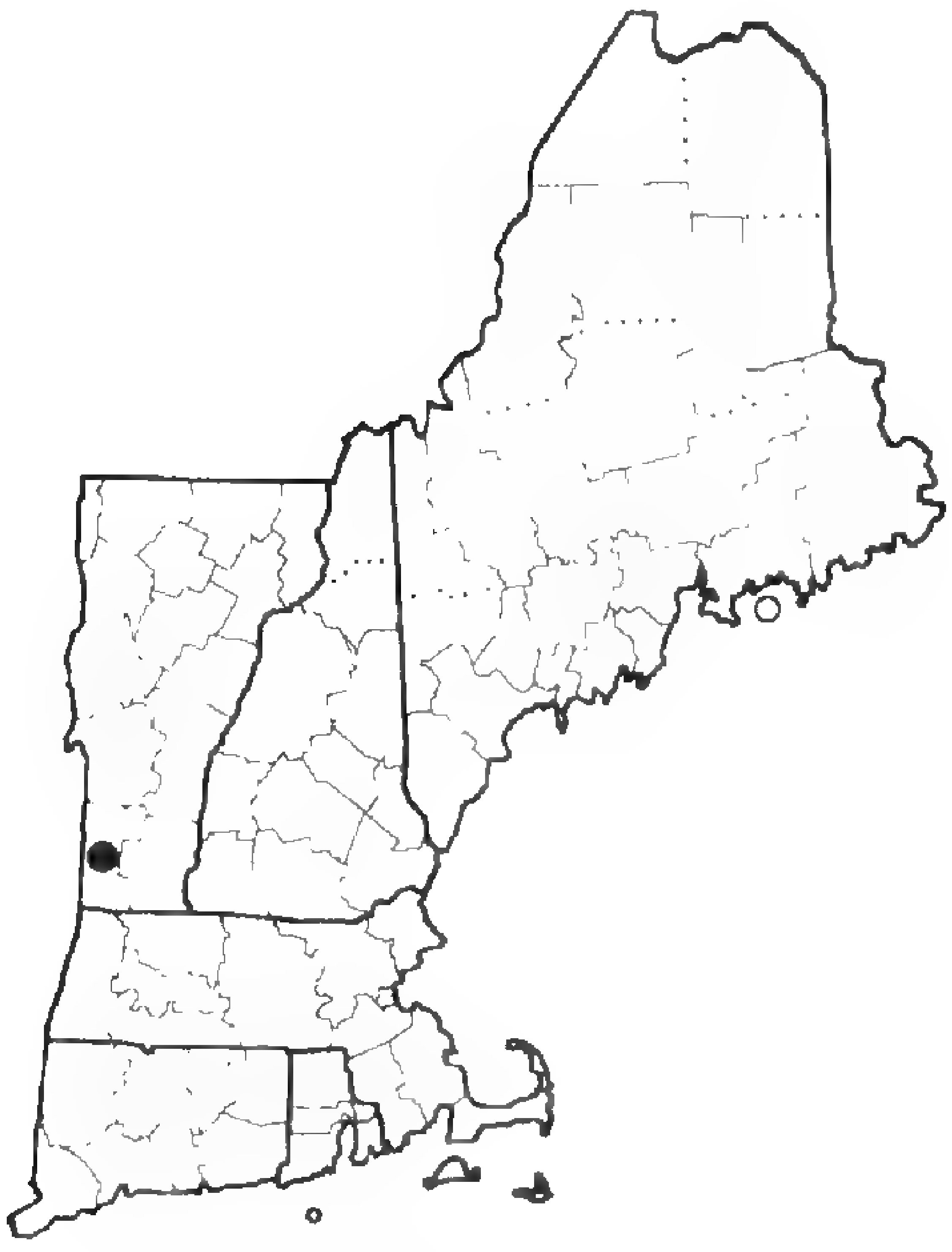
Potamogeton X *nitens*



Potamogeton perfoliatus X *P. richardsonii*

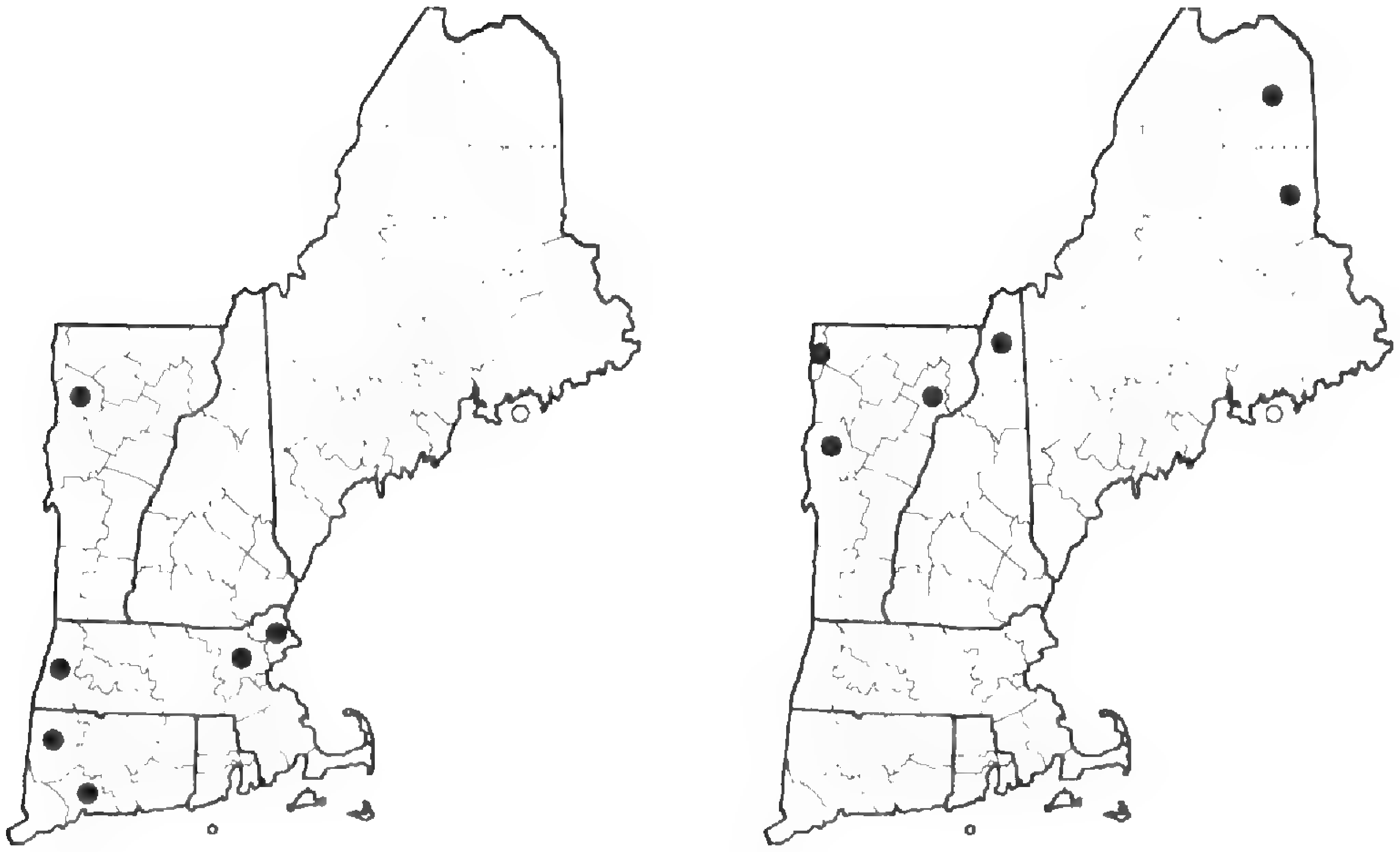


Potamogeton praelongus X *P. richardsonii*



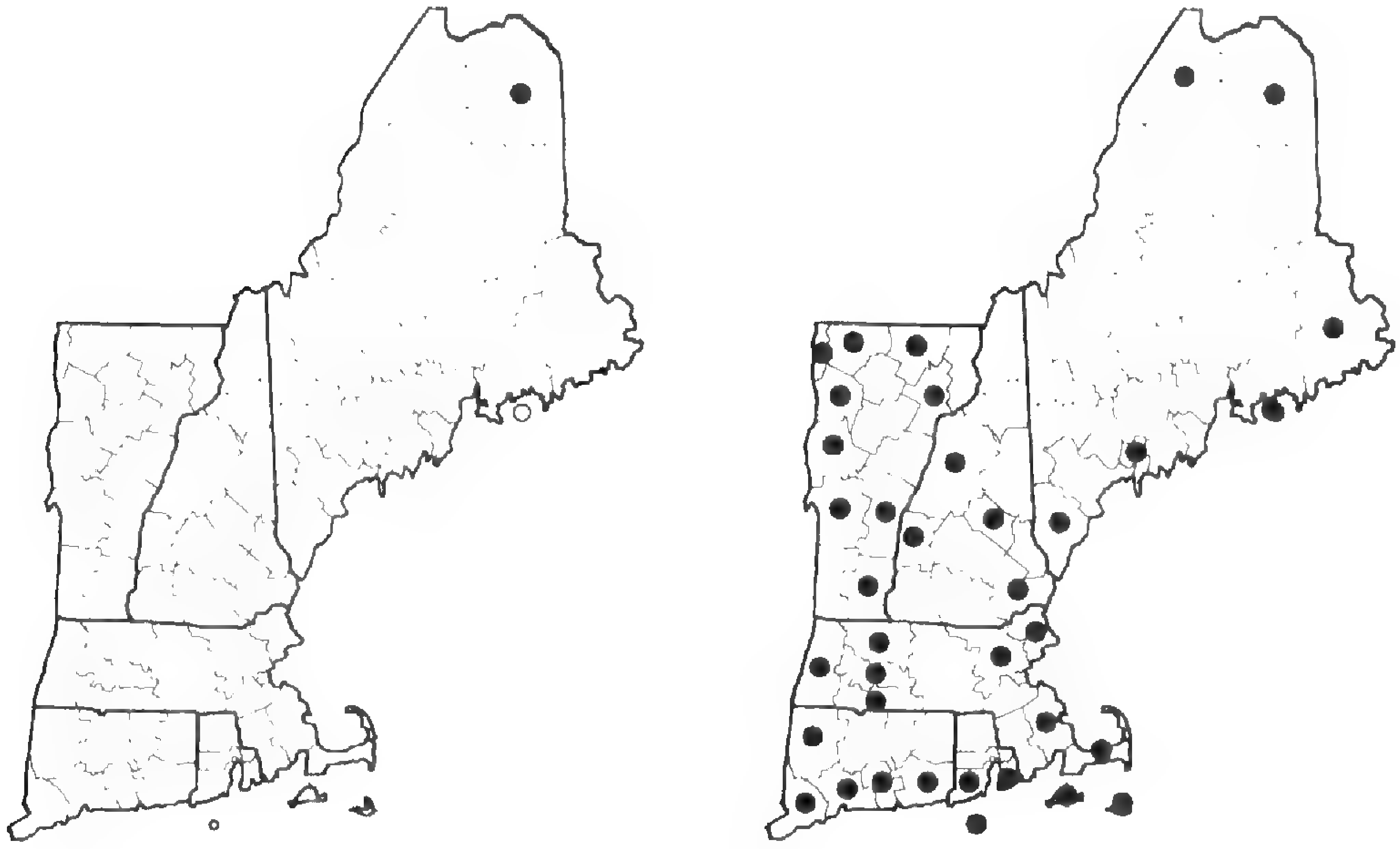
Potamogeton X *prussicus*

Figure 75. Distribution maps for *Potamogeton* X *nitens, P. perfoliatus* X *P. richardsonii, P. praelongus* X *P. richardsonii,* and *P.* X *prussicus.*



Potamogeton X *spathuliformis*

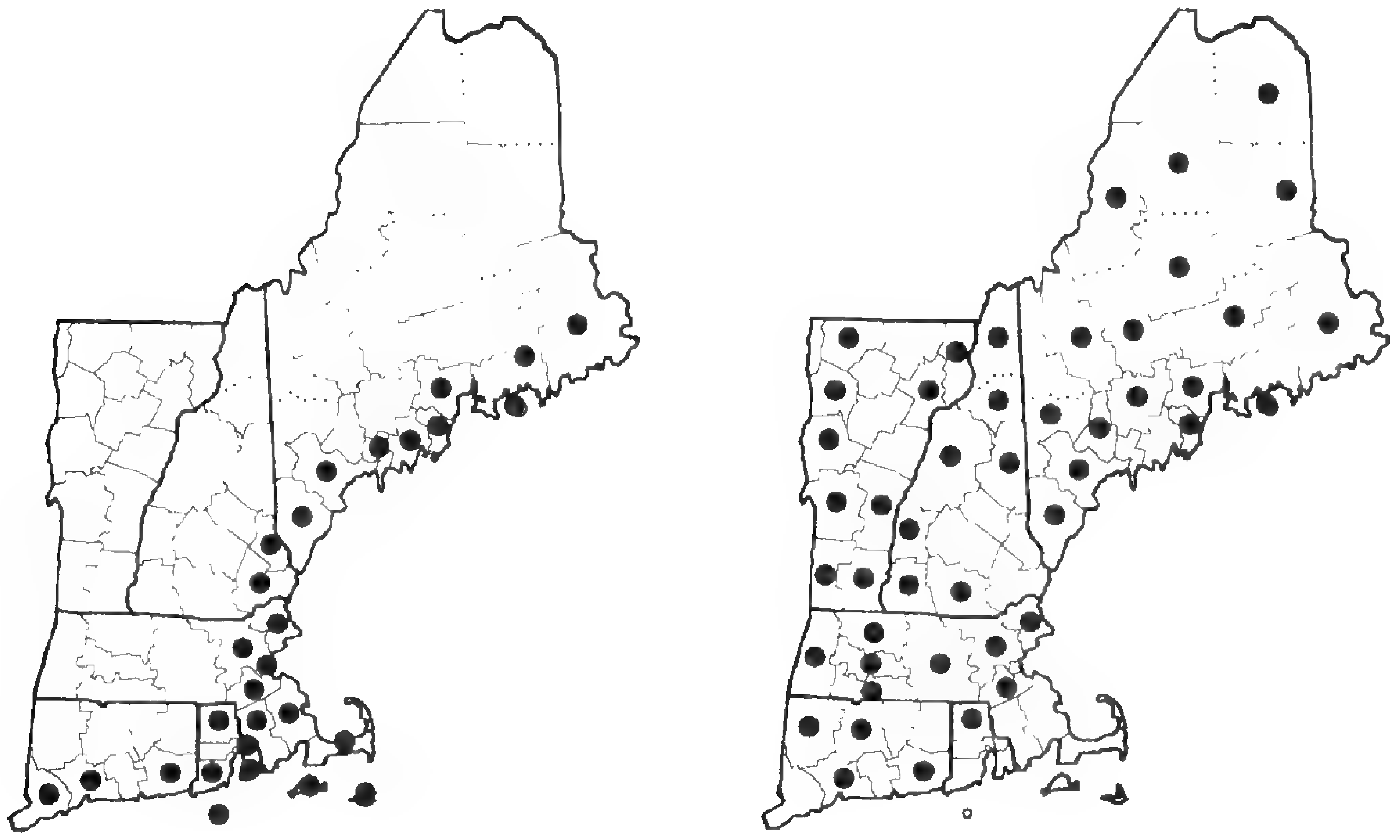
Stuckenia filiformis
subsp. *alpina*



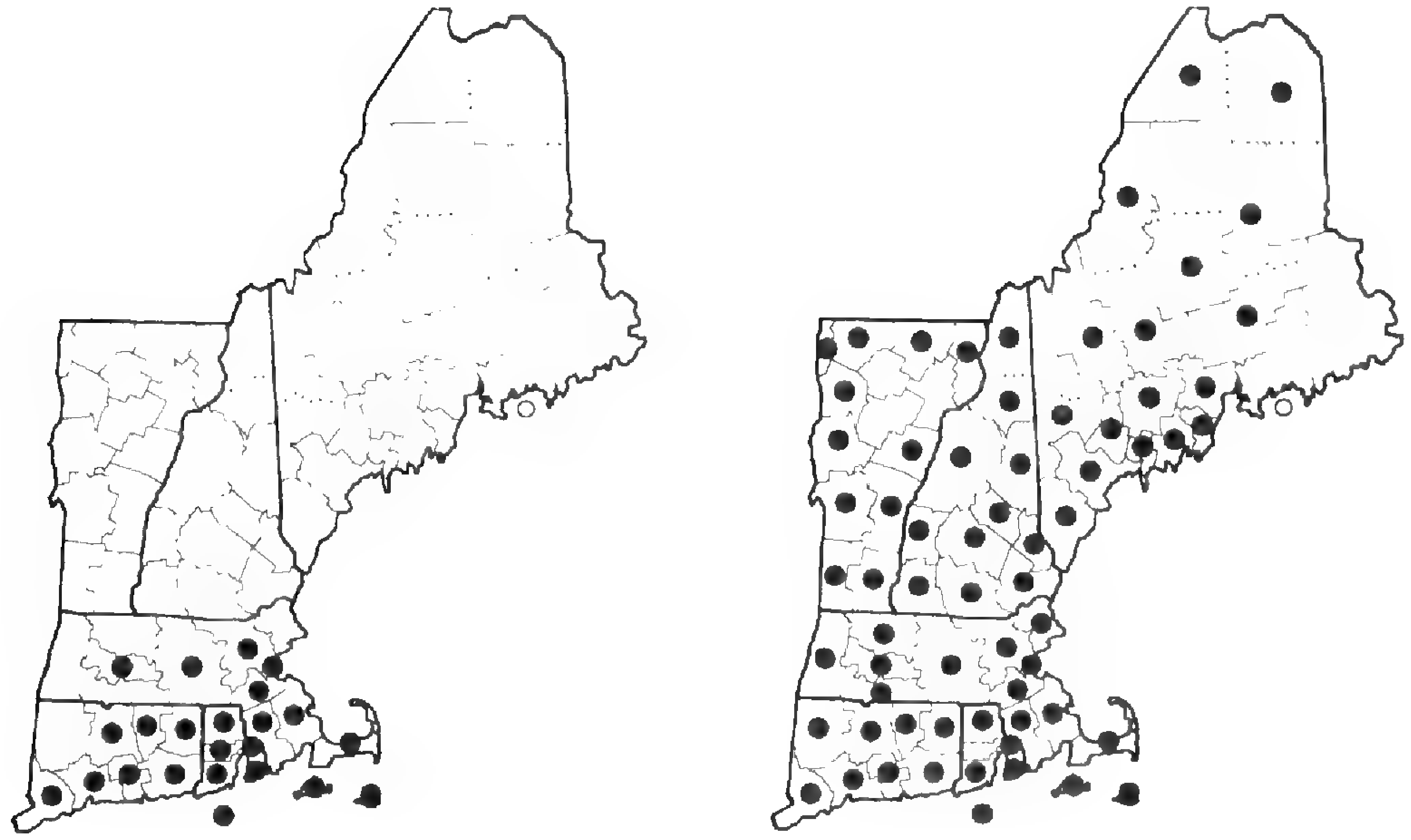
Stuckenia filiformis
subsp. *occidentalis*

Stuckenia pectinata

Figure 76. Distribution maps for *Potamogeton* X *spathuliformis*, *Stuckenia filiformis* subsp. *alpina*, *S. filiformis* subsp. *occidentalis*, and *S. pectinata*.

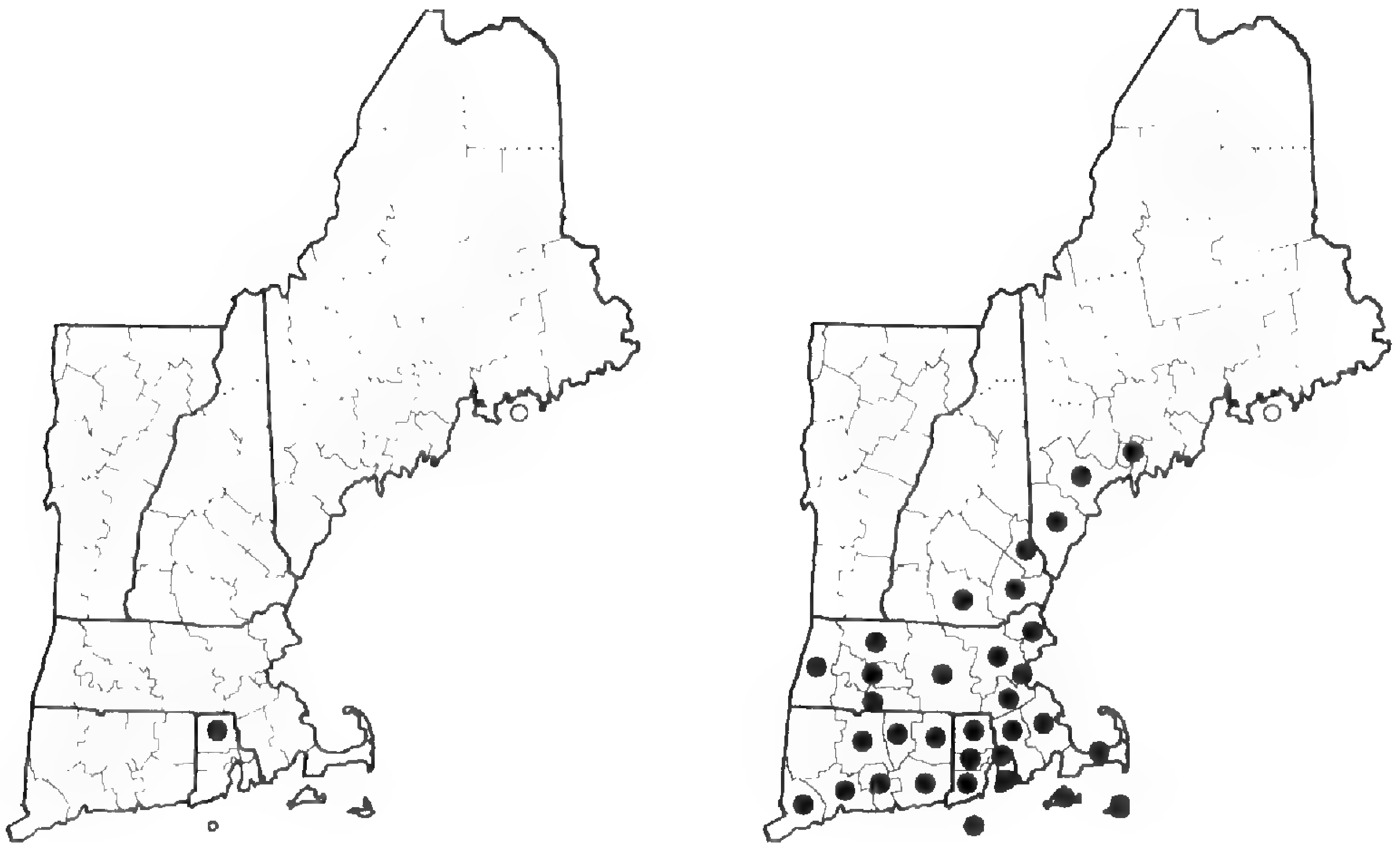


Ruppia maritima *Scheuchzeria palustris*

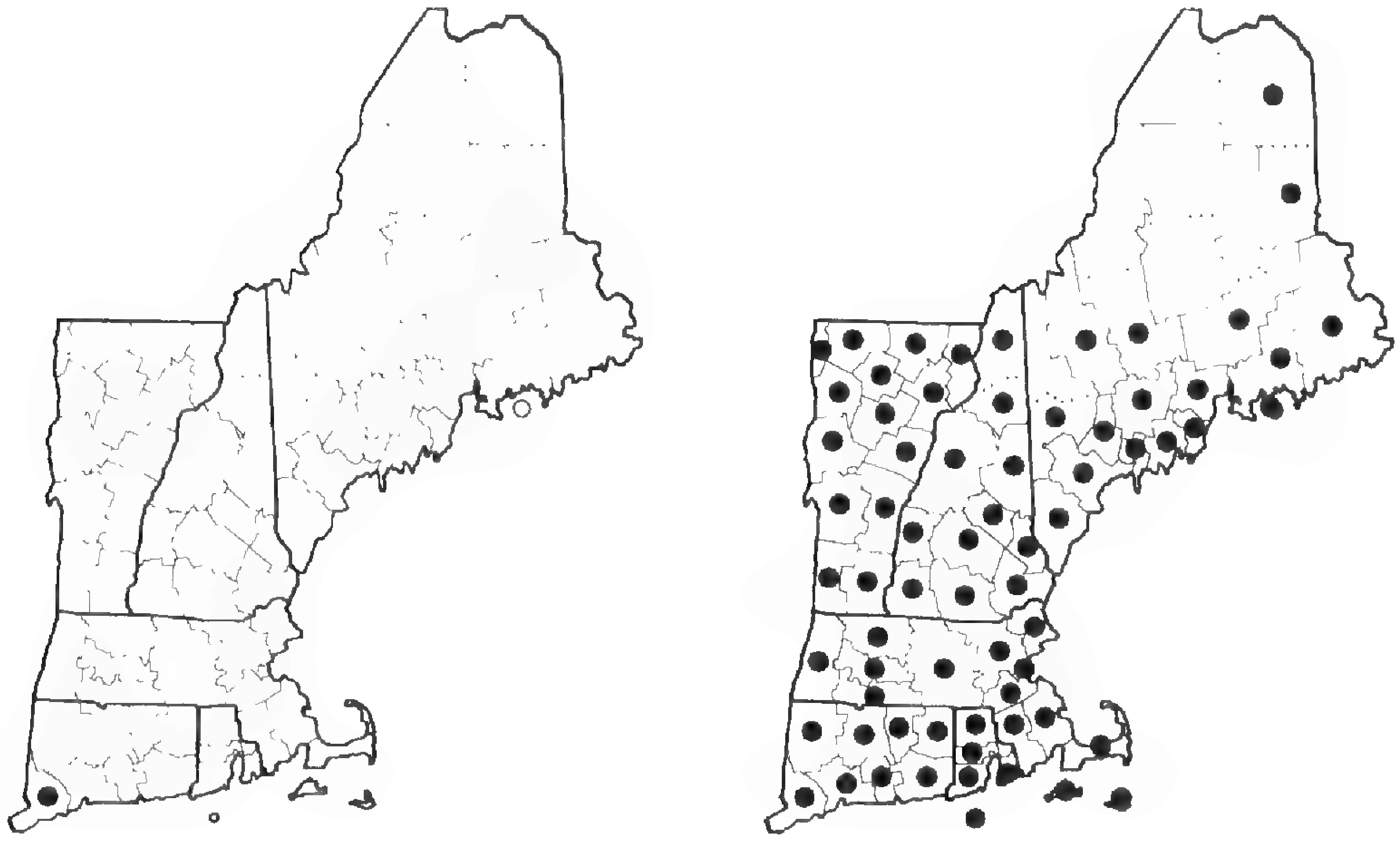


Smilax glauca *Smilax herbacea*

Figure 77. Distribution maps for *Ruppia maritima, Scheuchzeria palustris, Smilax glauca,* and *S. herbacea.*

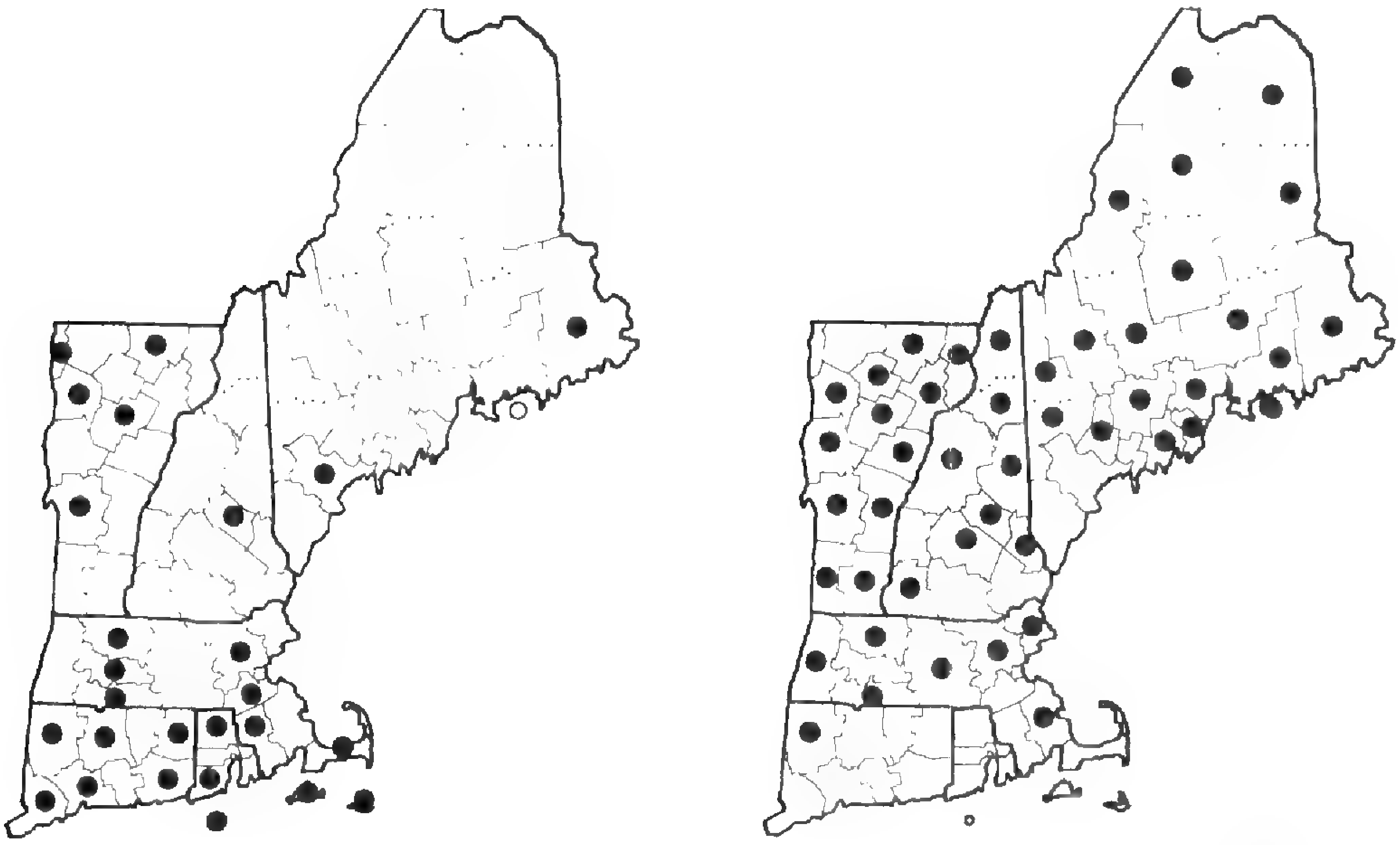


Smilax pulverulenta *Smilax rotundifolia*

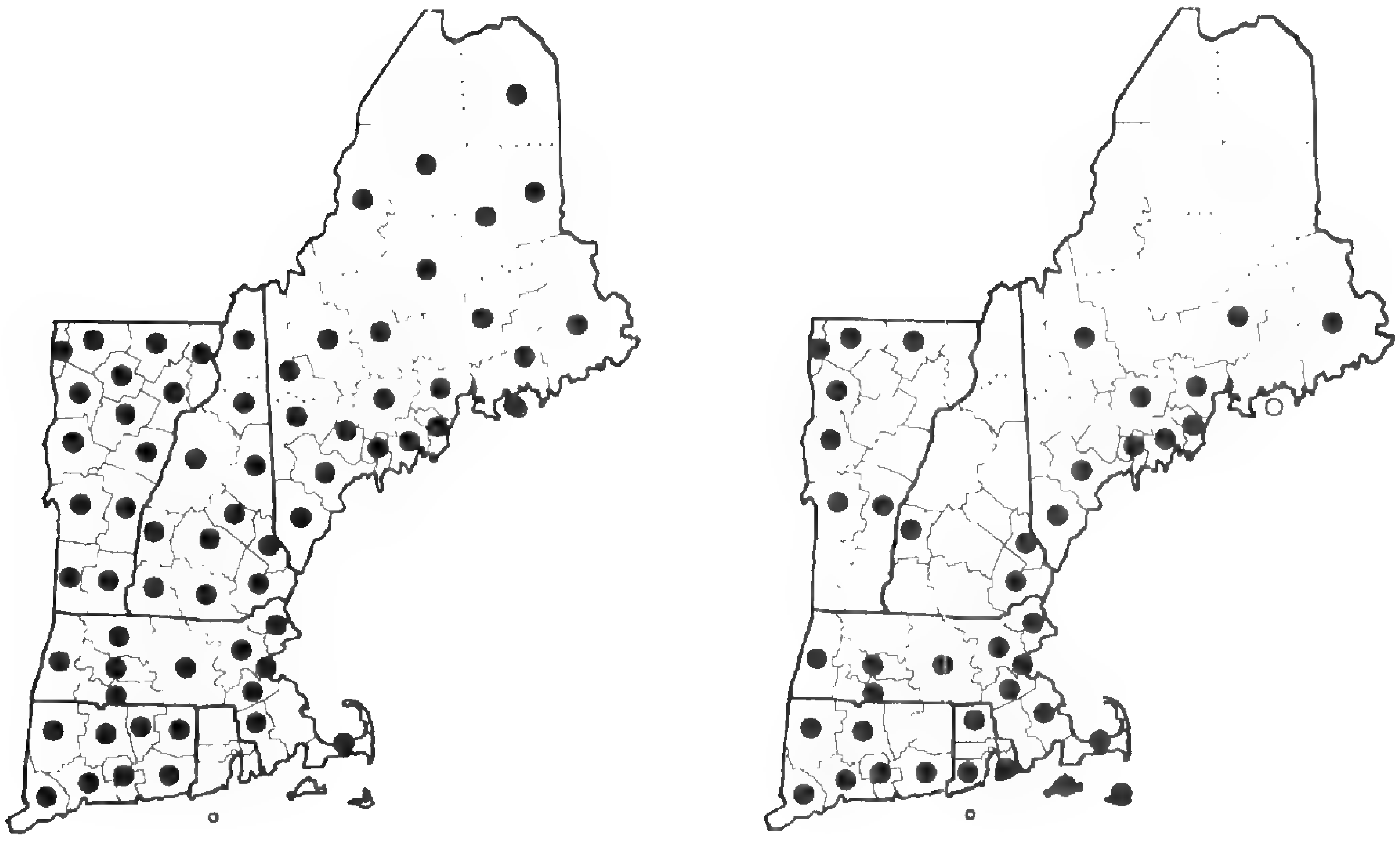


Smilax tamnoides *Sparganium americanum*

Figure 78. Distribution maps for *Smilax pulverulenta, S. rotundifolia, S. tamnoides,* and *Sparganium americanum.*

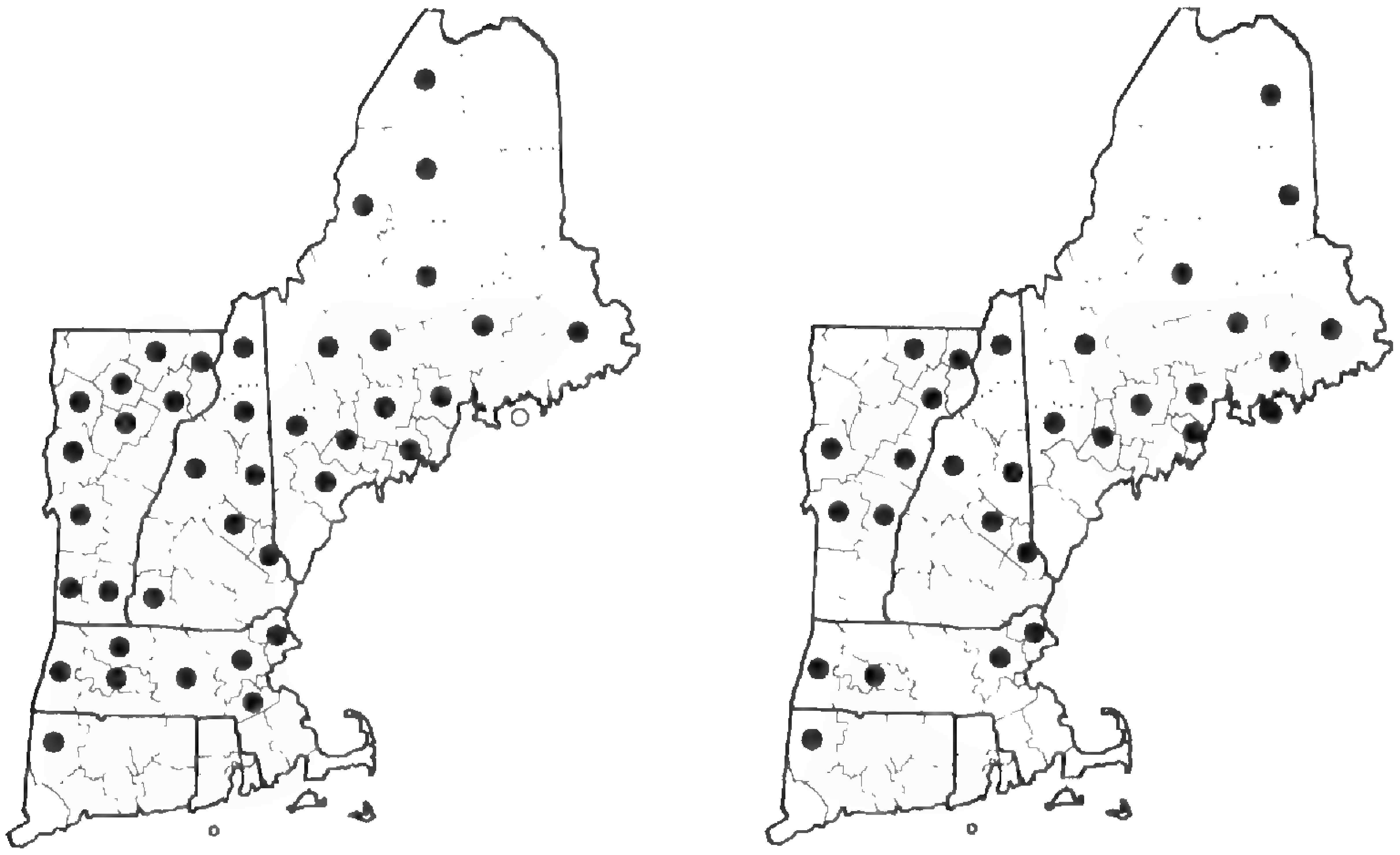


Sparganium androcladum *Sparganium angustifolium*



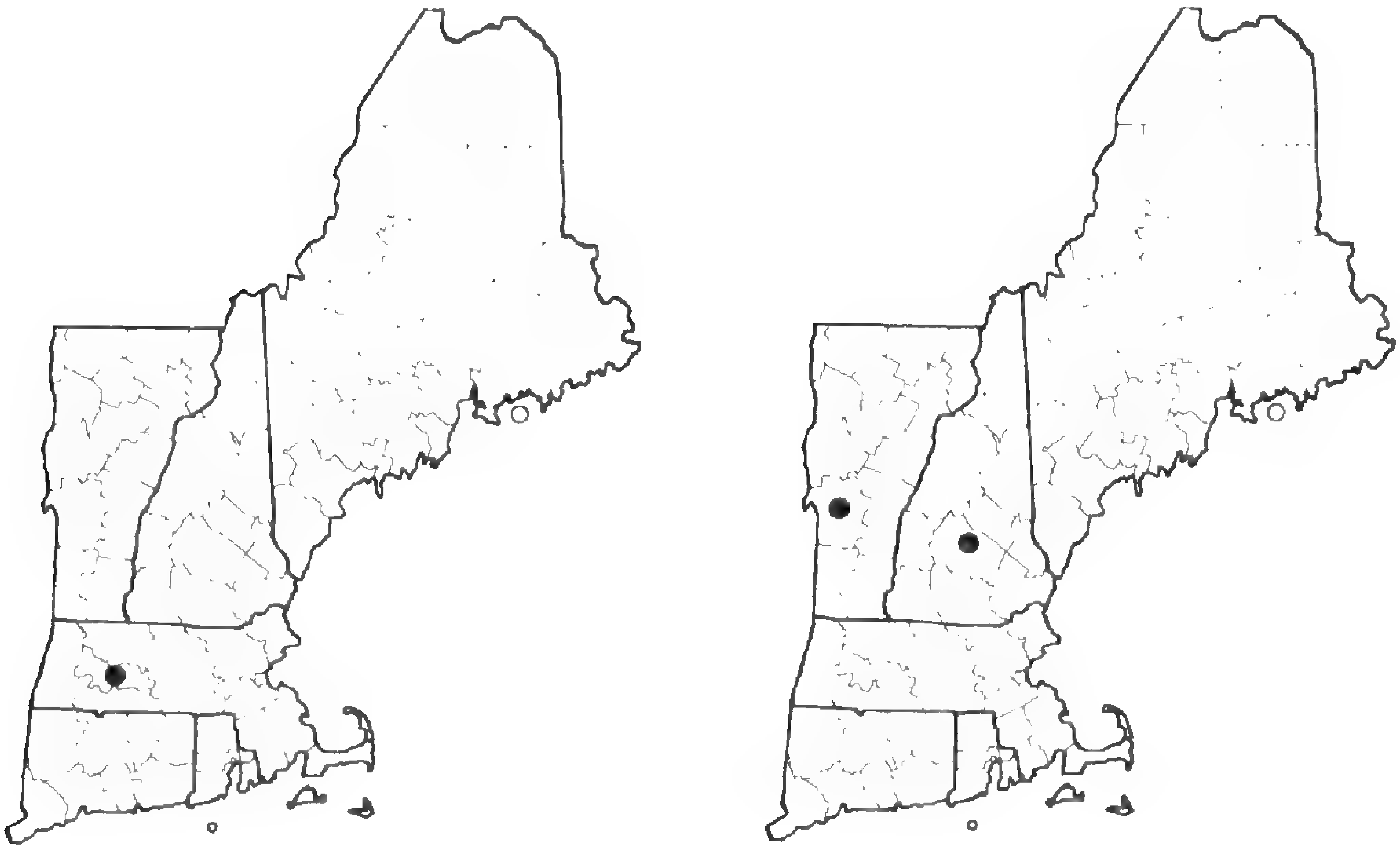
Sparganium emersum *Sparganium eurycarpum*

Figure 79. Distribution maps for *Sparganium androcladum*, *S. angustifolium*, *S. emersum*, and *S. eurycarpum*.



Sparganium fluctuans

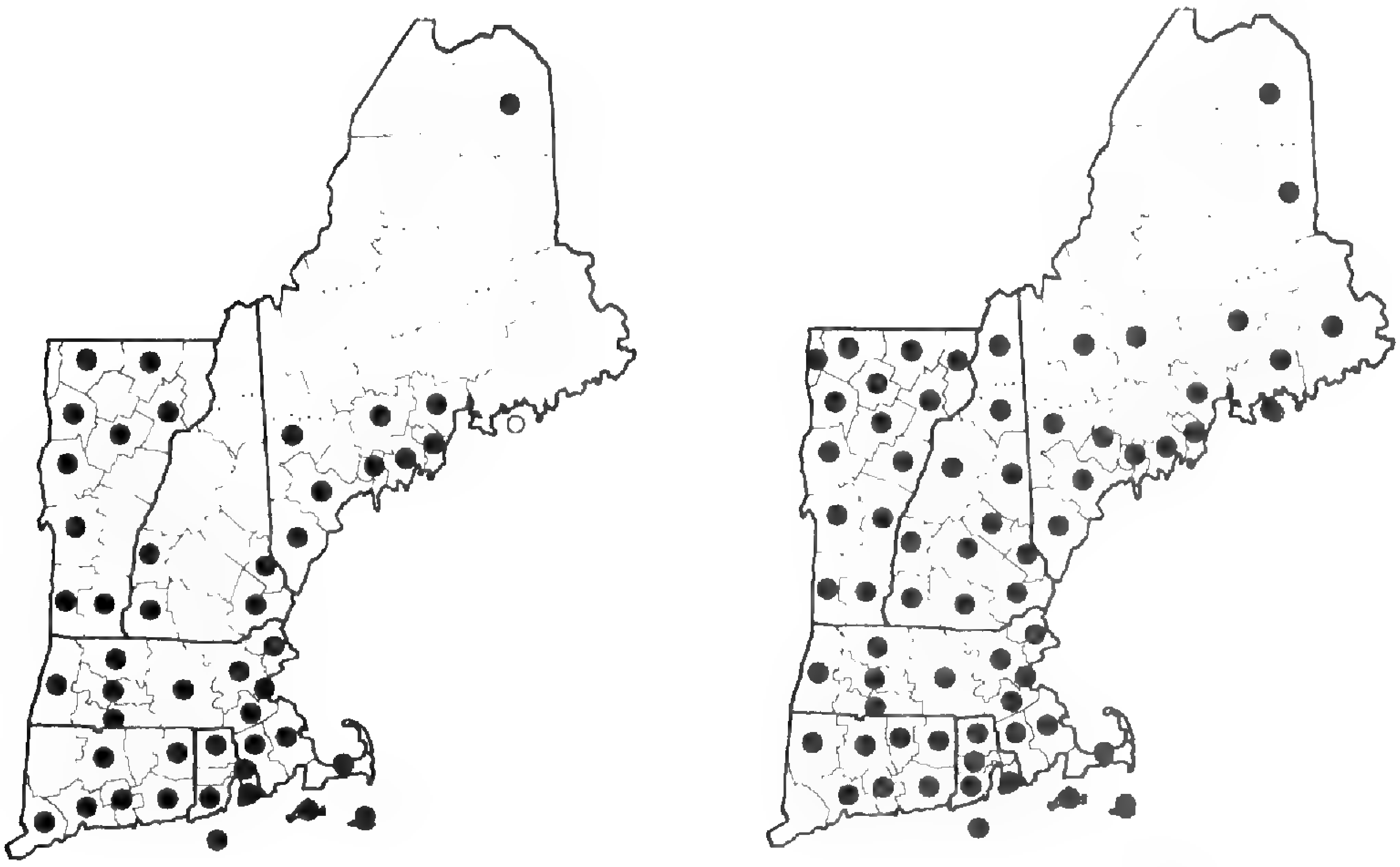
Sparganium natans



Sparganium americanum
X *S. fluctuans*

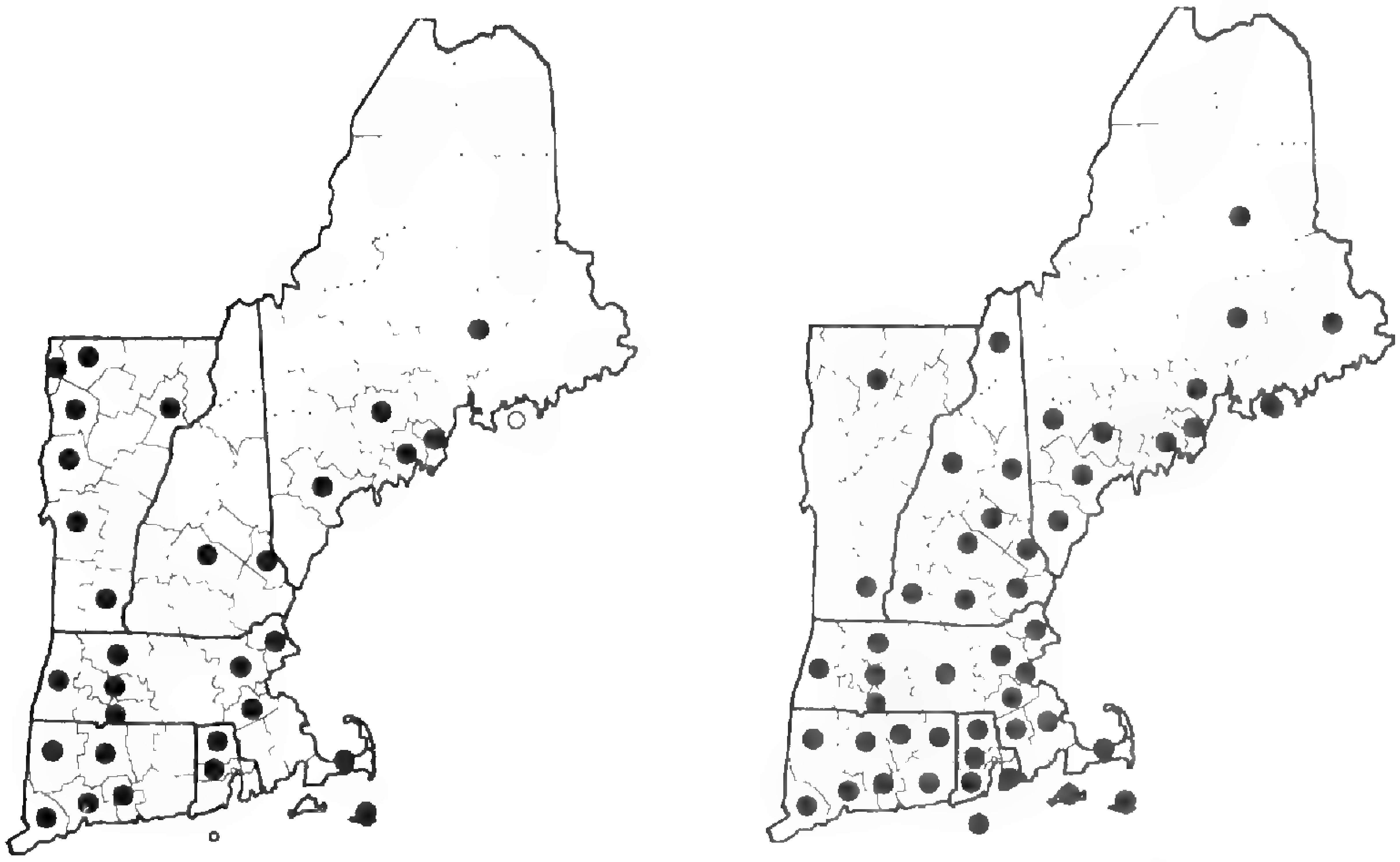
Sparganium angustifolium
X *S. emersum*

Figure 80. Distribution maps for *Sparganium fluctuans, S. natans, S. americanum* X *S. fluctuans, S. angustifolium* X *S. emersum.*



Typha angustifolia

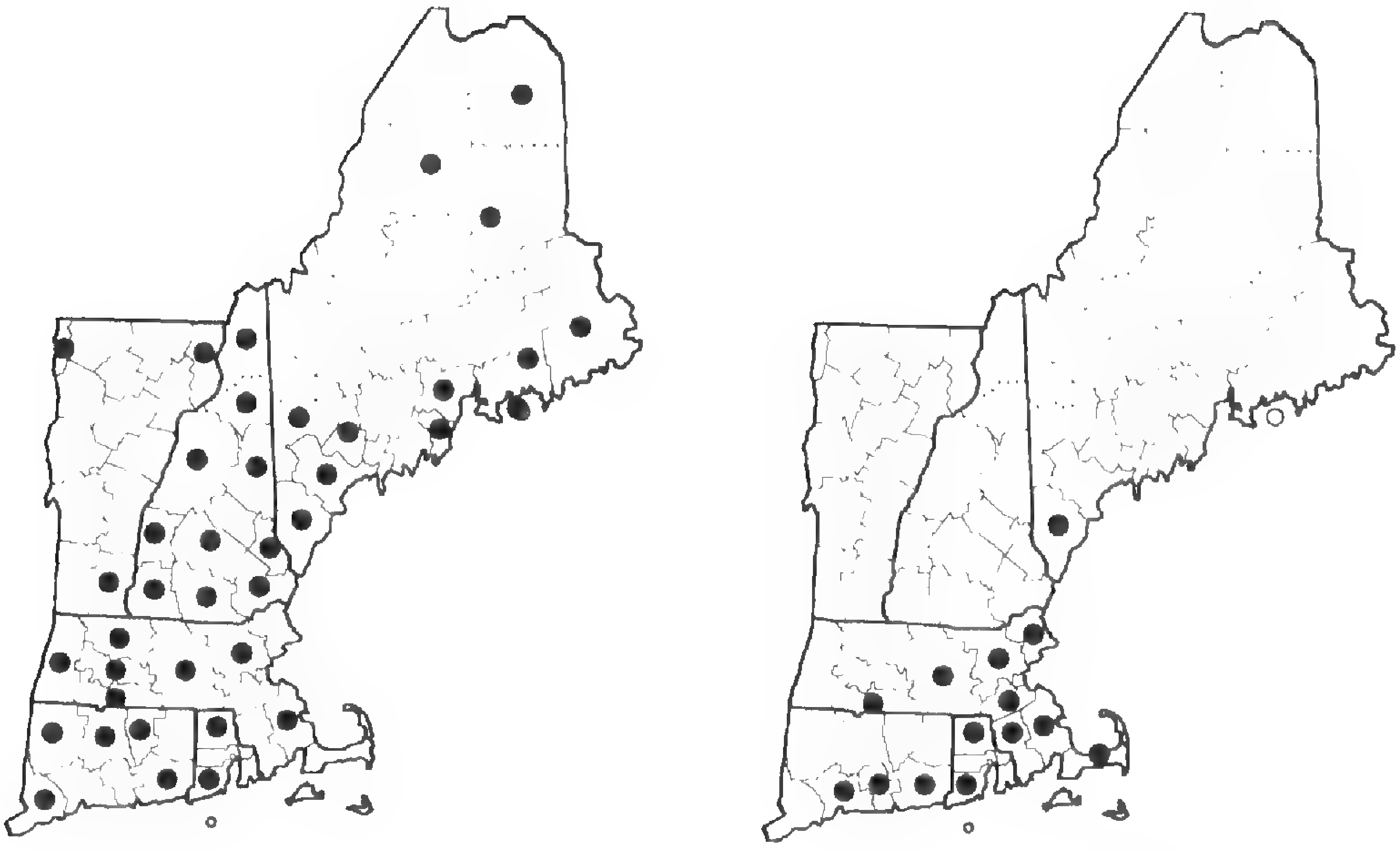
Typha latifolia



Typha X *glauca*

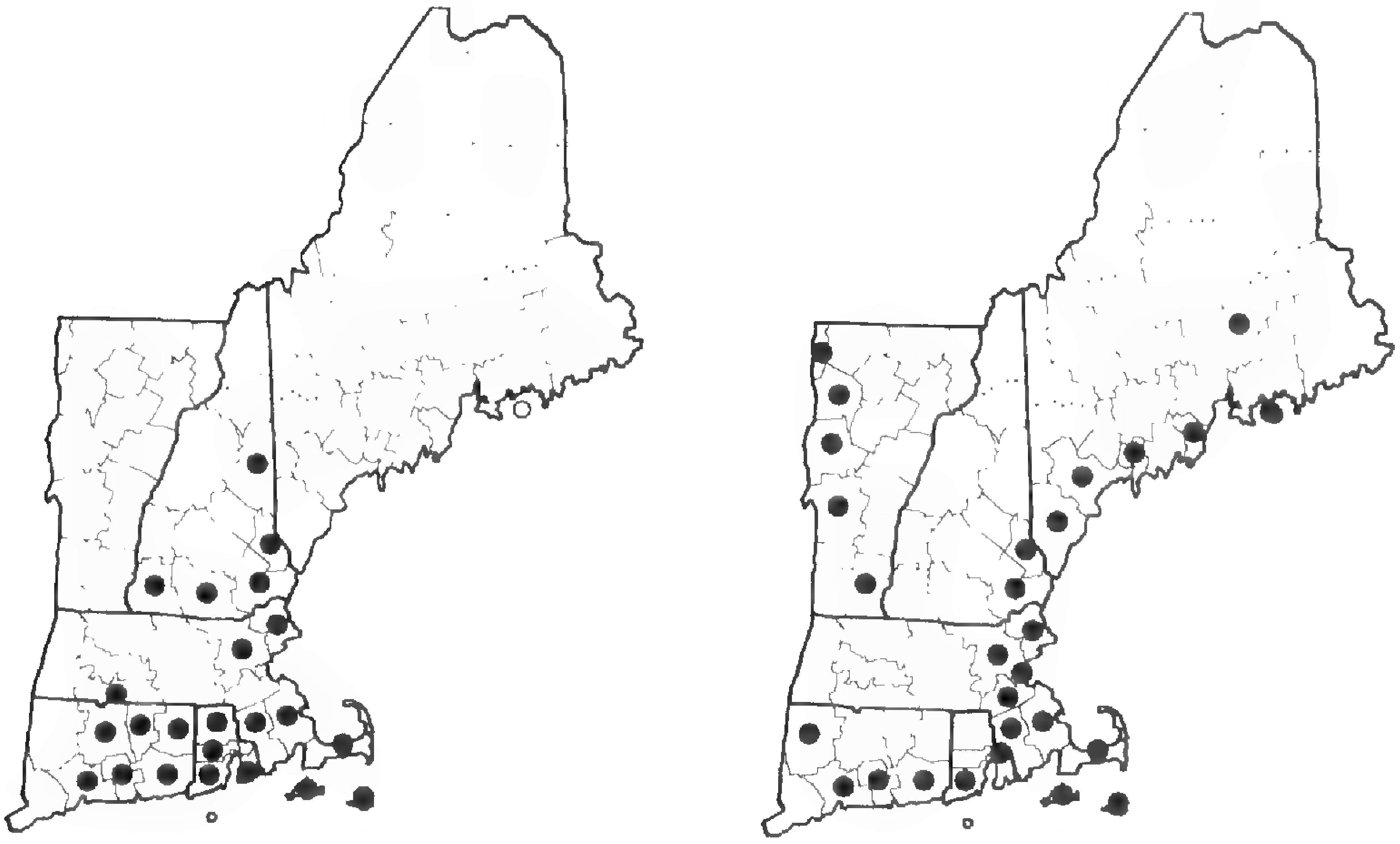
Xyris difformis
var. *difformis*

Figure 81. Distribution maps for *Typha angustifolia, T. latifolia, T.* X *glauca,* and *Xyris difformis* var. *difformis.*



Xyris montana

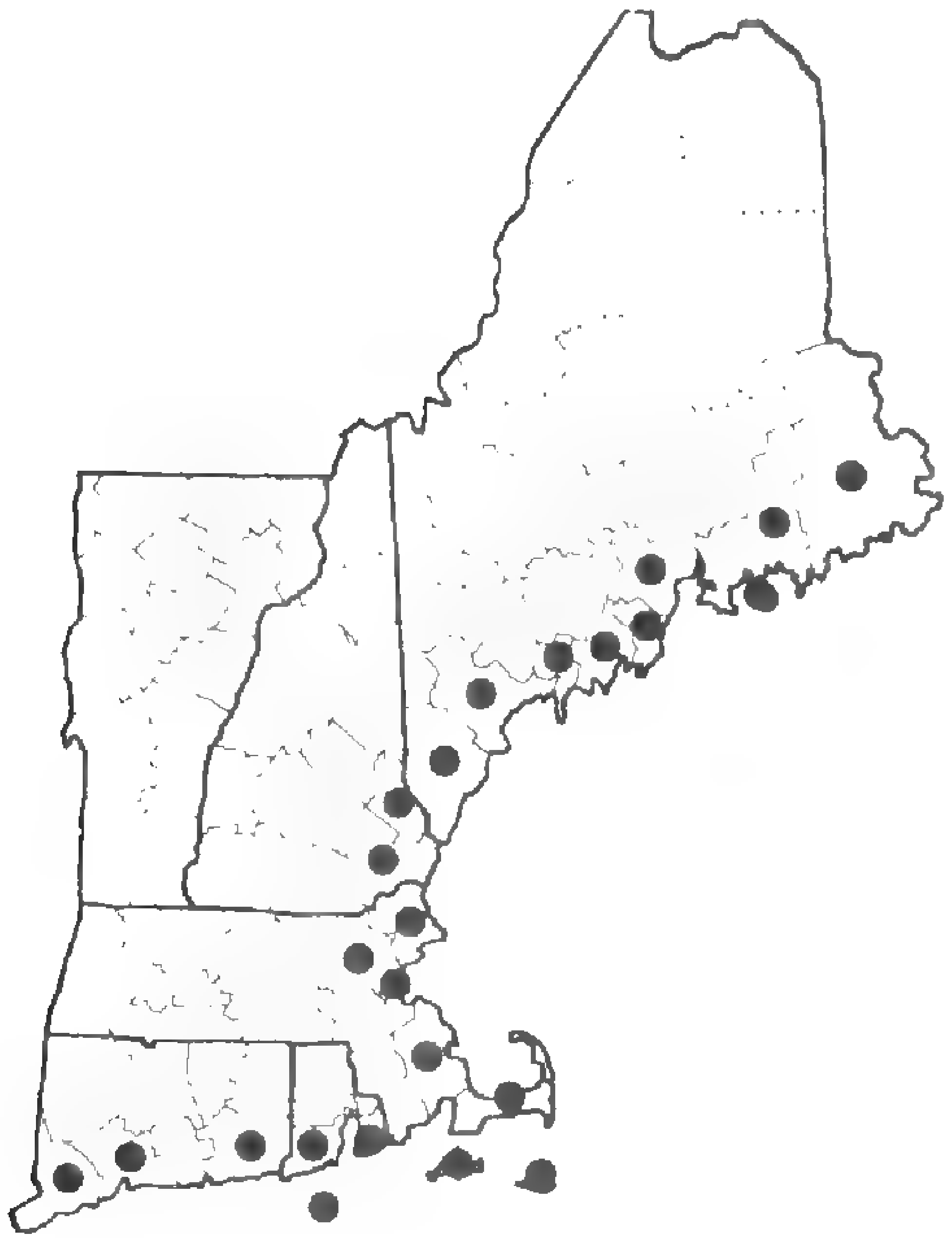
Xyris smalliana



Xyris torta

Zannichellia palustris

Figure 82. Distribution maps for *Xyris montana, X. smalliana, X. torta,* and *Zannichellia palustris.*



Zostera marina

Figure 83. Distribution map for *Zostera marina.*

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NEBC MEETING NEWS

September 1999. Dr. Les Mehrhoff, curator of the G. Safford Torrey Herbarium at the University of Connecticut, addressed the topic, "The Non-native Invasive and Potentially Invasive Flora of New England: A Regional Perspective." He explained first that his concern was primarily about non-native species that are outcompeting native flora in portions of the "minimally managed" landscape. Where once we had old fields succeeding to *Rubus,* now we are likely to see the ubiquitous *Rosa multiflora* conquering the abandoned opening. Although early American botanist John Bartram complained in print about the proliferation of *Narcissus* cultivars into the natural environment around Philadelphia, there was little mention in the scientific literature of problematic plant introductions until a pair of papers authored by M. L. Fernald in 1905 and 1939 described certain "fugitives that had escaped." Reflective of the change in sentiment toward certain species, Fernald commented that the common name for *Hieraceum aurantiacum* in his native Maine changed from Venus' paintbrush to Devil's paintbrush. In the later paper, he noted a number of Asian taxa, such as *Lonicera japonica,* that were "crossing the landscape like a horde of huns." Mehrhoff pointed out that the term "invasive" should apply only to non-indigenous species, because technically a species cannot invade its own territory. When natives behave aggressively, he recommends we use the word "explosive." So as not to malign any species as inherently "bad," Les cited a line from an Aldo Leopold paper in the 1940s that says that "the invasive species problem is an attribute of numbers, not species." If not for herbarium records, Mehrhoff pointed out, it would be hard to know whether certain taxa were native or weedy introductions. An example given was the widespread Dusty Miller, *Artemesia stelleriana,* a species for which Fernald found the first American collection to be from 1879—a specimen collected by William Farlow in Nahant, Massachusetts.

Mehrhoff then discussed current efforts by himself and others in New England to develop definitions and criteria to be used for determining which species are invasive or potentially invasive in the New England region. He listed the following as characteristics of invasive species: 1) being non-native, 2) having high seed production, 3) being capable of rapid dispersal, 4) having the ability to establish easily, 5) having a competitive advantage over associated plants, and 6) being persistent on the landscape. He then recognized two categories of non-native invasive species: "Widespread and Invasive," and "Restricted and Invasive." He and New England colleagues are calling a third "watch-list" group "Potentially Invasive Species." To determine to which of these three groups a species might belong, Mehrhoff, being a good taxonomist, has developed a work sheet that progresses through a set of criteria like a dichotomous key. The four primary questions are: (1) Is it naturalized? (2) Is it capable of rapid and widespread dispersion and establishment? (3) Is it capable of dispersing over spatial gaps? (4) Is it capable of existing in high numbers away from artificial habitats? Four additional basic criteria are: (5) Is it currently widespread or at least common in the region or in one or more habitat types? (6) Is it known to have numerous individuals in many populations in the region? (7) Does it out-compete other species in the same natural plant community? (8) Does it have the potential for rapid growth, high seed or propagule production, dissemination, and establishment in natural areas? To be considered truly invasive the answer must be "yes" to the eight questions or criteria. To distinguish between Widespread and Restricted Invasives, one must determine whether the species is widespread with many occurrences in minimally managed natural areas or simply common in part of the region or in one or more habitat types in the region. The species qualifies as Potentially Invasive if the answer is "yes" to the first four questions, but "no" to one or more of the remaining four questions. Over 50 slide images were used to illustrate taxa being considered for status as Invasive or Potentially Invasive. A draft list for New England was also distributed along with a request for feedback on it.

What else is needed to deal with the problem of invasive species? Among Mehrhoff's answers to this question was to do further inventory and research, including that aimed at getting a better understanding of species biology for many of the purported invaders. Early detection and removal of new invaders would be another important action, he said. Another avenue he encouraged was working with the nursery and landscaping industries to find native alternatives, to test and monitor new exotic introductions, and to educate their customers. A final item fitting into Mehrhoff's solutions would be a computerized "Atlas of Non-native Invasive Species in New England" that would serve as a database of current and historical records. This, along with other information about invasive plants, he envisioned being available at a web site. Currently, the web site for the herbarium at the University of Connecticut (www.eeb.uconn.edu/collections/herbarium/herbarium.html) has a draft of Mehrhoff's list for the state.

October 1999. Rick Enser, State Botanist with the Rhode Island Natural Heritage Program, presented a slide lecture entitled "The Flora of Block Island, Rhode Island." Introducing his talk, Enser explained that in his overview of Block Island's flora, he would attempt to answer three questions about the island: how it came to be, what habitat types are present, and what factors are influencing the current vegetation and flora? Addressing the first question, he stated that Block Island's flora and fauna relate to the island's glacial history. The island is a product of glaciation, resulting from an ice sheet pushing up ocean sediments consisting primarily of clay to form much of the island's mass and characteristic bluffs. Glacial till and debris cap the sediments in places and bedrock is absent. The island is about 4.5 miles wide at its widest point and possesses 6030 acres. Using maps of the coastal islands and the continental shelf as they appeared following the retreat of the glaciers, he suggested that the flora and fauna of Block Island became isolated from the mainland about 8–9000 YBP, much earlier than occurred on Martha's Vineyard and Nantucket, which he dated at about 4000 YBP. This long isolation, he feels, is a primary reason for the depauperate flora and fauna on the island relative to some other islands of its size in the region. The indigenous fauna of the island, he pointed out, includes only two mammals, four amphibians, and six reptiles. Another reason suggested for the depauperate biota is the island's lack of a glacial outwash-plain.

Documentation of the early flora and vegetation of the island is limited. Livermore, in 1875, cited historic records from the 1600s about certain trees being used as boundary markers and surmised from this that forest must have been present on the island previously, even though it and the boundary trees were absent by this time. Pollen and wood fragment data suggest that a deciduous forest was once present on the island, too. From the time of the Revolutionary War to the present, the island has been largely an open, agricultural landscape grazed by livestock such as horses, cows, and sheep. Early botanical exploration by Robbins in 1829 documented two Rhode Island records, *Arenaria caroliniana* and *Hydrocotyle verticillata,* not seen since on the island. Other botanical explorers of the island to follow were Henri Young, Stephen T. Olney, and William W. Bailey. In an 1893 article in the *Bulletin of the Torrey Botanical Club,* Bailey reported an island flora of 294 species. An interesting record by Bailey was *Ranunculus cymbalaria,* which he described as abundant around the perimeter of Great Salt Pond. This once-brackish pond has since been permanently breached and the buttercup can no longer be found there, Enser said. Botanists following on Bailey's heels included Arthur Hollick, James F. Collins, and M. L. Fernald. Interestingly, in 1913 Fernald was the first to collect *Liatris scariosa* var. *novae-angliae* on Block Island. "Could this conspicuous species have been overlooked by the earlier botanists?" Enser asked. Grazing by livestock and deer, he added, is now widespread on the island and threatens this species and others. Fenced exclosures are being used by conservationists to protect selected sites for the species. Some species such as *Platanthera lacera,* he suspects, are gone due to the heavy deer browsing activity. Despite some losses, the number of species documented for the island has increased to around 760, Enser said, but primarily due to intensive exploration and the increase in the number of nonindigenous species present. Block Island's flora includes most of the region's most invasive taxa, and Enser estimated that about 30% of its current flora is introduced. *Populus alba,* for instance, was introduced about 1850 and now has dense colonies established about the island.

Habitats on the island include extensive dunes; salt flats and marshes; freshwater ponds; sedge meadows; shrub thickets; inland shrub communities dominated by *Viburnum dentatum, Myrica pensylvanica,* and *Amelanchier* spp.; managed open grasslands used for grazing and hay fields; and a depression area with a pocket of forest possessing *Nyssa sylvatica* and *Fagus grandifolia.* Also in this depression are the island's only woodland wildflowers such as *Maianthemum canadense,* first found by Fernald, and *Anemone quinquefolia,* discovered for the first time on the island only a couple of years ago. Perhaps the most important plant community on the island in Enser's eyes are small areas of open moraine with maritime grasses and herbs, located on slopes and tops of knolls. Here, indigenous species prevail and rare plant taxa for the island and state persist. In these areas one can find

Liatris, Helianthemum dumosum, Aristida purpurascens, and *Chrysopsis mariana.*

In closing remarks, Enser said that the future for natural vegetation on the island appears dim despite 25% of the land base being in conservation management. Nonindigenous species, including many invasive species, comprise more than 50% of the island's vegetative cover, and development pressures for additional housing and recreation are on the rise.

October 1999 Field Trips. On Friday afternoon, preceding the Club's evening meeting, about 15–16 enthusiastic Club members and friends explored the south shoreline of Worden Pond in South Kingstown, Rhode Island. Rick Enser led the outing. The water level was relatively low, so walking was mainly on mudflats among beds of exposed wetland plants that are typically emergent from standing water. The area was scoured for plants, both familiar and new. Dominant species included *Juncus militaris, Euthamia tenuifolia,* and *Gratiola aurea.* Locally dense patches of basal rosettes belonging to *Sabatia kennedyana* could be found below the taller vegetation, but not a single flowering stem was seen; it was suspected that this was due, in part, to two successive high water years. Some of the more uncommon finds of the day were occasional fruiting stems of *Ludwigia sphaerocarpa,* a plant or two of *Glyceria obtusa* bearing dense panicles of long spikelets, and a few clumps of *Rhynchospora macrostachya.* Aquatic finds included *Elatine minima* and *Vallisneria americana,* the latter possessing mature fruits attached to elongated scapes, coiled as they do following anthesis.

On Saturday a small group of 8–10 Club members, led by Dr. Keith Killingbeck of the University of Rhode Island and by Rick Enser, toured Ell Pond in Hopkinton, Rhode Island. The site is owned by The Nature Conservancy and is the only designated National Natural Landmark in Rhode Island. The vertical relief of the site surprised many as we scrambled upward along a trail of granitic bedrock and boulders. Alongside the trail we examined a mature, mixed hardwood/conifer forest where we found *Chamaecyparis thyoides, Pinus strobus, Tsuga canadensis* (some infested with hemlock adelgid), *Nyssa sylvatica, Pinus rigida, Quercus coccinea,* and *Q. prinus:* an uncommon mixture of species characteristic of either wet, mesic, or dry, well-drained sites. Another special feature of the site was the abundance of *Rho-*

dodendron maximum in the understory, giving one the feeling of being in the Southern Appalachians. The group could not resist a quick foray to the edge of Ell Pond where some typical bog species such as *Rhynchospora alba, Vaccinium macrocarpon, V. oxycoccos,* and *Sarracenia purpurea* were seen on a narrow *Sphagnum* mat that edged the pond.

—Paul Somers, Recording Secretary.

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FIVE NEW SPECIES OF *VERBESINA* FROM THE NORTHERN ANDES (HELIANTHEAE; ASTERACEAE)

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ABSTRACT. Five new species of *Verbesina* are described, *V. biserrata, V. clarkae, V. maldonadoensis,* and *V. pichinchensis* all from Ecuador, and *V. perijaensis* from Colombia.

Key Words: *Verbesina,* new species, Heliantheae, Asteraceae, Ecuador, Colombia, Northern Andes

Studies in the Heliantheae of the northern Andes, mostly for the *Flora of Ecuador*, have resulted in the discovery of the following five undescribed species of *Verbesina.* The species are in addition to the over 200 species already known in the New World genus *Verbesina* (Olsen 1985). The four Ecuadorian species are in addition to the 18 listed for Ecuador in Jørgensen and León-Yánez (1999). The Colombian species is in addition to the ca. 25 already known from that country (including those of Díaz-Piedrahíta 1985). A number of the following species are distinguished by rays being white, yellow, or lacking, and they would potentially fall within the artificial sections *Leucactinia, Ochractinia,* or *Lipactinia,* but these sections are not recognized here. For a partial discussion of some of past artificial segregates in *Verbesina* see Blake (1925). Most of the true diversity of the genus seems to be centered in Mexico.

Verbesina biserrata H. Rob. & Panero, *sp. nov.* TYPE: ECUADOR. Prov. Cotopaxi: approximately 10.9 km W of Pilaló along road to Latacunga, 3200 m, 15 Jul 1992, *J. Panero & B. L. Clark 3000* (HOLOTYPE: TEX; ISOTYPE: QCA). Figure 1.

In habitus ad Verbesinam lloensem superficialiter simila sed in foliis oppositis valde biserratis et floribus radii nullis differt. In

Figure 1. *Verbesina biserrata* H. Rob. & Panero, holotype, Herbarium of the University of Texas (TEX).

foliis oppositis ad V. rivettii et V. pichinchensem proximius sed in caulibus puberulis et marginis foliorum distincte biserratis et foliis subtus sparce tomentellis et floribus radii omnino nullis et floribus disci 20–25 et corollis sordide albis praeter in lobis nigrescentibus distincta.

Trees 3–6 m tall; stems brownish, terete, striate, without wings, minutely brownish puberulous. Leaves opposite, with petioles 1–8 cm long, upper leaves sometimes narrowly winged to base; blades of lower leaves oblong-ovate, to 30 cm long, 14 cm wide, with rounded base, upper leaves ovate-elliptical, 6–15 cm long, 3–6 cm wide, with base acute or acuminate, margins doubly serrate, often serrulate or with minute mucronate dentations in upper leaves, apex acute, upper surface sparsely pilose, lower surface thinly tomentellous, pale yellowish, not obscuring green surface except on immature leaves, denser and brownish on veins; veins pinnate or slightly subpinnate, with 6–9 ascending veins on each side, basal veins of larger leaves more spreading. Inflorescence terminal on leafy branches, broadly corymbiform; primary branches mostly opposite, ascending, densely puberulous with sordid hairs. Heads 10–12 mm high, ca. 7–9 mm wide; involucral bracts ca. 18, dark green to brown, narrowly oblong, flat, 4–8 mm long, 1.5–2.5 mm wide, rounded at tip, puberulous with pale hairs outside; pales similar to inner involucral bracts, acute, ca. 8 mm long. Ray florets lacking. Disk florets 20–25; corollas sordid white, blackish on lobes, ca. 7 mm long, pilosulous on tube, with few hairs on lobes, tubes ca. 1.8 mm long, throat ca. 4.5 mm long, lobes ca. 1 mm long, with fringe of long papillae on inner margins; anther thecae black, ca. 2.5 mm long; apical appendage black, ca. 0.6 mm long, 0.35 mm wide. Cypselas immature, ca. 4 mm long, glabrous on sides, few small setulae along upper margins, with wings not expanded; awns of pappus straight, ca. 6 mm long.

Verbesina biserrata is known only from the type collection. The plant was found in Cotopaxi at 3200 m in disturbed Andean forest. The species superficially resembles *V. lloensis* Hieron., but differs by the opposite, strongly serrate leaves and lack of ray florets. The species is probably more closely related to other primarily opposite-leaved species such as *V. rivettii* S. F. Blake to the north and *V. pichinchensis* to the south, both of which have dense tomentum on the leaf undersurfaces and have some ray florets.

Verbesina clarkae H. Rob. & Panero, *sp. nov.* TYPE: ECUADOR. Prov. Carchi: 10.4 km E of Julio Andrade along road to El

Carmelo and El Aljún, around town of El Aljún, 2880 m, 21 Jul 1992, *J. Panero & B. L. Clark 3040* (HOLOTYPE: US; ISOTYPES: QCA, TEX). Figure 2.

In radiis albis brevibus et caulibus puberulis vel glabrescentibus ad Verbesinam maldonadoensem simila sed in capitulis majoribus in floribus radiis ca. 8 et in bracteis involucri ca. 22 differt.

Shrubs or small trees 4–10 m tall, moderately branched; stems terete, unwinged, brownish, puberulous, glabrescent. Leaves alternate, petioles distinct, unwinged, 3.5–9.0 cm long; blades ovate, 18–28 cm long, 10–15 cm wide, base obtuse with short acumination, margins remotely and minutely denticulate, apex broadly acuminate, upper surface minutely scabridulous, lower surface densely pale hirtellous, denser and more brownish on veins; venation pinnate, with 8–10 veins on each side, lowest secondary veins narrower, closer, spreading at ca. 90°. Inflorescence from apices and upper axils of leafy branches, broadly corymbiform cymes with many heads, ca. 30 cm wide and high; peduncles 3–18 mm long, densely brownish hirtellous with broad-sharp hairs. Heads campanulate, 10–12 mm high; involucre 7–8 mm wide; involucral bracts ca. 22 in ca. 3 graduated series, narrowly oblong, 2–7 mm long, 1.0–1.3 mm wide, apices obtuse, densely puberulous with pale hairs outside; pales similar to inner involucral bracts, ca. 8 mm long. Ray florets ca. 8; corollas white, sometimes with tinge of yellow, tube and tip of limb pilosulous, tube 1.3 mm long, limb ca. 3.5 mm long, 1.3 mm wide. Disk florets ca. 20; corollas whitish yellow, 6.0–6.8 mm long, pilosulous throughout, sparsest on middle of throat, tube ca. 1.8 mm long, throat 3.8–4.0 mm long, lobes ca. 1 mm long, with dense fringe of long papillae on inner margin; anther thecae black, 2.5 mm long; apical appendage black, 0.5 mm long, ca. 0.3 mm wide. Cypselas immature; ray cypselas ca. 3 mm long, with single outer awn ca. 3 mm long; disk cypselas ca. 3.8 mm long, essentially glabrous, wings not expanded, pair of pappus awns ca. 6 mm long.

The new species is named for the co-collector on the 1992 expedition, Bonnie L. Clark, previously a student of Ted Barkley at Kansas State University, more recently of Shawnee Mission, Kansas.

Verbesina clarkae is known only from the type locality. The

PLANTS OF ECUADOR

Verbesina

CARCHI: 10.4 km E of Julio Andrade along the road to El Carmelo and El Aljún, around the town of El Aljún. Shrubs or small trees 4-10 m tall, ray corollas few and white sometimes with a tinge of yellow, disk corollas whitish yellow, herbage covered with a brownish pubescence. Growing in disturbed Andean forest
2880 m
Occasional

Jose L. Panero 3040 Jul 21 1992
with Bonnie Clark

Pontificia Universidad Católica del Ecuador (QCA)
Michigan State University Herbarium

Fieldwork supported by NSF grant [illegible]

Figure 2. *Verbesina clarkae* H. Rob. & Panero, holotype, United States National Herbarium (US).

species occurs in easternmost Carchi at 2880 m in disturbed Andean forest. It is one of the few species in Ecuador in which white rays are present. The closest relative is probably *V. maldonadoensis* of eastern Carchi, but the present species has larger heads with more numerous florets, ca. 8 ray florets and ca. 20 disk florets. The rays have small limbs, and their number is distinctive within Ecuador. A possibly closely related Colombian species from Dept. Valle is *V. barragana* Cuatrec., but the latter has lanuginose pubescence on the stems, more lanceolate leaves, and five or fewer ray florets with limbs 7 mm long.

Verbesina maldonadoensis H. Rob. & Panero, *sp. nov.* TYPE: ECUADOR. Prov. Carchi: 9 km E of Maldonado, ca. 55 km W of Tufiño along road Maldonado–Tufiño–Tulcán, 2100 m, small trees to 7 m tall, corollas whitish, growing in disturbed Andean forest, 20 Jul 1992, *J. Panero & B. L. Clark 3035* (HOLOTYPE: US; ISOTYPES: QCA, TEX). Figure 3.

In radiis albis brevibus et caulibus puberulis vel glabrescentibus ad Verbesinam clarkae simila sed in capitulis minoribus in floribus radiis ca. 3 et bracteis involucri ca. 14 distincta.

Shrubs to 7 m tall, moderately branched, with brownish hairs; stems brown, terete to slightly angled, without wings, slightly deflected at nodes, minutely puberulous or with sparse arachnoid hairs; internodes mostly 2–3 cm long. Leaves alternate, petioles 2–8 cm long, 1/5 to more than half as long as blade, unwinged; blades elliptical, 10–17 cm long, 3–8 cm wide, base acute to slightly acuminate, margins minutely mucronate-serrulate except near base, apex short and narrowly acuminate, upper surface dark, minutely pilosulous, densely hirtellous on veins, lower surface densely pilosulous, subtomentellous on veins; secondary veins pinnate, ca. 8 on each side, spreading at ca. 55°, arched before margins. Inflorescence from apices and upper axils of leafy branches, broadly flat-corymbiform, with many heads, ca. 25 cm high and wide; peduncles 1–12 mm long, densely hirtellous. Heads narrowly campanulate, 5–6 mm high; involucre 3–4 mm wide; involucral bracts ca. 14, in ca. 3 graduated series, narrowly oblong, 1.5–4.0 mm long, 0.5–1.2 mm wide, apices acute, thinly herbaceous, pilosulous outside; pales greenish on keel and distally, elliptical-lanceolate, 5.0–5.5 mm long, ca. 1 mm wide, pilosulous distally on keel. Ray florets ca. 3; corollas white, tube ca. 1.5 mm long, pilosulous, limb oblong, ca. 4 mm long, 1.5–

PLANTS OF ECUADOR

Verbesina maldonadoensis H.Rob. & Panero
Holotype
CARCHI: 9 km E of Maldonado, ca. 55 km W of Tufiño along the road Maldonado-Tufiño-Tulcán. Small trees to 7 m tall, corollas whitish, most heads attacked by insects. Growing in disturbed Andean forest.
2100 m
Occasional

José L. Panero 3035 Jul 20 1992
with Bonnie Clark

Figure 3. *Verbesina maldonadoensis* H. Rob. & Panero, holotype, United States National Herbarium (US).

2.0 mm wide. Disk florets 8–12; corollas yellowish, ca. 4.5 mm long, pilosulous on tube and lobes, tube ca. 1 mm long, throat ca. 2.5 mm long, lobes ovate-oblong, ca. 0.8 mm long, with dense fringe of long papillae on inner margin; anther thecae black, ca. 1.8 mm long; apical appendage yellowish distally, ca. 0.35 mm long, ca. 0.2 mm wide. Cypsela immature, ca. 2 mm long, with wings to 1.5 mm wide, glabrous; awns of pappus straight, 2.0–3.5 mm long.

PARATYPE: **Ecuador.** Prov. CARCHI: above Maldonado, in secondary cloud forest and pastures, 2500 m, 1 Aug 1989, *van der Werff & Gudiño 10852* (US).

Verbesina maldonadoensis is known only from secondary cloud forests at 2100–2500 m elevation in the western part of the Province of Carchi near the Colombian border. The species probably also occurs in the immediately adjacent areas of Colombia. The rather small heads with white ray florets, alternate leaves, and the sometimes very long petioles distinguish this species.

Verbesina pichinchensis H. Rob., *sp. nov.* TYPE: ECUADOR. Prov. Pichincha: Páramo and shrub vegetation on eastern slopes of Cerro Pichincha, 3600–4000 m, 26 Jan 1977, *G. Harling, U. Eliasson, & L. Andersson 14832* (HOLOTYPE: US; ISOTYPE: GB). Figure 4.

Ad Verbesinam ecuatorianam simila sed in foliis suboppositis in foliis plus ovatis et in ramis inflorescentium densius tomentosis distincta.

Shrubs to 2 m tall, moderately branching; stems pale brownish, terete, unwinged, densely lanulose with pale slender hairs, internodes between pairs of leaves 3–5 cm long, internodes between leaves of pairs ca. 0.5–1.0 cm long. Leaves subopposite, petioles 1–2 cm long; blade narrowly ovate, 8–14 cm long, 2.5–4.5 cm wide, base short-acute, slightly acuminate on petiole, margins closely serrulate from below widest part, apex acute, upper surface dark green, densely scabridulous with sharp hairs of many sizes, lower surface paler, almost completely covered with bases of hairs, subtomentose to sublanulate with long and short hairs, main secondary veins 5 or 6 on each side, ascending at 25–40°, with a few smaller closely spreading secondaries nearer base. Inflorescence terminal and from upper axils on leafy stems, broadly corymbiform with many heads, to 13 cm wide, with

Figure 4. *Verbesina pichinchensis* H. Rob., holotype, United States National Herbarium (US).

branches ascending, tomentose; peduncles 0–12 mm, covered with dense pale tomentum. Heads campanulate, 9–11 mm high, 7–8 mm wide; involucral bracts ca. 15, in 2–3 series, oblong to oblong-lanceolate, 4–6 mm long, 1.5–2.0 mm wide, apices obtuse, densely puberulous to sublanulate outside and near tip inside, inner bracts acute, densely puberulous outside; pales similar to inner involucral bracts, to 8 mm long. Ray florets 0–3; corolla fertile, yellow, tube ca. 2.5 mm long, pilosulous, limb oblong, ca. 5 mm long, 2.5 mm wide, sparsely puberulous. Disk florets ca. 15; corolla yellow, 4.5–5.0 mm long, tube ca. 1.5 mm long, pilosulous, limb sparsely puberulous, throat ca. 3.5 mm long, lobes 0.5 mm long and wide, with dense fringe of long papillae on inner margins; anther thecae black, ca. 2 mm long; apical appendage mostly yellowish, partially black. Cypsela (immature) 6 mm long, ca. 1.5 mm wide, with few slender hairs on sides, wings present; pappus with 2 awns, straight, 4.5–5.0 mm long.

PARATYPE: **Ecuador.** PROV. PICHINCHA: Pichincha, 30 Oct 1930, *R. Benoist s.n.* (P, US).

Verbesina pichinchensis is known from páramo and shrub vegetation at 3600–4000 m on Mt. Pichincha in north-central Ecuador. The specimens were determined at one time as *V. ecuatoriana* Sagást. (Sagástegui-Alva 1970), to which they seem closely related, but the leaves are subopposite with long internodes between the pairs, the leaf blades are more ovate, and the branches of the inflorescence have denser and longer tomentum. The habit is also similar to the common *V. sodiroi* Hieron., but the latter has 10–15 ray florets in a head.

Verbesina perijaensis H. Rob. *sp. nov.* TYPE: COLOMBIA. Dept. Cesar: "Magdalena", Sierra de Perijá, east of Manaure, Quebrada de Floridablanca, Andean forest and bushes, 2700–2800 m, 11 Nov 1959, *J. Cuatrecasas & R. Castaneda 25236* (HOLOTYPE: US). Figure 5.

In caulibus et foliis glabris ad Verbesinam laevifoliam et V. negrensis et V. simulans simila sed in bracteis involucri exterioribus 6–8 erectis obovatis et floribus radii ca. 14 in corollis longis et albis vel lilacinis differt.

Trees 2–3 m tall, with pendulous branchlets; stems brownish, glabrous, weakly angled. Leaves alternate, petioles 5–7 mm long;

Figure 5. *Verbesina perijaensis* H. Rob., holotype, United States National Herbarium (US).

blades subcoriaceous, oblanceolate, 6–9 cm long, 2–3 cm wide, base slightly acuminate, margins serrulate, apex acute, surfaces glabrous, shining, dark yellowish green above, veinlets forming dark reticulum below; venation pinnate, 6–8 upwardly curving secondary veins on each side. Inflorescence from apex and upper axils of leafy branches, laxly corymbiform with few large heads; branches glabrous at base, branchlets sparsely hirsute on one or more sides; peduncles 1–4 cm long. Heads broadly campanulate, 1.2–1.5 cm high, 2–3 cm wide; involucre of 6–8 spreading rounded herbaceous outer bracts, to 10 mm long, ca. 8 mm wide, mostly glabrous with some hairs near base and distal margins, apex rounded to obtuse, ca. 8, more erect, darker, obovate, glabrous, inner bracts with rounded thinly herbaceous often slightly recurved tips, 8–9 mm long, 5 mm wide above middle, with pale margins below; pales narrowly oblong, ca. 9 mm long, paler base clasping floret, distal 3 mm flat, darker, oblong, shortly acute. Ray florets ca. 14 in a head; corollas white or lilac, tube ca. 2 mm long, hirsutulous, limb narrowly elliptical, ca. 19 mm long, 4 mm wide. Disk florets ca. 40; corollas ca. 6.8 mm long, tube ca. 2 mm long, hirsutulous, throat ca. 3.5 mm long, lobes ca. 0.8 mm long, with fringes of long papillae on inner margins; anther thecae ca. 2.8 mm long; apical appendage rather pale, ca. 0.45 mm long, ca. 0.35 mm wide. Cypsela ca. 5.5 mm long, glabrous, wing immature; pappus awns 2–3 mm long.

Verbesina perijaensis is known only from the type, collected in the Perija region along the Venezuelan border. It appears to be related to some species in the Venezuelan Andes with glabrous leaves such as *V. laevifolia* S. F. Blake and *V. negrensis* Steyerm. of Venezuela (Aristeguieta 1964) which lack ray florets, and *V. simulans* S. F. Blake which has small white rays. The new species differs from all of these by the large white rays and the very large foliose involucral bracts.

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DO REPRODUCTIVE HISTORY TRAITS RELATE TO SEED MATURATION IN A CLONAL HERB?

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ABSTRACT. A field experiment tested whether seed maturation in Canada mayflower (*Maianthemum canadense*) was pollen limited and whether ramets flowering for the first time differed from ramets flowering for the second time in the number of seeds that they matured. Addition of pollen increased the number of seeds matured by ramets and therefore seed maturation was pollen limited. No difference in the number of seeds matured by ramets flowering for the first time and ramets flowering for the second time was detected and thus previous flowering did not appear to affect current seed maturation. There was a positive relationship between the number of seeds matured by ramets and the total weight of these seeds. This relationship did not differ between ramets flowering for the first and second times.

Key Words: ramet, genet, Canada mayflower, *Maianthemum canadense*

Plants must allocate limited resources to structures associated with growth, defense, and reproduction (Bazzaz et al. 1987). Over a plant's lifetime, allocation patterns must balance survivorship and fecundity (Bazzaz et al. 1987).

A tradeoff between current fecundity and subsequent growth and fecundity has been reported for the orchids *Cypripedium acaule* (Primack and Hall 1990), *Epidendrum ciliare* (Ackerman and Montalvo 1990), and *Tipularia discolor* (Snow and Whigham 1989). Current fecundity also reduced growth in mayapple (*Podophyllum peltatum*; Sohn and Policansky 1977, although see Benner and Watson 1989) and reduced the probability of producing females in jack-in-the-pulpit (*Arisaema triphyllum*; Bierzychudek 1984).

Current fecundity in self-incompatible, insect-pollinated plants may be influenced by a number of variables including the availability of compatible pollen (Bierzychudek 1981; Thompson and Stewart 1981) and also by a plant's reproductive history. This is not to suggest that a plant shown to be pollen limited in a given year is not ultimately resource limited (Bierzychudek 1981) as the addition of pollen in one year may increase current fecundity at the expense of future fecundity (Janzen et al. 1980).

Canada mayflower (*Maianthemum canadense* Desf.; Gleason and Cronquist 1991) is a rhizomatous, perennial herb with genets that consist of dimorphic ramets. Flowering ramets have 2–3 leaves with a terminal inflorescence consisting of 4–35 perfect flowers, while vegetative ramets have only one leaf. Fruits contain 1–4 seeds. Canada mayflower is self-incompatible (Worthen and Stiles 1986).

In the fall, ramets "die back," leaving an overwintering bud that will become the ramet in the following year. At this time it is possible to determine "by touch" whether a bud is vegetative or flowering (Ganger 1998). The status of this bud appears to be determined much earlier, and flower primordia are visible under the microscope as early as May (Kana 1982). With the dieback of the ramets, an abscission scar is left. The scars left by vegetative and flowering ramets are distinctive so it is possible to determine the age of a ramet and whether this ramet has been vegetative or flowering for each of its previous years (Ganger 1997; Silva et al. 1982). It is possible to make this determination in the field with a hand lens, but not as reliably as with a dissecting scope in the lab. It is sometimes possible to identify a ramet that has flowered previously by the presence of a dead flowering stalk.

The flowering ramets of Canada mayflower vary with respect to the number of times they have flowered previously and the number of years spent vegetative prior to flowering or since flowering (Ganger 1997). It is not known whether ramets that remain vegetative longer mature more seeds. It is also not known whether ramets experience a cost of previous flowering. If there were such a cost, then ramets flowering for the second time may mature fewer seeds than ramets flowering for the first time. This cost may also be reflected in the resources allocated to these seeds. Specifically, previously flowering ramets may allocate fewer resources to a similar number of seeds than other ramets.

A field experiment was undertaken to address the following questions: (1) Do ramets that remain vegetative for a longer period of time mature more seeds? (2) Is there evidence of a cost of flowering such that ramets flowering for the first time mature more seeds than ramets flowering for the second time? (3) Is

Canada mayflower pollen limited in local populations? (4) Is there a relationship between the number of seeds matured by ramets and the total weight of these seeds? and (5) Does this relationship differ between ramets flowering for the first and second time?

MATERIALS AND METHODS

Field work was conducted in a mixed coniferous-hardwood forest in the University of New Hampshire woodlands, Durham, NH. Sixty ramets that were flowering for the first time were identified as well as 60 ramets that were flowering for the second time. Ramets flowering for the first and second time occurred together, often within millimeters of one another. These two "flowering" treatments represented one of the factors in a two-factor experiment. Seed maturation in Canada mayflower has been demonstrated to be pollen limited in New Jersey populations (Worthen and Stiles 1988) and in previous years in the University of New Hampshire woodlands (Ganger 1997). Therefore, a second factor, "pollination," was included. Half of the flowering ramets in each of these treatments were randomly assigned to either of two treatments: hand pollinated or open pollinated. Including this factor reduced the likelihood that differences in seed maturation between first- and second-time flowering ramets would be obscured by low levels of pollination.

Each of the flowers of the hand-pollinated ramets were pollinated each day for the life of the flowers. Pollen was collected immediately prior to use from 10–20 flowering ramets not more than 20 m away and applied to stigmas with a wooden toothpick. Flowers from the open-pollinated ramets were not manipulated and presumably received natural levels of pollination. At the end of the fruiting season, all of the flowering ramets were excavated and taken to the laboratory. The numbers of fruits and seeds matured by each ramet was noted. Seeds were removed by gently pushing on the fruits. Seeds were dried for 72 hours at 80°C in a drying oven and then weighed to the nearest 1×10^{-5} g using a Mettler AE 63 balance. The total weight of all seeds matured by ramets was calculated. For each of the ramets that flowered for the first time, the number of years prior to flowering was noted. For each of the ramets that flowered for the second time, the number of years since flowering was noted.

In order to determine if ramets that remained vegetative for a longer period of time were able to mature more seeds, two regressions were performed. For hand-pollinated, first-time flowering ramets, the number of seeds they matured was regressed on the number of years prior to flowering. For hand-pollinated, second-time flowering ramets, the number of seeds that they matured was regressed on the number of years since flowering.

If ramets that were flowering for the first and second time differed in the amount of resources that were allocated to seed maturation, then this difference may have been apparent either as a difference in the number of seeds matured or as a difference between the two types of ramets, in the resources allocated to a similar number of seeds.

In order to test whether the number of seeds matured by ramets flowering for the first time differed from ramets flowering for the second time and whether seed maturation in ramets overall was pollen limited, a two-way analysis of variance (ANOVA) was performed. The statistical model consisted of two factors: flowering (first-time flowering vs. second-time flowering ramets) and pollination (hand pollinated vs. open pollinated). Both flowering and pollination were fixed, categorical variables. The dependent variable was the number of seeds matured. If there was a difference in the number of seeds matured between ramets flowering for the first and second time, then this effect would more likely be observed in ramets that received an overabundance of pollen. In other words, if resource limitation was occurring to a greater extent in either the first- or second-time flowering ramets, then the difference in seed maturation would more likely be detected statistically if pollen-limited ramets were not included. Therefore one *a priori* contrast was considered: the number of seeds matured by hand-pollinated, first-time flowering ramets was compared to the number of seeds matured by hand-pollinated, second-time flowering ramets.

In order to determine if ramets that were flowering for the first and second time differed in their allocation of resources to seeds, two analyses of covariance (ANCOVA) were performed. ANCOVA allowed for a determination of whether there was a relationship between the number of seeds matured by ramets and the total weight of these seeds, and whether this relationship varied between first- and second-time flowering ramets. Two separate ANCOVAs were performed, one for open-pollinated ramets and another for hand-pollinated ramets. In order to determine what variables influenced seed maturation, the number of seeds was the dependent variable. The number of times flowering was the independent, categorical variable and the total weight of seeds per ramet was the covariate. In these analyses, only those ramets that matured seeds were considered.

RESULTS

Forty-six of 60 open-pollinated ramets matured one or more seeds while 51 of 60 hand-pollinated ramets matured one or more seeds. Six ramets were excluded from the analyses because they were found to have flowered more than twice, they could not be accurately aged, or their reproductive history could not be determined due to decay.

The average number of years prior to flowering for ramets flowering for the first time was 3.9 years (SD = 1.81) and thus the average age of these ramets was 4.9 years (SD = 1.81). For ramets flowering for the second time, the average number of years since flowering was 2.9 years (SD = 0.75) and the average age of these ramets was 8.4 years (SD = 1.87). The number of seeds matured by hand-pollinated ramets was not correlated with the number of years prior to flowering for first-time flowering ramets ($F_{1,20,0.05} = 0.53$, $p = 0.47$) nor with the number of years since flowering for second-time flowering ramets ($F_{1,28,0.05} = 2.34$, $p = 0.14$).

Ramets that were hand pollinated matured more seeds than ramets that were open pollinated ($F_{1,107,0.05} = 127.22$, $p < 0.005$, $r^2 = 0.11$; Figure 1). There was no difference in the number of seeds matured by ramets flowering for the first and second time ($F_{1,107,0.05} = 0.50$, $p = 0.48$; Figure 1). There was no interaction between the pollination and flowering factors ($F_{1,107,0.05} = 0.90$, $p = 0.35$). The *a priori* contrast was also not significant; there was no difference between the number of seeds matured by hand-pollinated, first-time flowering ramets and hand-pollinated, second-time flowering ramets ($F_{1,106,0.05} = 0.63$, $p = 0.43$; Figure 1). In concluding that there was no difference in the number of seeds matured between these two treatments, there is an associated probability of being wrong. This is Type II error or β. Following Winer et al. (1991) it was possible to determine β and therefore the statistical power ($1 - \beta$) of this comparison, given specific

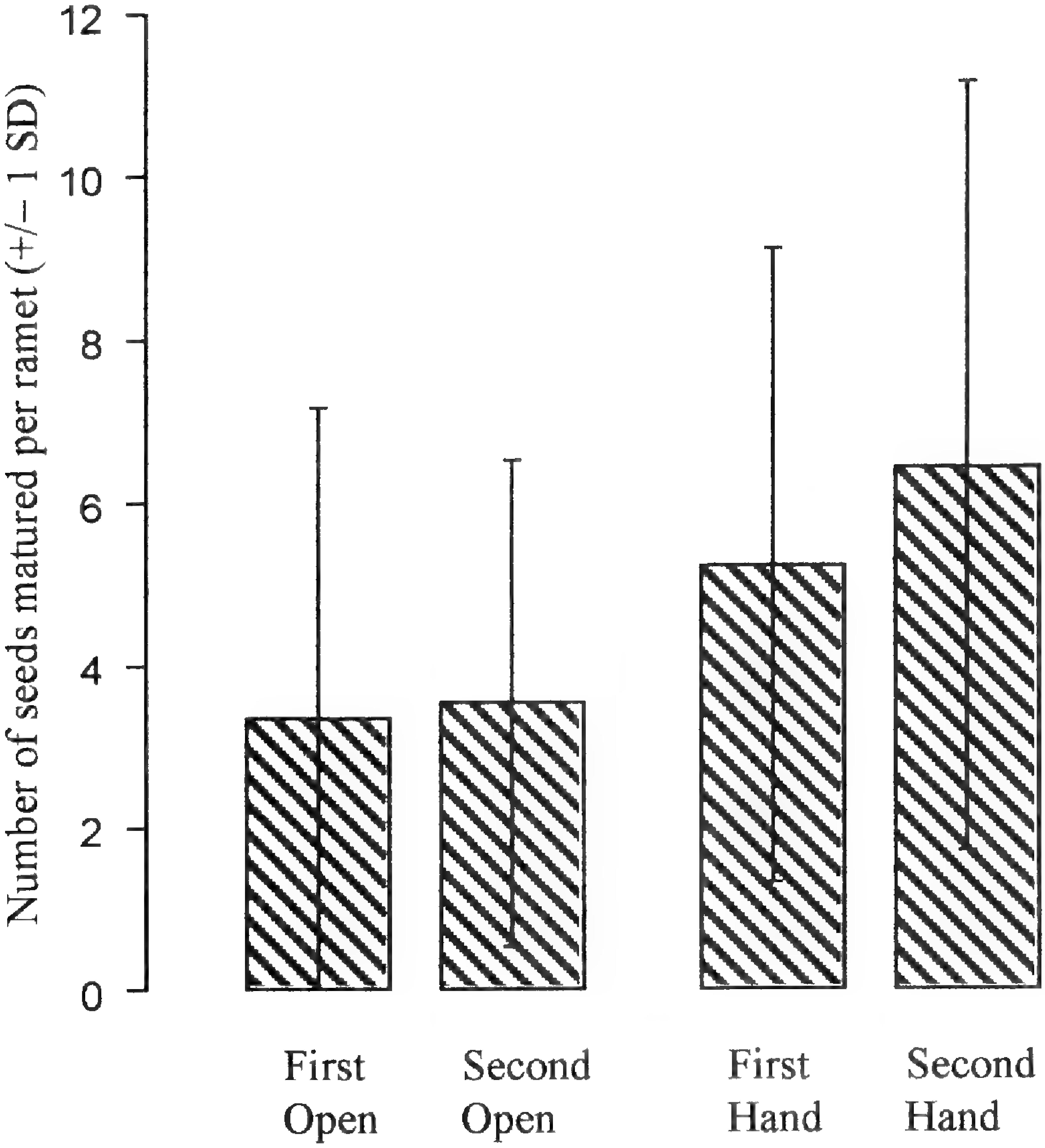

Figure 1. Mean number of seeds matured by *Maianthemum canadense* ramets in each of the four experimental treatments. First = first-time flowering ramets; Second = second-time flowering ramets; Open = open-pollinated ramets; and Hand = hand-pollinated ramets.

alternative hypotheses. The statistical power of the test, assuming a true difference between the treatment means of 1, 2, and 3 seeds, was determined to be 0.21, 0.51, and 0.80, respectively.

Seeds varied in weight from 3 to 18 mg. For open-pollinated, first- and second-time flowering ramets, there was no difference in the relationship between the number of seeds matured and the total weight of these seeds with respect to either the slopes of these relationships ($F_{1,40,0.05} = 1.37$, $p = 0.25$; Figure 2A) or the y-intercepts ($F_{1,41,0.05} = 1.89$, $p = 0.17$; Figure 2A). There was a positive relationship between the number of seeds matured and

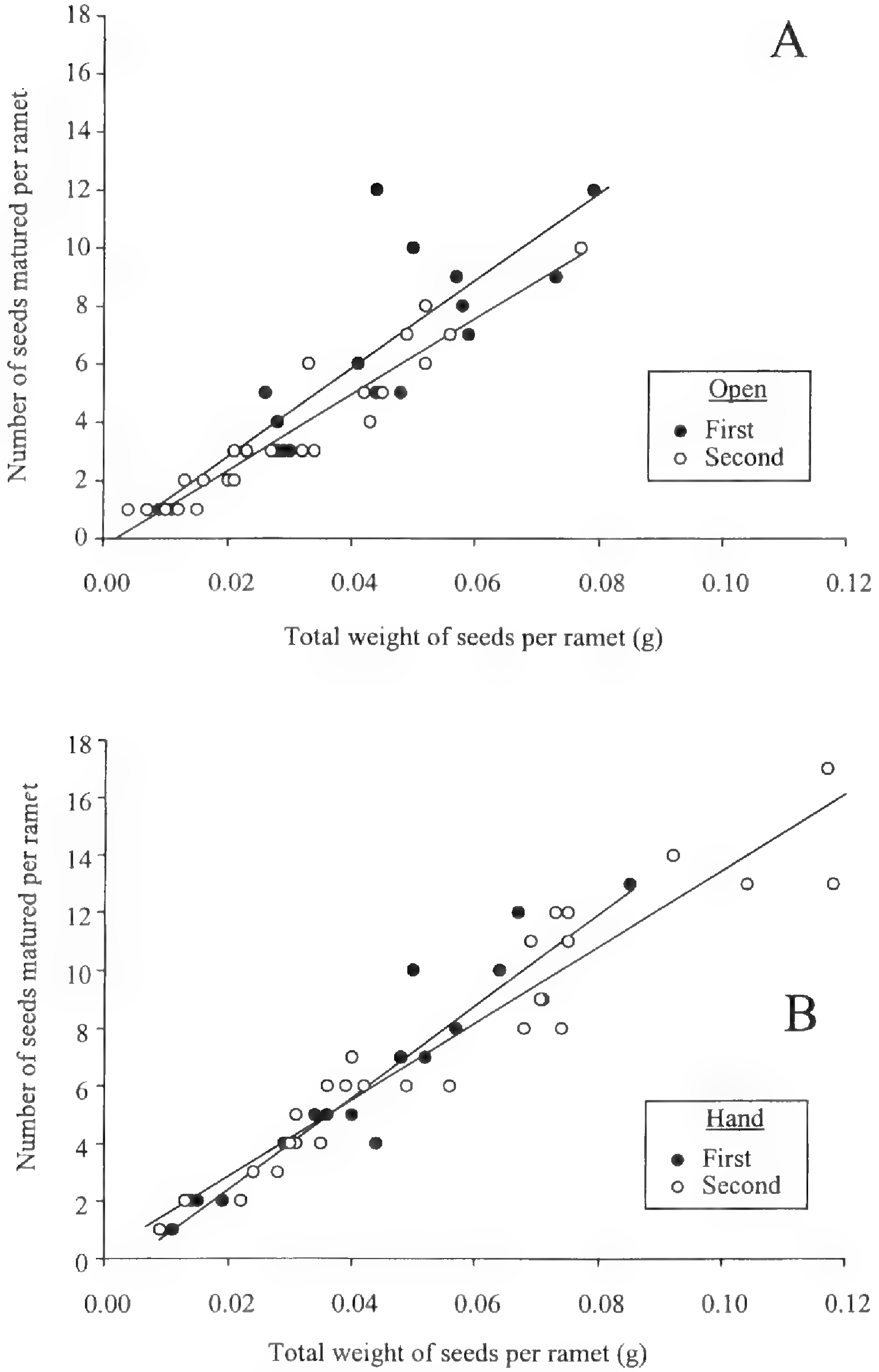

Figure 2. Plots of the number of seeds matured by *Maianthemum canadense* ramets and the total weight of these seeds for (A) open-pollinated ramets and (B) hand-pollinated ramets. First = first-time flowering ramets; Second = second-time flowering ramets; Open = open-pollinated ramets; and Hand = hand-pollinated ramets.

the total weight of these seeds ($F_{1,40,0.05} = 176.25$, $p < 0.001$, $r^2 = 0.83$). For hand-pollinated, first- and second-time flowering ramets, there was no difference in the relationship between the number of seeds matured and the total weight of these seeds with respect to the slopes ($F_{1,41,0.05} = 2.57$, $p = 0.12$; Figure 2B) or the y-intercepts ($F_{1,42,0.05} = 0.55$, $p = 0.46$; Figure 2B). There was a relationship between the number of seeds matured and the total weight of these seeds ($F_{1,41,0.05} = 290.78$, $p < 0.001$, $r^2 = 0.90$).

Seed number was used as the dependent variable in both the ANOVA and the ANCOVAs in order to focus on what factors influenced seed maturation in Canada mayflower. It would also be valid in the ANCOVAs to use seed number as the independent variable and the total weight of seeds per ramet as the dependent variable. This, however, would change the focus from what factors influenced seed maturation to what influence did seed number have on seed weights. The results of such analyses did not differ from those presented above and this is likely due to an overall correlation between seed number and the total weight of seeds ($p < 0.001$, $r^2 = 0.92$).

DISCUSSION

The number of years prior to flowering for first-time flowering ramets and the number of years since flowering for second-time flowering ramets were not related to the number of seeds matured by ramets. Therefore ramets that waited longer to flower did not necessarily mature more seeds. Watson (1984, 1990) has referred to ramets as "mouths" which accumulate resources for use by the genet and for the ramet itself in the future. It is possible that with Canada mayflower, a vegetative ramet continues to accumulate resources until a specific threshold is reached and that this triggers the transition to a flowering ramet. The number of years since flowering may then be related to two variables: (1) the cost incurred by the ramet for past flowering and seed maturation (this may be influenced by the degree of ramet integration) and (2) the quality of the habitat. In other words, a ramet that waited a greater number of years to flower again may have incurred a great cost of previous reproduction, one that the genet was not able to offset, or the quality of the habitat was such that resources were able to be replenished only very slowly, or even some combination of the two. It may also be that another part of the genet was flowering during the intervening years between flowering and that the ramet in question was subsidizing the seed maturation of another part of the genet.

Ramets matured comparable numbers of seeds regardless of whether this was their first- or second-time flowering. Thus the act of flowering did not appear to influence the success of future seed maturation. This was true as well for ramets that received an overabundance of pollen. For this contrast, statistical power was low for a hypothesized difference of one seed. However, at a hypothesized difference of three seeds (approximately the difference between the pollination treatment means) power was quite high.

The addition of pollen resulted in an increase of, on average, 2.7 seeds per ramet. This suggests that seed maturation in ramets was pollen limited during the experiment. Moreover, the addition of pollen had a similar effect on ramets flowering for the first and second time.

There was a strong relationship between the number of seeds matured and the total weight of these seeds for both open- and hand-pollinated ramets. Furthermore this relationship did not differ between ramets flowering for the first and second time. This is further evidence that there was not a cost of having flowered in the past.

While it was possible to determine if ramets had previously flowered, nothing is known about the success of previous flowering. It could be that seed maturation in the past was low and therefore the costs incurred by ramets at that time was also low. The cost of having flowered and reproduced in the past may also have been mitigated by other ramets at the time of flowering. Canada mayflower ramets are known to have increased seed maturation if they receive ample pollen and their rhizomes are left intact, but not if ramets receive ample pollen and their rhizomes are severed (Ganger 1997). This suggests that resources may be translocated to the flowering ramet, either from the rhizome or from other ramets, and may offset the cost of reproduction incurred by the ramet. It is important to note that second-time flowering ramets are much rarer than first-time flowering ramets and that second-time flowering ramets are a subset of ramets that have flowered before. Therefore these results should be viewed with caution.

Canada mayflower is not the only example of a plant in which a cost of previous flowering was not detected. In fact some plants show an increased likelihood of future flowering with greater current reproductive allocation. In the orchid *Spiranthes cernua,* Antlfinger and Wendel (1997) found that individuals producing fewer flowers were less likely to flower in the following year than individuals producing more flowers. This was despite the fact that individuals producing many flowers had a tendency to decrease in size in the following year. In the early spider orchid *Ophrys sphegodes,* Hutchings (1987) found that individuals flowering in the current year were: (1) more likely to flower in the following year than either vegetative or dormant individuals, (2) less likely to enter dormancy than either vegetative or dormant individuals, and (3) had greater survivorships than dormant individuals.

Other species show no effect of current flowering on future reproduction. Horvitz and Schemske (1988) experimentally created high and low levels of reproductive effort in *Calathea ovandensis* and found no difference in the growth, survival, and reproduction of individuals between treatments in the following year. Smith and Young (1982) found that individuals of *Senecio keniodendron* that had high levels of reproduction were more likely to die than other individuals. However those that did survive had higher levels of reproduction than other individuals in the following year.

The notion that previous reproduction should negatively affect present reproduction seems plausible. Since in plants, size and reproduction and size and survivorship tend to be positively correlated, allocation of resources to reproduction in the current year may not only reduce growth in the current year, but may also reduce future fecundity and survivorship due to decreased size (Lovett Doust 1989; Stephenson 1981). This relationship in plants such as Canada mayflower appears to be difficult to establish, in part because of the ability of Canada mayflower to be vegetative for a number of years between flowering and also due to Canada mayflower's clonal habit. These would allow Canada mayflower ramets to mitigate the cost of previous and current reproduction. It is possible then that the cost of previous reproduction, while not apparent at the level of the ramet, would be evident at the level of the genet.

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LONG-TERM VEGETATION DYNAMICS OF THE LOWER STRATA OF A WESTERN MASSACHUSETTS OXBOW SWAMP FOREST

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ABSTRACT. The structure, composition, and floristics of understory swamp forest vegetation in Ned's Ditch, a segment of a regularly flooded oxbow in Northampton, Massachusetts, has been investigated at intervals from 1973 through 1996. The forest canopy is dominated by *Acer saccharinum* in association with *Quercus palustris* and *Fraxinus pennsylvanica*; these species are regenerating despite the deaths of a number of trees between 1975 and 1985. The shrub stratum, dominated by *Cephalanthus occidentalis*, has remained relatively unchanged. In the herbaceous stratum, species abundances fluctuate from year to year in relation to flooding and other aspects of hydrology with aquatics such as *Lemna minor* increasing during wet years and annuals, particularly *Bidens* spp., growing to maturity in times of drought. The abundance of *Osmunda regalis* and *Onoclea sensibilis* has remained relatively constant over the 23 year period, but tree seedlings have become increasingly important though few have been recruited to the upper strata. Overall, emergent and floating hydrophytes in the herb stratum have tended to decline although the composition of the flora of the herb stratum continues to strongly resemble the flora of adjacent marshes. These observations suggest that preserving and successfully managing Ned's Ditch and similar floodplain forests will require the maintenance of species of diverse ecological requirements adapted to a range of habitat conditions.

Key Words: swamp forest, floodplain vegetation, herbaceous flora, forested wetlands, Connecticut River, Massachusetts

Although the importance of forests along floodplains within river ecosystems has been increasingly recognized (Decamps

1996; Gregory et al. 1991), the dynamics of floodplain forest vegetation remain poorly understood. Not surprisingly, investigations of economically important floodplain forest trees (Jones et al. 1994; Megonigal et al. 1997; Robertson et al. 1978) have been more common than studies of floodplain herbs and shrubs (Menges and Waller 1983). Kearsley (1999a) has recently inventoried Massachusetts floodplain forests and devised a classification that includes understory species; however long-term studies of the composition and structure of lower floodplain forest strata continue to be scarce.

In western Massachusetts, studies of vegetation within Connecticut River oxbows have been in progress since 1969 (Robinton and Burk 1971). Four of these oxbows form an apparent chronosequence, a "spatial array" of sites of different ages (Barbour et al. 1987) in various stages of seral development ranging from open water through freshwater marsh to mature swamp forest (Holland and Burk 1990). The most thoroughly studied of these sites, Ned's Ditch, is the northwestern segment of an oxbow that was cut off from the main stream of the Connecticut River around 710 (±130) YBP as determined by stratigraphy and radiocarbon dating (Holland and Burk 1982). Now owned by the Massachusetts Audubon Society as a part of Arcadia Wildlife Sanctuary, Ned's Ditch contains one of the largest stands of floodplain swamp forest in New England. The vegetation of the area within the old river bed includes this forest, stands of buttonbush (*Cephalanthus occidentalis*), and relic marsh communities surrounding ponds and remnants of the abandoned channel of an adjacent stream (Holland and Burk 1984, 1990). Ned's Ditch is regularly flooded during periods of heavy precipitation and/or high water on the Connecticut River with floodwaters entering its eastern section from an adjacent oxbow that was cut off from the main stem of the Connecticut River in 1840 (Holland and Burk 1982). During unusually heavy flooding, floodwaters also enter from the channel of the Mill River on the western margin of Ned's Ditch. Studies conducted during the period 1973–1977 (Holland and Burk 1984) indicated that the canopy trees, particularly the most prominent species, *Acer saccharinum, Quercus palustris,* and *Fraxinus pennsylvanica,* were well represented by seedlings in the understory and apparently replacing themselves. Hence the Ned's Ditch forest community was thought to be in a state of "hydric disclimax" (Daubenmire 1968) or "pulse stability" (Odum 1969) that might persist indefinitely (Holland and Burk 1984).

A resampling of the Ned's Ditch canopy in 1985, however (Holland and Burk 1986), indicated that a number of trees of all species had died since 1975, with highest mortalities in the lower size classes (3.0–13.5 cm diameter). In addition, recruitment from the herb stratum had been extremely low. Comparable tree deaths and low recruitment were also observed by studies in a regularly flooded oxbow in Hatfield, Massachusetts, a "younger" stage in the oxbow chronosequence (Holland 1998; Holland and Burk, in press), but not in an "older" rarely flooded stage on a higher Connecticut River terrace in Whately, Massachusetts (Holland and Burk 1986, in press, and unpubl. data). Field studies a decade later in Ned's Ditch indicated that few canopy trees died between 1985 and 1995/96. Nonetheless, although seedlings of *Acer saccharinum, Quercus palustris,* and *Fraxinus pennsylvanica* were abundant, few trees had been recruited into the smaller stem classes of the canopy (Burk et al. 1996).

This study compared the shrub and herb strata of Ned's Ditch during the interval 1973–1977 with their state in 1985 and again in 1995/96. Specific goals of the study were:

(1) to document the abundance and distribution of the vascular plant species comprising the shrub and herb strata of the Ned's Ditch swamp forests throughout this 23 year interval;
(2) to assess changes in the abundance and distribution of vascular plant species in these strata throughout the study period;
(3) to attempt to identify long-term changes in vegetation between 1973 and 1995/96, and to distinguish long-term changes from changes that reflect short-term fluctuations in hydrological conditions, including drought and flooding;
(4) to examine relationships between the vegetation of the lower strata of the swamp forest and the vegetation of adjacent marshes.

MATERIALS AND METHODS

Quantitative sampling of the canopy, shrub, and herb strata of the Ned's Ditch forest was initiated in the summer of 1973 and repeated during 1974, 1975, 1977, 1985, and 1995–1996. Quantitative sampling of marsh vegetation in Ned's Ditch was conducted in 1973, 1974, 1975, 1984, and 1994.

As a part of the 1973 sampling, five transects were laid out at 285 m intervals across Ned's Ditch, beginning near its eastern margin. Each transect extended from the old Connecticut River bank through the former river bed to the opposite bank, a distance of approximately 306 m. Along each transect, swamp forest vegetation occurred within the former Connecticut River bed, adjacent to the old Connecticut River bank on both sides but at a lower elevation. Stands of buttonbush swamp and ponds with relict marsh communities occurred farther towards the centers of the transects; transitions between swamp forest and the buttonbush swamp and marsh communities were abrupt and boundaries between each vegetation type were easily delimited.

To sample swamp forest vegetation, ten 10 m × 10 m permanent plots were established, two on each transect beginning 3.3 m in from the edge of the forest closest to the bank at each end. In 1996, the four corners of each plot were marked with buried rebar which could be re-located by means of a metal detector during successive sampling periods. The shrub stratum in each plot was sampled within a 5 m × 5 m quadrat located in one corner of each plot. Presence and coverage were estimated for each woody vascular plant species occuring as a shrub or sapling. To sample the herbaceous stratum within each 10 m × 10 m plot, ten 1 m × 1 m quadrats were laid out, five at regular intervals along the transect and five at regular intervals along a baseline perpendicular to the transect. Presence and coverage as determined by visual estimate were noted for all vascular plants including herbs, vines, and woody seedlings under 60 cm height in each of the 100 smaller quadrats. In addition the presence and cover of the aquatic moss *Amblystegium riparium* (Hedw.) BSG. (Amblystegiaceae) was also recorded for each smaller quadrat. Sampling of the ten 5 m × 5 m shrub quadrats was conducted during July and August of 1973, 1975, and 1985. Because of time constraints, six shrub quadrats were sampled in July and August of 1995 and the remaining four in 1996. Sampling of all 100 1 m × 1 m quadrats was conducted during July and August of 1973, 1974, 1975, 1977, and 1985. Sampling of 60 smaller quadrats within six 10 m × 10 m plots was conducted in 1995 and the remaining 40 smaller quadrats within the four other 10 m × 10 m plots were sampled in 1996. During each sampling

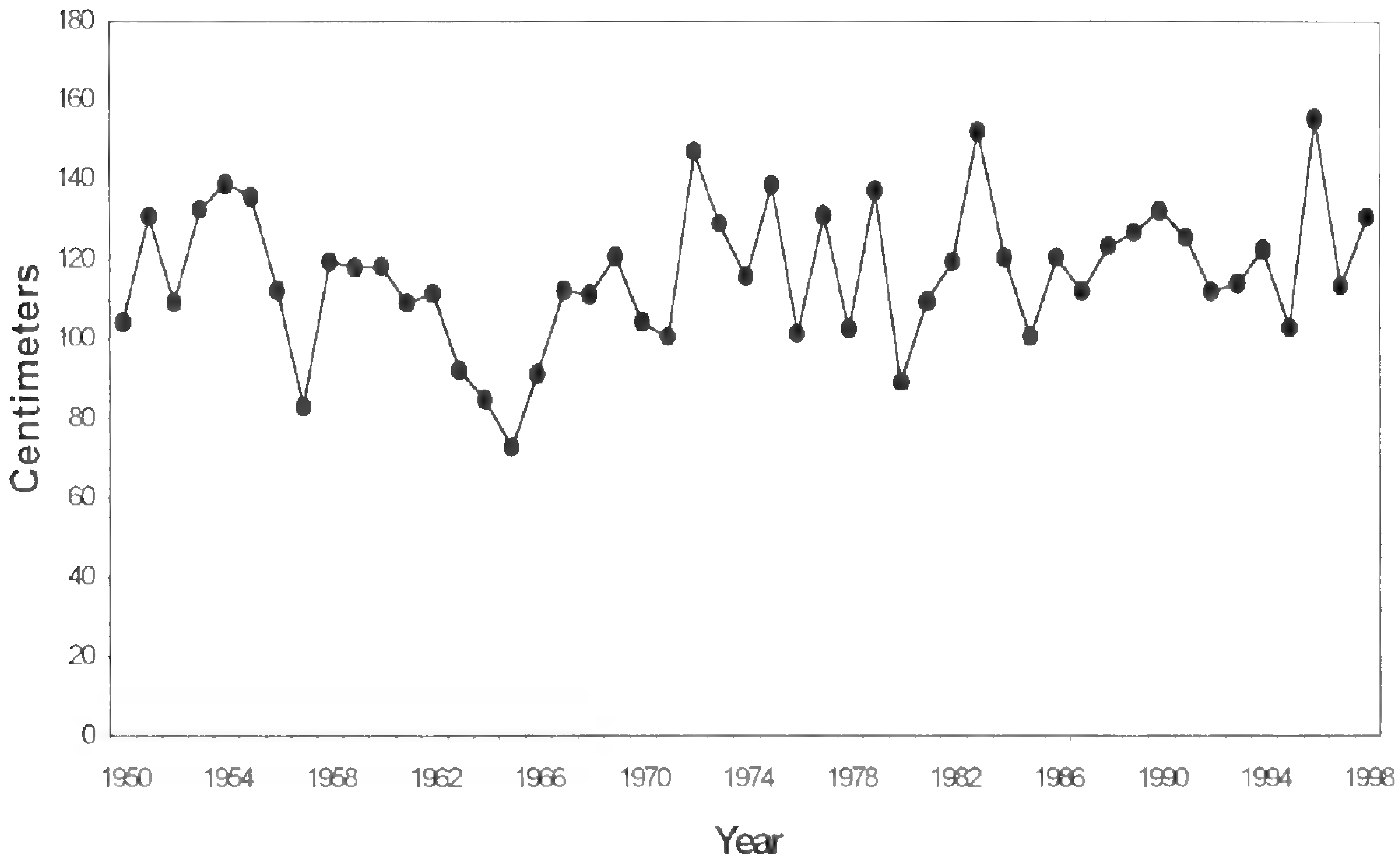

Figure 1. Total annual precipitation (cm) in the study area, 1950 through 1998. See text for sources.

period, studies of the shrub and herb strata were coordinated with sampling of the canopy within each plot.

In some instances, particularly in years when growth was delayed or disrupted by late spring or summer flooding, a number of very small plants in the quadrats could be identified only at the generic level. Because of this, immature specimens of several regularly or sporadically encountered genera that might be represented in the sampling by more than one species are grouped together under their respective genera. Nomenclature of fern species follows *Flora of North America North of Mexico* (Flora of North America Editorial Committee 1993). Nomenclature of seed plants follows Fernald (1950) except for *Bidens tripartita* L. to include *B. comosa* (A. Gray) Wieg. and *B. connata* Muhl. Voucher specimens have been deposited in SCH.

For analysis and comparison, average percent cover and frequency were recorded for each species with cover values rounded off to the nearest whole number. Summed cover values for each year's sampling were calculated using actual rather than rounded data. Species richness, the total number of species present in each stratum, was calculated by counting all species present. Species grouped to genera as a single unit were counted only once in determining richness. For example, seedlings listed as *Cornus* spp. were counted as such, even though mature specimens of *C.*

alternifolia L.f., *C. amomum* Miller, and *C. stolonifera* Michx. were present at the site as potential seed sources. Discussions of the value of cover and frequency data in assessing vegetational change are in Daubenmire (1968) and Mueller-Dombois and Ellenberg (1974), and are summarized with reference to the adjacent oxbow marshes in Holland and Burk (1990).

The permanent plots and all quadrats were systematically placed, and we have attempted to re-locate each individual quadrat at each sampling period; hence probability statistics cannot be used as aids in interpreting the data (Barbour et al. 1987; Mueller-Dombois and Ellenberg 1974). As in earlier studies of changes in floristic composition over a series of collecting periods (Holland and Burk 1990; Holland and Sorrie 1989; Lauermann and Burk 1976), the Simpson Index of Resemblance (Simpson 1965) was used to compare the taxonomic composition of the herb stratum in successive years of sampling. Simpson's Index of Resemblance (100 c/n1, in which c is the number of species common to the two floras and n1 is the number of species in the smaller flora) is helpful in comparing floras of approximately equal sizes in a common area. In addition, to assess interrelationships between the composition of the Ned's Ditch swamp forest and floras of adjacent Ned's Ditch marshes, Simpson's Index was also used to compare the swamp forest in 1977, 1985, and 1995/96 with the composition of the Ned's Ditch marshes. The marshes were sampled in 1974 and 1984 (Holland and Burk 1990) and again in 1994, one year prior to the sampling of the forest (Holland and Burk, unpubl. data).

Data on yearly precipitation (Figure 1) were obtained from the website www.ncdc.noaa.gov/onlineprod/drought/temp/drought_15006 for western Massachusetts from 1950 through 1998. Data on the times of major flooding were obtained from our own observations of the site.

RESULTS

As in earlier studies (Holland and Burk 1984, 1990) tables were prepared listing all vascular plant species in any quadrat for each sampling period. Data from 1973 are available in Sackett (1974) and data from 1973, 1974 and 1975 in Sackett (1977). The 1975 data are also included in Holland and Burk (1984) with an indication of species sampled earlier but not in 1975 and spe-

Table 1. Composition of the herb stratum in Ned's Ditch in 1977, 1985, and 1995/96. Numbers represent mean and standard deviation (in parentheses) of percent cover (C), frequency (F), and total number of species sampled. [1]mostly *B. tripartita* L. and *B. cernua* L., [2]mostly *S. nigra* Marshall.

	1977		1985		1995/96	
Species	C	F	C	F	C	F
Herbs and vines						
Agrostis alba L.	<0.5 (0.83)	4	—	—	—	—
Agrostis perennans (Walter) Tuckerman	1 (3.25)	11	—	—	—	—
Alisma subcordatum Raf.	<0.5 (0.88)	5	<0.5 (0.06)	1	<0.5 (0.66)	4
Apios americana Medikus	3 (8.14)	11	7 (14.68)	19	2 (4.34)	16
Arisaema triphyllum (L.) Schott	<0.5 (0.48)	5	<0.5 (0.13)	5	<0.5 (0.72)	8
Bidens frondosa L.	4 (4.85)	61	3 (6.27)	34	<0.5 (0.68)	14
Bidens spp.[1]	<0.5 (0.70)	18	7 (5.24)	75	<0.5 (0.16)	8
Boehmeria cylindrica (L.) Swartz	1 (1.35)	46	4 (7.97)	50	2 (4.46)	19
Cardamine pensylvanica Muhl.	<0.5 (0.28)	6	<0.5 (0.02)	1	—	—
Carex tribuloides Wahlenb.	3 (10.25)	10	<0.5 (0.20)	<0.5	—	—
Carex spp.	1 (1.12)	18	<0.5 (0.27)	<0.5	1 (1.24)	7
Celastrus scandens L.	—	—	<0.5 (0.03)	1	—	—
Cicuta bulbifera L.	—	—	<0.5 (0.17)	6	—	—
Cuscuta gronovii Willd.	—	—	<0.5 (0.03)	1	—	—
Dryopteris carthusiana (Villars) H. P. Fuchs	1 (2.14)	3	1 (2.37)	4	—	—
Dulichium arundinaceum (L.) Britton	<0.5 (0.09)	5	<0.5 (0.13)	4	—	—
Echinochloa crusgalli (L.) P. Beauv.	—	—	<0.5 (0.03)	1	—	—
Eleocharis acicularis (L.) Roemer & Schultes	6 (13.4)	25	<0.5 (0.16)	16	1 (1.26)	5
Erechtites hieracifolia (L.) Raf.	—	—	<0.5 (0.52)	9	—	—
Eupatorium spp.	<0.5 (0.32)	1	—	—	—	—

Table 1. Continued.

Species	1977		1985		1995/96	
	C	F	C	F	C	F
Galium spp.	1 (0.54)	31	1 (1.52)	32	<0.5 (0.47)	9
Geum virginianum L.	—	—	<0.5 (0.22)	6	—	—
Glyceria fernaldii (Hitchc.) St. John	—	—	12 (14.56)	54	3 (6.25)	20
Hieracium spp.	—	—	<0.5 (0.04)	2	—	—
Hypericum virginicum L.	<0.5 (0.09)	1	<0.5 (0.88)	7	<0.5 (0.19)	2
Impatiens capensis Meerb.	<0.5 (0.09)	3	<0.5 (0.68)	6	<0.5 (0.16)	4
Leersia oryzoides (L.) Swartz	1 (1.44)	11	<0.5 (0.90)	15	—	—
Lemna minor L.	4 (7.71)	36	<0.5 (0.14)	3	<0.5 (0.22)	26
Ludwigia palustris (L.) Ell.	1 (2.35)	25	<0.5 (0.14)	17	—	—
Ludwigia polycarpa Short & Peter	<0.5 (0.69)	2	<0.5 (0.40)	2	—	—
Lycopus uniflorus Michx.	—	—	—	—	<0.5 (0.68)	10
Lycopus virginicus L.	<0.5 (0.19)	5	<0.5 (1.10)	5	<0.5 (0.47)	1
Lysimachia ciliata L.	<0.5 (0.13)	5	<0.5 (0.13)	1	—	—
Lysimachia nummularia L.	<0.5 (0.06)	2	<0.5 (0.13)	3	1 (0.89)	9
Lysimachia terrestris (L.) BSP.	1 (0.84)	13	1 (1.09)	25	1 (1.09)	11
Onoclea sensibilis L.	6 (13.97)	13	5 (9.27)	27	6 (14.72)	18
Osmunda regalis L.	5 (10.47)	15	8 (16.27)	13	6 (10.94)	14
Panicum clandestinum L.	<0.5 (0.54)	3	—	—	—	—
Parthenocissus quinquefolia (L.) Planchon	—	—	—	—	<0.5 (0.22)	6
Penthorum sedoides L.	1 (2.74)	8	<0.5 (0.14)	3	—	—
Phalaris arundinacea L.	—	—	<0.5 (0.28)	2	—	—
Pilea pumila (L.) A. Gray	<0.5 (0.68)	16	—	—	—	—
Polygonum amphibium L.	—	—	1 (1.64)	6	—	—
Polygonum hydropiperoides Michx.	—	—	<0.5 (1.22)	7	—	—

Table 1. Continued.

Species	1977		1985		1995/96	
	C	F	C	F	C	F
Polygonum punctatum Elliott	<0.5 (0.82)	9	—	—	—	—
Polygonum spp.	<0.5 (0.03)	1	—	—	<0.5 (0.16)	2
Prunella vulgaris L.	—	—	<0.5 (0.02)	1	—	—
Ranunculus flabellaris Raf.	8 (10.54)	38	1 (0.67)	40	<0.5 (0.82)	12
Rhus radicans L.	<0.5 (0.04)	2	<0.5 (0.18)	9	1 (2.78)	6
Sagittaria latifolia Willd.	—	—	<0.5 (0.19)	1	—	—
Scutellaria lateriflora L.	1 (0.75)	23	1 (1.02)	18	<0.5 (0.44)	6
Sium suave Walter	1 (0.97)	17	1 (1.25)	43	<0.5 (1.00)	7
Smilax herbacea L.	<0.5 (0.28)	3	<0.5 (0.35)	3	<0.5 (0.32)	1
Solanum dulcamara L.	—	—	<0.5 (0.25)	6	<0.5 (0.16)	2
Solidago spp.	<0.5 (0.03)	1	—	—	—	—
Spirodela polyrhiza (L.) Schleiden	<0.5 (0.32)	8	—	—	—	—
Thelypteris palustris Schott	—	—	—	—	2 (4.60)	5
Woody seedlings						
Acer saccharinum L.	9 (6.03)	77	8 (8.90)	78	7 (9.64)	60
Alnus rugosa (DuRoi) Sprengel	—	—	<0.5 (0.06)	1	—	—
Catalpa speciosa Warder	—	—	<0.5 (0.02)	1	—	—
Cephalanthus occidentalis L.	7 (5.36)	62	5 (4.92)	60	3 (2.62)	37
Cornus spp.	1 (0.99)	20	<0.5 (0.73)	4	<0.5 (0.81)	4
Fraxinus pennsylvanica Marshall	2 (3.06)	51	2 (3.00)	36	3 (3.94)	42
Ilex verticillata (L.) A. Gray	1 (1.24)	13	<0.5 (0.33)	5	<0.5 (0.47)	1
Populus deltoides Marshall	—	—	<0.5 (0.05)	2	—	—
Quercus palustris Muenchh.	1 (2.36)	7	<0.5 (0.28)	19	1 (1.28)	17
Robinia pseudoacacia L.	<0.5 (0.38)	14	—	—	<0.5 (0.06)	11
Salix spp.[2]	<0.5 (0.35)	7	<0.5 (0.03)	1	<0.5 (0.02)	1

Table 1. Continued.

	1977		1985		1995/96	
Species	C	F	C	F	C	F
Ulmus rubra Muhl.	<0.5 (0.05)	3	<0.5 (0.09)	10	<0.5 (0.25)	8
Viburnum recognitum Fern.	—	—	—	—	<0.5 (0.06)	1
Vitis spp.	1 (1.39)	27	2 (2.67)	24	1 (2.20)	5
Total species	50		57		39	

cies not in any quadrat but present elsewhere in swamp forest at the site. Data from 1977, 1985, and 1995/96, all previously unpublished, are included here in Table 1.

Despite the changes in the canopy of the Ned's Ditch swamp forest that were evident by 1985 (Burk et al. 1996; Holland and Burk 1986), the shrub stratum has remained relatively unchanged during the interval 1973–1995/96 (Table 2). Coverage of the dominant *Cephalanthus occidentalis* declined between 1973 and 1975 but returned to near 1973 levels by 1985. A decline of *Acer saccharinum* and *Fraxinus pennsylvanica* observed in the 1995/96 sampling of the shrub stratum probably reflects the recruitment of saplings of these tree species from the shrub stratum into the canopy.

Changes in the herb stratum for the period 1973 through 1977 were presented in Holland and Burk (1984). Within the herb stratum, total vegetative cover rose from a low of 14% in 1973 to 71% by 1975 and continued at a slightly higher level through 1977. The very low cover in 1973 resulted from damage caused by an atypical flood that had completely inundated the herb stratum for at least ten days in early July, less than a month before the sampling period (Holland and Burk 1984). Species richness rose from a low of 27 in 1973 to 47 by 1975 (Holland and Burk 1984) and continued at a somewhat higher level through 1977 (Table 1).

Total cover in the herb stratum remained relatively constant from 1975 through 1985 and then declined over the next ten year period (Table 3). Overall cover was lowest in years with late spring or summer floods and highest in wet years without late spring or early summer flooding. Species richness reached a high of 57 species in 1985 but had declined to 39, little above its 1974 level by 1995/96 (Table 1). The higher diversity in 1985 resulted, in part, from the presence of weedy species such as *Erechtites hieracifolia* and *Prunella vulgaris,* which had become established in small numbers under the unusually dry conditions of that season, and possibly, in part, because of the higher light levels in lower strata resulting from the extensive mortalities among canopy trees. Most invaders of this sort did not persist through 1995/96 (Table 1).

From 1977 through 1995/96, the abundance of the prominent rhizomatous ferns, *Onoclea sensibilis* and *Osmunda regalis* remained relatively constant, presumably in large part because the

Table 2. Variation in the cover of shrubs in Ned's Ditch. Numbers represent mean and standard deviation (in parentheses) of percent cover of each vascular plant species and percent total cover.

	Year			
Species	1973	1975	1985	1995/96
Acer saccharinum	8 (15.22)	11 (31.35)	8 (15.10)	1 (1.75)
Alnus rugosa	—	<0.5 (0.32)	<0.5 (0.63)	<0.5 (0.95)
Cephalanthus occidentalis	37 (32.65)	20 (26.38)	33 (31.24)	35 (39.08)
Cornus spp.	5 (5.77)	4 (4.86)	<0.5 (0.95)	2 (4.83)
Fraxinus pennsylvanica	—	2 (4.69)	8 (23.68)	<0.5 (0.34)
Ilex verticillata	1 (2.71)	2 (5.25)	4 (6.34)	5 (11.07)
Quercus palustris	1 (1.63)	<0.5 (0.42)	—	—
Salix spp.	—	1 (3.48)	—	—
Viburnum recognitum	—	<0.5 (0.32)	—	—
Vitis spp.	<0.5 (1.26)	1 (1.90)	—	4 (11.01)
Total cover (%)	52	45	54	48

Table 3. Variation in percent relative cover of vascular plant species in the herb stratum of Ned's Ditch. Relative cover of species at 5% or more total cover at any sampling period and total cover—see discussion of *Amblystegium riparium* in text.

	Year and Hydrology					
Species	1973 July Flood	1974 Dry	1975 Wet	1977 Wet	1985 Dry	1995/96 Dry/Wet
Acer saccharinum	7	11	6	12	11	17
Apios americana	1	<0.5	1	3	10	5
Bidens spp.	<0.5	1	1	4	14	2
Boehmeria cylindrica	<0.5	<0.5	<0.5	1	5	4
Cephalanthus occidentalis	1	8	6	10	7	6
Dulichium arundinaceum	29	17	10	<0.5	<0.5	0
Eleocharis acicularis	1	3	3	8	<0.5	1
Fraxinus pennsylvanica	1	1	1	2	3	6
Glyceria fernaldii	—	—	—	—	16	7
Lemna minor	7	3	48	7	<0.5	<0.5
Onoclea sensibilis	14	11	1	8	7	15
Osmunda regalis	14	14	4	7	11	14
Ranunculus flabellaris	1	3	3	11	1	1
Total cover (%)	14	36	71	73	74	43

same clones have been encountered at each sampling period. In addition, three major trends were noted within the vegetation of the herb stratum:

(1) The relative abundances of the more important species continued to fluctuate from year to year, apparently in relation to hydrology (Figure 1; Table 3). Hydrophytes increased during wet years such as 1975 and 1977 (Holland and Burk 1984). During dry seasons, annuals, particularly *Bidens* spp. grew to maturity and, while flowering, achieved "aspect dominance" (Oosting 1956) as in 1985 (Table 3 and field observations during dry years when sampling was not conducted).
(2) The relative cover of tree seedlings, particularly seedlings of *Acer saccharinum* and *Fraxinus pennsylvanica* increased (Table 3). In 1973, *Dulichium arundinaceum, Onoclea sensibilis,* and *Osmunda regalis* were the most prominent species, in descending order of abundance. By 1995/1996, *A. saccharinum* was most abundant, followed by *Onoclea sensibilis* and *Osmunda regalis.*
(3) Hydrophytes generally declined from previous levels of abundance. These included both "errant hydrophytes" (Mueller-Dombois and Ellenberg 1974) such as *Lemna minor, Ranunculus flabellaris,* and *Spirodela polyrhiza* (Table 1), and emergents. *Potamogeton pectinatus* L. and *Utricularia vulgaris* L. were sampled in 1975 (Holland and Burk 1984) but not later. A nonvascular errant hydrophyte, the moss *Amblystegium riparium* was present at every sampling period in the 1970s, reaching a peak cover of 21% of the total substratum in 1977, occurring in 81% of the quadrats sampled. The peak abundance of *A. riparium* appeared to be inversely related to the abundance of *L. minor,* which had reached its maximum in 1975 and declined by 1977 (Table 3). *Amblystegium riparium* was not seen during 1985, a dry season, nor identified in 1995; it was encountered again in nearly half the plots sampled in 1996 with an average cover of 2% of the substratum.

Several emergent hydrophytes also found in the high- and mid-marsh zones of the adjacent ponds declined markedly as well. *Dulichium arundinaceum,* the most abundant species of the herb stratum in 1973 and 1974, was present only at very low levels

Table 4. Simpson's Index of Resemblance comparing the flora of the Ned's Ditch swamp forest herb stratum at each sampling period to the flora of successive samplings of that stratum.

Year of Initial Sampling	Years of Successive Sampling				
	1974	1975	1977	1985	1995/96
1973	88.9	81.5	77.8	70.4	63.0
1974		77.8	83.3	77.8	63.9
1975			72.3	70.2	74.4
1977				72.9	81.6
1985					81.6

in 1977 and 1985 and not sampled at all in 1995/96. *Eleocharis acicularis* persisted at generally low levels throughout the period, reaching its greatest abundance in 1977 and then declining.

Table 4 compares the herb flora of Ned's Ditch at each sampling period from 1973 to 1985 to the floras of successive sampling periods at the specific level. Floras from sampling periods closer in time tended to be more similar than floras from longer intervals, and the least similar floras were those of the first and last collections of data, 1973 and 1995/96. When Ned's Ditch marshes were compared with the swamp forest herb stratum in successive years of sampling, similarities tended to be higher when comparisons were made between marsh and forest floras at the closer time intervals (Table 5). Levels of forest/marsh similarity fall within the range of forest/forest similarities. The Simpson Index comparing the composition of the Ned's Ditch swamp forest in 1974 with the forest in 1995/96 is identical with Simpson's Index comparing the Ned's Ditch marsh in 1974 with the forest in 1995/96.

Table 5. Simpson's Index of Resemblance comparing the flora of the Ned's Ditch marshes to the herbaceous flora of the adjacent swamp forest herb stratum at each successive sampling.

Year of Marsh Sampling	Years of Swamp Forest Sampling			
	1973/75	1977	1985	1995/96
1974	75.8	75.0	72.2	63.9
1984			74.1	71.1
1994				79.5

DISCUSSION

Fluctuations in the composition of the herb stratum of Ned's Ditch in response to seasonal variations in hydrology may represent a community response to conditions associated with a particular form of hydric disclimax, i.e. a persistent state maintained by recurrent but irregular flooding. During wet seasons, hydrophytic species become abundant; during dry seasons these are largely replaced by mesophytic forms (Holland and Burk 1984). Together the understory flora represents a spectrum of life forms including annuals, woody seedlings, emergent perennial graminoids, perennial forbs, errant hydrophytes, annuals, and vines.

Previous comparisons of the herb stratum of the Ned's Ditch swamp forest to the floras of adjacent marshes have shown a stronger resemblance than that of other oxbow swamp forests and their marshes (Holland and Burk 1990). While the low marsh dominants *Nuphar variegata* Durand and *Potamogeton pectinatus* did not extend into the forest, many species were shared by both communities (Table 5), and despite the decline of hydrophytes in the swamp forest over the last two decades of the study, the floras of the marshes and the herb stratum of the forest continued to be strongly similar. In part this similarity reflects dispersal during periods of flooding when high water extended throughout the oxbow, connecting ponds and forest. In addition, the ponds occasionally dried out and species more frequently found in the forest became established on exposed pond bottoms.

The increased relative abundance of woody seedlings and overall decline in hydrophytes in Ned's Ditch may have resulted, in part, from drier conditions associated with changes in elevation resulting from sedimentation and from reduced available light on the forest floor associated with the growth of the canopy trees. Studies of comparable Wisconsin floodplain forests have characterized *Bidens* spp. and *Lemna* spp. as high-light specialists at the lowest elevations of the herb strata and *Acer saccharinum* and *Onoclea sensibilis* as light generalists at somewhat higher elevations; seedlings of *A. saccharinum* have been shown to germinate well in either light or shade (Peterson and Bazzaz 1984). Scouring through heavy flooding and high mortalities of the dominant trees before 1985 (Burk et al. 1996) may have slowed or reversed these trends since long periods of flooding are particularly harmful to young seedlings of *A. saccharinum* (Peterson and Bazzaz 1984).

Similar effects of different flood regimes have also been observed in Louisiana swamp forests that contain understory species in common with Ned's Ditch (Conner and Day 1976). Stands that were flooded to a depth of 0.6 m much of the year possessed constantly saturated soil and herb strata containing only floating and emergent aquatics, including *Lemna minor* and *Spirodela polyrhiza.* Forests that were inundated for two to three months in the spring but surface-dry in summer supported more diverse lower strata of "briars, grasses and annual herbs" along with seedlings, saplings, and woody vines.

Related studies (Conner et al. 1981) contrasted the effects of altered flood regimes in swamp forests that had shared similar vegetation and seasonal flooding through the 1950s. In an undisturbed control site, growth of aquatics and understory woody vegetation was limited by shading and periodic flooding. In a site now permanently flooded, the resultant deaths of canopy trees, particularly *Fraxinus* spp., increased light penetration and allowed the spread of aquatics, including *Lemna minor* and *Spirodela polyrhiza.* After permanant inundation, flood-tolerant shrubs also invaded, including *Cephalanthus occidentalis,* the seeds of which are capable of germinating underwater (see references in Conner et al. 1981). In a site now managed by controlled winter/spring flooding followed by an annual summer/fall drawdown, aquatic species were absent. The managed site was increasingly dominated by *Acer rubrum* var. *drummondii* and *Fraxinus,* taxa with seeds that germinate during the dry period to produce seedlings that become established before flooding.

Since the initial sampling of vegetation in Ned's Ditch, the concept of a vegetation type that may persist indefinitely through "pulse stability" (Odum 1969) has been explored with reference to floodplain forests in particular. Odum et al. (1979), using data from Conner and Day (1976) for examples, have suggested that moderate or seasonal flooding may result in increased tree growth in mature floodplain forests composed of species already well adapted to the flooding regime. Continuous high levels of flooding, however, may result in impounded and stagnant conditions that stress canopy vegetation and reduce productivity. More recent studies (Megonigal et al. 1997) conclude that the results of flooding are complex and affected by the timing and length of floods and the relative strength of their flow. In addition, stresses resulting from drought and anaerobic soils may offset any benefits of flooding (Mitsch and Rust 1984).

CONSERVATION

The integrity of the Ned's Ditch swamp forest community is largely dependent on dynamic hydrological conditions resulting from periodic flooding on the Connecticut River. In 1973, at the time of the initial sampling, much of the site was privately owned and subject to intermittent logging, dumping of wastes, and other disruptive human activities. The entire Northampton oxbow including the Ned's Ditch forest is now owned by the Massachusetts Audubon Society and preserved as a natural area with a management plan (McGuire 1988) that includes control of potentially invasive exotic species. With the exception of *Lysimachia nummularia,* non-native species have not been regularly encountered in Ned's Ditch; although *Solanum dulcamara, Prunella vulgaris,* and seedlings of *Catalpa speciosa* were sampled in 1985, only *S. dulcamara* persisted until 1995. Nonetheless, a number of potentially invasive species, several of which are now frequently encountered in other Massachusetts floodplain forests (Kearsley 1999b) are well established nearby. These include *Acer platanoides* L., *Berberis thunbergii* DC, *Celastrus orbiculatus* Thunb., *Polygonum cuspidatum* Sieb. & Zucc., *Rhamnus frangula* L., and *Catalpa speciosa,* which is spreading along the Mill River at the western margin of Ned's Ditch (Burk and Prabhu 1988). Spread of these species should be monitored and, if necessary, curtailed because of their potential harm to native species (Weatherbee et al. 1998). Of particular concern is *Ludwigia polycarpa,* currently threatened in Massachusetts (Massachusetts Natural Heritage and Endangered Species Program 1997) and not seen at its former locations in Ned's Ditch since 1985 (Holland and Burk 1990).

Sustaining biological diversity may be particularly critical in ecosystems such as floodplain forests that experience seasonal or longer fluctuations in hydrology (Grime 1997; Keddy and Reznicek 1982). Our studies, along with other investigations of floodplain forest vegetation, suggest that preserving and successfully managing these communities will require the maintenance of species of diverse ecological requirements adapted to a range of habitat conditions. In these dynamic systems, individual species tend to fluctuate in abundance and may sometimes disappear completely from a given floodplain forest site. Hence a range of similar protected sites within the region may be essential in providing reservoirs from which species may be recruited as habitat conditions change. Since our earliest vegetation studies in Ned's Ditch, we have argued for the conservation of floodplain forests and other wetland habitats (Holland and Burk 1984, 1990); and Kearsley's recent inventory (Kearsley 1999a) reinforces the necessity for maintaining these increasingly scarce plant communities, particularly transitional and "Small-river" floodplain forests, few of which are now protected, on a broader scale within the state and region.

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VASCULAR FLORA OF BEAVER WETLANDS IN WESTERN MASSACHUSETTS

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ABSTRACT. The composition and structure of vegetation in beaver wetlands located in Franklin and Hampshire Counties of western Massachusetts were studied from 1980 to 1995. A flora of 231 vascular plants was recorded within fifteen selected field sites including seven new county records and one state-listed species (*Ophioglossum vulgatum* var. *pseudopodum*). Relatively few species (5.6% of the total flora) were introduced. Factors contributing to high vascular plant diversity included 1) steep hydrological gradients created by beaver dams; 2) spatial heterogeneity caused by beaver artifacts, human structures and geological features; and 3) temporal heterogeneity resulting from beaver activity and hydrological fluctuations. While beaver activity has helped maintain regional vascular plant diversity in western Massachusetts since the reestablishment of beaver populations in the 1920s, current increases in beaver densities may pose a threat to later successional wetland species.

Key Words: beaver (*Castor canadensis*), vascular flora, wetlands, Massachusetts

The beaver (*Castor canadensis*) has had a profound impact on the landscape of western Massachusetts. Trapped to regional extinction in the mid-18th century, it returned in 1924 when a colony immigrated into West Stockbridge (Berkshire County). Augmented by reintroductions by the Massachusetts Department of Conservation, the state-wide population expanded rapidly, totaling approximately 52,000 in 1999 (S. Langlois, pers. comm.).

Beavers alter the structure and composition of both upland and riparian vegetation. They forage on woody vegetation 60 m or more from a stream course, girdling and felling trees, shrubs, and vines (Hall 1960; Rutherford 1955) and utilizing over 90 woody food species throughout their range (McMaster 1989).

Beaver dams in Massachusetts are constructed of branches, vines, shrubs, herbaceous plant material, boulders, sand, gravel, and mud. They range from 0.3 to 2 m in height and 3 to 300 m in length (Shaw 1948). Often placed against stone walls or culverts, they span stream channels and extend to the edges of the adjacent uplands.

New dams create impoundments up to 8 ha in area extending upstream and into the uplands along the stream margins. Above dams, soils are saturated, stream velocity is reduced, and sediment accumulates. Below dams, discharge rates decline and sediment loads are reduced (Naiman et al. 1988). These hydrological alterations in turn influence stream biogeochemistry including carbon cycling (Naiman et al. 1986), methane evasion rate (Ford and Naiman 1988), soil redox potential (Naiman et al. 1988), pH and acid-neutralizing capacity (Smith et al. 1991), and biological oxygen demand and dissolved oxygen concentration (Naiman et al. 1988).

Following inundation, most woody vegetation is killed within one or two growing seasons. Within five years shallower areas, particularly along the pond margins or adjacent to the dams or lodges, are colonized by floating-leaved and submerged aquatics and emergent hydrophytic plants.

When beaver colonies are removed by trapping or predation or when they migrate to another site as food supply dwindles, unmaintained dams deteriorate and sites gradually drain. The upstream end of a site and the lateral margins usually drain first while the areas immediately above the dam and surrounding the lodge are often among the last to drain. Eventually the stream cuts a channel in the bottom sediments before exiting through one or more openings in the abandoned dam.

An unmaintained beaver dam may impound water during spring meltout and after periods of heavy precipitation, thus affecting site hydrology for years, sometimes decades, after abandonment. Factors that influence the frequency, extent, and duration of reflooding include the condition of the old dam, the topographical gradient of the site, and the size of the watershed upstream of the site (McMaster 1997).

The goals of the study initiated by Nancy D. [Mosher] McMaster in 1980 were to describe the composition and structure of the vascular vegetation in beaver-impacted wetlands, to analyze vegetational changes over the duration of the study, and to develop a model for succession in beaver-impacted wetlands. She initially sampled all vascular vegetation in fifteen sites over the period from 1980 to 1984 and began resampling in 1985, a process that continued until her death in 1990 (McMaster 1989). In 1991 Robert T. McMaster resumed the sampling schedule, employing the transects and methodology of the previous work (McMaster 1997).

This paper presents a combined list of vascular plant species found in all fifteen sites over the period 1980–1995 from both studies, as well as abundance data, descriptions of plant communities, county and state records, and changes in species diversity. A more detailed analysis of the structure and dynamics of vascular vegetation over the fifteen-year interval will be presented in a forthcoming paper.

MATERIALS AND METHODS

Eighty sites in Franklin and Hampshire Counties were initially identified from topographic maps and aerial photographs as likely beaver-impacted wetlands. After field reconnaissance, sites currently occupied by beavers and sites subject to human disturbance such as burning, logging, and excavation were eliminated. The fifteen sites thus selected (Figure 1; Table 1) ranged in area from 0.6 to 8.0 ha and in elevation from 164 to 465 m above sea level. All were located on the eastern slope of the Berkshire Plateau in an area of finely corrugated muscovite schist interbedded with layers of gneiss and white quartzite (McMaster 1989). Soils were a combination of glacial tills, alluvium, and muck (Egler 1940). Five sites were adjacent to paved roads, six to unpaved roads, and four were accessible only by footpath.

Site histories were reconstructed by examination of USDA Soil Conservation Service maps and panchromatic black and white aerial photographs (scale 1:24,000), US Geological Survey maps, deeds, town histories, by communication with property owners, and by field observation. Sites were monitored regularly for presence or absence of active beaver colonies throughout the period of the study. Site age (i.e. number of years since last beaver occupation of a site) was determined from communication with property owners or local residents for activity previous to 1980 and from direct observation in the field for sites occupied since 1980.

Vegetation was sampled along transects established across each site parallel to the remains of the beaver dam. Along each transect, 0.5 m × 0.5 m quadrats were located at 2 m intervals. Five categories were used to estimate abundance based on criteria de-

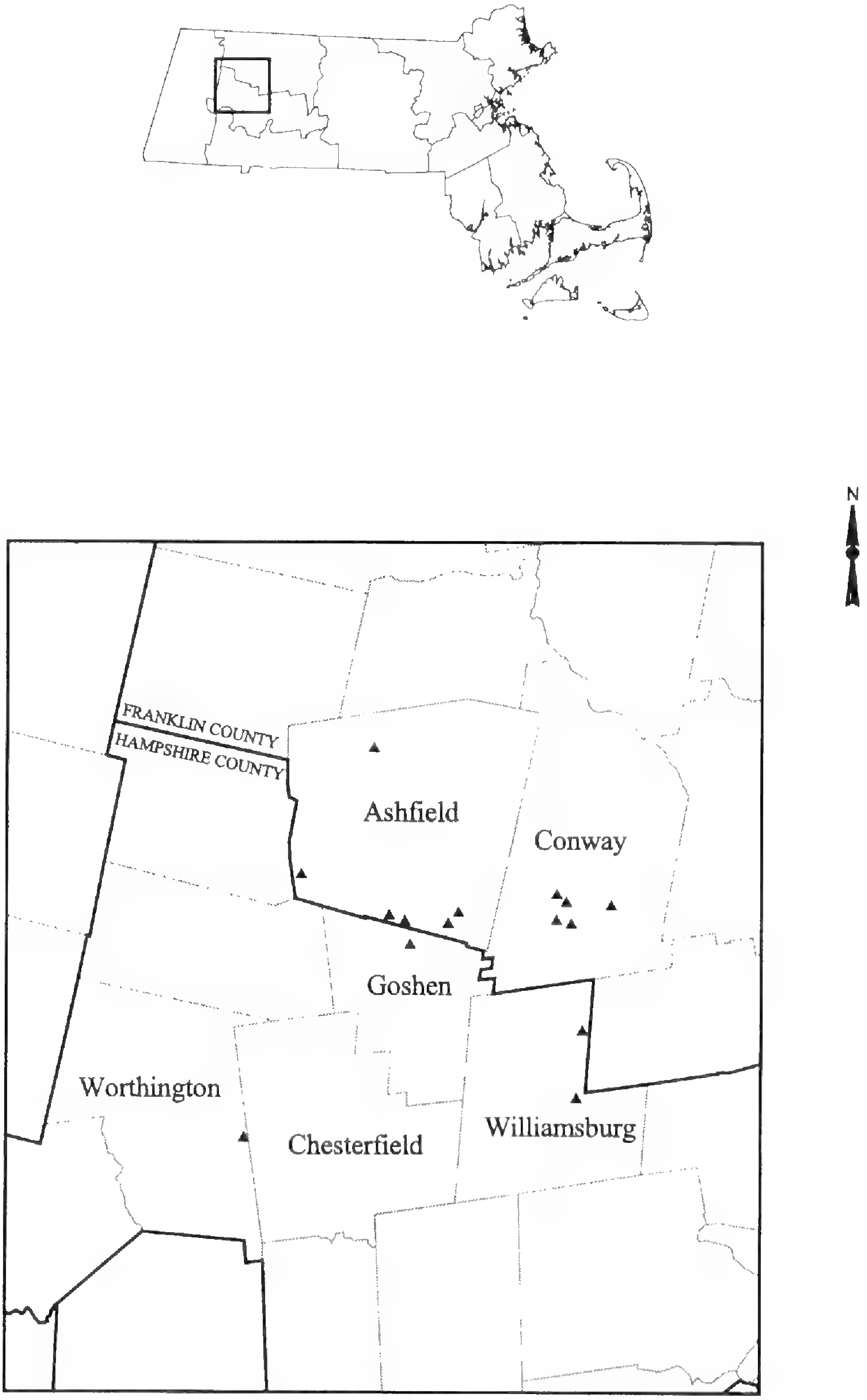

Figure 1. Location of field sites.

Table 1. County, watershed, elevation above sea level (m), area (ha), and age (years) since last beaver occupation (as of 1995) for the fifteen study sites. [1]Refers to the Mill River with headwaters in Conway, which enters the Connecticut River at Hatfield. [2]Refers to the Mill River with headwaters in Goshen and Ashfield, which enters the Connecticut River at Easthampton.

Site	County	Watershed	Elevation (m)	Area (ha)	Age (years)
Ashfield 1	Franklin	Westfield River	417	3.8	20
Ashfield 2	Franklin	Westfield River	417	1.4	40
Ashfield 3	Franklin	Westfield River	393	2.5	1
Ashfield 4	Franklin	Mill River[1]	453	6.2	1
Ashfield 5	Franklin	Mill River[1]	453	2.5	1
Ashfield 6	Franklin	Deerfield River	465	1.8	16
Conway 1	Franklin	Mill River[1]	369	1.8	25
Conway 2	Franklin	Mill River[1]	362	2.5	35
Conway 3	Franklin	Mill River[1]	338	3.2	18
Conway 4	Franklin	Mill River[1]	329	1.0	15
Conway 5	Franklin	Mill River[1]	243	3.5	16
Goshen 1	Hampshire	Mill River[2]	417	2.1	18
Williamsburg 1	Hampshire	Mill River[1]	220	7.8	26
Williamsburg 2	Hampshire	Mill River[2]	164	0.6	16
Worthington 1	Hampshire	Westfield River	375	8.0	10

scribed by Palmer et al. (1995): abundant, frequent, occasional, infrequent, and rare.

All sites were originally sampled in mid-summer between 1980 and 1984 (McMaster 1989; Mosher 1981). Three sites, Conway 1, 2, and 3, were resampled at five year intervals. The remaining twelve sites were to be resampled at ten year intervals when possible. Seven of these were resampled on schedule. Ashfield 3, which had been reoccupied by beavers in 1992, was resampled in 1993 after the site was once again abandoned. Four sites, Ashfield 6, Conway 5, Goshen 1, and Worthington 1, which were first sampled in 1984, could not be resampled in 1994 or subsequently due to continued beaver occupation but were revisited at regular intervals.

Percent species turnover for a site (T) was calculated as follows:

$$T = (E + R)/S \times 100$$

where,

E = Number of extinctions between samplings;

Table 2. Floristic summary of plant taxa in fifteen beaver-impacted wetlands, Franklin and Hampshire Counties, Massachusetts.

Group	Families	Genera	Native Species	Introduced Species	Total Species
Pteridophytes	7	8	12	0	12
Gymnosperms	2	3	3	0	3
Angiosperms					
Dicots	45	89	138	10	148
Monocots	14	32	65	3	68
TOTAL	68	132	218	13	231

R = Number of recruitments between samplings;

S = Total number of species present in both samplings of the site.

The species list presented includes all vascular plant taxa found in systematic sampling of the fifteen sites as well as in general reconnaissance of the sites from 1980 to 1995. Nomenclature for all species and identification of introduced species are based on Gleason and Cronquist (1991). State and county records are based on Magee and Ahles (1999) and lists obtained from the Massachusetts Natural Heritage and Endangered Species Program. Voucher specimens for all taxa are held in the Smith College Herbarium (SCH).

RESULTS

The flora of the 15 study sites included 231 vascular plant taxa in 68 families and 132 genera (Table 2; Appendix). The distribution of taxa by life-form was as follows: 108 forbs, 55 graminoids, 30 shrubs, 22 trees, 12 ferns and fern allies, and 4 vines. Plant families best represented in the flora were Cyperaceae (30 species), Asteraceae (19 species), Rosaceae (16 species), and Poaceae (15 species). All but four species were perennials. Two species are county records for Hampshire County and five are county records for Franklin County (Table 3). One species is currently listed as threatened in Massachusetts, *Ophioglossum vulgatum* var. *pseudopodum,* the northern adder's-tongue fern (Massachusetts Natural Heritage and Endangered Species Program 1997). The population in this study was the largest in the state with approximately 900 sporophytes counted in 1991 (McMaster

Table 3. County records among the flora of the fifteen study sites.

Species	Site
Hampshire County	
Galium trifidum	Williamsburg 1 and 2, Worthington 1
Juncus conglomeratus	Williamsburg 1
Franklin County	
Carex eburnea	Conway 5
Carex lacustris	Ashfield 3, 4, 5
Juncus brachycephalus	Conway 3, 4
Oenothera fruticosa	Conway 3
Potentilla palustris	Ashfield 2

1994, 1996). Currently, *O. vulgatum* var. *pseudopodum* is also state-listed in Connecticut (Connecticut Department of Environmental Protection 1995) and Rhode Island (Enser 1998).

Species richness per site ranged from 32 species in Conway 2 (1995) to 79 species in Conway 5 (1984). Number of families represented in each site ranged from 19 families in Conway 2 (1995) to 34 families in Conway 5. Over one-third (84) of the species occurred in only one site. Ten species occurred in all fifteen sites: *Acer rubrum, Carex stipata, Impatiens capensis, Leersia oryzoides, Ludwigia palustris, Onoclea sensibilis, Salix sericea, Scirpus cyperinus, Spiraea alba* var. *latifolia,* and *S. tomentosa* (Appendix).

Thirteen species or 5.6% of the total vascular flora were introduced species: *Achillea millefolium, Agrostis gigantea, Berberis thunbergii, Cirsium arvense, Conium maculatum, Echinochloa crusgalli, Hypericum perforatum, Juncus conglomeratus, Lonicera* × *bella, Myosotis scorpioides, Potentilla norvegica, Rorippa nasturtium-aquaticum,* and *Solanum dulcamara.* This compared to 20% for eastern and central North America according to Fernald (1950). Eight of the thirteen introduced species occurred in only one site. The most common introduced species was *Agrostis gigantea,* which occurred in nine of the fifteen sites. Surprisingly, the site with the most introduced species was Conway 3, the most remote of all the sites.

A typical beaver-impacted wetland may best be characterized as a complex mosaic of five physiographic zones, each with its own characteristic plant community. The precise arrangement of the zones varied from site to site depending on geomorphology, beaver activity, and human disturbance.

Zone 1, open water. This zone included standing water above the dam and moving water in the stream channel that persisted throughout the growing season. Areas of deeper water were dominated by floating-leaved aquatics such as *Lemna minor* and *Utricularia vulgaris* or rooted hydrophytes such as *Brasenia schreberi, Najas flexilis, Nuphar variegata, Polygonum amphibium,* and *Potamogeton* spp. while shallower waters were colonized by emergents such as *Sparganium* spp., *Carex* spp., and *Scirpus* spp. The stream channel was often vegetated by *Potamogeton* spp. and *Ludwigia palustris.*

Zone 2, mud flats. Upstream of the open water, saturated bottom sediments were exposed through most of the growing season but were frequently reflooded for short periods. Mud flats were often dominated by stands of *Leersia oryzoides, Lysimachia terrestris,* or *Eleocharis acicularis.*

Zone 3, wet meadows. Farther upstream, the partially drained soils of wet meadows occasionally were reflooded during the growing season. They were most often dominated by species of *Carex, Scirpus, Juncus, Solidago,* and *Eupatorium* as well as by *Impatiens capensis.* In some sites tussock-forming graminoids such as *Calamagrostis canadensis, Carex stricta, Phalaris arundinacea,* and *Scirpus cyperinus* created a hummock-and-hollow microtopography (McMaster 1989).

Zone 4, drier meadows. Still farther upstream and adjacent to the site margins were drier meadows, areas of well-drained soils which rarely were reflooded during the growing season. Here emergent hydrophytic graminoids such as *Carex crinita, Eleocharis* spp., *Glyceria canadensis, Juncus effusus,* and *Typha latifolia* occurred in association with herbaceous species including *Aster puniceus, Eupatorium maculatum, Galium tinctorium,* and *Impatiens capensis.* In some sites *Typha latifolia* formed large pure stands in this zone.

Zone 5, dry meadows and upland margins. Along the wetland/upland boundaries of sites where reflooding seldom oc-

Table 4. First and last sampling years, species richness at first sampling, number of recruitments and extinctions, species richness at last sampling, net change in species richness, and percent species turnover for eleven study sites.

Site	Years Sampled	Species Richness First	Recruitments	Extinctions	Species Richness Last	Net Change	Species Turnover
Ashfield 1	82–92	47	20	22	45	−2	63%
Ashfield 2	82–92	41	12	19	34	−7	58%
Ashfield 3	82–93	40	24	19	45	+5	67%
Ashfield 4	84–94	72	18	36	54	−18	60%
Ashfield 5	84–94	68	12	41	39	−29	66%
Conway 1	80–95	57	10	15	52	−5	37%
Conway 2	80–95	44	13	25	32	−12	67%
Conway 3	80–95	70	16	27	59	−11	50%
Conway 4	84–94	55	38	23	70	+15	66%
Williamsburg 1	84–94	49	19	23	45	−4	62%
Williamsburg 2	84–94	52	22	20	54	+2	57%

curred, the emergent hydrophytes and herbaceous species found in Zone 4 mixed with a variety of woody wetland species including *Spiraea alba* var. *latifolia, Ilex verticillata,* and *Alnus incana.* Also occasionally found in this zone were saplings of woody species common in the surrounding upland, especially *Acer rubrum, Betula alleghaniensis, B. lenta, B. papyrifera, B. populifolia,* and *Prunus serotina.*

Disturbed areas. Some areas of a site including beaver dams, lodges, and food caches; stone walls; roadway embankments; and outcrops of bedrock were above high water but were subject to frequent disturbance from beaver or human activity. Vegetation in these areas included woody upland species such as *Fagus grandifolia, Fraxinus americana, Pinus strobus,* and *Tsuga canadensis,* shrubby pasture species such as *Juniperus communis* and *Berberis thunbergii,* and herbaceous species including *Conium maculatum, Achillea millefolium,* and *Solanum dulcamara.*

Table 4 lists the number of vascular plant species occurring in sampled plots over ten-to-fifteen-year intervals between sampling in eleven sites (the other four sites were not resampled due to reoccupation). Recruitments exceeded extinctions (i.e. species richness increased) in three sites over the interval between sampling while extinctions exceeded recruitments in eight sites. All but one of the eleven sites had a percent turnover of 50% or more. Mean percent turnover for the eleven sites was 67%.

DISCUSSION

Total vascular plant diversity of the fifteen field sites, 231 taxa, was relatively high considering the small area (48.7 ha) represented. In a study of the herb strata of three Connecticut River oxbows in western Massachusetts, Holland and Burk (1984) identified 130 taxa of herbs, vines, and woody seedlings over a single growing season in three sites totaling 64 ha. M. Hickler reported 177 vascular species in a three-year survey of fifteen oxbows of the Nashua River (Massachusetts) totaling 12.5 ha (pers. comm.). In a botanical survey of a 162 ha natural area in Franklin County, McMaster (1987) identified 532 vascular plant species in a single season.

High plant diversity in the study sites resulted from several factors. Spatial variability within a site may be attributed to the steep hydrologic gradient created by the dam and to the topographical heterogeneity created by beaver artifacts (dams, lodges, food caches, canals, etc.), human structures (walls, roadways, utility lines, etc.), and geological features (glacial erratics and outcrops of bedrock). Temporal variability within a site resulted from beaver activity (building of dams, lodges, and other artifacts; maintenance of beaver structures; eventual abandonment), human impacts (destruction of dams, trapping, filling, dredging, burning, grazing cattle), and hydrological effects (reflooding, draining, and drought). Invasion of dominant forest species that could shade out herbaceous species was controlled by the saturated soils over most of the area of a site. Finally, vascular plant diversity among the fifteen sites appeared to be enhanced by variations in soil and water chemistry (McMaster 1997).

The small number of introduced species may be attributed to two factors. Many of the non-native plants of eastern North America are associated with agriculture, adapted to dry, disturbed habitat such as fields or road edges, and are unlikely to germinate in the saturated soils found in beaver-impacted wetlands. Those able to germinate as soils drained in late spring or early summer may not have been able to reach maturity in the short period before reflooding occurred and conditions again became intolerable.

Two wetland plant species, *Lythrum salicaria* and *Phragmites australis*, are of particular concern in the northeastern United States due to their aggressiveness and ability to drive out native wetland species. Both are common in disturbed areas and appear to follow major transportation arteries. While *L. salicaria* is found in abundance in many wetlands of eastern and central New England, it has not yet appeared in any of the study sites. This may be due in part to elevation, climate, soil type, or to the relative remoteness of these sites from major highways. *Phragmites australis* was present in only one of the fifteen study sites where it occurred in a very limited area along an abandoned utility right-of-way.

Decline in species richness observed in eight sites was primarily among shrubs and trees, probably the result of repeated beaver occupation and reflooding during the 10–15 year interval (while all sites were inactive at the onset of the study, at least one reoccupation occurred in ten of the fifteen sites over the period of this study). Increase in species richness observed in the other three sites was due primarily to recruitment of woody species from the surrounding upland or from the seed bank as draining proceeded in the absence of reoccupation. Vascular plant diversity began to decline again in sites unoccupied for more than twenty years, however, probably due to the loss of herbaceous species unable to compete with invading shrubs and trees. Additional data on changes in species composition, zonation, and diversity in the fifteen sites over the duration of this study will be presented in a forthcoming paper.

Most of the vascular plant species found in beaver-impacted wetlands depend on the presence of saturated soils and full sun, a rare combination of conditions in New England in the absence of beaver activity. As beaver population density increases and available habitat declines, reoccupation of abandoned sites is likely to occur at shorter intervals. Under these conditions plant species such as *Ophioglossum vulgatum* var. *pseudopodum* that favor older successional sites may be expected to decline. Active management of beaver populations may be necessary to promote regional vascular plant diversity. Any anthropogenic activities that alter hydrology such as draining or filling wetlands, and diverting or channelizing streams may also have a negative impact on vascular plant diversity in these habitats.

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APPENDIX

ANNOTATED LIST OF THE VASCULAR PLANTS OF BEAVER WETLANDS IN FRANKLIN AND HAMPSHIRE COUNTIES, MASSACHUSETTS.

Species name is followed by habitat preference (Zone 1 = open water, Zone 2 = mud flats, Zone 3 = wet meadow, Zone 4 = drier meadow, Zone 5 = dry meadow and upland margin, or disturbed areas), abundance (abundant, frequent, occasional, infrequent, or rare; based on criteria described by Palmer et al. 1995), and the number of sites in which it occurred (e.g. 4/15 indicates the species occurred in 4 of the 15 sites). Introduced species are indicated by an asterisk (*). Nomenclature follows Gleason and Cronquist (1991).

LYCOPODIOPHYTA (Clubmosses)

SELAGINELLACEAE

Selaginella apoda (L.) Spring – Zone 3, rare, 1/15

EQUISETOPHYTA (Horsetails)

EQUISETACEAE

Equisetum arvense L. – Zone 5, occasional, 6/15
Equisetum sylvaticum L. – Zones 3,4,5, rare, 4/15

POLYPODIOPHYTA (Ferns)

ASPLENIACEAE

Dryopteris carthusiana (Villars) Fuchs – Zones 4,5, rare, 2/15
Thelypteris noveboracensis (L.) Nieuwl. – Zone 5, rare, 1/15
Thelypteris palustris Schott – Zones 3,4,5, frequent, 14/15

DENNSTAEDTIACEAE

Dennstaedtia punctilobula (Michx.) T. Moore – Zone 4, rare, 1/15

ONOCLEACEAE

Onoclea sensibilis L. – Zones 2,3,4,5, frequent, 15/15

OPHIOGLOSSACEAE

Ophioglossum vulgatum L. var. *pseudopodum* (S. F. Blake) Farw. – Zones 3,4, rare, 1/15

OSMUNDACEAE

Osmunda cinnamomea L. – Zones 3,4,5, rare, 6/15
Osmunda claytoniana L. – Zone 4, rare, 1/15

Osmunda regalis L. – Zones 4,5, occasional, 8/15

PINOPHYTA (Gymnosperms)

CUPRESSACEAE

Juniperus communis L. – Zone 5, disturbed areas, rare, 1/15

PINACEAE

Pinus strobus L. – Zones 4,5, disturbed areas, rare, 5/15
Tsuga canadensis (L.) Carrière – Zones 4,5, disturbed areas, rare, 3/15

MAGNOLIOPHYTA (Flowering Plants)

MAGNOLIOPSIDA (Dicots)

ACERACEAE

Acer pensylvanicum L. – Zone 5, rare, 1/15
Acer rubrum L. – Zones 4,5, occasional, 15/15
Acer spicatum Lam. – Zone 5, rare, 2/15

ANACARDIACEAE

Toxicodendron radicans (L.) Kuntze – Zones 4,5, rare, 2/15

APIACEAE

Cicuta bulbifera L. – Zones 3,4,5, rare, 1/15
**Conium maculatum* L. – Zone 4, disturbed areas, rare, 1/15
Hydrocotyle americana L. – Zones 2,3,4,5, occasional, 11/15
Sium suave Walter – Zones 1,2,5, rare, 4/15
Zizia aurea (L.) Koch – Zone 3, occasional, 1/15

AQUIFOLIACEAE

Ilex verticillata (L.) A. Gray – Zones 4,5, frequent, 11/15
Nemopanthus mucronatus (L.) Loes. – Zone 5, rare, 2/15

ARALIACEAE

Aralia nudicaulis L. – Zone 5, rare, 1/15

ASCLEPIADACEAE

Asclepias incarnata L. – Zone 3, infrequent, 1/15

ASTERACEAE

**Achillea millefolium* L. – Zone 3, disturbed areas, rare, 1/15

Aster novae-angliae L. – Zone 4, rare, 1/15
Aster puniceus L. – Zones 3,4, occasional, 11/15
Aster racemosus Elliott – Zones 3,4,5, rare, 3/15
Aster umbellatus Miller – Zone 4, rare, 1/15
Bidens cernua L. – Zones 4,5, frequent, 6/15
Bidens connata Muhl. – Zones 2,5, frequent, 6/15
Bidens frondosa L. – Zone 3, rare, 1/15
**Cirsium arvense* (L.) Scop. – Zone 3, rare, 1/15
Eupatorium maculatum L. – Zones 2,3,4,5, frequent, 12/15
Eupatorium perfoliatum L. – Zones 2,3,4,5, frequent, 14/15
Eupatorium purpureum L. – Zones 2,3,4, infrequent, 3/15
Euthamia graminifolia (L.) Nutt. – Zones 2,4, occasional, 13/15
Senecio aureus L. – Zones 3,4, rare, 3/15
Senecio obovatus Muhl. – Zone 2, rare, 1/15
Solidago caesia L. – Zone 5, rare, 1/15
Solidago canadensis L. – Zones 2,3,4, occasional, 11/15
Solidago patula Muhl. – Zones 3,4,5, infrequent, 3/15
Solidago rugosa Miller – Zones 2,4, occasional, 11/15

BALSAMINACEAE

Impatiens capensis Meerb. – Zones 2,3,4,5, frequent, 15/15

BERBERIDACEAE

**Berberis thunbergii* DC – Zone 3, disturbed areas, rare, 1/15

BETULACEAE

Alnus incana (L.) Moench – Zones 2,3,4,5, abundant, 11/15
Alnus serrulata (Aiton) Willd. – Zone 5, rare, 1/15
Betula alleghaniensis Britton – Zones 2,5, occasional, 7/15
Betula lenta L. – Zones 4,5, infrequent, 3/15
Betula papyrifera Marshall – Zone 5, infrequent, 2/15
Betula populifolia Marshall – Zones 4,5, rare, 7/15

BORAGINACEAE

**Myosotis scorpioides* L. – Zone 4, rare, 1/15

BRASSICACEAE

Cardamine pensylvanica Muhl. – Zone 1, rare, 2/15
**Rorippa nasturtium-aquaticum* (L.) Hayek – Zones 2,3, rare, 1/15

CALLITRICHACEAE

Callitriche palustris L. – Zone 1, rare, 3/15

CAPRIFOLIACEAE

**Lonicera* × *bella* Zabel – Zones 4,5, rare, 1/15
Lonicera canadensis Marshall – Zone 4, rare, 1/15
Sambucus canadensis L. – Zones 3,4,5, disturbed areas, rare, 6/15
Viburnum alnifolium Marshall – Zone 5, rare, 1/15
Viburnum dentatum L. var. *lucidum* Aiton – Zones 2,3,4,5, disturbed areas, occasional, 9/15
Viburnum lentago L. – Zone 5, rare, 2/15
Viburnum nudum L. var. *cassinoides* (L.) T. & G. – Zone 5, occasional, 4/15

CLUSIACEAE

Hypericum canadense L. – Zones 2,5, occasional, 4/15
Hypericum ellipticum Hook. – Zones 2,3, occasional, 12/15
Hypericum majus (A. Gray) Britton – Zone 4, rare, 1/15
Hypericum mutilum L. – Zones 2,4, infrequent, 12/15
**Hypericum perforatum* L. – Zones 2,3,4, rare, 3/15
Triadenum virginicum (L.) Raf. – Zones 2,3,4,5, frequent, 2/15

CORNACEAE

Cornus amomum Miller – Zones 2,3,4, disturbed areas, occasional, 4/15

DROSERACEAE

Drosera rotundifolia L. – Zones 4,5, infrequent, 7/15

ERICACEAE

Lyonia ligustrina (L.) DC – Zones 3,4,5, infrequent, 2/15
Vaccinium corymbosum L. – Zone 5, occasional, 8/15

FABACEAE

Amphicarpaea bracteata (L.) Fern. – Zone 4, rare, 1/15
Apios americana Medikus – Zone 5, rare, 1/15

FAGACEAE

Fagus grandifolia Ehrh. – Zone 5, rare, 1/15
Quercus rubra L. – Zone 5, rare, 1/15

GENTIANACEAE

Gentiana clausa Raf. – Zones 2,3, infrequent, 1/15

HAMAMELIDACEAE

Hamamelis virginiana L. – Zones 4,5, occasional, 2/15

JUGLANDACEAE

Juglans cinerea L. – Zone 5, rare, 1/15

LAMIACEAE

Lycopus americanus Muhl. – Zones 2,4,5, infrequent, 6/15
Lycopus unifolorus Michx. – Zones 2,3,4, occasional, 6/15
Lycopus virginicus L. – Zones 2,4,5, infrequent, 12/15
Mentha arvensis L. – Zone 2, disturbed areas, infrequent, 7/15
Prunella vulgaris L. – Zone 3, rare, 1/15
Scutellaria galericulata L. – Zones 2,3,4, rare, 5/15
Scutellaria lateriflora L. – Zones 3,4,5, rare, 4/15

LAURACEAE

Lindera benzoin (L.) Blume – Zone 5, rare, 1/15

LENTIBULARIACEAE

Utricularia vulgaris L. – Zone 1, occasional, 3/15

MYRICACEAE

Myrica gale L. – Zones 2,3,4,5, occasional, 1/15

NYMPHAEACEAE

Brasenia schreberi J. F. Gmelin – Zone 1, rare, 1/15
Nuphar variegata Durand – Zone 1, infrequent, 1/15

OLEACEAE

Fraxinus americana L. – Zone 5, disturbed areas, rare, 1/15

ONAGRACEAE

Circaea alpina L. – Zones 3,4, rare, 1/15
Epilobium coloratum Biehler – Zones 3,4, rare, 7/15
Epilobium glandulosum Lehm. – Zone 2, occasional, 2/15
Epilobium leptophyllum Raf. – Zone 2, rare, 1/15
Epilobium strictum Muhl. – Zones 3,4,5, infrequent, 7/15
Ludwigia palustris (L.) Elliott – Zone 2, occasional, 15/15
Oenothera fruticosa L. – Zones 4,5, rare, 1/15

OXALIDACEAE

Oxalis acetosella L. – Zones 3,4,5, infrequent, 5/15

Oxalis stricta L. – Zones 3,4,5, rare, 2/15

POLYGONACEAE

Polygonum amphibium L. – Zones 1,2, rare, 1/15
Polygonum arifolium L. – Zones 3,4,5, rare, 4/15
Polygonum hydropiper L. – Zones 2,3, infrequent, 9/15
Polygonum pensylvanicum L. – Zone 1, rare, 2/15
Polygonum sagittatum L. – Zones 2,3,4, disturbed areas, occasional, 13/15

PRIMULACEAE

Lysimachia ciliata L. – Zones 3,4, rare, 1/15
Lysimachia terrestris (L.) BSP. – Zones 2,3,4,5, frequent, 9/15
Trientalis borealis Raf. – Zone 5, rare, 1/15

RANUNCULACEAE

Caltha palustris L. – Zones 2,3,4, occasional, 4/15
Clematis virginiana L. – Zones 3,4,5, occasional, 7/15
Coptis trifolia (L.) Salisb. – Zones 4,5, rare, 2/15
Ranunculus tricophyllus Chaix – Zone 1, occasional, 1/15
Thalictrum pubescens Pursh – Zones 1,3,4, disturbed areas, rare, 5/15

ROSACEAE

Aronia arbutifolia (L.) Elliott – Zones 3,4,5, infrequent, 3/15
Fragaria virginiana F. V. Duchesne – Zone 3, rare, 2/15
Geum laciniatum Murray – Zones 3,4, rare, 2/15
Geum rivale L. – Zones 3,4, rare, 2/15
Potentilla fruticosa L. – Zones 3,4,5, rare, 2/15
**Potentilla norvegica* L. – Zone 4, rare, 1/15
Potentilla palustris (L.) Scop. – Zone 3, rare, 1/15
Potentilla simplex Michx. – Zones 2,3,4,5, rare, 10/15
Prunus serotina Ehrh. – Zones 4,5, infrequent, 7/15
Prunus virginiana L. – Zone 4, rare, 1/15
Rubus hispidus L. – Zones 2,3,4,5, disturbed areas, occasional, 13/15
Rubus idaeus Michx. – Zones 2,3,4,5, occasional, 7/15
Rubus pubescens Raf. – Zone 5, infrequent, 1/15
Rubus setosus Bigelow – Zone 4, rare, 1/15
Spiraea alba DuRoi var. *latifolia* (Aiton) Dippel – Zones 2,3,4,5, disturbed areas, abundant, 15/15
Spiraea tomentosa L. – Zones 2,3,4,5, occasional, 15/15

RUBIACEAE

Cephalanthus occidentalis L. – Zones 4,5, rare, 1/15
Galium asprellum Michx. – Zones 2,3, occasional, 6/15
Galium palustre L. – Zone 2, occasional, 1/15

Galium tinctorium L. – Zones 2,3,4,5, abundant, 14/15
Galium trifidum L. – Zones 2,3,4,5, occasional, 9/15
Galium triflorum Michx. – Zone 5, rare, 1/15

SALICACEAE

Populus balsamifera L. – Zone 3, rare, 1/15
Populus tremuloides Michx. – Zone 5, infrequent, 3/15
Salix bebbiana Sarg. – Zones 3,4,5, rare, 3/15
Salix discolor Muhl. – Zones 2,5, infrequent, 5/15
Salix eriocephala Michx. – Zones 4,5, infrequent, 2/15
Salix lucida Muhl. – Zones 3,4,5, infrequent, 2/15
Salix nigra Marshall – Zone 5, rare, 1/15
Salix sericea Marshall – Zones 3,4,5, occasional, 15/15

SAXIFRAGACEAE

Penthorum sedoides L. – Zone 2, infrequent, 4/15
Saxifraga penysylvanica L. – Zone 4, rare, 1/15
Tiarella cordifolia L. – Zone 2, rare, 1/15

SCROPHULARIACEAE

Chelone glabra L. – Zones 3,4,5, infrequent, 4/15
Mimulus ringens L. – Zones 2,3, infrequent, 11/15
Veronica americana (Raf.) Schwein. – Zones 2,3,4, rare, 2/15
Veronica scutellata L. – Zone 3, rare, 1/15

SOLANACEAE

**Solanum dulcamara* L. – Zones 3,4,5, disturbed areas, rare, 3/15

ULMACEAE

Ulmus rubra Muhl. – Zone 4, rare, 1/15

URTICACEAE

Boehmeria cylindrica (L.) Swartz – Zones 2,3,4, infrequent, 1/15

VERBENACEAE

Verbena hastata L. – Zones 2,3,4, rare, 3/15

VIOLACEAE

Viola cucullata Aiton – Zone 5, rare, 1/15
Viola lanceolata L. – Zones 3,4, rare, 2/15
Viola macloskeyi Lloyd – Zones 2,4,5, infrequent, 14/15

VITACEAE

Parthenocissus quinquefolia (L.) Planchon – Zone 3, rare, 1/15

LILIOPSIDA (Monocots)

ALISMATACEAE

Sagittaria latifolia Willd. – Zones 2,4, occasional, 4/15

ARACEAE

Arisaema triphyllum (L.) Schott – Zone 3, rare, 1/15

CYPERACEAE

Carex atlantica L. Bailey – Zones 2,3,4,5, occasional, 11/15
Carex canescens L. – Zones 2,4, infrequent, 2/15
Carex comosa F. Boott – Zones 2,3,4,5, abundant, 8/15
Carex crinita Lam. – Zones 2,4, frequent, 7/15
Carex debilis var. *debilis* Michx. – Zones 3,4, rare, 2/15
Carex eburnea F. Boott – Zones 4,5, rare, 1/15
Carex flava L. – Zones 2,4,5, infrequent, 10/15
Carex intumescens Rudge – Zones 2,3, abundant, 4/15
Carex lacustris Willd. – Zones 3,4, occasional, 3/15
Carex lupulina Muhl. – Zone 3, rare, 1/15
Carex lurida Wahlenb. – Zones 2,3,4, occasional, 14/15
Carex scabrata Schwein. – Zones 3,4, rare, 1/15
Carex scoparia Schkuhr – Zones 2,4, occasional, 11/15
Carex stipata Muhl. – Zones 2,3,4,5, occasional, 5/15
Carex stricta Lam. – Zones 3,4,5, abundant, 13/15
Carex vulpinoidea Michx. – Zones 4,5, occasional, 4/15
Cyperus bipartitus Torr. – Zone 5, rare, 1/15
Cyperus strigosus L. – Zone 3, rare, 1/15
Dulichium arundinaceum (L.) Britton – Zones 3,4,5, abundant, 9/15
Eleocharis acicularis (L.) Roemer & Schultes – Zones 2,3,5, occasional, 8/15
Eleocharis ovata (Roth) Roemer & Schultes – Zone 2, frequent, 13/15
Eleocharis palustris L. – Zones 2,5, occasional, 6/15
Eleocharis tenuis (Willd.) Schultes – Zones 2,4,5, frequent, 12/15
Rhynchospora capitellata (Michx.) Vahl – Zone 1, rare, 3/15
Scirpus atrovirens Willd. – Zones 2,4, occasional, 5/15
Scirpus cyperinus (L.) Kunth – Zones 2,3,4,5, occasional, 15/15
Scirpus microcarpus C. Presl. – Zones 2,4,5, occasional, 9/15
Scirpus polyphyllus Vahl – Zone 1, rare, 2/15
Scirpus smithii A. Gray – Zones 2,3,4, rare, 5/15
Scirpus validus Vahl – Zones 2,4, infrequent, 8/15

ERIOCAULACEAE

Eriocaulon aquaticum (Hill) Druce – Zone 2, rare, 1/15

IRIDACEAE

Iris versicolor L. – Zones 1,2,3,4, rare, 10/15
Sisyrinchium montanum Greene – Zone 1, rare, 1/15

JUNCACEAE

Juncus brachycephalus (Engelm.) Buchenau – Zones 3,4, rare, 2/15
Juncus brevicaudatus (Engelm.) Fern. – Zones 2,4, occasional, 11/15
Juncus canadensis J. Gay – Zone 4, infrequent, 6/15
**Juncus conglomeratus* L. – Zone 4, rare, 1/15
Juncus effusus L. – Zones 2,3,4, occasional, 14/15
Juncus marginatus Rostk. – Zone 1, rare, 1/15

LEMNACEAE

Lemna minor L. – Zone 1, occasional, 6/15
Spirodela polyrhiza (L.) Schleiden – Zone 1, rare, 2/15

LILIACEAE

Lilium canadense L. – Zone 2, rare, 1/15

NAJADACEAE

Najas flexilis (Willd.) Rostkov & Schmidt – Zones 1,2,3, frequent, 2/15

ORCHIDACEAE

Habenaria psycodes (L.) Sprengel var. *psycodes* – Zone 3, rare, 1/15
Liparis loeselii (L.) Rich. – Zones 2,3, rare, 1/15

POACEAE

**Agrostis gigantea* Roth – Zones 2,3,4, frequent, 10/15
Agrostis hyemalis (Walter) BSP. – Zone 3, rare, 1/15
Brachyelytrum erectum (Schreber) P. Beauv. – Zone 3, rare, 1/15
Calamagrostis canadensis (Michx.) P. Beauv. – Zones 2,3, abundant, 10/15
**Echinochloa crusgalli* (L.) P. Beauv. – Zone 5, rare, 1/15
Glyceria canadensis (Michx.) Trin. – Zones 2,3,4,5, occasional, 14/15
Glyceria grandis S. Wats. – Zone 4, rare, 1/15
Glyceria melicaria (Michx.) C. E. Hubbard – Zone 4, rare, 2/15
Glyceria striata (Lam.) A. Hitchc. – Zones 2,3,4, infrequent, 9/15
Leersia oryzoides (L.) Swartz – Zones 2,3,4,5, abundant, 15/15
Muhlenbergia mexicana (L.) Trin. – Zones 2,5, infrequent, 4/15
Panicum lanuginosum Elliott – Zones, 3,4, infrequent, 2/15
Panicum rigidulum Nees – Zones 2,3,4, rare, 1/15
Phalaris arundinacea L. – Zones 2,3,4, frequent, 7/15
Phragmites australis (Cav.) Trin. – Zone 3, rare, 1/15

SPARGANIACEAE

Sparganium americanum Nutt. – Zones 1,2,3,4,5, frequent, 7/15
Sparganium androcladum (Engelm.) Morong – Zones 2,3,5, occasional, 9/15
Sparganium chlorocarpum Rydb. – Zones 2,3,5, occasional, 6/15

TYPHACEAE

Typha latifolia L. – Zones 2,3,4,5, abundant, 12/15

ZOSTERACEAE

Potamogeton epihydrus Raf. – Zone 1, rare, 3/15
Potamogeton natans L. – Zone 1, rare, 2/15

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NEW ENGLAND NOTE

REDISCOVERY OF *SYMPHYOTRICHUM ANTICOSTENSE* IN THE UNITED STATES

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Symphyotrichum anticostense (Fern.) Nesom (synonyms: *Aster anticostensis* Fern., *A. gaspensis* Victorin) was first described by Merritt Lyndon Fernald from Anticoste Island, Quebec (Fernald 1915). Since its discovery, this species has had a complicated taxonomic history. It has been considered by various authors to be a distinct species (under each of the above names), a variety, or a form unworthy of recognition. In the third case, it has been placed with *Symphyotrichum novi-belgii* (L.) Nesom (synonym: *Aster novi-belgii*), which it closely resembles. Studies by Brouillet and Labrecque (1987) have shown *S. anticostense* (as *Aster*) to be an allopolyploid derivative of *S. novi-belgii* and *S. boreale* (Torr. & Gray) Nesom.

Recent work by Xiang (1994), Xiang and Semple (1996), and Nesom (1993, 1994) has shown that the genus *Aster,* as treated by Fernald (1950) and Gleason and Cronquist (1991), is polyphyletic. Some of the plants traditionally considered to be asters are more closely related to *Erigeron,* the fleabanes, than to *Aster sensu stricto.* In addition, the genus *Solidago* is nested within *Aster sensu lato* and necessitates name changes (i.e., renaming all the goldenrods as *Aster,* or subdividing *Aster* into smaller, monophyletic groups). Their approach, after carefully weighing the data, has been to split *Aster* into a number of small, morphologically similar groups to create a nomenclatural system that matches the phylogeny of these plants.

Identification of *Symphyotrichum anticostense* is somewhat problematic because of its intermediate morphology between *S. boreale* and *S. novi-belgii,* and because it is known to hybridize with the latter. In many respects it resembles a robust *S. boreale,* with firm, ascending leaves that barely clasp the stem, erect branches of the capitulescence, and appressed phyllaries that are herbaceous at the apex and chartaceous at the base. However, unlike *S. boreale,* it has a thicker stem and rhizome (>2.0 mm wide) and larger leaves (width and length). *Symphyotrichum novi-belgii* is distinguished from both of these species by its phyllaries, that are usually foliaceous and squarrose, its open-branched capitulescence, and herbaceous to fleshy, clasping leaves. A detailed description of this species' morphology, a photo of the type specimen, and key to related species are provided in Labrecque and Brouillet (1990; as *Aster*).

Symphyotrichum anticostense is endemic to northeastern North America, known only from Anticoste Island, the Gaspé, and the St. John and Aroostook River watersheds (Labrecque and Brouillet 1990). It was first collected in the United States by M. L. Fernald in 1901 in Fort Fairfield, Maine (under the name *Aster junceus* Ait.). It was found in circumneutral gravel on the shore of the Aroostook River, near the U.S.–Canada border. Unfortunately, this site was destroyed by a rise in water level caused by Tinker Dam in the early part of the century. Though field surveys have revealed new populations in Quebec and New Brunswick (Luc Brouillet, pers. comm.), this aster has not been collected from Maine for nearly a century. It is listed in *Flora Conservanda*: New England (Brumback and Mehrhoff, et al. 1996) as historic and presumed extirpated in the state (SX). Recent reports of this aster in Maine in Gleason and Cronquist (1991) are based on annotations of historic material by Labrecque and Brouillet (1990).

Utilizing natural community and historic range information gathered from articles (Fernald and Wiegand 1910; Labrecque and Brouillet 1990) and herbarium labels (at MAINE), I surveyed sites along river shores on 5 and 6 September 1998 in seven townships on the St. John and Aroostook Rivers that are known presently, or were known historically, to possess the appropriate substrate and/or associated species. *Symphyotrichum anticostense* is usually found on well-drained, circumneutral, cobble shores that are kept open by water and ice scour. It often grows with other well-known species that favor this habitat, such as *Anemone multifida* Poiret, *Oxytropis campestris* (L.) DC var. *johannensis* Fern., and *Tanacetum bipinnatum* (L.) Shultz-Bip. ssp. *huronense* (Nutt.) Breitung (Labrecque and Brouillet 1990). Searches at most of these areas revealed only common asters, including *Doellingeria umbellata* (P. Mill.) Nees, *S. novi-belgii, S. puniceum* (L.) Nesom, and *S. lanceolatum* (Willd.) Nesom.

On a section of scoured, cobble shore on the Aroostook River in Caribou, Maine, I located twelve stems of *Symphyotrichum anticostense* growing in a 0.5 × 0.5 m area. This site seemed least likely for discovery of this aster due to lack of circumneutral plant indicators and its invasion by field species, such as *Phalaris arundinacea* L. and *S. lanceolatum.* Additionally, *Prunus pumila* L. var. *depressa* (Pursh) Gleason, *Rosa blanda* Ait. var. *blanda,* and *Salix interior* Rowlee were found in the area. The plant's identity was confirmed by Luc Brouillet and a specimen deposited at Herbier Marie-Victorin (MT). This find indicates that additional riverbank habitats may harbor populations of *S. anticostense.*

Symphyotrichum anticostense is considered globally imperiled (ranked G2; Labrecque and Brouillet 1990). Three major threats to its survival in the northeast are: (1) water flow alteration due to damming; (2) riverbank disturbance; and (3) crowding by invasive plants. Dams are likely the most significant threat to *S. anticostense.* In addition to inundation of the plants, dams decrease the effect of spring ice scour by regulating a river's flow, thereby allowing woody species to invade the riverbanks. *Symphyotrichum anticostense* appears to be similar to *Pedicularis furbishiae* S. Wats. in its need for cyclical river shore disturbance to remove woody competitors. Riverbank disturbance by motorized vehicle traffic and development on the river shores have impacted populations of the aster on the Bonaventure River in Quebec (Labrecque and Brouillet 1990). *Symphyotrichum anticostense* is apparently unable to tolerate crowding by invasive plants. At the Caribou station, where much of the region is utilized for agricultural purposes, *Phalaris arundinacea* and *S. lanceolatum* form a dense cover on the shore. Further survey effort is needed to determine the full extent of *S. anticostense*'s presence in Maine and identify methods of mitigating its threats.

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NEW ENGLAND NOTE

AEGAGROPILOUS *DESMARESTIA ACULEATA* FROM NEW HAMPSHIRE

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Although most seaweeds are anchored solidly by their holdfasts, unattached populations are common in calm bays, fjords, salt marshes, and estuaries throughout the world (Benz et al. 1979; Dawes et al. 1985; Josselyn 1977; Orth et al. 1991; Phillips 1961; Zobell 1971). Five somewhat arbitrary and overlapping categories of unattached seaweeds can be recognized (Norton and Mathieson 1983): (1) entangled: highly branched and intertwined plants [e.g., *Bonnemaisonia hamifera* Har., *Gracilaria tikvahiae* McLachlan, and *Hypnea musciformis* (Wulfen in Jacq.) J. V. Lamour.] that occur among other drifting seaweeds and may include multiple plants or taxa; (2) loose-lying: completely unattached plants such as the saltmarsh fucoids *Ascophyllum nodosum* (L.) Le Jol. ecad *scorpioides* (Hornemann) Reinke and *Fucus vesiculosus* L. ecad *volubilis* (Hudson) Turner; (3) embedded: plants that lack a holdfast and are partially buried in sand or mud (e.g., *Fucus cottonii* Wynne et Magne); (4) free-floating: entangled and drift plants like *Sargassum natans* (L.) Gaillon; and (5) aegagropilous: spherical masses of radially arranged branches that are composed of either single or multiple plants held together by interlocking branches [e.g., *Pilayella littoralis* (L.) Kjellm. and *Spermothamnion repens* (Dillwyn) Rosenv.].

Of the 328 species of unattached seaweeds recorded by Norton and Mathieson (1983), 146 were loose-lying, 62 free-floating, 58 entangled, 53 aegagropilous, and 9 embedded. The aegagropilous taxa included 25 red, 18 green, and 10 brown algae. Some of the best known ball-forming algae are produced by freshwater and marine species of *Cladophora* (Hoek 1963; Newton 1950; Sakai

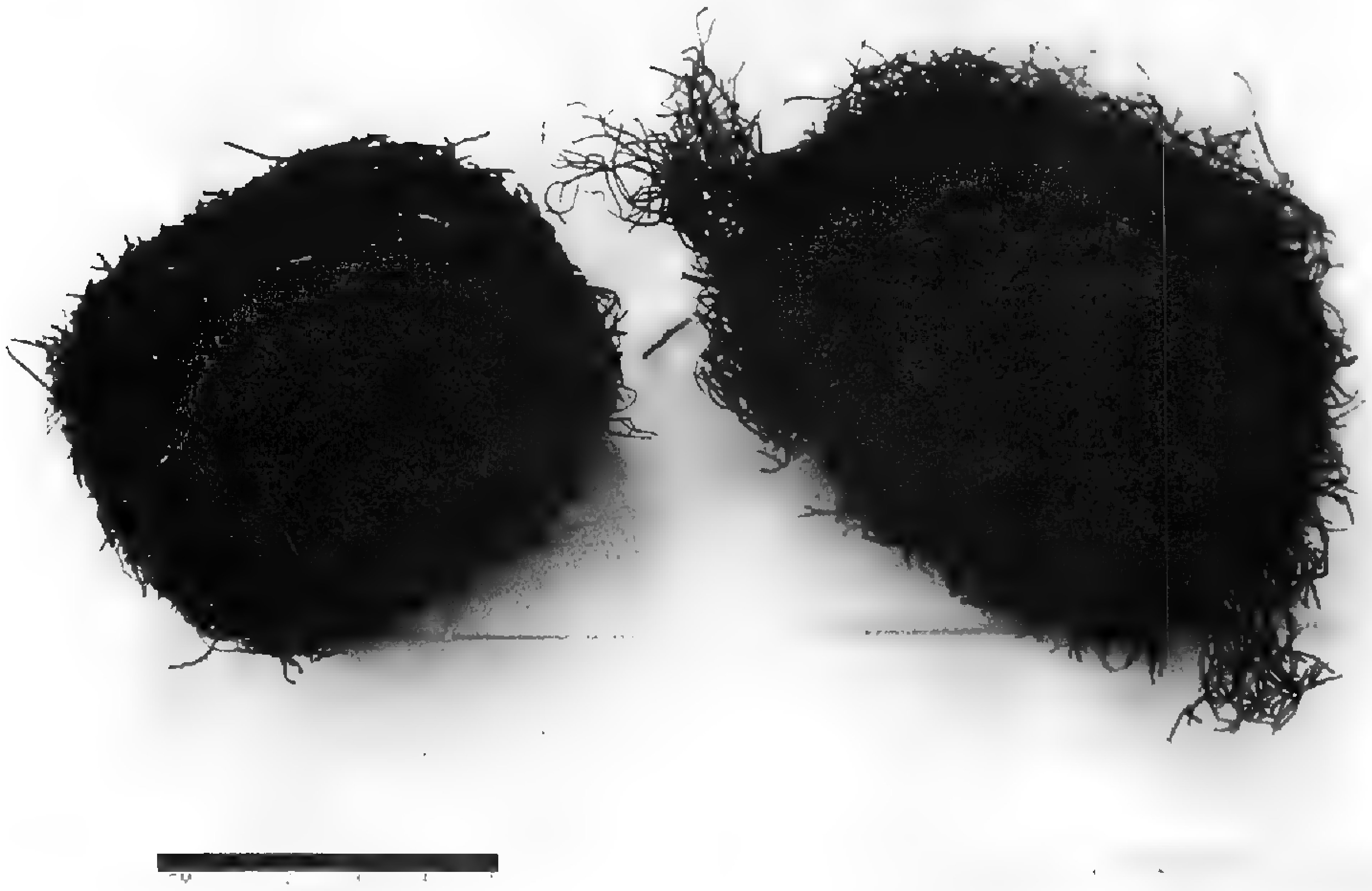

Figure 1. Two aegagropilous specimens of *Desmarestia aculeata,* with the sample on the left being more compacted and spherical than the one on the right; scalar = 5 cm.

1964), with the famous Japanese "lake-balls" designated as natural monuments (Kurogi 1980). According to Newton (1950), *Cladophora* balls occur sporadically, sometimes cast up in enormous numbers and at other times totally absent. Aegagropilous species, like most other unattached seaweeds, originate from attached plants, and they usually become infertile and reproduce entirely by vegetative means (Fritsch 1935, 1945).

The present paper reports the occurrence of two aegagropilous specimens of *Desmarestia aculeata* (L.) J. V. Lamour. (Desmarestiales, Phaeophyceae; Figure 1) that were collected at Concord Point (43°01′00″N, 70°43′55″W), Rye, New Hampshire on February 6, 1998. It is a common perennial (cf. Mathieson and Hehre 1982; Taylor 1957) that grows attached to solid substrata within subtidal environments throughout the eastern (Portugal to Iceland and Greenland) and western North Atlantic (New Jersey to the Canadian Maritimes), the North Pacific from Oregon to the Aleutian Islands of Alaska, the Bering Sea, Kurile Islands, and Russia (Mathieson 1979; Scagel et al. 1986; South and Tittley 1986). We believe this represents the first record of *D. aculeata* growing in an aegagropilous habit, as only free-floating or entangled masses have been previously reported (Norton and Mathieson 1983). Drift material of *D. aculeata* is common in the Gulf of Maine, where biomass values in excess of 11 kg wet wt. m^2 may occur after major winter storms (Mathieson, unpubl. data).

One of the two *Desmarestia* balls was found within a deep tidal pool, while the other occurred within a tidal channel that was closed at one end and open to strong wave action at the other. The specimens (Figure 1) were approximately the size of a tennis ball (7.5 × 7.5 cm and 7.5 × 8.5 cm). They were composed primarily of entangled, "wiry", and very spiny *Desmarestia* fronds, which were flatter than most terete, attached specimens. A diverse assemblage of plants, animals, and shell fragments was associated with the *Desmarestia* balls: the cord grass *Spartina alterniflora* Lois.; the seaweeds *Chaetomorpha linum* (O. F. Müll.) Kütz., *Rhizoclonium tortuosum* (Dillwyn) Kütz., *Chondrus crispus* Stackh., *Polysiphonia fucoides* (Huds.) Grev., and *Ptilota serrata* Kütz.; plus the invertebrates *Dynamena pumila* (L.), *Membranipora membranacea* (L.), *Tubularia* sp., and *Mytilus edulis* L.

As noted by several investigators (cf. Fritsch 1935, 1945; Gibb 1957; Nakazawa and Abe 1973; Sakai 1964; Yoshida 1963), the aegagropilous morphology results from a variety of factors, including detachment/breakage, oscillating movement of fragmented materials, meristematic injury, scar tissue development, and extensive regeneration and/or proliferation of new growth. Subsequent rolling and further injury causes pruning, proliferation, and compaction, resulting in a dense, spherical structure.

In the case of *Cladophora,* aegagropilous specimens are composed of entangled masses of filaments bound by rhizoids. In old *Cladophora* balls the center often decays, leaving a cavity; younger balls may form several concentric layers. The "beach form" of the temperate North Atlantic *Ascophyllum nodosum* [i.e., either *A. mackaii* (Turner) Holmes et Batters or *A. nodosum* ecad *mackaii* (Turner) Cotton of different investigators] is one of the most highly modified spherical forms (Gibb 1957; South and Hill 1970). Two temperate aegagropilous seaweeds form extensive blooms, including the persistent nuisance brown alga *Pilayella littoralis* in Massachusetts and the ceramialean "red tide" alga *Spermothamnion repens* in southern New England (Wilce et al. 1982). Tropical and subtropical seaweeds form similar structures; detached *Caulerpa racemosa* (Forsskål) J. Agardh and *Bryotham-*

nion seaforthii (Turner) Kütz. form ball-shaped masses after exposure to gentle water motion near coral reefs and within mangrove canals (Almodovar and Rehm 1971). Nuisance populations of lagunal ball-forming *Cladophora prolifera* (Roth) Kütz. occur in Bermuda (Bach and Josselyn 1978).

The crustose coralline red alga *Lithothamnion glaciale* Kjellm. may form free-living balls or rhodoliths on sandy or gravelly substrata in quiet bays in Newfoundland (Hooper 1981). Ice is instrumental in these habitats as it breaks off the calcareous crusts, allowing small fragments to roll around and acquire a distinctive ball-shaped configuration. Extensive populations of rhodoliths (*Lithophyllum* and *Lithothamnion* spp.) also occur in the Gulf of California (cf. Bosence 1983; Foster and Riosmena-Rodriguez 1999; Steller and Foster 1995) where they constitute major sources of carbonate sediment and habitats of high diversity (Foster et al. 1997). In contrast to the production of ball-shaped structures from living, photosynthetic seaweeds, balls are also produced from dead leaf and rhizome materials of the Mediterranean seagrass *Posidonia oceanica* (L.) Delile. In a series of experimental evaluations, Cannon (1979) demonstrated the importance of oscillating water motion, clumping, compaction, and disintegration of detrital materials in the formation of *Posidonia* balls.

Apparently, frond detachment in *Desmarestia* is followed by injury to its intercalary meristem, resulting in the loss of trichothallic hairs and a lack of proliferations. Its ball-shaped morphology probably develops because of rolling and compaction of residual branches, plus the incorporation of "foreign" materials. The retention of detached *Desmarestia* fragments within deep tide pools or semi-enclosed tidal channels may provide a vehicle for consistent movement (rolling) and compaction.

ACKNOWLEDGMENT. We are indebted to Ms. Jenna Wanat and Ms. Kim Mayer who collected the two samples of *Desmarestia* balls during field investigations in association with a Marine Botany class in the spring of 1998. The paper is issued as Contribution Number 347 from the Jackson Estuarine Laboratory and the Center for Marine Biology.

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NEW ENGLAND NOTE

TWO MORE WEEDS IN MAINE

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Senecio viscosus L. (Asteraceae) was discovered in Maine in August 1969 by Frank Seymour on a field trip of the Josselyn Botanical Society. His specimen (*Seymour 27886* VT) is from a roadside at the foot of Boarstone Mt., Eliotville, Piscataquis Co. (Seymour 1982). This collection was overlooked by recent authors in Maine (e.g., Campbell et al. 1995; Haines and Vining 1998). *Senecio viscosus* was found again in Maine in July 1999, as a weed at both ends of a culvert on Route 162, where McLean Brook enters the southwestern arm of Long Lake (*Zika 13921* NEBC, WTU). The site is dry, gravelly, and sunny, at an elevation of 180 m, in T17 R4 WELS, Aroostook Co. About 100 plants were seen, growing with *Plantago major* L. *Senecio viscosus* is a European native, known as an occasional adventive in Nova Scotia and in the northeastern United States.

A second addition to the flora of Maine is *Corynephorus canescens* (L.) Beauv. (Poaceae), collected in July 1999 as a rare weed in a cultivated cranberry crop on Route 1A about 2 km east of the Millbridge town line (*Zika 13946* NEBC). The inconspicuous plants were in sunny, moist, and sandy soil, at an elevation of 12 meters, in the town of Harrington, Washington Co. Angelo and Boufford (1998) recorded this European grass from southeastern Massachusetts, but nowhere else in New England. The species is similar to *Festuca ovina* L. in general habit, and perhaps is overlooked.

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NEW ENGLAND NOTE

NEW RECORDS FOR *SCIRPUS ANCISTROCHAETUS* IN NEW HAMPSHIRE

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In 1992, the New Hampshire Natural Heritage Inventory (NHNHI) procured a Section 2 grant from the U.S. Fish and Wildlife Service (USFWS) to perform de novo inventories for northeastern bulrush (*Scirpus ancistrochaetus* Schuyler) in New Hampshire. While the site location for this bulrush was in Vermont, across the Connecticut River from Walpole, New Hampshire (see Schuyler 1962), it had not been found at that time in New Hampshire. Northeastern bulrush was listed by USFWS as endangered in 1991 and a recovery plan was prepared and signed in 1993. Listing was based on the lack of protection for nearly all of the known sites and the high degree of threat from imminent development pressure (United States Fish and Wildlife Service 1991). The Natural Heritage Program lists this species as globally rare (G3) since its discovery at over 50 sites along the Appalachians between western Virginia and southwest New Hampshire (A. E. Schuyler pers. comm. 1996). It is listed as S1 (critically imperiled with five or fewer occurrences) in four states, S2 (imperiled with six to 20 occurrences) in three states, extirpated (SX) in one state, and as a Division 1 species in the *Flora Conservanda* (Brumback and Mehrhoff, et al. 1996).

The NHNHI hired Woodlot Alternatives, Inc. to perform searches for northeastern bulrush during three-to-four days each in 1992, 1993, and 1994. Aerial photographs were reviewed before initiating searches in the towns of Acworth, Charlestown, Langdon, and Unity in Sullivan County, and the towns of Alstead, Gilsum, Surry, and Walpole in Cheshire County, New Hampshire. Fifty-four sites were selected out of 125 potential sites and seven of these contained populations of northeastern bulrush. A sample from the first population found was verified by A. E. Schuyler in the field the following year. Each population was found growing in wetlands where natural water levels had been altered by either beaver or human-caused draining of small ponds by culverts and beaver dam removal.

In 1992 likely sites along the Connecticut River were visited by canoe but no new populations were found there, although it was re-located at the type locality originally described by Schuyler. Other sites were visited on foot in 1992 and the following two years. When an area was found to have the appropriate habitat (open graminoid/sedge swales, evidence of fluctuating water levels, and bulrushes) the wetland was searched intensively for *Scirpus ancistrochaetus.*

Scirpus ancistrochaetus was found in wetlands with the following characteristics: saturated to slightly inundated (to 18 in. deep) emergent benches found next to slightly deeper emergent zones (e.g. areas too shallow for floating-leaf emergent plant species, and too deep for woody plants); fluctuating water levels (stagnant water levels allow succession to shrub and forested natural communities); associated plant species included *S. cyperinus* (L.) Kunth, *S. atrovirens* Willd., *Leersia oryzoides* (L.) Swartz, *Schoenoplectis tabernaemontani* (C. C. Gmel.) Palla, and *Sparganium androcladum* (Engelm.) Morong, which was almost always found close by in an "off shore" zone.

The most useful field characteristics for identification of the species were: (1) drooping, glomerular fruiting heads (these are similar looking to the fruiting heads of *Schoenoplectis tabernaemontani*—drooping heads are supported by curved inflorescence rays that rarely project upwards or straight out, as the inflorescence of *Scirpus cyperinus* may, and as *S. atrocinctus* Fern. and *S. hattorianus* Makino almost always do); (2) dark, chocolate-brown florets (*S. cyperinus* has tawny brown florets); and (3) broad bracts (close to 3/4 in. wide, while *S. cyperinus* has narrow acuminate bracts).

Once identified, the number of fruiting heads and the number of vegetative shoots per clone were counted in small patches of plants (less than 100), and estimated from counts of subsamples in large patches of plants. Collections of *Scirpus ancistrochaetus* were made if more than 20 fruiting culms were present, otherwise portions of the inflorescence were sampled for a voucher specimen and photographs were taken. Voucher specimens have been deposited in the Hodgdon Herbarium (NHA) at the University of New Hampshire in Durham. Wetland communities were described using The Nature Conservancy Eastern Heritage Task Force 1991 Site Survey Summary and Special Plant Forms, and using Natural Community Forms developed by NHNHI. Inventories of associated plants and their relative abundance were recorded for the field forms. In addition, the population's location in relation to present and former water levels, topography, and juxtaposition to other vegetation zones was mapped and/or described. All data forms and site specific information reside at NHNHI in Concord, New Hampshire and with the USFWS in Hadley, Massachusetts.

SPECIMEN CITATION: NEW HAMPSHIRE: Sullivan Co., Langdon, (elev. ca. 235 m), 22 foliose culms and 7 fruiting stems, growing on the edge of a breached headwater beaver pond in four clonal clumps, 9 Oct 1992, *Royte s.n.* (NHA); Charlestown, western bay of a pond, 119 fruiting stems and 150 leafy shoots were found in five patches, 18 Aug 1993, *Royte, von Oettingen, Schuyler & Schuyler s.n.* (NHA); (elev. 235 m) a large beaver flowage with beaver-impounded meadows in two tributaries (elev. 244 m and 250 m) there were a total of 400+ foliose shoots and 250 fruiting stems, found growing with *Scirpus cyperinus, Leersia oryzoides,* and *Dulichium arundinaceum,* 19 Aug 1993, *Royte s.n.* (NHA); marsh on the west side of road, (elev. 260 m), 115 fruiting stems and 75 foliose shoots were found growing on the wetland edge 2–5 cm above a large emergent zone dominated by *Sparganium androcladum,* 19 Aug 1993, *Royte s.n.* (NHA); headwater wetland (elev. ca. 260 m), 23 foliose culms and 15 fruiting stems were found in two clumps in two areas, both clumps were isolated islands near larger island clumps of *Scirpus cyperinus* and *Leersia oryzoides,* the water depth of 38–61 cm appeared to be higher than normal, 15 Aug 1994, *Royte s.n.* (NHA); wetland, along the northern shore of a beaver flowage (elev. ca. 319 m), 40–50 foliose culms and 23 fruiting stems in an emergent bench of *Leersia oryzoides* with 38–46 cm of water, 19 Aug 1994, *Royte s.n.* (NHA).

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NOTE

SAGINA (CARYOPHYLLACEAE) IN ILLINOIS: AN UPDATE

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The genus *Sagina* L. is circumboreal and was most recently monographed by Crow (1978). Only one species, *S. decumbens,* was noted by Mohlenbrock and Ladd (1978) and Mohlenbrock (1986) from Illinois until *S. procumbens* was reported from the Chicago area (Swink and Wilhelm 1994). Examination of specimens in Illinois herbaria revealed an additional adventive species in the state, *S. japonica.* Also, the occurrence of *S. apetala* in Illinois noted by Crow (1978), seems to have been overlooked by recent workers on the Illinois flora.

KEY TO *SAGINA* SPECIES IN ILLINOIS

1. Flower parts in 4s (rarely 5s on the same plant); sepals reflexed in fruit; matted wiry perennials, spreading by offshoots . . . . *S. procumbens*
1. Flower parts primarily in 5s (rarely 4s on the same plant); sepals erect or appressed in fruit; annuals with erect-ascending (or decumbent) often capillary stems and slender taproots, not strongly tufted, not spreading by offshoots . . . . (2)
    2. Leaves with cilia at base . . . . *S. apetala*
    2. Leaves glabrous at base . . . . (3)
        3. Seeds pale brown, triangular with a dorsal groove; capsules longer than broad; pedicels and sepals glandular or glabrous; leaves not succulent . . . . *S. decumbens*
        3. Seeds dark brown to black, plump, ellipsoid-ovoid, lacking a dorsal groove; capsules globose; pedicels and sepals glandular; leaves succulent . . . . *S. japonica*

NOTES ON THE SPECIES

Sagina apetala Ard. This species was first recorded from Illinois (Crow 1978) as follows: Union Co., no date, *Forbes s.n.* (MICH). I have not located duplicates in any of the herbaria I have checked. Crow also cited this European species from New Jersey, Maryland, and Lousiana, as well as Washington, Oregon, and California. Cronquist (Gleason and Cronquist 1991) did not include *S. apetala* in the revised manual, apparently unaware of Crow's records from the *Manual* range.

Sagina decumbens (Sw.) Ohwi. Our only native species was noted from 25 counties by Mohlenbrock and Ladd (1978). The following specimens appear to be additional county records: Effingham Co., Wildcat Hollow NE of Mason, 6 Jun 1967, *Evers 90778* (ILLS); Washington Co., Nashville, 2 Jun 1990, *Shildneck 16361* (ISM).

Sagina japonica (Sw.) Ohwi. The widespread occurrence of this eastern Asian species in the northeastern states was noted by Mitchell and Tucker (1991) and Mitchell (1993). In the Midwest, it has only been reported from northwestern Ohio (Rabeler 1996). The following specimen appears to be the first Illinois record: Sangamon Co., near Oak Ridge Cemetery, damp soil in grass, rare, 21 Sep 1951, *Lola Carter 15667* (ISM). In 1997, I noted this species in Charleston, Coles County in a limited area covering several dozen blocks, between the Eastern Illinois University Campus and the county courthouse approximately one km to the north. Searches of herbaria (noted below) and field work in eastern and central Illinois have not turned up any additional records. Specimens: Coles Co., Charleston, 1049 11th St., 28 May 1997, *Tucker 11273* (EIU); 1400 block of 7th St., 14 Jun 1997, *Tucker 11275* (EIU, ILLS, ISM); 7th St. and Buchanan Ave., 24 Jun 1999, *Tucker 11731* (EIU).

Sagina procumbens L. This native of Europe (Crow 1978) is widely naturalized in the northeastern states. It was first noted in Illinois from the Chicago area by Swink and Wilhelm (1994). The Morton Arboretum has specimens from Cook and Kane counties. The following record suggests it may be more widely distributed: Peoria Co., Peoria, 200 block North Garfield St., growing with moss in brick sidewalk cracks, 15 Jun 1955, *Chase 14252* (EIU; ILL det. R. K. Rabeler, 1993).

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NOTE

NOTES ON THE LENTIBULARIACEAE IN BOLIVIA: A NEW GENUS RECORD (*GENLISEA*) FOR THE COUNTRY, WITH TWO ADDITIONAL SPECIES RECORDS IN THE GENUS *UTRICULARIA*

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As part of our investigations in the wetlands of Parque Nacional Noel Kempff Mercado in eastern Bolivia, we have encountered two species of Lentibulariaceae that were previously not known for the country's flora: *Utricularia nana* A. St.-Hil. & Girard and *Genlisea guianensis* N. E. Brown. The latter constitutes the first record of this genus in Bolivia. Furthermore, while studying specimens at the Missouri Botanical Garden (MO), we encountered an unidentified specimen of *Utricularia* that had been collected from a large inselberg (granitic outcropping) just outside of the western border of Parque Noel Kempff. We were able to determine this specimen as *U. oliveriana* Steyermark, a third member of the Lentibulariaceae that had not previously been known for Bolivia.

The presence of *Genlisea guianensis* and *Utricularia nana* in eastern Bolivia represents only a small extension of their previously known distribution, as both are known to occur in the nearby state of Mato Grosso, Brazil (Taylor 1989). On the other hand, the population of *U. oliveriana* at Cerro Pelão represents an impressive disjunction from other known populations.

Parque Nacional Noel Kempff Mercado (Figure 1) is situated in the northeastern corner of the Department of Santa Cruz, in the Province of Velasco. As currently delineated, the park encompasses an area of approximately 15,300 km^2 (Killeen and Schulenberg 1999). *Genlisea guianensis* and *Utricularia nana* were encountered growing in seeps in a small clearwater stream on top of the Serranía de Huanchaca, a massive, steep-sided plateau situated along the eastern border of the park. The stream was fairly narrow (1–2 m), widening in a few areas to form small, still pools, with numerous wet seepy habitats present along the edges.

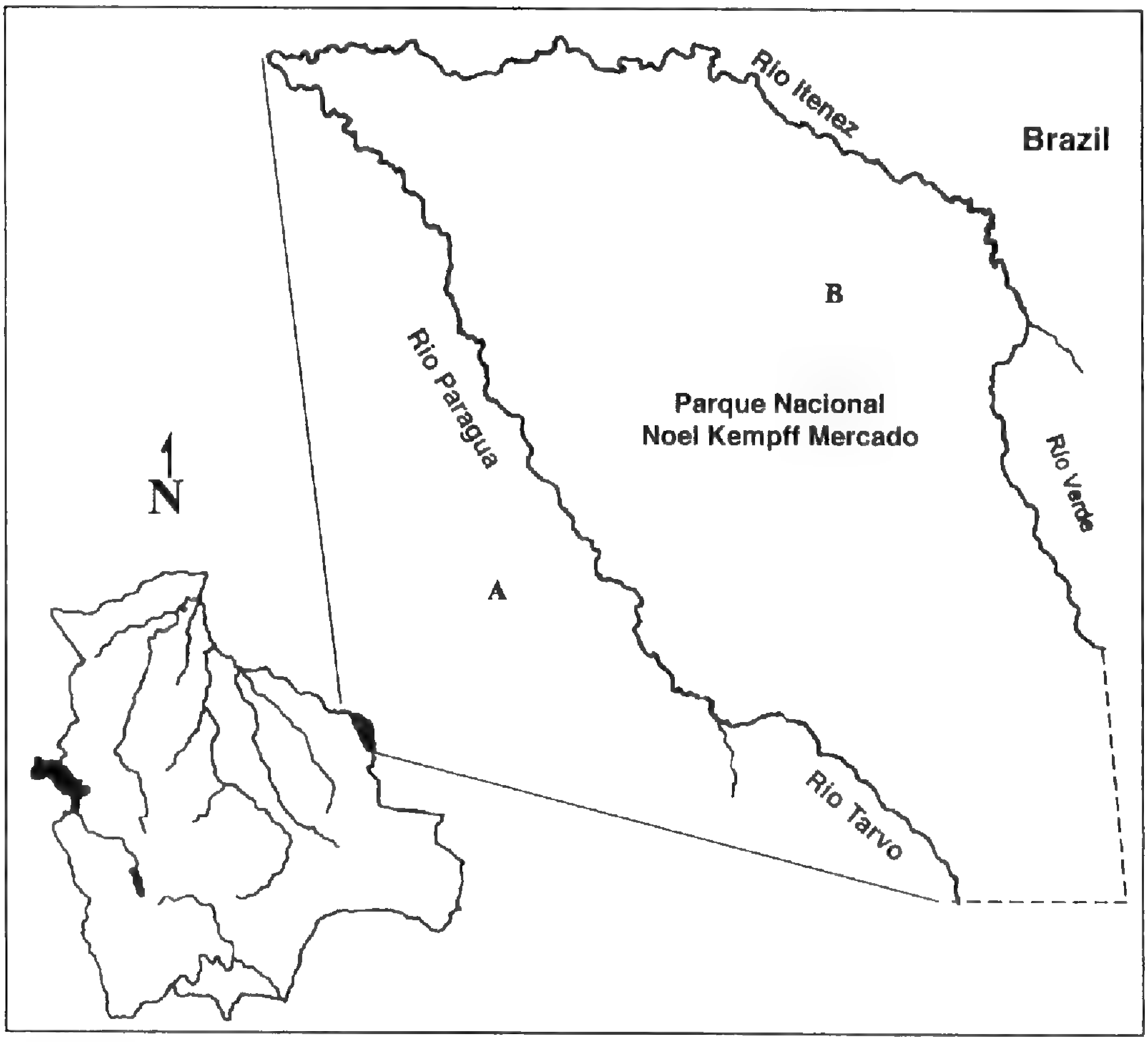

Figure 1. Parque Nacional Noel Kempff Mercado. **A**: Cerro Pelao. **B**: The stream on the Meseta. (Redrawn from Killeen and Schulenberg 1999)

Typical species in the seeps were *U. amethystina* Salzmann ex A. St.-Hil. & Girard and *U. pusilla* Vahl, and small, ephemeral, semi-aquatic herbs, such as *Polygala microspora* Blake (Polygalaceae) and *Burmannia flava* Mart. (Burmanniaceae).

Cerro Pelão (Figure 1) is a large inselberg located just outside the western border of the park (Killeen 1996), in the Reserva Forestal Bajo Paraguá. As with some areas of the Meseta, large expanses of exposed rock (lajas) are present. Where small seasonal streams and springs flow over these outcroppings, hydrophilic species in the genera *Utricularia* and *Rhynchospora,* and the family Eriocaulaceae can become established on the rocks and in the shallow sand and sediments that accumulate in pockets in the lajas. It was in this type of habitat that the third new record, *U. oliveriana,* was observed.

Genlisea guianensis is an erect herb with a rosette of elongate, strap-shaped leaves and purple flowers. This species is considered to be relatively large for the genus (Taylor 1991), attaining heights up to about 30 cm (Brown 1900). Prior to its discovery in Bolivia, *G. guianensis* was thought to be limited to Venezuela, Guyana, and Brazil (Fromm-Trinta 1984; Taylor 1991).

Although superficially quite similar to *Utricularia, Genlisea* can be clearly differentiated on the basis of sepal number and trap morphology. The calyx is composed of five sepals, as compared to the typical 2 sepals in *Utricularia* (Cook 1990; Taylor 1991), while the traps are forked and possess two helically twisted branches, in contrast to the globose and bladder-like traps of *Utricularia* (Cook 1990; Reut 1993; Taylor 1991). Although the traps have long been thought to be involved in some form of carnivory, their function in trapping protozoa was only recently identified by Barthlott et al. (1998), who demonstrated that the traps lured protozoa through a chemical attractant.

The fruits of *Genlisea* are capsular, with the capsules of some species said to be unique among flowering plants in possessing an unusual circumscissile dehiscence that ruptures along three different planes (Taylor 1991). In describing this pattern of dehiscence, Taylor (1991) likened the capsule to a globe and depicted the planes of dehiscence as occurring not only at the equator, but also at two additional latitudes between the equator and one pole.

Utricularia nana is typically a diminutive herb, although the species is quite variable, ranging in height from 1.5 to 12.0 cm (Taylor 1989). All individuals we observed were extremely small (2.0–2.5 cm tall). We had never before encountered a *Utricularia* of such small stature, and it wasn't until we were able to ascertain that what at first appeared to be grains of sand trapped among the base of the plant were actually miniscule traps, that we became convinced that this was, indeed, a species of *Utricularia*. According to Taylor (1989), *U. nana* has a fairly wide distribution in South America, and was previously known from Venezuela, Guyana, Surinam, French Guiana, Brazil, and Paraguay.

Utricularia oliveriana is a small rheophytic, apparently perennial herb (Taylor 1989). This species is extremely similar to *U. neottioides* A. St.-Hil.—another rheophyte that is frequently encountered in streams and in water flowing over expanses of rock on the Meseta. These two species—which are the sole members of Section *Avisicaria* Kamiénski—are most easily distinguished

Table 1. Species of *Utricularia* known for Bolivia. Species names in parenthesis are as given by Foster (1958).

Species	Foster (1958)	Taylor (1989)	Parque Noel Kempff M.
U. alpina Jacq.	+	+	
U. amethystina Salzmann ex A. St.-Hil. & Girard (*U. velascoënsis* O. Ktze.)	+	+	+
U. breviscapa Wright ex Grisebach		+	+
U. cornuta Michx. (misidentified: almost certainly *U. meyeri* Pilg.)	+		
U. erectiflora A. St.-Hil. & Girard		+	
U. foliosa L.		+	+
U. gibba L. (*U. obtusa* Sw.)	+	+	+
U. cf. *guyanensis* A. DC			+
U. hispida Lam.		+	
U. hydrocarpa Vahl		+	
U. lloydii Merl.		+	
U. meyeri Pilg.		+	+
U. myriocista A. St.-Hil. & Girard		+	+
U. nana A. St.-Hil.			+
U. neottioides A. St.-Hil. (*U. Herzogii* Lützelberg)	+	+	+
U. nervosa G. Weber ex Benj.		+	+
U. oliveriana Steyermark			+
U. poconensis Fromm-Trinta		+	
U. pusilla Vahl	+	+	+
U. simulans Pilger		+	+

Table 1. Continued.

Species	Foster (1958)	Taylor (1989)	Parque Noel Kempff M.
U. subulata L.	+	+	+
U. tricophylla Spruce ex Oliver (*U. globulariaefolia* Mart. ex Benj.)		+	
U. tricolor A. St.-Hil.	+	+	+
U. triloba Benj. ex Mart.		+	
U. unifolia Ruiz & Pavón	+	+	
U. warmingii Kamiénski		+	

on the basis of leaf shape, with *U. oliveriana* possessing tiny (2–8 mm total length) leaves with obovate simple laminae, while the leaves of *U. neottioides* are finely divided into pinnately arranged capillary segments and range in length from a few mm to several cm (Taylor 1989). The two species also differ in stature, with *U. oliveriana* characteristically possessing shorter inflorescences and thinner rhizoids than *U. neottioides.* Dimensions of the specimens from Cerro Pelao were slightly smaller than the lower limits listed for the species by Taylor (1989), with inflorescences from 12–17 mm in height (vs. 2 cm, Taylor), and leaves scarcely reaching 2 mm in length. *Utricularia oliveriana* was previously thought to be restricted to the Guyana Highland region, with populations known from Venezuela, Colombia, and Brazil (Taylor 1989).

To date, the most comprehensive floristic account of Bolivia is the checklist published over 40 years ago by Foster (1958). In his checklist, Foster listed nine species of *Utricularia* for Bolivia. In contrast, based on distributional information included by Taylor (1989) in his monograph of *Utricularia,* 22 of the 214 species that he recognized world-wide are known from Bolivia. With the additions of *U. nana* and *U. oliveriana,* 14 species of *Utricularia* are now known for Parque Noel Kempff Mercado, with a provisional fifteenth species awaiting confirmation (Table 1). According to Taylor (1989) 70 species occur within the entirety of South America, therefore, this one small corner of Bolivia contains one fifth of the continent's species of *Utricularia.* Based on Taylor's (1989) monograph, augmented by these new records, there are now 24 (possibly 25) species of *Utricularia* known for Bolivia (Table 1). Therefore, greater than half (58%) of the country's *Utricularia* species are now known to occur in Parque Nacional Noel Kempff Mercado. Furthermore, this level of diversity exceeds the number of species known for a number of other Neotropical countries, such as Panama (13 species; D'Arcy 1987), Peru (12 species; Brako and Zarucchi 1993), Ecuador (11 species; Jørgensen and León-Yánez 1999), and Costa Rica (10 species; Crow 1992).

EXSICCATAE

Genlisea guianensis N. E. Brown. Parque Nacional Noel Kempff Mercado. "La Meseta"; east of Los Fierros. Elev. ca. 760 m. Semi-aquatic, emergent herb. Growing along the edges of the stream. Common. Corolla purple-blue.

Fruits present. The stream bottom varies from exposed bedrock to sand. Numerous small pools are present. Surrounding vegetation: Cerrado. 16 Aug 1996, *N. Ritter, G. Crow, M. Garvizu, M. Ritter & J. Crow 3614.* (MO, NHA, USZ).

Utricularia nana A. St.-Hil. & Girard. Parque Nacional Noel Kempff Mercado. "La Meseta"; east of Los Fierros. Elev. ca. 760 m. Diminutive herb. Growing in small seeps along the edges of the stream. Only a small number of individuals were noted. Corolla yellow; subtended by red sepals. The stream bottom varies from exposed bedrock to sand. Numerous small pools are present. Surrounding vegetation: Cerrado. 16 Aug. 1996, *N. Ritter, G. Crow, M. Garvizu, M. Ritter & J. Crow 3600.* (MO, NHA, USZ).

Utricularia oliveriana Steyermark. Santa Cruz, Provincia Velasco. Parque Nacional Noel Kempff Mercado. Cerro Pelão. Bosque Seco con *Talisia, Dilodendron, Amburana, Hymenaea, Anadenanthera, Chorisisa, Luehea, Metrodorea, Rhamnidium, Sebastiana, Spondias, Astronium, Aspidosperma . . .* Substrato con poco suelo sobre roca granítica. 14°32′23″ S 61°29′53″ W. 300m. Hierba; sobre roca húmeda, inclinada. 1 Apr 1994, *A. Jardim,* with *Saldias, Guillen, Ramos, Jensen, & Surubí 484* (MO, USZ).

ACKNOWLEDGMENTS. We are grateful to the New York Botanical Garden and the Missouri Botanical Garden for providing additional herbarium specimens of South American *Genlisea* for study, with further thanks due to the latter for making their facilities available to us during our time in St. Louis. We also wish to thank Peter Jørgensen, Susana León-Yánez, and the Missouri Botanical Garden for providing us with an electronic copy of their checklist of Ecuadorian plants. Additionally, Timothy Killeen of Museo Noel Kempff Mercado in Santa Cruz, Bolivia deserves special thanks for his assistance in facilitating our fieldwork in the Park and for his suggestions regarding potential study areas. Appreciation is also due to all those individuals who assisted us with the fieldwork: Marisol Garvizu, Juan Surubí, Martha Ritter, and Jason Crow. Additional appreciation is due to the following: the park guards and administrators of Parque Nacional Noel Kempff, the Dirección General de Biodiversidad, the Servicio Nacional del Áreas Protegidas (SERNAP), and the Vice-Ministerio del Áreas Protegidas. This research was supported in part by a grant from the Vice President for Research and Public Service, University of New Hampshire. This paper is Scientific Contribution Number 2037 from the New Hampshire Agricultural Experiment Station.

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BOOK REVIEW

A Guide to the Algae of New England as Reported in the Literature from 1829–1984, Parts I and II (in 2 volumes), by LeBaron C. Colt, Jr. 1999. vi+1019 pp. maps. $100.00 plus shipping (softbound). Available from L. C. Colt, 61 Philip St., Medfield, MA 02052.

The two volume compilation by Barry Colt represents an exhaustive and important documentation of New England's algal flora, covering both microalgae and seaweeds. The value of such work is priceless, providing critical information regarding historical records, biodiversity patterns, biogeographic comparisons, potential environmental impacts, etc. The compendium represents a "labor of love" from a very talented and committed phycologist. Its dedication to Hannah T. Croasdale and the late Gerald W. Prescott is particularly fitting, as they both produced analogous and exhaustive publications on freshwater microalgae. Having followed the author's progress for more than a decade I can only imagine the difficulties, frustrations, effort, and many, many years involved! Certainly he is to be commended for finalizing such a major synopsis on New England algae.

The two-volume compendium contains a general Introduction (3 pages) describing the total project, plus four other major sections. The first section (the New England Region, 3 pages) describes the area, including all of the counties where collections have been made; some special geographical areas (e.g. Narragansett Bay, Rhode Island) are designated when individual counties are not easily ascribed. Generally the format follows that of a vascular plant flora, with listings of algal taxa given by counties and a standardized format utilized for authors, dates, etc. Two maps describe specific site identifications and locations within the region. The second section (The Algae of New England 1829–1984, 775 pages) gives a detailed listing of all known algae (i.e. freshwater and marine microalgae, plus seaweeds) from New England during this 155 year period; it is by far the largest part of the compendium, being approximately three-quarters of the entire text. A standardized format is used for the listings of algal taxa, being initially arranged alphabetically by genus and then by descending hierarchy (i.e. species, variety, forma, or other taxonomic levels as appropriate). Collection data for each taxon is also reported alphabetically by state and then chronologically by date of publication. A series of fourteen examples is given, using a uniform set of abbreviations for different states and counties. A third section (Authors and Contributors, 43 pages) gives a synopsis of author name(s), plus dates of publication(s) and pages on which the listed species are reported. Three levels of author citations are given: (1) individual, (2) coauthored, and (3) contributed material cited by other authors; all of these listings are arranged chronologically according to publication dates. The fourth section (Literature Cited, 175 pages) gives an exhaustive synopsis of supporting literature that is arranged alphabetically. It is also annotated to provide a variety of specific information: (1) site(s) of collections (i.e. state, county, or specific geographical area); (2) habitat (brackish, freshwater, marine, and terrestrial); (3) the presence of maps; (4) the presence or absence of descriptive materials; (5) the occurrence of figures and plates; and (6) the numbers of genera, species, varieties, forma, etc.

Barry Colt has synthesized an exhaustive set of information, providing direct citations to diverse taxa, authors, and the potentials for detailed cross-referencing. I've already found it very helpful in identifying several references and geographical data; the volumes also provide a logical tool for diverse searches, etc. While I am genuinely impressed with the author's efforts, no work of such a magnitude can be finalized without minor errors. For example, some typos and grammatical errors are evident within the text, including a few sentences that are incomplete or have mixed tenses. I assume that the term alpha really means alphabetical, but it is not clarified in several places. A few of the descriptive sections seem to have been run-on, while some handwritten parts also seem to be present. Lastly, the second part (i.e. Volume II) might be improved by a brief transitional paragraph showing its context and interrelationships to the first part (Volume I). No doubt these minor points can be rectified if there are future revisions or updates of literature. In summary, my few constructive comments should in no sense take away from the importance and value of this compendium. Congratulations to the author for a fine job!

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BOOK REVIEW

Thoreau's Country: Journey Through a Transformed Landscape, by David R. Foster. 1999. xiv + 270 pp. illustrations, bibliographic essay, index. ISBN 0-674-88645-3 $27.95 (hardcover). Harvard University Press, Cambridge, MA.

If you have ever crossed paths with a lichen-encrusted stone wall or a lonely cellar hole on a walk through a New England forest, you may have wondered how such things came to be in the middle of the woods. Who built them, and why? New England's stone walls have maintained a constant presence across the land over the centuries, but what changes have they witnessed in their lifetimes? How have the forests changed? How has the human impact on the landscape changed?

Such are the questions that can be answered by combining the observations of a nineteenth century naturalist with those of a twentieth century ecologist. In *Thoreau's Country: Journey Through a Transformed Landscape,* David R. Foster provides us with a window through which we can look back on New England's past. This window is actually the eye of one of New England's most keen 19th century observers, Henry David Thoreau. Though Thoreau is probably most well known for his philosophical writings, his daily journals afford an invaluable source of insight on daily life and nature in the mid-1800s. Foster, Director of the Harvard Forest since 1990, masterfully weaves Thoreau's observations into a tapestry that illustrates the origins of today's forests. Through his thoughtful introductions to each chapter, Foster makes a convincing case that it is necessary to know the cultural and natural history of New England in order to more fully understand the present day ecology of our own landscape.

Foster has tastefully selected and organized hundreds of Thoreau's journal entries into chapters that illustrate many aspects of the mid-1800s, when New England was at its peak in agricultural production. In Thoreau's time, more than 60 percent of the land in southern New England had been cleared and tamed, while the remaining sections were constantly subject to the axe and saw to supply an increasing demand for firewood and timber. Foster uses Thoreau's talent for imagery and detail to conjure up a striking picture of the 19th century countryside: pockets of isolated woodlands in a matrix of cultivated fields, meadows, and pastures, much the opposite of what we see today. The land was kept in this unnatural state by the endless toil of the New England farmers, who Thoreau described as heroic in their year-round work to improve their land and their livelihoods. The book contains a wealth of information about 19th century land use practices, which are ultimately responsible for determining the destiny of the forests that followed.

The reader will be amazed to discover that Thoreau, through his years of very detailed observations, was able to describe modern ecological concepts years before scientists would actually publish them. It was Thoreau who coined the term "forest succession" after he watched different species of trees reclaim the land that was increasingly being abandoned by farmers as they moved west or to the cities. He also recognized that each kind of tree had a situation in which it grew best, in essence that each species had its own niche. Foster points out that if 20th century ecologists had paid more attention to the works of Thoreau, much time and effort might have been saved in the rediscovery of these concepts. The fruitless attempts to grow white pine on clear-cut pine stands in the early part of this century could have been avoided if anyone had studied Thoreau; he anticipated that the dominance of white pine in New England would be a direct result of 19th century land use practices, and that hardwoods naturally recruit underneath the pines.

Although the changes that brought about the forests of today were well under way by the mid-1800s, the landscape was a vastly open one compared to today, and the communities of organisms were very different. Thoreau's journal entries are invaluable in that they describe an ecosystem that is completely outside of the experience of anyone living in our time. In his journals, Thoreau romanticized about the songs of bobolinks and meadowlarks, but bewailed the loss of the "noble" animals such as deer and bear. Today the situation is reversed, and we are concerned with preserving the diversity of the once common field species, which are declining at an alarming rate. Thoreau also observed the passenger pigeon and the American chestnut fulfilling their original ecological roles. Today the pigeon is extinct and the chestnut has been reduced to a shadow of its former stature by the chestnut blight.

Thoreau's Country: Journey Through a Changing Landscape would be of great interest to both the beginning naturalist and the experienced ecologist. Detailed and often romantic accounts of 19th century life and nature are combined with ecological principles and thoughtful reflections in such a way that readers gain a new appreciation for the hard life of their ancestors and for their ancestors' legacy, the woods through which we walk today. The book is well organized and enjoyable to read, complete with beautiful line drawings that depict life in a time gone by.

Having read the book, one can find new meaning in the forest landscape and be able to picture where it may have come from. You will find that the wall you discovered on your walk was most likely built from stones removed from a plowed field, and positioned to divide a pasture on the hill from the fertile soils in the lowland. The stones for the wall were relocated by the strain and sweat of a farmer who once lived in the house that sat upon the mossy foundation. The old oak tree with the spreading lower branches, another witness to more than a century of change, probably once shaded his livestock in the sweltering heat of a summer day. The other trees are the products of a predictable and ongoing succession of species that started when the farmer and his family abandoned their New England home to seek gold in California. You will also realize that as you stand on the same spot as the old farmer and look upon the same wall, you are just taking another snapshot, observing an instant in the continuous story of natural change that shapes and forms our reality.

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NEBC MEETING NEWS

November 1999. Bruce A. Sorrie, former botanist for the Massachusetts Natural Heritage and Endangered Species Program and now a botanical consultant in the southeastern United States, spoke on the topic, "Diversity and endemism in the Coastal Plain Flora." Sorrie defined the coastal plain as the exposed portion of the continental shelf that extends from Cape Cod, Massachusetts to a portion of eastern Mexico and northward into the area known as the Mississippi embayment. It is an area composed of Cretaceous age and younger deposits, which are mostly oceanic but augmented by materials derived from the older adjacent physiographic provinces. Its inland boundary is defined by "the Fall Line," where one encounters rocks of Paleozoic age. "The coastal plain occupies about 8% of the North American landmass," he said. The geologic boundaries of the coastal plain match the boundaries of what Sorrie considers to be the Coastal Plain Floristic Province. To put the coastal plain flora in perspective, Sorrie compared it to the Appalachian Floristic Province, a much older area geologically, and one regarded as a refuge for plants during periods of widespread inland seas and global climate change. While it has long been considered a major center of evolution from which most eastern North American species evolved, the Appalachian Floristic Province, Sorrie points out, has only seven endemic genera: *Cymophyllus, Galax, Rugelia, Diamorpha, Amphianthus, Jamesianthus, Nestronia,* and *Rugelia.* Many other genera often thought of as endemic to the Appalachian Province, e.g., *Astilbe, Disporum, Jeffersonia,* and *Menziesia,* are actually Arcto-Tertiary disjuncts with species also occurring in eastern Asia or elsewhere. Sorrie also mentioned a number of genera centered in the Appalachians which have spread well beyond the borders of the Province, e.g., *Chamaelirium, Clintonia, Epigaea,* and *Liriodendron.* He estimated that there might be about 200–300 endemic species in the Province, but he has not seen a figure on this.

Using a quote from the late Alwyn Gentry, Sorrie explained that the southeastern coastal plain is "a conspicuous but often overlooked center of endemism in temperate North America." Gentry said, "It is remarkable that Florida, only 152,000 km^2 and with virtually no topographic relief, should rank second only to California in number of endemic species; it is even more remarkable when we consider that the endemic plant species are concentrated in northern and central Florida, not in the subtropical southern part." According to Sorrie, there are 215 species wholly confined to Florida, and another hundred or so that extend but a short distance from its borders into Alabama and/or Georgia. For the coastal plain as a whole, there are two endemic plant families, 48 endemic genera, 35 of which are monotypic, and about 1400 endemic species, he said. Endemism occurs in many other coastal plain plant genera, 98 of which have five or more endemic species, he added. He felt that 60 million years of partial exposure of the coastal plain had allowed for considerable *in situ* plant colonization and evolution of new taxa. Sorrie's slides illustrated many of the endemic genera. Among them were: *Balduina, Ceratiola, Dicerandra, Franklinia, Harperocallis, Lachnanthes, Macranthera, Pinckneya, Pyxidanthera, Schwalbea, Sclerolepis, Stokesia, Warea,* and *Zenobia.*

Sorrie joked about the seemingly monotonous, pine-dominated landscape of the coastal plain. He quoted Roland Harper, a pioneering botanist in the southeastern coastal plain, who described a 700-mile train trip from Augusta, Georgia to Richmond, Virginia, where he did "not remember seeing any rocks, bluffs, escarpments, hills, ravines, gullies, springs, or hammocks, or passing through any railroad cuts deep enough to obstruct the view." Sorrie commented that some topograpic maps for eastern North Carolina even lack topographic contour lines! Why then, he rhetorically asked, does the coastal plain support such botanical diversity? Answering his own question, he gave seven possible reasons: (1) subtle shifts in soil composition and chemistry with eight of ten global soil orders represented; (2) subtle shifts in soil moisture; (3) subtle elevational differences that have profound effects on plant communities; (4) high humidity and percentage of sunshine; (5) the highest frequency of lightning strikes in the U.S., which results in many fire-adapted communities with high herb diversity; (6) up to 60 million years of vegetational history that has provided, at least, some localized refuges for temperate species during times of maximum glacial advance; and (7) the derivation of the flora from multiple source areas, including the tropics, subtropics, prairies and deserts, as well as from *in situ* speciation. A summary of ten different geographic patterns of floristic endemism in the coastal plain, followed by some questions from the audience, ended the meeting.

December 1999. Dr. Leila Shultz, Research Associate Professor at Utah State University, presented a lecture entitled "Breaking new ground in floristics: Using geographic information systems to predict species distributions in western North America." For the neophytes on Utah geography and flora, she started by describing 4–6 floristic provinces of Utah, the exact number depending on one's interpretation. The Colorado Plateaus define the southeastern portion of the state while the southwestern corner is considered an eastern extension of the Mojave Desert floristic province. A western fifth of the state consists of the Great Basin (formerly occupied by the pleistocene Lake Bonneville) and 35 associated mountain ranges including the calcareous Wasatch Mountains that form the Basin's eastern border. The northwestern corner has mountains of igneous origin and a flora influenced by migrations from the Pacific Northwest. This leaves one or more provinces in the east that include the Uinta Mountains, with floristic affinities to the Rocky Mountains; the Uinta Basin, considered by some to be part of the Colorado Plateaus; and the La Sal Mountains along the border with Colorado. The Utah flora includes 2602 native and 682 introduced species, and these numbers are increasing due to new discoveries and introductions. Between 1974 and 1994, 88 new species were described from Utah, a number of them by Shultz herself. Also, newly naturalized introductions have contributed about 100 new taxa to the flora since 1987, she said. It is a state where 10–15% of the flora is considered endemic and about 250 species have been proposed for federal listing.

Dr. Shultz described the collaborative efforts between herself, Martha Aiken, and other researchers at Utah State University to develop and test a geographic information system (GIS) for floristic data that would have the capability of predicting new locations for the state's rare plants. A first step toward this end was to create a rare species specimen database from which geographic coordinates could be extracted. A rare species appendix to the *Atlas of Vascular Plants of Utah* published in 1988 by Albee, Shultz, and Goodrich helped with this effort. Herbarium specimens that could be mapped at a 10 × 10 km scale or finer were selected and digitized, so that each mapped species represented a data layer in the GIS. The predictive modeling research was largely that of Aiken who completed a Master's thesis entitled "Predictive modeling of rare plant habitat in the eastern Great

Basin," a project funded by the Bureau of Land Management and the Hill Air Force Base. A field key was developed from environmental attributes and associated species data collected at 467 site plots. Approximately 20% were presence plots for rare species. Four rare plant species were selected for their representation of different kinds of habitats: *Sphaeralcea caespitosa* (valley & foothill sites), *Penstemon concinnus* (pinyon-juniper woodland), *Primula domensis* (faces of dolomite cliffs), and *Jamesia tetrapetala* (granite canyons). New data layers with site-specific data were then added to the baseline information provided by the coarse grid-distributions provided by the Atlas. Additional data for the GIS models came from four existing geographic databases: one elevational, both state and national soil databases, and a surficial geology database. Probability of occurrence maps were then developed from the GIS data containing 13 environmental variables encompassing slope, elevation, aspect, soil, and geologic data.

The predictive model used a tree-classification system to sort data using binary recursive partitioning. The attribute data for each variable were examined sequentially to identify the optimal partition resulting in the most homogeneity within classes and the most heterogeneity between classes. The procedure was repeated for each branch of the key. The result was a dichotomous key that was then incorporated into a computer program for extrapolation of the classification over large areas. The dichotomous key produced in S-Plus was written as a series of conditional statements for GRID, such that each variable in the model was represented by a unique grid coverage. GRID is a cell-based geoprocessing software that is integrated with ARC/INFO. As GRID reads the conditional statement, each grid cell is analyzed and simultaneously a new grid is generated in which each cell reflects the predictions of the terminal leaves of the conditional statement. The new grid is then converted to polygon coverage and the predictions are mapped using ARCPLOT.

Models were evaluated for total percentage of correct predictions and analyzed using two statistical tests for utility and bias. Both field-based and GIS-based models performed well for all four species of plants tested. For the GIS, based on 12 different models, mean accuracy was 97% for all predictions; for the Field Key, based on 16 models, the mean for correct predictions exceeded 95%. The models with the highest utility and lowest bias used elevation and aspect in predicting distributions. Over-prediction occurred for all species but was considered less of a problem than under-prediction.

The presentation included habitat pictures for a number of rare species from the vast remote areas of Utah. Most of the species shown were discovered and described in the 1970s–80s. Although the rate of new discoveries has declined, a respectable number of new finds occurred in the 1990s, demonstrating a need for continued botanical exploration in remote areas of the intermountain west. Shultz emphasized the importance of using separate fields for spatially explicit data (e.g., latitude and longitude) in herbarium databases, thus providing a means for transporting floristic data to geographic information systems. She encouraged the employment of different spatial scales depending on the data source, i.e., 10 km grids for the generalized localities provided by most herbarium collections and 1 km grids for records with latitude and longitude given in seconds. Databases developed from site-intensive studies such as those used in the Utah predictive model can serve the dual role of providing floristic information for herbarium vouchers and ecological data for mathematical models that investigate the relationship of plant distributions to climate and ecology.

January 2000. The first program of the year 2000 was titled "First Friday Foray into Fantastic Flora," better known as the annual "show and tell," where members are invited to make short presentations that typically involve showing and narrating a small number of slide images. As exemplified by first presenter, Donald Lubin, however, slides are not a necessary prerequisite. Don explained that he had prepared 62 laminated fronds of fern taxa and would have them available for examination after the meeting. He also spoke of fern exploration with Ray Abair that resulted in three wood fern hybrid taxa being discovered in the Blue Hills south of Boston and the verification of 39 pteridophyte taxa at Wachusett Mountain in Worcester County, including eight that had not been reported previously. Lisa Standley started the slides with images from the Okavango Delta in Botswana. We were shown a relatively flat landscape with enormous wetlands that resemble, according to Lisa, marshes of Manitoba. Here she saw many familiar genera such as *Typha, Phragmites, Nymphaea, Eleocharis,* and *Scirpus,* but mixed with them stems of *Papyrus.*

Several trees from upland habitat were featured including the sausage tree, *Kigelia* (with bat-pollinated orange flowers and large, sausage-shaped fruits), and baobabs, all large trees up to 10–12 ft. in diameter at their bases. Not seeing any immature baobabs, Lisa expressed concern about whether or not they were reproducing. Close-ups of African large game, including one showing a group of side-by-side lionesses in crouched position lapping water, ended the brief glimpse of Africa.

Nancy Eyster-Smith brought us back to the U.S. for a look at vegetation management activities witnessed in national parks on a family trip across country this past summer. At Glacier National Park, she saw propagated native species being planted along walkways as part of a revegetation project, and new metal boardwalks that had been installed to prevent further trampling near Logan Pass. She also observed sites where exotic taxa had been spot-sprayed with herbicides. At Little Bighorn Battlefield National Memorial, people were seen pulling an invasive species of *Hypericum* by hand. Jumping to the Caribbean, Richard Falcona illustrated some arid landscapes and scenic views from the island of St. John in the U.S. Virgin Islands. Plant taxa shown were turk's cap cactus, *Melocactus intortus,* and century plant, *Agave missionum,* both native to the island. Paul Somers illustrated a few nonindigenous species encountered on a trip to the islands of Nevis and St. Kitts. Examples shown were *Momordica charantia* (Cucurbitaceae) and *Calotropis procera* (Asclepiadaceae), both indigenous to the Old World tropics, and cashew trees, *Anacardium occidentale,* a native of northern South America. Paul also showed a few shots of wetland plants taken in Massachusetts, including *Utricularia cornuta* and *U. inflata* from Plymouth County, *Potamogeton ogdenii* from Berkshire County, and a possible new record of *Lycopodiella alopecuroides* from northern Worcester County. Sticking with the Massachusetts theme, Pam Weatherbee illustrated some habitats and plants encountered during a biological survey of the Hop Brook Wildlife Management Area in southern Berkshire County. Despite a long history of land utilization, Pam reported finding some relatively natural wetlands with species such as *Iris versicolor, Galium palustre, Salix candida,* and *Salix serissima*; forest communities containing an interesting association of *Quercus bicolor* and *Carpinus caroliniana*; and even a couple of rare plant species. Also catching Pam's eye during the survey was a beautiful Baltimore checkerspot, a butterfly species thought to be switching from *Chelone* to *Plantago* as a food plant.

Andy Finton then took us across the Berkshires to the Hudson River Valley of New York for a presentation on plant community inventory work recently completed there by himself and colleagues at the New York Natural Heritage Program. We learned about remnant serpentine barrens on Staten Island; oak-dominated forests with heath understories in the river valley and rocky summit communities; and beech-maple and spruce-dominated old growth forests in the Catskills, where one conifer swamp yielded a black gum aged at 485 yrs. Other communities highlighted were calcareous cliff communities with calciphile ferns in Albany and Greene Counties and bog, sedge meadow, and spruce flat communities of the Rensselaer Plateau.

The closing presentation was by George Newman who visually transported us to the Gaspé Peninsula for a preview of sites to be visited and things to do during the NEBC summer field trip in July, 2000. George emphasized the extensive serpentine barrens above timberline on Mont-Albert and the many calciphiles that could be found in sea cliffs around Mont Ste. Pierre. At Forillon National Park, options of boating to watch sea lions and seals or botanizing the talus slopes of Cap-Bon-Ami were offered as enticements. In the Percé vicinity, exploring calcareous conglomerate formations of Mont Ste-Anne, sea cliffs occupied by gannets and puffins on Ile Bonaventure, or limestone river beds of Grand Rivière were presented as interesting options.

—PAUL SOMERS, Recording Secretary.

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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 102nd year and contains about 400 pages per volume. Visit our web site at http://www.herbaria.harvard.edu/nebc/

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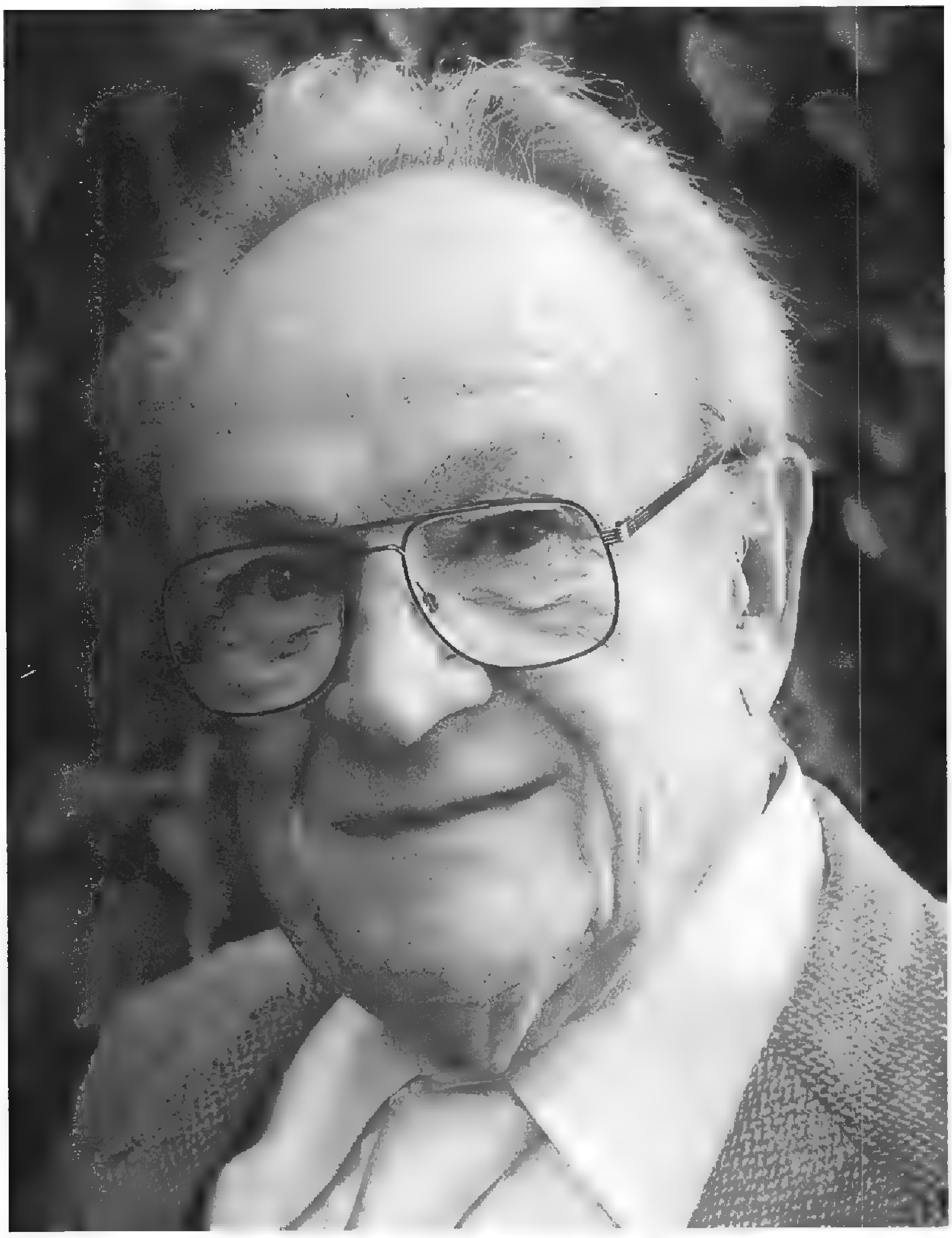
DEDICATION

WARREN HERBERT WAGNER, JR.
1920–2000



This issue of *Rhodora* is dedicated to Dr. Warren Herbert Wagner, Jr.—botanist and friend to botanists, professor, and student. Club members will long remember his spirited defense of field botany and whole-plant biology given at the symposium.

Largely responsible for rejuvenating the systematic study of North American pteridophytes, Herb considered thorough field knowledge of the plants in question a prerequisite to any laboratory investigation. He demonstrated the efficacy of this policy with major advances in the systematics of spleenworts (*Asplenium*), woodferns (*Dryopteris*), and moonworts (*Botrychium*). Herb's legacy extends beyond the study of pteridophytes, however, since his students and others have applied his lessons across the botanical spectrum. In particular, his demonstration of reticulate evolution in many fern genera led to a general inquiry about the significance and evolutionary consequences of natural hybridization. Many of us will remember him also for the development of "Wagner Trees" during the infancy of cladistics, which is ironic since clades can be obscured by hybrid reticulation.

In his later years Herb returned increasingly to field work, and ended his career immersed in the discovery and naming of new species. Within the past 20 years he named more than a dozen new species of *Botrychium* from the Great Lakes region and western North America, and during his last summer he traveled to Alaska to investigate a new moonwort there. In addition, he recently named numerous species of Hawaiian ferns, on which he was an expert, based on his many years of field experience there.

Young at heart, always curious and inquisitive, never accepting dogma (old or new), Herb was a most enthusiastic teacher, a prolific writer, and a superb field companion. He was always ready to talk about the nature of plants, either on a broad scale or a narrow one, and he enlivened any field trip with his broad range of knowledge.

Although his main research efforts lay outside New England, we all have benefitted from his work and his teachings. The NEBC is especially grateful that Herb gave freely of his time and spirit to the symposium.

—ARTHUR V. GILMAN, *Rhodora* Centennial Symposium Committee.

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OPENING REMARKS

PLANT CONSERVATION GLOBALLY AND LOCALLY

PETER H. RAVEN

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What I want to do here is to paint the broadest picture possible of the current crisis in biological conservation around the world, and in particular in the United States. This crisis is so extreme, and so important to us all, that I want to stimulate thinking about the issues involved and invite dialogue about strategies for combating the problem.

Our planet is four and a half billion years old and life has existed for at least 3.8 billion years, as far as we can tell. During that time, five great extinction events have occurred. The first three were restricted entirely to marine life. The fourth occurred at the end of the Permean, approximately 280 million years ago. This event changed the character of life on Earth, and led into the Mesozoic, the era of dinosaurs and cycads. During this era, angiosperms and other modern groups evolved and life on Earth became more and more complex. The fifth great extinction event occurred at the end of the Mesozoic, 65 million years ago.

The fifth extinction was probably precipitated by a meteorite, which landed somewhere in the vicinity of the Yucatan in Mexico. The result was an opaque cloud that restricted photosynthesis and disrupted life; two-thirds of the terrestrial species became extinct and the character of life on land again changed completely. Approximately ten million years went by before recovery of the evolutionary pathways that led to modern groups. It's estimated that, after the extinction, there were 500,000 to 1,000,000 terrestrial species remaining. Currently, the Earth is estimated to house between 7 and 10 million species of eukaryotic organisms. Of these, only one in four has a valid name. In the tropics, the ratio is much less, around one in twenty. Even for the described species of organisms, our knowledge of relationships and ecosystem dynamics is extremely limited.

Homo sapiens appeared on Earth approximately 200,000 years ago. During the past 200,000 years, our species has developed agriculture, migrated around the world, and increased in population to approximately six billion. Much of this population increase has occurred during the past century. Human population growth has been fueled by the use of oil, gas, and coal, causing tremendous atmospheric destruction. In the coming century, we are faced with the important questions: can we achieve sustainability and can we maintain the Earth's biological diversity? These questions are two sides of the same coin; the results of the past 50 years are not encouraging.

Americans first became aware of the concept of biodiversity in the 1980s. At this time, biodiversity was thought of as a kind of inventory of species, but gradually, the definition expanded to include all relationships and biological variations within communities and within ecosystems. In 1992, Americans became acutely aware of this situation, when President George Bush declined to sign the treaty "International Convention on Biological Diversity" at the World Summit held in Rio de Janeiro. At this convention, the United States was one of only seven countries to decline ratification.

Over the last fifty years, the population in the United States has increased from 135 million to 270 million. Also during this time, approximately 25% of the world's topsoil has been lost permanently, and 15–20% of the world's agricultural land has been lost to forces such as urban sprawl and deforestation. In addition, carbon dioxide levels have increased more than 30% and the stratospheric ozone layer has been depleted by 8%. Most seriously, there has been a drastic increase in the proportion of biological extinction in the past fifty years. We know from documented extinctions of birds and mammals that we can expect any given species to last about two million years. Since the Renaissance, extinction rates have increased hundreds of times. Current extinction rates are 1,000 × background rate and are accelerating towards 10,000 × background rate in the next century. Stuart Pimm of the University of Tennessee, using island biogeography models, has calculated that 1/3 of all tropical species will be extinct or nearly extinct within the next 25 years, and that 3/4 of all tropical species will be extinct or nearly extinct by the end of the next century.

It has been projected that, worldwide, 2/3 of all organisms will be extinct by the end of the next century. One species, *Homo sapiens,* is driving an extinction event comparable in scope and intensity to the one 65 million years ago, which completely changed the character of life on Earth. Nothing we could do could be more short-sighted or damaging to our own future, since we depend on the 350,000 species of photosynthetic organisms for all productivity in the biosphere.

We say that the 21st century will be the "Age of Biology," but how can it be if we are eliminating species at a rate comparable to the great extinctions of the past? How can we harness the power of genetic variability of organisms, which we are only just beginning to understand, when we are driving extinction rates to such phenomenal levels? Doesn't it make sense for us to be interested in sustainability? Doesn't it make sense for us to be interested in the rest of the world? Over the past 50 years, the industrialized world's population has fallen from 30% to 20%, but that 20% controls 85% of the world's economy and creates 80–90% of the world's pollution. The United States, as the wealthiest nation, can and must make a difference in reversing this trend for the benefit of ourselves and the rest of the planet.

What can we, as citizens, as scientists, do to maintain a world in which beauty, music, poetry, philosophy, literature, biological diversity, and all the things that we cherish can thrive? What do we have to do to create a world that will go on? It is important that we create a world that can continue to function sustainably. It is important that we not lose the biological diversity that would sustain us in the future. Our future depends on how we live now, on the choices we make. If we want to be optimistic about the world's future, we need to exercise our personal determination to do something about it. We should: (1) be leaders in developing new forms of energy conservation and alternative sources of energy; (2) pay attention to internationalism and acknowledge that the people living in non-industrialized countries are of profound importance to the earth's future; (3) vote, and encourage others to do so; (4) support like-minded conservation groups that are devoted to sustainability and internationalism; and (5) make wise choices and decrease our personal levels of consumption.

New Englanders have always looked to the world far beyond conventional boundaries. New Englanders have traditionally understood the world from a perspective of trading, knowledge, culture, and art. This is a great and traditionally defined region of our country, and one that has made wonderful contributions, and is set to make wonderful contributions for the future. In that vein, I hope that the remarks I have offered here have given you something to think about and to act on.

RHODORA, Vol. 102, No. 911, pp. 246–247, 2000

POST-GLACIAL CHANGES IN VEGETATION AND CLIMATE IN NORTHERN NEW ENGLAND

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SUMMARY. Quaternary research in several disciplines has produced strong independent evidence about the post-glacial vegetation and climate of northern New England and adjacent Canada. Late-glacial environments in the region included extensive areas of treeless tundra—more so than was the case in glaciated areas of mid-continental North America. Tree taxa spread gradually from the south, with most current forest elements present by the early Holocene. Subsequent changes in climate have greatly affected the distribution and abundance of those taxa.

Stratigraphic changes in physical and biological characteristics of lake sediments indicate that early to middle Holocene temperatures were as much as 2°C warmer and that the moisture balance (precipitation minus evaporation) was considerably lower than today. These reconstructions are consistent with known orbital variability (especially precession of the equinoxes) which resulted in as much as 8% more summer insolation than at present.

Several lines of paleoecological data corroborate this paleoclimatic reconstruction. White pine (*Pinus strobus* L.) was widespread and abundant in the early to middle Holocene, probably because frequent fires created conditions favorable for seedling establishment. During that same time, both white pine and hemlock [*Tsuga canadensis* (L.) Carrière] were present at elevations as much as 300 to 400 m higher than their present upper limit in the White Mountains of New Hampshire and the Adirondack Mountains of New York.

Conditions changed considerably during the past few thousand years, however, as the climate became cooler and moister. Fossil-pollen evidence shows that the distribution of white pine, which had been so extensive during the drier early and middle Holocene, has diminished consistently during the past 4000 years. This decline appears to have resulted from a reduction in frequency of forest fires during the late-Holocene shift toward a cooler, moister climate.

Within the past 1000 years, populations of several boreal forest

taxa, including spruces (*Picea* spp.) and balsam fir [*Abies balsamea* (L.) Miller] expanded along the southern margins of their distribution in Canada and the northern tier of the United States—from Minnesota to Maine. The strong expansion of spruce in the Great Lakes-New England region, especially the past 500 years, appears to have been associated with summer cooling of about 1°C during the Little Ice Age.

What can be said about the future? General Circulation Model (e.g., NCAR CCM3) projections for a future with twice the present atmospheric concentration of CO_2 suggest that both summer and winter conditions in northern New England may be as much as 3°C warmer than at present and that precipitation may also be greater. If the models are correct, the summer conditions may be as warm as or warmer than those 6000 to 8000 years ago, but possibly also wetter.

RHODORA, Vol. 102, No. 911, pp. 248–249, 2000

IMPLICATIONS OF POST-GLACIAL CHANGES IN CLIMATE AND VEGETATION ON THE FLORA OF THE WHITE MOUNTAINS, NEW HAMPSHIRE

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SUMMARY. Steep environmental gradients along the slopes of the White Mountains support a diverse flora in several distinct vegetation zones. Deciduous hardwood forests with white pine and hemlock occur at low elevations. Coniferous forests of spruce and fir with paper birch grow at mid-elevations. Subalpine fir forests are found at tree-line (~1500 m). The alpine meadows on the highest ridges and peaks have a flora that includes 73 species of vascular plants and a number of species of bryophytes that are essentially alpine.

Paleoecological studies in the mountains have recorded the broad-scale postglacial climate and vegetation changes over the past 13,000 years. These changes fit the regional patterns described for northern New England. However, because of the mountains' elevational range, two paleoecological changes are unique to the White Mountain region. Pollen and plant macrofossil evidence indicates that tree-line reached the valleys 11,500 years ago and reached its modern position on slopes 10,000 years ago. The contemporary alpine flora is widely assumed to be the remnant of the arctic flora that followed the retreating ice sheet. The mid-elevation coniferous forest of spruce, fir, and paper birch is relatively recent in origin, expanding several thousand years ago. Elevational range extension of white pine and hemlock and the mixtures of deciduous tree species in mid-elevational forests from 10,000 to roughly 4000 years ago indicate warmer climatic conditions than today. Tree-line may have also stood above its current elevation during the early to mid-Holocene 9000 to 4000 years ago.

While the patterns of vegetation and climate change are well known on the scale of thousands of years, short-term changes on the order of tens or even hundreds of years are poorly documented. Evidence from the Greenland ice-cores, the North Atlantic marine record, the Atlantic Canada terrestrial record (midges, pollen, and plant macrofossils), and the southern New England

pollen record show dramatic short-term climatic oscillations during the late-glacial (14,000 to 10,000 years ago). The ice-core and marine records show that these oscillations may have extended into the Holocene (the last 10,000 years). High (temporal) resolution studies are underway in the White Mountains to find evidence of these climatic oscillations. Preliminary loss-on-ignition (percent organic matter in the sediments), midge, and pollen studies document that two of these short-term oscillations, the Killarney Oscillation (KO) and the Younger Dryas (YD) did occur in the White Mountains. The mean annual temperature is estimated to have changed as much as 5–10°C within a period of less than 50 years during the YD 10,700 to 10,000 years ago. The magnitude and abruptness of these events may have created bottlenecks that reduced the size of the alpine and lower elevation floras in the White Mountains.

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VEGETATION OF THE PRESETTLEMENT FORESTS OF NORTHERN NEW ENGLAND AND NEW YORK

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ABSTRACT. The lotting surveys from northern New England and New York provide a unique opportunity to derive quantitative documentary evidence on past forests. Due to the distinctive "proprietory town" land tenure system, northern New England has an extensive and virtually untapped archive of land division surveys done prior to settlement (1763–1820). I searched archives throughout Vermont, New Hampshire, and northern New York and located records from 179 towns documenting 48,260 individual trees across the region. Surveyors used 131 separate vernacular names representing at least 49 recognizable species. This collection of town-wide witness tree relative frequencies is a consistent and unbiased empirical estimate of the composition of the natural vegetation before confounding land use. Five ubiquitous taxa (beech, spruces, maples, hemlock, birches) comprised 79% of the witness trees. Beech (32%) consistently dominated the region with greater than 60% of the trees in some towns. Spruce (14%) was the second most abundant species and found throughout the region. Maples (12%) were consistently distributed with peak abundance in Vermont. Hemlock (12%) had a patchy distribution with pockets of abundance, including the eastern Adirondacks. Birches (9%) were a species group with higher abundance in the mountains or to the north. White pine was consistently uncommon with very low (<1%) abundance on the uplands. A dramatic "oak–beech" tension zone or ecotone separated the oak–pine vegetation in the major southern valleys from the spruce–maple–beech composition northward. The central tendency was toward spruce–hardwoods with distinctive variants in the north, the Taconics, and the Champlain Valley. Major fires and blowdowns were equally rare and affected only 0.5% of the region. Fire was frequent only in the Hudson-Champlain corridor and windthrow was a low-level background disturbance. The most dramatic changes documented over the past 200 years have been the decline of beech and the profound effects of human land use.

Key Words: Adirondacks, historical ecology, New Hampshire, northern hardwood forest, plant biogeography, presettlement vegetation, proprietory town, surveyor's records, Vermont, witness tree

The first Europeans in northeastern North America saw the forest as "daunting terrible . . . infinite thick woods" (Josselyn 1675). Historical views of the land are subjective and anecdotal, but we are still influenced by their lasting metaphors: "This is the forest primeval. The murmuring pines and the hemlocks/ Bearded with moss, and in garments green, indistinct in the twilight/ Stand like Druids of eld, with voices sad and prophetic" (Longfellow 1854). Indeed the 18th century was *le grand dérangement* for both the people and forests of Acadia and New England. The 1700s began the clearing and harvesting of upland New England and within a century the land was profoundly changed (Whitney 1994). Since much of the region is forested today, we often assume a similarity to, if not continuity with, forests of the past. Was the forest dominated by the pines and hemlocks of Longfellow or the "hemlock–white pine–northern hardwoods" of Braun's (1950) classic treatise? Was the vegetation the thick woods of Josselyn or filled with decadent behemoths of "old growth" stands? Were the "bearded" trees long undisturbed and waiting to die of old age? Reconstructing the nature of the "primeval" forests is not just an academic exercise in historical ecology, but is necessary to establish an empirical baseline for ecological, educational, and management activities.

The characteristics of present forests can be projected backward to elucidate the composition and structure of historic forests. The response of trees to environmental factors or the current composition of long undisturbed forests are potential models for past conditions. Each of these models has limitations. Correlation with environmental variables is usually linear and deterministic. It tends to produce broad zones of vegetation responding to a single factor (e.g., climate) or stereotyped vegetation types based on distinctive topography or substrates. More appropriate models would be more sophisticated (i.e., non-linear, multivariate, stocastic) and be spatially explicit (e.g., Pacala et al. 1993). In addition, environmental conditions, especially in glaciated regions, are not a constant background and shift (e.g., climate) or develop (e.g., soils) in the interim. Paleoecological studies show the vegetation in northern New England is in flux due to long- and short-term environmental changes, land use history, and stochastic factors (Jacobson 2000).

A more practical approach to extrapolation is to use surviving forest remnants, especially those unconfounded by human activities. Even the largest of these areas in the Northeast (e.g., The Nature Conservancy's Big Reed Forest Reserve in northern Maine, The Bowl Research Area in the White Mountain National Forest of New Hampshire, and the Five Ponds Wilderness of the

Adirondack Park in New York) are few in number, have been repeatedly naturally perturbed (i.e., wind, ice, insects, fire), and escaped human activities exactly because they were "odd-balls" or "out-of-the way" (Cogbill 1996). Remnants, by definition, have escaped expected disturbances and are necessarily atypical of the "normal" or prevailing "common" landscape at any time.

Since the nature of the primeval forest is shrouded by myths, unrealistic models, and atypical remnants, historical methodology must be used to discover their reality. Actual "eye-witness" accounts are needed to document the details, variation, and dynamics in the landscape. Contemporary observations of explorers, naturalists, diarists, authors, and publicists abound, but they are very subjective and generally qualitative (Whitney 1994). Paleohistorical studies are more scientific and "see" the forest through reconstruction. They examine the physical evidence from earlier forests (e.g., dead wood, charcoal, pollen, macrofossils) at a site, testifying of the past occupants. Regional paleoecological syntheses give a long-term and relatively low resolution history of regional vegetation (Jacobson 2000; Spear 2000). We do not, however, have to resort only to scientific studies of remains to discover aspects of the vegetation that covered the historic landscape. Although the trees are no longer available for scientific inquiry, there is a contemporary and empirical documentary record. Surveyors at the time actually saw and recorded forest composition during land division and survey (Whitney 1994). Early surveys from northern New England, generally 1763 to 1820, clearly document the actual, not theoretical, abundance of particular trees in the forest before human improvements.

A distinctive land tenure system arose in the 18th century in the northern English colonies in North America (Clark 1983; Price 1995; Woodard 1936). The unsettled lands in northern New England were divided into areas, ideally six miles square on a side (= 100 km^2), called "towns." The "outlines" of the towns were commonly surveyed in anticipation of settlement and then the land was granted by the crown or the colonial government to a group of persons "in common," so-called "proprietors." The main occupation of the absentee proprietors was to subdivide the town into "lots," survey those (typically 40–60 ha) lots, and transfer ownership by means of a "lottery" among shareholders. Surveyors traditionally documented distances and corners of the outlines and lot boundaries by blazing and recording trees ("witness trees"). An unintended consequence of this "lotting survey" was a sample of the trees in the town on a predetermined grid. Significantly, the surveyors also often recorded general forest conditions, the suitability for settlement, and unusual character of each lot.

The proprietory town system was continued by the New England states after independence until disposal of ungranted land was completed in the mid-1800s. In northern New York much of the land was not granted to proprietors, but starting about 1791 the various units (i.e., tracts, purchases, patents) were transferred to individuals by the state (McMartin 1994). Significantly, in the Adirondack region, many units or subdivisions called "townships" were nominally the same size (100 km^2) as the New England town. Although most of the New York tracts do not correspond to towns today or were never settled, many were surveyed by the state into lots in the proprietory town tradition. Taken all together, these surveys inadvertently produced a systematic and widespread sample of the forest of northern New York and New England in the late 1700s and early 1800s ("presettlement surveys"). These records are official documents, but the local and transitory nature of the proprietors resulted in the manuscript lotting surveys, typically recorded in the "Proprietors' Book," or the resultant maps being scattered in various repositories. The New England town lotting methods were incorporated into the Land Ordinance of 1785, which mandated the "rectangular system" for land division in the western United States (Price 1995; White 1984). The resultant federal General Land Office (GLO) surveys have been the primary resource for numerous studies of the historical landscape (e.g., Delcourt and Delcourt 1996; Schwarz 1994; Whitney 1994).

Not as formalized as the GLO surveys, the unstandardized and dispersed town proprietors' surveys have received remarkably little interest (cf. Bourdo 1956; Irland 1999; Whitney 1994). In the Northeast, studies of the presettlement surveys have been done in northern Vermont (Siccama 1971), northern Maine (Lorimer 1977), upstate New York (Marks and Gardescu 1992; McIntosh 1962; Seischab 1990, 1992) and eastern Canada (Lutz 1997; Moss and Hosking 1983). All these studies used town outline surveys, except Siccama (1971) who used lotting surveys within 6 towns in northern Vermont to look at local vegetation patterns. In contrast, there are several towns in both New Hampshire and

Connecticut with readily available manuscript maps or other summaries of lotting surveys (Cogswell 1880; Hamburg and Cogbill 1988; Torbert 1935; Winer 1955). In addition, several researchers at Harvard Forest have begun to analyze town-wide lotting surveys in over 40 towns in southern New England (Foster et al. 1998; M. Burgi, pers. comm.). Whitney (1994) integrated many of these surveys into maps depicting the pattern of species' abundances over the northeastern quarter of the United States. His small-scale maps show broad continental distributions within the Northeast. The wealth of information from the underutilized and numerous town surveys is an unparalleled opportunity to fill in geographic gaps in coverage and display details of species distributions. Thus this study's purpose is to locate, collate, and summarize the available town witness tree surveys to derive a quantitative empirical database on the presettlement vegetation and its variation over northern New England and New York.

MATERIALS AND METHODS

I searched archives throughout Vermont, New Hampshire, and New York to locate manuscripts, maps, and published records of lotting surveys before settlement. The collation of witness trees in the presettlement surveys resulted from three separate projects. The Vermont collection was commissioned by the Vermont Biodiversity Project to provide background for the classification of vegetation in the state. The majority of the recorded surveys found were in the Proprietors' Books typically housed with the town land records in their respective Town Halls. Copies of many of the early town records are on microfilm at the Public Records Office in Middlesex. In addition, surveys of the towns granted by colonial New York within the present borders of Vermont were found in the New York State Archives (NYSA) in Albany. In the 1790s, the leased lots in the Rensselaer Manor towns adjacent to Vermont were also surveyed using similar techniques (Rensselaerwyck Papers, NYSA). The New Hampshire surveys were collected in a collaboration between the Hubbard Brook Long-Term Ecological Research (LTER) and the Harvard Forest LTER projects to create a baseline for historical land use studies. New Hampshire surveys were also usually recorded in the Proprietor's Books, commonly housed in the town office. Microfilm copies of many town records in New Hampshire were found at the New

Hampshire State Library in Concord. I collected the New York surveys in a follow-up project to document further the characteristics of old growth forests in the Adirondacks (Woods and Cogbill 1994). The New York records were found in the state's collection (NYSA) of Field Books (also available from the LDS [Mormon] Family History Centers) or Surveyor General's Books. Other sundry surveys and summary maps were collated from published papers and from manuscripts in various repositories (Town offices, State Historical Societies, State Archives, State offices) in all three states.

Records containing witness tree data or descriptions of the forest were carefully read, noting all trees cited by name and any descriptions of the forest composition or its disturbance (e.g., "open", "burnt", "fallen"). Throughout proprietary lotting surveys, virtually all witness tree citations were of a single tree at each sample point, so species associates were only known from supplemental line or lot descriptions. Whenever possible the trees were located on a map of the original lots ("lotting map" or "town plot"), and a special effort was made to avoid duplication of trees on shared boundary lines or the corners of adjacent lots. All witness tree "mentions" within each town were classified and tallied by the most exact taxa inferred by the surveyor's name. When possible, appropriate taxa were combined and frequencies summed into functionally similar groups (e.g., soft maples, white oaks, hard pines, wet ashes, white birches). In order to maintain a consistency in the identifications across all towns, the taxa and their frequencies were further lumped into 26 exclusive genera groups. For each town with more that 50 witness trees, the relative frequency of each taxon was treated as the presettlement composition (ca. 1800) at that location. To reveal the distribution pattern of each group or taxon, the relative frequencies were plotted on basemaps using Street Atlas USA® (DeLorme Co., Yarmouth, ME). Following Whitney (1994), isopleths of equal witness tree frequency ("isowits") generalize the patterns within the region.

Due to availability of wide ranging and detailed presettlement surveys, the forest was arguably better documented before settlement than it is today. The most detailed current data on the forest composition is in the decennial Forest Inventory and Analysis (FIA) project of the United States Forest Service. A comparison of these two data sets highlights changes over the past 200 years.

I calculated the ratio of the 1983 Vermont FIA (Frieswyk and Malley 1985) relative density of trees (> 5 in. DBH) to the average witness tree frequency in equivalent species' groups in the state ca. 1800.

RESULTS

This study located 179 "towns" in northern New England and New York with extensive lotting surveys (Table 1). The proprietory surveys date primarily from 1763 to 1810. Some non-proprietory towns' lots were surveyed as early as 1673 (Clark 1983), while late-granted tracts in the mountains were surveyed as late as 1850. In Vermont and New Hampshire the Proprietor's Books have survived in at least 185 (37%) of the towns and 105 (57%) of these books contain numerous witness tree mentions. Although 21 other town witness tree records were uncovered, the vast majority (83%) of the New England surveys were from the proprietors' records themselves. Due to the more exhaustive searches, Vermont has a slightly higher "yield" of books or surveys than New Hampshire; at least 33% of the Vermont towns have surviving presettlement surveys. In New York's Adirondacks, 49 (37%) of the larger tracts and townships have equivalent surveys available. The towns in the witness tree database come from throughout the region. There is the greatest representation from the heavily settled Merrimack Valley and western Vermont towns and the least representation from east-central New Hampshire and southeastern Vermont towns. Overall 48,260 witness trees were tallied with a median of 179 trees in a town and a rough sample density of 2.7 trees per km^2.

Vernacular names. In 1609, Samuel de Champlain (1925) saw ". . . fine trees of the same varieties (*espèces*) we have in France" along the New York shore of Lake Champlain. Although the early European observers were familiar with the genera in the flora of eastern North America, the species were novel. Surveyors invariably used colloquial names for trees, but virtually all citations can be associated with known scientific taxa. The lack of Latin names is not surprising given the short time since the introduction of the Linnaean system in 1753 and lack of useful manuals or floras until the turn of the century. Despite their isolation and lack of formal botanical education, the surveyors were

Table 1. Number of towns and witness trees represented in existing surveys from Proprietors' Books and other archival documents.

Region	Current Number of "Towns"	Number of Towns with			Survey Dates	Number of Witness Trees
		Prop. Book	Prop. Book Lotting	Total Lotting		
New Hampshire	245	77	35	44	1673–1850	16,781
Vermont	251	108	70	82	1763–1820	21,150
Adirondacks	132	—	—	49	1771–1831	8960
Taconics	4	—	—	4	1790–1795	1369
TOTAL	628	195	105	179	1673–1850	48,260

Table 2. Cited tree names in presettlement (1763–1820) forest surveys from 179 towns in Vermont, New Hampshire, and northern New York. Brackets indicate possible taxonomic ambiguity. Nomenclature follows Gleason and Cronquist (1991).

Surveyor Name	Surveyor Synonyms	Spelling Variant	Taxa Referenced
Generic Names			
Ash			*Fraxinus* sp.
Birch		Burch, Berch, Birtch, Burtch	*Betula* sp.
Spruce	Black spruce		*Picea* sp.
Cherry	Wild cherry		*Prunus* sp.
Elm		Holm, Ealm	*Ulmus* sp.
Hickory			*Carya* sp.
Maple		Mapel, Maypole, Mepall	*Acer* sp.
Oak		Oke, Oake, Och, Ock, Ocke	*Quercus* sp.
Pine			*Pinus* sp.
Poplar		Popler, Popular, Popplr	*Populus* sp.
Shadwood		Shadbush	*Amelanchier* sp.
Thorn bush	Hawthorn		*Crataegus* sp.
Willow	Osier, White willow		*Salix* sp.
Specific Names			
Alder	Alder birch		*Alnus incana*
Apple			*Pyrus malus*
Basswood		Bass, Baft	*Tilia americana*
Beech		Beach, Bectch	*Fagus grandifolia*
Black ash	Brown ash, Yellow ash		*Fraxinus nigra*
Black birch	Cherry birch		*Betula lenta*
Black cherry			*Prunus serotina*

Table 2. Continued.

Surveyor Name	Surveyor Synonyms	Spelling Variant	Taxa Referenced
Blue beech	Water beech		*Carpinus caroliniana*
Boxwood	Box tree		*Acer negundo?*
Butternut	White walnut, Lemon walnut, Oylnut, Oilnut, Butterwood	Butnut, Buternut	*Juglans cinerea*
Buttonwood	Sycamore	Buttinwood	*Platanus occidentalis*
Cedar	White cedar		*Thuja occidentalis*
Chestnut		Chisnut, Chesnutt	*Castanea dentata*
Chestnut oak	Rock oak, Yellow oak		*Quercus prinus*
Fir	Balsam fir	Firr, Fur	*Abies balsamea*
Hemlock	Hemlock pine	Hamlock, Hemloc	*Tsuga canadensis*
Leaverwood		Lear wood, Liverwood	*Ostrya virginiana*
Moosewood	Moose willow, Moose maple, Moosebush, Stripped willow		*Acer pensylvanicum*
Mountain ash		Mt. Ash	*Sorbus americana*, [*S. decora*]
Norway pine	Red pine		*Pinus resinosa*
Pepperidge		Pepraige	*Nyssa sylvatica*
Pin oak			*Quercus palustris*
Pitch pine		Pich pine	*Pinus rigida*
Popple		Pople, Popel, Poppel	
Red ash		Read ash, Reed ash	
Red birch		Read burch	*Betula cordifolia*, [*B. alleghaniensis*]

Table 2. Continued.

Surveyor Name	Surveyor Synonyms	Spelling Variant	Taxa Referenced
Red cedar			*Juniperus virginiana*
Red cherry		Reed cherry	*Prunus pensylvanica*
Red elm			*Ulmus rubra*
Red oak		Read oak, Reed oak, Reid oak	
Sassafras		Saxefax	*Sassafras albidum*
Shagbark	Shag walnut		*Carya ovata*
Soft maple	Red maple		*Acer rubrum,* [*A. saccharinum*]
Spruce	Double spruce, spruce pine	Sprusse	*Picea rubens,* [*P. mariana*]
Sugar maple	Hard maple, Rock maple, Sugar tree, Black maple		*Acer saccharum*
Swamp maple			*Acer rubrum,* [*A. saccharinum*]
Swamp white oak		Swamp oak	*Quercus bicolor*
Tamarack	Hacematac, Larch	Tamarac, Tamarisk	*Larix laricina*
Water ash			*Fraxinus nigra*
White ash			*Fraxinus americana*
White birch		White burtch	*Betula papyrifera,* [*B. cordifolia*]
White elm			*Ulmus americana*
White maple	Silver maple		*Acer saccharinum,* [*A. rubrum*]
White oak		Whight oak, Whit ocke	*Quercus alba*
White pine			*Pinus strobus*
White spruce			*Picea glauca*
Yellow birch			*Betula alleghaniensis*

Table 2. Continued.

Surveyor Name	Surveyor Synonyms	Spelling Variant	Taxa Referenced
Yellow pine			Pinus rigida, [*P. resinosa*]
Ambiguous Names			
Balsam			*Abies balsamea,* [*Populus balsamifera*]
Bastard maple			Acer spicatum, [*A. pensylvanicum*]
Hornbeam			*Ostrya virginiana,* [*Carpinus caroliniana*]
Juniper			*Juniperus virginiana, Thuja occidentalis*
Moose elm			*Acer pensylvanicum*
Peach			*Prunus*?
Plum			*Prunus* sp.
Rock birch	Rock white birch		*Betula* sp.
Wild pear			*Prunus* sp.
Witch elm			*Ulmus rubra, U. americana*
Whitewood			not *Liriodendron, Populus deltoides*?
Deceptive Names			
Black oak			*Quercus rubra,* [*Q. velutina*]
Dogwood			not *Cornus*?
Hacmetack			*Picea rubens,* [*Larix laricina*]
Walnut			*Carya* sp.
Witch hazel	Hazel, Hazelnut		*Ostrya virginiana*

Table 2. Continued.

Surveyor Name	Surveyor Synonyms	Spelling Variant	Taxa Referenced
Enigmatic names			
Beattlewood			?
Bilberry tree			?
Greenwood			?
Jerwood			?
Laurel			*Kalmia latifolia*?
Pegwood			?
Remmon		Remmond, Ammon, Remon	?
Roundwood			*Sorbus* ?
Shittum wood			*Sorbus* ?
Spoonwood bush			?
Tobaccowood	Moose(wood)		*Acer pensylvanicum* ?
Wicerpee			not *Dirca*

competent naturalists. The early lotting surveys recorded 131 vernacular tree names or synonyms (excluding quaint spellings) representing 65 distinct taxa (Table 2). Interestingly, the colloquial names were influenced by transferred English usage, and so the most ambiguous attributions are in taxa not shared with the British flora (i.e., *Ostrya, Carya,* shrubby *Acer*). The surveyors were very discerning and consistent in usage. For example, they often made subtle species distinctions (e.g., red ash, red elm). Overall 49 recognizable species are found in the presettlement species list for the 179 towns (Table 2). All these cited species are prominent current members of the approximately 65 species in the region's tree flora. Several infrequent species were not explicitly acknowledged (e.g., bur oak, big-toothed aspen, grey birch, bitternut hickory), but they are certainly present, submerged in amorphous genera or by misunderstood terms. There have been no apparent extirpations, but some terminology (e.g., lemon walnut, leaverwood, pepperidge) has fallen out of use.

Although the surveyors used many explicit vernacular names, there are still various degrees of uncertainty in some species (Table 2). For many of the most common trees only a generic name was cited (i.e., maple, oak, pine, birch, ash). In these genera there is an unavoidable confusion of species, but within their range and proper habitat many of the common species are unambiguous (i.e., sugar maple, red oak, white pine, yellow birch, white ash). Even in context, in some genera (i.e., cherry, poplar) the cited species remains ambiguous. Some specific names are still equivocal (e.g., swamp maple, yellow pine, red birch) or are occasionally misapplied (i.e., balsam, hornbeam, juniper). The most confusing are anachronistic names that have a deceptive common meaning today (cf. Marks and Gardescu 1992; Seischab 1992; Siccama 1963). Thus in late 18th century vernacular usage, hacmetack referred to any conifer, especially *Picea,* rather than its current exclusive use for *Larix*; witch hazel was *Ostrya* rather than *Hamamelis*; walnut meant *Carya* rather than *Juglans*; dogwood did not refer exclusively to *Cornus*; black spruce included red spruce, whose species concept did not exist until the late-1800s; and black oak was regularly used for red oak. A few names remain enigmatic; those used several times might be lost vernacular terms (i.e., remmon, shittum wood, pegwood, tobaccowood), but those used a single time were more likely confu-

Table 3. Composite presettlement composition of witness trees (n = 48,260) in 179 towns in northern New England and New York.

Taxa	Constancy (%)	Mean (%)	Maximum (%)	Coefficient of Variation (%)
Beech	98.9	32.1	68.2	42
Spruces	87.2	14.2	52.6	96
Maples	99.4	12.1	33.1	51
Hemlock	97.2	11.6	39.3	73
Birches	99.4	8.8	37.8	67
Pines	60.6	4.8	56.8	177
Oaks	52.2	4.8	58.8	195
Fir	55.0	2.9	25.0	165
Ashes	78.3	2.2	11.7	94
Basswood	66.1	1.4	10.0	121
Ironwoods	57.8	1.2	9.5	149
Elms	50.0	1.0	8.2	157
Cedar	30.6	0.5	7.1	216
Poplars	33.3	0.4	4.3	198
Chestnut	10.0	0.4	12.9	406
Tamarack	16.7	0.3	12.1	362
Hickories	20.6	0.3	4.3	254
Moosewoods	21.7	0.2	3.9	264
Butternut	17.8	0.2	5.3	326
Cherries	22.8	0.2	2.4	263
Willow & Alders	18.9	0.1	1.6	262
Buttonwood	7.2	0.0	1.7	499
Mountain Ash	2.2	0.0	1.7	740
Other		0.2		

sions (i.e., wicerpee, laurel), misunderstandings (greenwood, jerwood), or inventions (beattlewood, bilberry tree, gumwood).

Species distributions. The composite composition over the 179 towns is an integrated view of the vegetation in the region in 1800 (Table 3). Five taxa (beech, spruces, maples, hemlock, birches) composed 79% of the witness trees and each occurred in virtually every town in the region. Each of these ubiquitous trees was abundant (mean > 8%), had relatively low variability between towns (coefficient of variation [CV] < 100%), and could dominate certain towns (maxima > 30%) across the region. Beech (mean 32%) was by far the most abundant species, exceeding 60% in widely scattered towns. It constituted greater than

30% of the trees throughout its range, falling off only in southeastern New Hampshire, in the high mountains, and in the far northeast. Spruce was second in abundance (14%), but still less than half that of beech. It had a more restricted range than the other dominants (constancy 87% of the towns) and was not recorded in a few towns of the Champlain, Hudson, or Merrimack Valleys. Spruce abundance was variable, reaching 15% at middle elevations across the region, 35% in the mountains, and maxima (> 50%) in the western Adirondacks and at the Canadian border. Maples (mean 12%) had an abundance greater than 6% throughout the region with high pockets (> 20%) scattered across the richer soils of Vermont. By far the majority of these maple trees consisted of sugar maple, but its abundance was necessarily less than the generic figures. An undetermined lesser percentage of the trees was red or silver maple, especially in lowlands or in the larger river valleys. Hemlock had the same mean abundance (12%), but had a more patchy distribution than maple. There were three large polygons (i.e., southwestern New Hampshire, central Vermont, and especially the eastern Adirondacks) of towns with hemlock greater than the 20% isowit. Birches were the least abundant (9%) of the dominants and this figure is inflated since the taxon is also a mixture of species. Overall birch distribution was variable with greater than 5% everywhere and maxima of greater than 25% in the mountains. These maxima are most likely due to white birch, but yellow birch was apparently most important in mid-elevations and below. Both white and yellow birch increased from south to north and upslope, and both the species were represented in all areas except the Merrimack Valley.

Pine and oak were found in slightly more that half of the towns. Both had low overall abundance, but in a restricted part of their range could dominate (maxima > 55%) certain towns (Table 3). Oaks (mean 5%) were commonly found only in the Champlain or large southern valleys. Oak was codominant (> 30%) with pine in the Merrimack Valley and was commonly abundant (> 15%) in the Taconics and Hudson-Champlain corridor; however, these were a mixture of oak species. In lowland valleys, areas of maximum oak abundance, white oak dominated, with high frequencies even at the northern limit of its range (13%) on Squam Lake, New Hampshire. Red oak was most abundant (to 25%) in the southern hills and valleys and scattered (< 5%) northward in the upper valleys, but not found on the uplands or in the mountains.

Pine (mean 5%) also showed a variable and restricted distribution (Figure 1). The 5% isowit bounds roughly three polygons: in the Hudson-Champlain corridor, southeastern New Hampshire, and the Connecticut River. The nested 20% isowit defines the high pine abundance in scattered pockets in the Champlain, Connecticut, Ausable, and Saco Valleys and a large extreme (maxima > 50%) area in the Merrimack Valley. Unfortunately, the distribution and composition were obscured by the lumping of pines (i.e., pitch, white, red) into a single group. In areas of maximum representation in the large southern valleys, the majority of the pattern is clearly due to pitch pine, as here it was regularly cited by name or as "pine plains". White pine co-occurred in these valleys and was probably most common in northern ones, particularly the Champlain Valley and the "Cohas" (Abenaki for "white pine place") in the upper Connecticut Valley (Whitney 1994). Evidently white pine was the only pine on the uplands outside of the Taconics; but remarkably, here on the hills and mountains, white pine was consistently uncommon with very low (< 1%) abundance. Despite its reputation and conspicuousness, white pine was a relatively minor component of the presettlement forest in most of northern New England (cf. Braun 1950; Clark 1983; Irland 1999; Pike 1967).

In addition to the seven most abundant trees, five other taxa (fir, ashes, basswood, ironwoods, elms) occurred in more than half of the towns (Table 3). All these secondary species had low average abundance (1–3%). Except for fir, which could be locally common (> 20%) in the mountains, these species were common associates of the dominants and had rather modest maximum expression (8–12%). Ash was the most widespread (78% of the towns), but its component species showed contrasting distributions: black ash was more northern and in the lowlands, white ash more in the uplands and southern, while red ash was less common and intermediate. The remaining secondary species (basswood, ironwood, elms) were scattered across the region, but each reached maximum abundance in the richer lowlands such as the Champlain Valley.

The rest of the trees in the flora were recorded in less than 33% of the towns (Table 3). All these infrequent species, including the minor species in the grouped genera, had low average

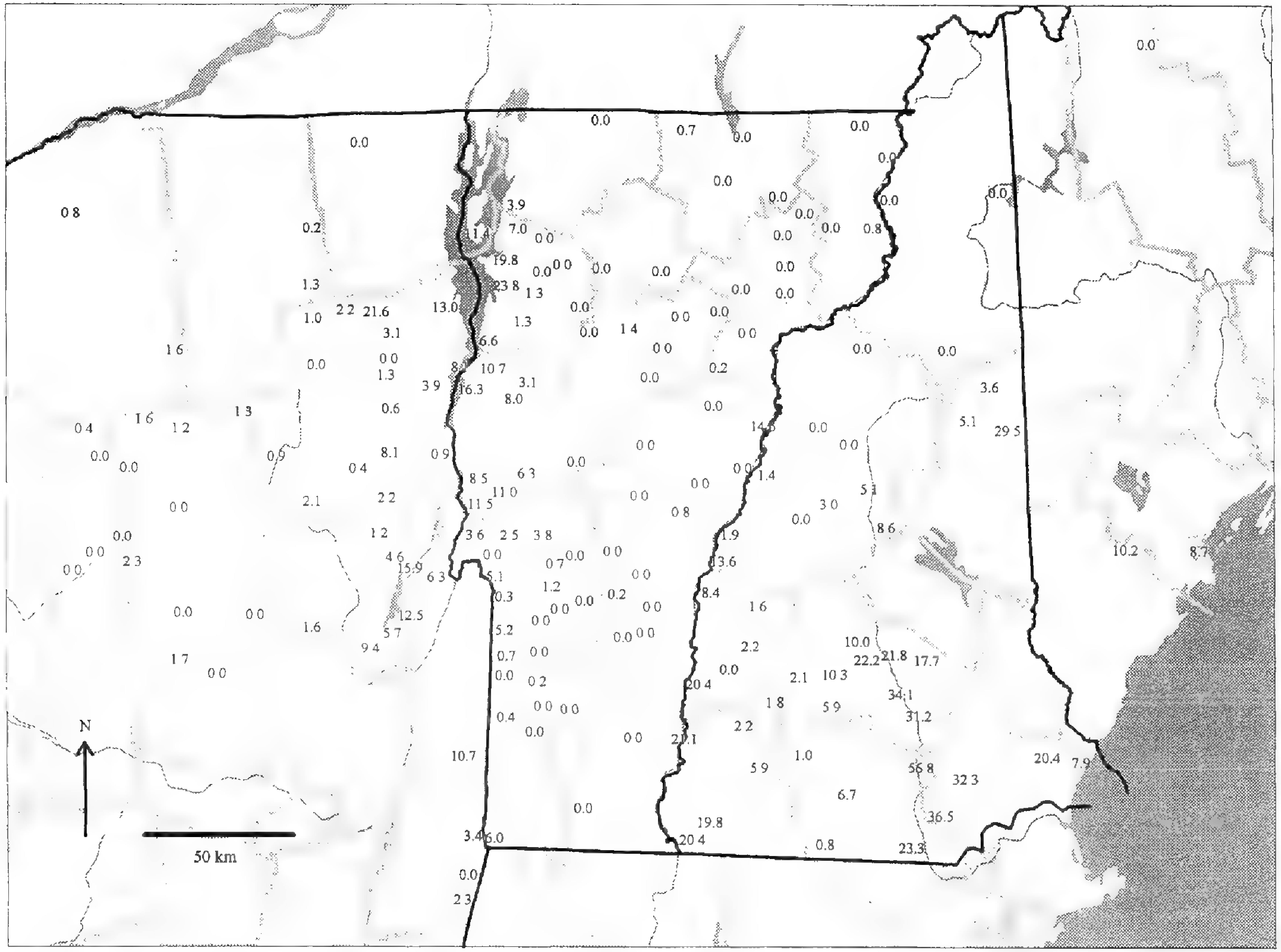

Figure 1. Relative frequencies (%) of pine in 179 town-wide presettlement lotting surveys in northern New York, Vermont, and New Hampshire. Base map is ® 1996 DeLorme Co., Yarmouth, ME.

Table 4. Number of towns (out of 179 surveyed) and lots affected by cited disturbances in presettlement surveys (1763–1820) in Vermont, New Hampshire, and northern New York.

Region	Total No. of Towns Disturbed	Fire		Windfall	
		Towns	Lots	Towns	Lots
New Hampshire	4	2	2	2	2
Vermont	8	2	2	6	10
Western Adirondacks	6	1	1	5	32
Eastern Adirondacks	14	13	71	4	6
Lake George	5	5	22	2	5
TOTAL	37	23	98	19	55

abundance (< 0.5%) and very patchy distributions (CV > 200%). Many of these minor species were restricted to special habitats (i.e., swamps, dry ridges, sand plains, riparian galleries, mountain slopes) and only three (chestnut, tamarack, cedar) with modest maximum abundance (> 6%) were locally common in particular habitats. Despite being distinctive indicators in the flora, all the remaining minor species averaged less than 1.2% abundance even when present, and were inconsequential to the prevailing composition of the forest

Dynamics. The presettlement surveys provide a static view of the forest development at the time, but the surveyors also indicated past disturbances in the forest. Lotting surveys commonly included "dead" or "dry" trees and "stubs" or "stumps" indicating a consistent low level of disturbance. The resulting forest often had numerous "staddle" (sapling) trees cited, but trees very rarely became large enough to merit the surveyor's "great" modifier. Significantly, there were 153 lots with instances of larger "burns" or "windfalls" worth recording (Table 4). Fire was the most prevalent disturbance with some two-thirds of the highly disturbed lots being burned. For example, in 1749 Peter Kalm (1987) noted that on the western shore of Lake Champlain "the mountains are covered with trees, but in some places the forests have been destroyed by fire." This is exactly the area in the Hudson-Champlain corridor where fire was most frequent. Beyond this valley, or in the under-cited Merrimack Valley, which obviously was an often burned "great pitch pine plain," fire had an extremely low frequency in the mountains of northern New

Table 5. Ratio of relative tree density in 85 towns across Vermont about 1800 to statewide FIA (Frieswyk and Malley 1985) relative tree density in 1983.

Increases (+)		Neutral		Decreases (−)	
Soft maples	25	Hard maples	1.3	Beech	0.2
White birches	23	Dry ashes	1.6	White oaks	0.2
Poplars	7	Sweet birches	1.0	Basswood	0.25
Cedar	4	Red oaks	0.9	Hard pines	0.4
Fir	4	Spruce	0.9	Wet ashes	0.4
Soft pines	2.3	Hemlock	0.7		
		Elm	0.7		

England and the western Adirondacks (Table 4). Evidently, catastrophic fires were restricted to sandy or rocky substrates, and generally near the settlement frontier. In contrast to fire, windfalls were found regularly across the region. Although commonly covering several lots at once, windfalls were smaller and more diffuse than burns. For example, in 1816 surveyor John Richards (Field Books, Vol. 4, NYSA) found "All the timber standing on it are large and thrifty, with very few exceptions, the wind has made havock [*sic*] among the timber in many places of [Township # 42]". Here in the western Adirondacks wind disturbance reached its maximum frequency (Table 4) and the pattern has been continued with the repeated blowdowns of 1950 and 1995 at the same site. As a result of the clumped and restricted distribution of burns, an equal number of towns was affected by fire (13%) as by wind (11%). Overall disturbances large enough to deserve mention, however, affected only 21% of the towns. In the affected towns an estimated 2.5% of the area was in burns or windthrow; overall roughly 0.5% of the region was affected by major disturbances at settlement.

The presettlement forest composition is a unique baseline for documenting the effects of land use in the region. Although all the species of the early forest were still prominent by 1983, the composition of the forests in Vermont have changed dramatically since 1800 (Table 5). Species of younger forests associated with the aftermath of human activities (i.e., soft maples, white birch, poplars) have increased by two orders of magnitude (up to 2500%). Even white pines have more than doubled in frequency, apparently due, in part, to the net gain between the loss due to harvesting and the regrowth in abandoned fields. Several species that originally grew in richer lowlands (i.e., white oaks, basswood, wet ashes) have also declined substantially (down to 20% of the original). Their maximum abundance was on the most productive land, which was intensively cleared and often remains unforested today, such as the Champlain Valley. Several species have remained roughly unchanged over the 200 years. Some of this is a balance between harvesting and woodlot improvement (maple) or a natural tendency for regeneration (ashes, sweet birches). Spruce has had substantial decline at mid-elevations due to climatic changes and forest harvesting, but this loss has been nearly balanced by substantial gains in the valleys due to regeneration in old fields (Hamburg and Cogbill 1988). The most dramatic change over the past 200 years is the loss of the absolute dominance of beech to 20% of its presettlement abundance. This decline is apparently not due to recent bark disease, to over utilization for wood, to lack of regeneration, or to land clearance. As first pondered by Siccama (1963, 1971), the reason for the incredible amount of beech in all northeastern presettlement surveys, and its subsequent decline, remains an enigma.

DISCUSSION

Accuracy. Quantitative analyses of the survey records depend on the data being an accurate estimate of tree composition within the towns. Lotting and outline surveys of proprietory towns are not a random sampling of the trees at the time; however, the survey design did produce samples in quasi-regular pattern at locations determined *a priori* and covering the whole town. As with much historical data, the methods were poorly documented, coverage was incomplete, and the observations were uncontrolled. For example, in 1772 in surveying the town of Mansfield, Vermont, Ira Allen (1928) professed that "(a) great proportion of said lots were made on spruce or fir trees, and if I described them as such, it would show the poorness of the town. In my survey bills I called spruce and fir gumwood, a name not known to the [proprietors]". Contrary to his claim, Allen's own proprietors' survey (Mansfield Proprietors' Book, Stowe [VT] Town Hall) shows 18% spruce and no "gumwood" at all. Nevertheless, the proprietor's surveys were done by numerous surveyors, over many years, with little incentive to skew the results.

In northern Vermont outline surveys, the corner-to-tree distances were statistically equal for all major species (Siccama 1971). Apparently in these systematic surveys there was little bias in the choice of trees (Bourdo 1956; Whitney 1994) and spatial bias, if any, was toward the more detailed surveys (e.g., lower reaches of the towns with the smallest lots), exactly the areas in town later most affected by settlement. At face value, the lotting tree tallies are a statistical sample and the relative frequencies are a consistent and unbiased estimate of overall composition of the forests at the turn of the 1700s.

Vegetation scale. The patterns of tree distribution exist at three distinct, albeit nested, vegetation scales: the community or forest type (~ 10 ^{2} km^{2}), the landscape or local combination of communities (~ 10^{2} km^{2}), and the regional or zonal arrangement of these landscapes (~10^{5} km^{2}). The town grain size (nominally 10^{2} km^{2}) is fixed by the mechanics of the presettlement surveys, but conveniently preserves species variation at the landscape scale (Delcourt and Delcourt 1996). The town-wide sample necessarily averages tree abundance over multiple forest types, but is an ideal size to reflect the local proportion of trees in those types. Thus the town sample is appropriate for the characterization of the landscape composition and advantageous for quantifying regional patterns. The minimum of 50 trees per town is low (Bourdo 1956) and limits the detection of infrequent species. Restricted types or infrequent species are incompletely sampled, but the analyses are accurate for the common species responsible for gross vegetational patterns. Moreover, many of the towns had large samples (> 400 trees) and this accounts for some estimates of range and abundance of uncommon species.

In mountainous or hilly terrain each town captured much of the elevational variation, so the town-wide data tend to cloud any elevational gradients. Moreover, each town supported many of the species in the region in a range of communities. Thus within-town variability was high compared to between-town variability. Therefore it is advantageous to have multiple samples within biophysical regions to elucidate regional patterns. The 179 towns in the region showed major range and abundance distributions not seen in the previous isowit maps derived from only 14 samples (Whitney 1994). Although the gross levels of common species abundance are similar, spatial and quantitative resolution is missing. For example, the small-scale maps (Whitney 1994) misrepresent the actual patterns: the oak dominance in the Merrimack Valley, the lack of pine on the uplands, the large amount of hemlock in the eastern Adirondacks, and the substantial presence of spruce in southwestern New Hampshire.

Vegetation types. The vegetation of the region varied from oak–pine in the warm southern valleys to beech–maple to spruce–fir in the northern mountains. In 1741, Richard Hazzen (1879), while surveying the northern boundary of Massachusetts near Whitingham, Vermont, found the land "exceedingly good and covered with Beach, Maple, Chestnutt &c. . . . the pigeon's nests were so thick that 500 might have been told on the beech [and] Hemlocks as well." The beech, maple, and hemlock still dominate, but the chestnut has been functionally eliminated and the pigeons are gone completely. At the opposite extreme of the compositional gradient, John Richards (1816, Field Books, Vol. 4, NYSA) while surveying Townships # 42 and 43 (now Five Ponds Wilderness) in the western Adirondacks saw "much fine spruce, yellow birch, beech, and maple . . . with few white pine and black cherry trees . . . [and an] abundance of the finest spruce and yellow birch on this land of any perhaps in the world." This was and remains the archetype of a red spruce–hardwood landscape in the Northeast. Even in this mixed-hardwood vegetation there was much local variation. The richer sites had more maple and less spruce. Thus in 1773 in Norbury, New York (now Calais, Vermont), Samuel Gale (Surveyor's General Book, Vol. 38, NYSA) found "choice land timbered with maple, beech, bass, some elm, ash, birch & in patches some butternuts, with Maidenhair and some nettles."

The ranges of the five dominant taxa in northern New England and New York overlapped in a broad zone, but they did not form a single landscape pattern. In the presettlement forest, beech was predominant and formed a series of conifer–northern hardwood types. Significantly, spruce was the typical conifer and neither white pine nor hemlock typified the entire zone (cf. Braun 1950). Although there were distinct regional variations (e.g., maple in Vermont hills, spruce in the western Adirondacks), numerous towns from all three states had a spruce–maple–beech composition. However common this central type, admixtures of secondary species caused the vegetation composition to diverge from this hub in three primary directions. One spoke was toward colder moosewood–fir–spruce towns of the north, the mountains, or the western Adirondacks; the second spoke was toward drier chestnut–hickory–poplar–oak ridges of towns in the Taconics-Lake George region; and the third spoke was toward the oak–pine lowland towns of the Merrimack Valley. Within this primary pattern, there were prominent variations, such as the abundance of hemlock in the eastern Adirondacks or the rich hardwoods (i.e., ashes, butternut, buttonwoods) of the Champlain Valley.

The one major vegetation boundary was the dramatic discontinuity between beech dominance on the uplands and oak–pine dominance in the major southern valleys. This rapid transition is akin to the "tension zone" between the prairie woodlands and the northern forest in Wisconsin (Curtis 1959). The similarity might even extend to the role of fire in maintaining the boundary. In the lower hills of the Taconics and southwestern New Hampshire there was an equivalent "oak–beech" tension zone at the edge of the Hudson and Merrimack Valleys. This ecotone marked a switch in dominance, as well as the coincidence of the general range limits of spruce, yellow birch, white oak, chestnut, and pitch pine. This major vegetation shift over a relatively short distance was even more surprising given the moderate elevational relief. A less distinct version of this tension zone ("pine–spruce") extended around the Champlain Valley and weakly up the Connecticut Valley. Due to the condensing of the elevation gradients and limited high elevation land, the distinct altitudinal ("coniferous–deciduous") ecotone was smoothed across towns in the presettlement compositions (Cogbill and White 1991).

Historical methodology. The lotting witness tree surveys from northern New England and New York are an empirical representation of the natural vegetation before confounding of land use. The presettlement dating, quantitative enumeration, unbiased estimates, and town-wide scale, are all unique advantages of this resource. Combined with the extensive available archival record, this tree composition database effectively documents the regional composition of the early forest. The summary isowits give higher resolution and temporal control than similar "isopoll" maps derived from paleohistorical sampling. This summary of regional vegetation, however, is still limited by its composite composition and landscape scale. Utilizing exact tree locations from lotting maps within individual towns would produce a truly detailed and spatially explicit view of the 18th century vegetation.

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FIFTY YEARS OF CHANGE IN *RHODORA* AND THE NEW ENGLAND FLORA

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SUMMARY. The major changes from 1950 to the present involve destruction of natural areas, effect of invasive species as well as species new to New England, and improved taxonomies. The period 1900–1950 was influenced mainly by the great Harvard botanist M. L. Fernald. *Rhodora* was one of the earliest North American regional journals. New techniques seem to be overtaking classical field and herbarium studies, and many of our field and herbarium workers feel eclipsed and no longer of value. Graduate students are giving up ambitions of becoming systematic botanists because they are not interested in purely laboratory or computer research. A comparison of studies of pteridophyte taxonomy between the period 1900–1950 and the present shows profound changes. The future of our research in New England should include careful comparison with other parts of North America, for example the western Great Lakes. There is still much to do, and field and herbarium studies are as important as ever. *Rhodora* continues to be an inspiration.

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LINKING THE DEEP AND RECENT PAST TO THE MODERN NEW ENGLAND LANDSCAPE

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Summary. The very long-term record provided by paleoecological studies indicates that rates of vegetation change during the relatively brief period since European settlement are the greatest since the last Ice Age. Interpreting the details of these changes and their persistent effects on modern landscapes at a range of spatial scales provides critical information for ecologists, conservation biologists, and natural resource managers. At a regional scale (i.e., New England excluding northern Maine) the landscape was largely deforested, farmed intensively, and, over the past 150 years, allowed to reforest naturally to produce extensive semi-natural woodlands interspersed with urban and suburban areas. One consequence of this history is that many open-land plants and animals, including several that are high priorities for conservation, thrived during the agricultural 18th and 19th centuries and have declined greatly over the recent past. In contrast, as forests have expanded and continued to mature there has occurred a remarkable expansion of native woodland species. At a sub-regional scale (i.e., north-central Massachusetts) this history is associated with a broad-scale homogenization of forest canopy composition. Although tree species abundance varied with climate gradients at the time of European settlement no such relationship exists today. In contrast, many herb and shrub species do exhibit striking variation in modern distribution with climate across the same area. Importantly, the change in tree composition apparently involves two processes: the very long-term decline in species such as hemlock and beech, which actually began more than 500 years ago in response to climate change, and a regional increase in successional and sprouting species due to land use.

On a landscape scale, vegetation structure and composition are apparently much more homogeneous and patchy than at European settlement as they currently vary on a fine scale with land-use histories. Site history, along with variation in soil conditions, is a strong determinant of modern species distributions because plant species vary so widely in their response and ability to re-

cover and re-establish after, for example, fire, forest cutting, grazing, or plowing. Stand-level pollen records suggest that the canopy composition of most forests was completely changed by this history and bears little resemblance to earlier forests on the same sites (Foster and O'Keefe 2000).

Recognition that New England is a cultural landscape shaped in most details by its history of intensive human activity is an essential background for understanding modern ecological processes. Interpretation of the details of this history at geographical and temporal scales relevant to specific concerns can afford tremendous insights into land management and conservation policy (Foster 1999).

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IMMIGRATION AND EXPANSION OF THE NEW ENGLAND FLORA

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ABSTRACT. Nonindigenous vascular plant species have been introduced, intentionally or unintentionally, since Europeans landed in what is now New England some time in 1496. We know little about the native flora of New England at that time. John Josselyn's *New England Rarities Discovered* recorded both the native and European plants he saw during his two visits to southeastern Maine and is the earliest report on the flora of what is now New England. Subsequent writers, such as Manasseh Cutler, also documented both the native and increasing number of non-native species that became naturalized in this region. This paper discusses both the intentional and nonintentional introductions from Europe and the later introductions from eastern Asia. Various modes of unintentional introductions such as ballast plants and agricultural "stowaways" are presented. Species that are native to other regions of North America and that have naturalized in New England are mentioned. Currently, over 1000 vascular plant species that are not considered indigenous to the region exist in the New England flora. A few introductions have become so aggressive in their establishment around New England that they are now acknowledged as invasive species. Early botanical works and herbarium records are used here to document arrivals and changes in the flora.

Key Words: introductions, non-native plants, nonindigenous plants, New England, flora

The flora of New England is a mosaic of native and non-native species. The ratio of native to non-native species varies from habitat to habitat, site to site, and time to time. Nonindigenous species have been arriving since the earliest European explorers set foot on New England shores. While some non-native species arrived accidentally, many were brought here for utilitarian or aesthetic reasons. Not surprisingly, the earliest introductions into New England were native to Europe, later ones coming from other regions of North America, Eurasia, Eastern Asia, or elsewhere.

The current New England flora is composed of between 24 to 45 percent nonindigenous species (Table 1). These percentages are only approximations because of different taxonomic circum-

Table 1. Tabular summary of species by state. [1]Seymour 1969; [2]Dowhan 1979, Mehrhoff 1987, 1995; [3]Gould et al. 1998; [4]Sorrie and Somers 1999; [5]Campbell et al. 1995.

State/Region	Total spp.	Native spp.	Non-native spp.	Percent Non-native
New England[1]	2882	1995	887	31%
Connecticut[2]	2625	1700	925	35%
Rhode Island[3]	1618	1226	392	24%
Massachusetts[4]	2814	1538	1276	45%
Maine[5]	2103	1469	634	30%

scriptions, nomenclature, different appraisals of what is considered naturalized, and recent discoveries. Published works vary depending on nomenclatural sources. Seymour's *Flora of New England* (Seymour 1969) and Dowhan's *Checklist for Connecticut* (Dowhan 1979) follow Fernald's nomenclature (Fernald 1950) for most treatments. The *Vascular Flora of Rhode Island* (Gould et al. 1998) follows Cronquist (Gleason and Cronquist 1991) and *Flora of North America* (Flora of North America Editorial Committee 1993+). Massachusetts' county checklist (Sorrie and Somers 1999) follows a mixture of Kartesz's nomenclature (Kartesz 1994) and that of the Flora of North America Project (Flora of North America Editorial Committee 1993+). Maine's checklist (Campbell et al. 1995) uses a variety of additional sources including experts who are preparing taxonomic treatments for the Flora of North America Project.

In New England, Rhode Island appears to have the lowest percentage of nonindigenous species, 24% (Gould et al. 1998), while Massachusetts appears to have the highest, 45% (Sorrie and Somers 1999). Published current figures are not available for Vermont or New Hampshire.

There are two complimentary ways of evaluating the history of the nonindigenous components of the New England flora. One way of approaching the expansion of the flora is temporal. The other is phytogeographic. Historical documents shed light on the increase in non-native species over time. Concurrently, there are elements of the introduced flora known to represent different phytogeographic origins. Although there were periods of introductions from different geographical regions, the temporal component and the phytogeographic component do not exactly coincide. Separating the two can be difficult because certain Asian taxa, such as Tree-of-Heaven, *Ailanthus altissima* (Mill.) Swingle, were introduced into North America from botanic gardens in Europe (Spongberg 1990).

TERMINOLOGY

For this paper I set the bounds of New England to be the cumulative political boundary of the six New England states. While this boundary is admittedly artificial, it helps clarify the meaning of the native and non-native.

Native or indigenous are used here for those species that existed within this boundary prior to AD 1496 when the Italian explorer John Cabot, sailing for King Henry VII of England, landed on what are now New England shores (Newby 1982). Native taxa are often mentioned in the early botanical literature for New England. Herbarium collections do not exist that document these early reports. In fact, the earliest herbarium collections for New England that still exist (at least in North American herbaria) appear to be from around the beginning of the 19th century. Most native taxa are North American endemics although some exhibit amphiatlantic or cosmopolitan distributions. Taxa that naturally occurred in the region near New England and recently arrived here by means of their own adaptations without the aid of human intervention are also considered native. *Eupatorium album* L., is considered native to Connecticut although it was only discovered there in 1981 (Mehrhoff 1996). It had been known for many years from Long Island (Miller and Young 1874) and is wind dispersed. Its discovery in southeastern Connecticut was not surprising.

Non-native or nonindigenous species as used here are taxa that appear to have arrived in New England sometime after AD 1500. Most of these are known to have extra North American origins. The majority of these taxa arrived with aid, intentional or accidental, from humans. As many species were intentionally introduced and subsequently escaped and became established here, there is often a known history of their introduction. In addition, many of these are known to be native elsewhere and their occurrence here accepted as human-assisted. There are no herbarium records until much later and often, as a newly discovered species is noteworthy, there may be numerous collections attesting to its recent discovery and novelty.

Introduction is used to describe an event. By itself it implies neither intentional introduction nor accidental introduction. These modifiers should be used when the history of an introduction is known or clarity of thought is necessary.

Naturalized is used to designate non-native taxa that are established, reproducing and persisting without human intervention and cultivation. Often, establishment can occur within natural plant communities. Many non-native taxa occur in New England but cannot be considered as naturalized because they must have human intervention in order to persist. Further, naturalized implies persistence over time. Some species not considered naturalized may exist away from cultivation for a year or two but populations do not establish and persist for long. These should be considered adventive (Fernald 1950).

Garden escapes are those taxa that originally were intentionally introduced as garden plants and subsequently became naturalized away from cultivation. The term garden escape here is used only for taxa that are completely naturalized into the New England flora, not for adventives. Notations on old herbarium specimens often indicate "in garden," "near garden," "escaped from garden," or "established."

Occasionally perceptions of a plant's desirability change when a garden plant escapes and becomes naturalized away from gardens. Fernald (1940) tells how *Hieracium aurantiacum* L. was a prized garden plant in the central Maine of his youth and was then known as Venus' Paint-brush. Once it had escaped and become established away from gardens it was often seen growing aggressively in these new sites. After a while, its colloquial name had changed to Devil's Paint-brush.

Invasion, invasive species, and invasives are used to imply both an arrival event and subsequent establishment and proliferation. These terms are only used here in reference to non-native species. Rapid spread or aggressive growth and proliferation are implicit with invasive species. No inference should be drawn about the arrival event; it can either be by the biological attributes of the species or with human assistance. The use of explosive species or native explosive species in reference to native species that exhibit the characteristics of invasive species might help avoid confusion.

A weed, commonly described as a plant growing where it is not wanted, can be native or non-native (Les and Mehrhoff 1999).

For this reason, and because personal preferences and biases exist, the term weed is not used here. Weedy, however, is a good descriptive term and clearly understood by most to imply rampant growth.

Nomenclature used here follows Cronquist (Gleason and Cronquist 1991) or the published volumes of the Flora of North America Project (Flora of North America Editorial Committee 1993+).

HISTORY OF INTRODUCTIONS

Early accounts of the pre-colonial flora are biased by interpretation (Whitney 1994) and rarely go beyond generic descriptions of the forest. The earliest written account of the flora was that of John Josselyn, an Englishman who published two books on the natural curiosities of the New World in the late 17th century. No one knows the dates of Josselyn's birth or death but we do know he twice visited his brother who lived in the region that is now Saco, Maine. The first visit was in 1638, when he stayed for 15 months. His second visit was in 1663, this time lasting for eight years (Tuckerman 1865). During these two visits he recorded his observations on the wildlife and flora he encountered. Shortly after his return to England in 1671, he published *New England Rarities Discovered in Birds, Beasts, Fishes, Serpents, and Plants of that Country* (Josselyn 1672).

In *New England Rarities Discovered,* Josselyn, as the title suggests, discussed five groups of organisms found in New England. Within the plants, he further divided his listings into five subdivisions: "Of such Plants as are Common with us in England," "Of such Plants as are proper to the Country," "Of such Plants as are proper to the Country, and have no Name," "Of such Plants as have sprung up since the English planted and kept Cattle in New England," and "of such Garden-Herbs amongst us as do thrive there, and of such as do not" (Josselyn 1672). Interspersed throughout the text are uses for the plants and animals about which he was writing. The author, with crude line drawings, illustrated nine of the plants. Josselyn's use of vernacular names is often confusing or difficult to decipher. He probably used Johnson's edition of Gerard's Herbal from 1636 as his source of information (Tuckerman 1865).

New England Rarities Discovered represents the first exposition of the New England Flora. In addition, it sets a benchmark for dates for early nonindigenous introductions. Josselyn's fifth section on plants is of interest as a list of garden plants that may represent one of the earliest accounts of what plants were cultivated for food by early settlers.

Josselyn's first section, "Of such Plants as are Common with us in England" includes native widespread species such as *Typha latifolia* L. that naturally occurred here as well as in Great Britain. Other taxa included in this first list are now considered to have conspecific species on either side of the Atlantic. Josselyn included here a number of species now considered nonindigenous in New England. One can infer, as Tuckerman (1865) did, that these nonindigenous taxa must have been introduced early in colonial history because they were so well established by the time of his visits that Josselyn mistook them for natives.

Josselyn used vernacular names known to him. Some of these such as "Hollow-leaved Lavender" (*Sarracenia purpurea* L.), "Rupter-wort" (*Euphorbia* sp.), or Trackle-berries" [*Smilacina racemosa* (L.) Desf.] are no longer used (Tuckerman 1865). It is often difficult to decide which taxon was meant by some of Josselyn's names. In 1865, Edward Tuckerman published an annotated version of *New England Rarities Discovered.* In this, he attempted to identify, using contemporary scientific names, all of the taxa included by Josselyn. Tuckerman's interpretations are extremely helpful though he was not always clear about the species to which Josselyn was referring. He attempted to interpret Josselyn's names in light of what was known about European and North American floristics at that time. For example, Tuckerman assumed that when Josselyn recorded St. John's-wort, he probably meant *Hypericum perforatum* L., now assumed by most botanists to be introduced here. However, he commented that Josselyn could have meant *Hypericum corymbosum* Muhl. (now *Hypericum punctatum* Lam.).

Josselyn's fourth section, "Of such Plants as have sprung up since the English planted and kept Cattle in New England," is the most interesting section when considering the nonindigenous flora. Here Josselyn listed 40 species that he felt were not native to New England and were brought here, intentionally or unintentionally, by Europeans. His section heading is interesting in that it implies he associated the keeping of cattle with the arrival of European species. Seeds of many species are known to have been "stowaways" with seeds intended for agricultural uses (Fernald

1905). Perhaps Josselyn had some reason to suspect that seeds were unintentionally introduced with livestock food or bedding. In a footnote following this section Tuckerman pointed out taxa mentioned mostly in Josselyn's first section that belong here.

The first and fourth parts of Josselyn's plant lists are of interest as lists of plants that had been introduced from the Old World by this time. These lists help narrow the period during which the taxa Josselyn included here were introduced. Given the state of floristic botany in the late 17th century, it is not surprising Josselyn included with his native species, taxa now thought to be introductions. For instance, Josselyn's Wild purcelane [*sic*], was thought by Tuckerman (1865) to be *Portulacca oleracea* L., a native of Europe. This report establishes this taxon as part of the flora of New England at a very early date. Josselyn's inclusion of Herb Robert in his first section is interesting. *Geranium robertianum* L. was considered by Tuckerman (1865) to be "common to us and Europe". Eastern North American populations have been viewed as native here by Fernald (1950) but naturalized by Cronquist (Gleason and Cronquist 1991). Many field botanists consider it a good indicator of rich, shaded colluvial slopes and cool, mesic woodlands. In western North America populations of *G. robertianum* are viewed as non-native and invasive (Brumback, pers. comm.). Josselyn's inclusion of this species in this section suggests it should be considered to be native in New England since it is unlikely it would have become so well established in such specific natural habitats in the short time after Europeans arrived here.

The second written record of plants, both native and non-native, existing in New England, is that of Manasseh Cutler. Cutler was born in Killingly, Connecticut, in 1742, educated at Yale College, and became a pastor in Ipswich Hamlet, Massachusetts, where he lived until his death in 1823 (Humphrey 1898). In spite of remaining in one town for 52 years, Cutler was far from sedentary. We know from his correspondence and diaries (Cutler and Cutler 1888) that he traveled widely throughout New England, collecting as he traveled. A diary entry from July 2, 1787 recounts how while traveling from Middletown, Connecticut, to New Haven he examined several plants he had collected, "for the heat was too intense for riding" (Cutler and Cutler 1888). Unfortunately, Cutler's large herbarium was destroyed by fire (Day 1901).

Cutler's "An Account of some of the vegetable Productions, naturally growing in this Part of America, botanically arranged [*sic*]" was published in the first volume of the Memoirs of the nascent American Academy of Arts and Sciences (Cutler 1785). "Botanically arranged" was according to the new Linnaean sexual system. In his introductory paragraphs, Cutler (1785) explained that he undertook this listing of plants from "this part of America" because he felt that while "*Canada* and the southern states . . . have been visited by eminent botanists from *Europe*" there had been "almost total neglect of botanical enquiries [*sic*], in this part of the county". He blamed this on the fact "*that Botany has never been taught in any of our colleges*, and to the difficulties that are supposed to attend to it; but principally to the mistaken opinion of its inutility in common life" [his italics]. Later he commented, "From the want of botanical knowledge, the grossest mistakes have been made in the application of the *English* names of *European* plants, to those of *America*." Cutler was well aware of nonindigenous plants in the landscape. On this subject he wrote, "We have it, also, in our power, from the recent settlement of the country, to determine, with great certainty, what vegetable productions are indigenous, and present those doubts and disputes hereafter, which have frequently taken place among botanist in old countries. For it is very improbable that any exotic plants are become so far naturalized as not to be distinguishable from the natives."

Cutler reported 66 European species established in New England. He made no attempt to correct the confusion of using European names for North American taxa. Because of this, some of his taxa must be suspect. Under *Ornithogalum,* he said about what he called Bethlemstar [*sic*], "Blossoms yellow. Common in grass lands and amongst bushes." The European *O. umbellatum* L., now commonly known as Star-of-Bethlehem, has white tepals. The native *Hypoxis hirsuta* (L.) Coville, common in New England grasslands and open woods, has yellow sepals and petals and was originally published as *Ornithogalum hispidum* by Linnaeus.

Possibly the most interesting inclusion is under the genus *Cardamine.* Cutler gave the common names "Impatient" and then "Impatient Ladysmock". These are followed by the comments, "Blossoms yellowish white. By springs in mountainous land." The European *C. impatiens* L. has yellowish-white petals whereas most other *Cardamine* that occur in New England have white or pinkish petals. The earliest herbarium specimen seen from New England was collected in Peterborough, New Hampshire, in 1916. It seems unlikely *C. impatiens* was here and established in Cutler's time as it is not included in the seventh edition of *Gray's Manual* (Robinson and Fernald 1908) and the eighth edition of *Gray's Manual* (Fernald 1950) has it only as local from southern New Hampshire and eastern Pennsylvania. It is possible, but unlikely, that Cutler was seeing *C. hirsuta* L. but this species was not known in New England until recently. *Cardamine parviflora* L. is native to Europe and represented in New England by its var. *arenicola* (Britt.) O. E. Schulz, but this is usually a taxon of dry, sandy soils and ledges, not of "springs in mountainous land". Cutler was probably reporting the native *C. pensylvanica* Muhl. that occurs commonly along streams, though this species usually has sharply white petals. The true identity of this taxon and its historical biogeography must await further elucidation.

Some of Cutler's other inclusions are less obscure. Many notes about non-native species are interesting in light of current distributions. *Ligustrum* "is not very common in the wild state." He made no mention of which species, but it must have been, given the time, the European Common Privet *L. vulgare* L. Thornapple or Jimsonweed, *Datura stramonium* L. "is said to be an exotic, and that it is not found growing at any great distance from the sea." *Solanum dulcamara* L. was "Common about fences in moist land." *Berberis,* taken by me to be *B. vulgaris* L. because of his comments "that rye and wheat will be injured by this shrub, . . ." is said to be "Common".

The next account of the region's flora was Jacob Bigelow's *Florula Bostoniensis* or *Plants of Boston* published in 1814. Bigelow included 83 introduced species in the first edition. By the third edition, published in 1840, there are 140 nonindigenous plants enumerated (Fernald 1905). In most cases, nonindigenous species are not distinguished in the text. Occasionally an entry will include a comment about a possible introduction. By the time the second edition was published in 1824, the Black Locust, *Robinia pseudoacacia* L. had become established in New England. Not included in the first edition of *Plants of Boston,* Bigelow said of it by 1924, "The Locust tree, exceedingly valued for the hardness and durability of its timber, is not, I believe, found native in the New England states, though abundantly naturalized near habitations and roads." He went no further than to explain that it is native to North America. It is commonly taken to have occurred as far east and north as central Pennsylvania (Elias 1987). This is indicative however, that by this time, people had started moving species native to other parts of North America into New England for utilitarian purposes.

Other floras produced in the first half of the 19th century add other species to the growing list of non-native species that had naturalized in New England. John Brace's flora of Litchfield, Connecticut (Brace 1822), includes both native and non-native species. Likewise, in 1831, Dr. Eli Ives, a professor of *materia medica* at Yale College, produced a list of plants growing without cultivation in the vicinity of New Haven, Connecticut (Ives et al. 1831). Both authors included native and non-native taxa but did not always distinguish between them.

The Massachusetts legislature commissioned a report on the botany of the Commonwealth that was ultimately separated into herbaceous plants by Chester Dewey (1840) and trees and shrubs by Emerson (1846). While Dewey's flora includes introductory remarks under the heading "Of the Useless Plants" that would lead one to believe he might have provided insight into some of the introductions, he actually provided little beyond commenting that a species is introduced, possibly introduced, or naturalized. Similarly, Emerson included nonindigenous species but shed no light on how they might have been introduced. These points apparently show, however, that while cognizant of the presence of non-native species, these botanists did not view them in a negative light.

Many collections made during this same period led to the naming of species of vascular plants from New England that were new to floristic botany. It is interesting to note that the scientific authorities for most of the taxa included in the early works on the New England flora were Europeans. During the first half of the 19th century, names of New Englanders such as Bigelow, Ives, Oakes, Robbins, Hitchcock, and Dewey appeared as authorities for New England plants. The species published by these botanists added to the numerical expansion of the regional flora.

By the last half of the 19th century lists of non-native plants by means of introduction were appearing in the literature. There are a number of plausible explanations for this beyond the scope of this paper, such as better communication between Europe and

North America, better training in botany, and botanists who traveled abroad and knew plants in native habitats as well as in their naturalized condition. Perhaps, too, there was an increase in the number of North American botanists, both professional and amateur, who were actively cataloging the local flora.

The effort of cataloging non-native species was perhaps pioneered by Lewis D. de Schweinitz, whose "Remarks on the Plants of Europe which have become naturalized in a more or less degree, in the United States" was published posthumously in 1832 (Schweinitz 1832). Schweinitz's work appears to have focused primarily on New York and Pennsylvania. He separated the 137 species he enumerated into 3 categories: 1) Plants which have become more or less *generally* naturalized in the United States; 2) Plants but *partially* spread; and 3) Introduced only in the vicinity in which they are or were cultivated. He further divided the more or less generally naturalized species into those introduced by cultivation, for agricultural or other purposes, and those introduced fortuitously with agricultural seeds (Schweinitz 1832).

SOURCES OF INTRODUCED PLANTS

Introductions occurring in the latter half of the 19th century were either intentional or unintentional. Plants were intentionally introduced as crops for humans or livestock, for natural products such as dyes, foods, and other intentional uses, or for esthetic reasons. Often these escaped and became naturalized. Robinson (1880), in the introduction to *The Flora of Essex County,* told of the prevalence of gardens for purely ornamental purposes. It is in this period that we see the rise of botanical gardens that served the multiple functions of education, research, and recreation. Noteworthy among these was Harvard's Botanical Garden in Cambridge, begun in 1806 by William Dandridge Peck and taken over by Asa Gray in 1842 (Dupree 1959), and later, in 1872, the Arnold Arboretum (Hay 1995; Spongberg 1990). During this period, the polymath Jacob Bigelow and others laid out the grounds of Mt. Auburn Cemetery in Cambridge as a kind of botanical garden.

Seed catalogs show that many non-native plants had been introduced into the trade during the first half of the 19th century (Mack 1991). Many well-known naturalized species were first introduced into New England as garden plants and later escaped. Sometimes these "escapes" were aided by plant-growers. Both *Trapa natans* L. and *Marsilea quadrifolia* L. were introduced into the wild near Boston by Louis Gauerineau, the gardener at Harvard's Botanical Garden (Les and Mehrhoff 1999). Other times, garden plants escaped. Many early labels for collections of *Vincetoxicum nigrum* (L.) Moench mention it as escaping from gardens. It is interesting to speculate that the source of the first New England specimen of this Swallowwort (BRU!), taken on the streets of Cambridge, Massachusetts, in 1876, was the Harvard Botanical Garden. Fernald (1900) explained how *Artemisia stelleriana* Besser probably escaped from late 19th century private gardens in which it was a popular bedding plant.

Ship's ballast was an early-recognized source of non-intentional introductions. Ships coming to the United States in order to bring natural resources back to Europe would arrive with rocks and dirt as ballast to be discarded before loading the valuable cargo for the return trip. Many port cities had "ballast grounds" or ballast piles to which the jettisoned ballast would be continually added. These became favorite haunts of local botanists in search of floristic novelties. One of the earliest works on this subject was by Aubrey H. Smith on "Colonies of Plants observed near Philadelphia" (Smith 1867). This was followed by other reports from the Philadelphia area (Burk 1877; Martindale 1876, 1877). In 1878, Judge Addison Brown began a series of five articles on ballast plants collected around the port of New York City (Brown 1878a, 1878b, 1879, 1880, 1881). Many of the plants, especially in Brown's lists for New York, occur in New England and it is not inconceivable that they arrived here in the same manner, given the thriving ports and navy yards along the coast from Connecticut to Boston and downeast to Maine. In fact, Smith (1867) referred to some of the ballast piles in Philadelphia near where the "coasters" docked.

In the early part of the 20th century a number of small papers were produced on plants found in the vicinity of factories where seeds or propagules would be introduced with the products with which the factory dealt. Some of the best known of these kinds of introductions were the plants found with "wool-waste". From 1901 to 1932 there were a series of articles in *Rhodora,* mostly by Emily F. Fletcher, dealing with plants found around woolen processing plants near Westford, Massachusetts (Collins 1901;

Fletcher 1912, 1913, 1915, 1916, 1917; Weatherby, 1924, 1932). The composting wool-waste was later used to fertilize fields (Fernald 1905).

Robinson (1880) mentioned introduced plants found along the Merrimac [*sic*] River down-stream from Lowell and Lawrence. An interesting group of non-native species was collected from the waste pile of a rubber reprocessing plant in Waterbury, Connecticut (Blewitt 1911, 1912). Apparently, used shoes were collected for rubber reclamation. The nonrubber parts were thrown on the waste piles where seeds that had hitchhiked there germinated and grew. In an interesting postscript that may explain why some of these species did not persist, Blewitt said, "For the past two years many plants in a portion of this place have been killed by fumes of an acid factory while those that survive are badly seared and burned by the deadly gases" (Blewitt 1911).

One of the most interesting cases of "factory-flora" was the discovery of *Lepidium latifolium* L. on the grounds of a glue factory in Danvers (Morse 1924). This European species is now abundant in parts of the southwest. In New England, it was found in eastern Massachusetts near the coast and at one inland site in Worcester County. It also occurs along the southwestern Connecticut coastline where it was thought to have been introduced at the site of a "dye and licorice works" (Eames 1935). In addition, *Paulownia tomentosa* (Thunb.) Steud., *Lepidium draba* L., and *Tamarix pentandra* Pall. were reported from the same area.

Railroads brought adaptable species, often ones with weedy tendencies, from the developing west. The now near ubiquitous Black-eyed Susan, *Rudbeckia hirta* L., is thought to have come east in that fashion. It had reached Philadelphia by 1826 and probably New England by 1855 (Robinson 1880). Fernald (1905) felt that *Senecio jacobea* L. arrived in Portland by way of the railroad from New Brunswick

Unintentional introductions and the escape of intentional introductions continue. *Froelichia gracilis* (Hook.) Moq., having reached New England by railroads, was first collected here in 1973. Although not currently known from New England, Mile-a-minute vine, *Polygonum perfoliatum* L., was first reported in Westchester County, New York, in 1995 (R. Mitchell, pers. comm.). At that time it was well established and within a mile of Connecticut. It seems plausible, since a natural dispersal from the nearest known occurrence in eastern Pennsylvania was unlikely, that it arrived here at this site in nursery stock and escaped. *Lonicera maackii* (Rupr.) Maxim. was first collected in the wild in Connecticut in 1978. This species is occasionally cultivated and it is likely, given its history as an invasive species in the Midwest (Luken and Theiret 1996), that its numbers will increase in the wild in southern New England.

BIOGEOGRAPHY OF PLANT INTRODUCTIONS

An equally informative way of looking at introductions is by considering species from different geographic origins. Most of the early introductions were of European plants that arrived with or after the earliest settlers (Fernald 1905). This continued until the opening of eastern Asia for trade after 1861 (Rehder 1936). After this, while it is still likely that some European plants were introduced into New England, most of the new introductions were from regions in East Asia such as Japan and China (Spongberg 1990). As they came from similar climates and geological histories, species from East Asia were well adapted to exist in New England. Often imported as ornamentals, some of these escaped and became quickly established in the local flora.

Again, the botanical gardens often provide the earliest records for introduced plants. In New England, the Arnold Arboretum was actively involved in plant importations from Japan and China by the beginning of the 20th century (Hay 1995; Rehder 1936). Rehder (1936) reported that after 60 years, the Arnold Arboretum had introduced at least 2500 species from around the world. Progeny of many of these reached American gardens.

A catalog of plants in the Harvard Botanical Garden, thought to have been written in 1879 (J. Warnement, pers. comm.), includes both *Elaeagnus umbellata* Thunb. and *Berberis thunbergii* DC. Although both are now considered highly invasive, at that point they were well-behaved members of the Garden's holdings. As with many invasive species, there is a variable period after introduction before offspring begin to appear in the wild.

Recent introductions from East Asia were not seen as a problem in 1905 when M. L. Fernald delivered his address on "Some Recently Introduced Weeds" to the Massachusetts Horticultural Society (Fernald 1905). Fernald stated that the number of nonindigenous plants in New England was then over 600 species. Further, he discussed only European species in spite of the fact that East Asian species had been introduced by that time (Rehder 1936). Later, in a presentation to the Franklin Society in 1939 (Fernald 1940) Fernald devoted a number of pages to the problems faced by rare plants from aggressive non-native species. One can infer from these two papers that in 1905 most Asian species were hardly, if at all, dispersing away from managed landscapes into the wild but that by 1939, many of the East Asian species were escaping and becoming well established in the wild.

CONCLUSIONS

The New England flora has steadily grown since the arrival of Europeans in the 17th century. While many species were intentionally introduced for utilitarian reasons some were also intentionally introduced for aesthetics. Many arrived unintentionally. These unintentional means of transport were often quite varied. Many, but not all species, persisted and are part of our regional flora today. Others that may or may not have become naturalized did not persist until present. As recently as the middle of this century, nonindigenous species were being imported as foods, medicines, or ornament (Rehder 1936). In addition, still other species, considered native to adjacent regions, have naturally expanded their ranges into New England. The most recent comprehensive list of New England vascular flora says there are 2882 vascular plant species reported from New England (Seymour 1969). Of these, 887 are considered nonindigenous (Seymour 1969). Given recent finds and the different nomenclature, these figures must only be accepted as approximations and it is likely that over 1000 species should be considered naturalized here.

Introductions can be looked at both from a historic perspective and a phytogeographic perspective. While these approaches compliment each other, clear divisions in each cannot be drawn. *Rosa multiflora* Thunb., a native of eastern Asia, was first introduced into the Elgin Botanic Garden in New York by way of European botanical gardens in 1811 (Rehder 1936).

Currently, the few non-native species that are aggressively invading natural plant communities are of paramount concern for conservationists (Brumback 1998). These invasive species are well known and exhibit biological characteristics of species adapted to habitat disturbance (Mehrhoff 1998). Efforts must be taken to control their spread. Concurrently, there are other non-native species that have the potential of becoming invasive in New England and their status must be assiduously monitored.

One final note: times have changed since Manasseh Cutler lamented how few botanists studied the New England flora (Cutler 1785). We know as much about our flora as we do because, for years botanists combing the fields, woods, and other habitats traipsed all over New England. Now there again seems to be a paucity of field botanists. Whether you ascribe to Eames (1935) who "had the good fortune . . . to find great quantities" of *Lepidium latifolium* or to Morse (1924) who sensed that the same species "seems to be liable to become a hardy weed of undesirable character" is not the point. What is important is that these two individuals had the ability and interest to recognize something new, to identify it, and to document its occurrence by collecting herbarium specimens. If we want to continue to monitor changes in the New England flora we must have botanists in the field to do so.

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RATES OF SUCCESS IN THE REINTRODUCTION BY FOUR METHODS OF SEVERAL PERENNIAL PLANT SPECIES IN EASTERN MASSACHUSETTS

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ABSTRACT. To prevent species from going extinct and to restore locally extinct species to conservation areas, conservationists have been attempting to create new populations of rare and endangered species. Such efforts are still at an early stage, with the basic methodology still being developed and many efforts resulting in failures or only modest success. The purpose of this work was to develop some general rules about how to carry out reintroduction efforts using four methods to create many new populations of eight perennial species. Our results demonstrate that the chances of success were greater when planting seedling and adult material rather than sowing seeds on the sites. Using larger adult material was more successful than using seedlings. Adult transplants also flowered and fruited right away, in contrast to plants derived from seeds, which rarely flowered even after several years. Digging up the site to expose the soil and reduce competition prior to sowing seed did not result in a greater establishment of seedlings. At many sites no plants survived at all, or success was low. These results emphasize the difficulties of establishing new plant populations. To increase the rate of success, attempts should utilize many sites, numerous seeds or plants, and various methods in order to develop a workable methodology for the species in question. Because of the difficulties of establishing new populations, conservation of rare and endangered species should first protect existing populations and only secondarily rely on reintroductions to ensure species survival.

Key Words: reintroduction methods, conservation, population re-establishment, restoration ecology

It has been estimated by the Center for Plant Conservation that perhaps 4200 of the 20,000 plant species of North America are under threat of extinction to some degree (Center for Plant Conservation 1993). A recent survey of the New England flora found 576 taxa judged to be "in need of regional conservation" (Brumback and Mehrhoff, et al. 1996; Stevens 1998). Worldwide, perhaps 25% of vascular plant species may become extinct in the coming 50 years (Raven 1987).

A primary cause of species extinctions is direct damage to the populations, whether by destruction of habitat, over-exploitation, or from competition from introduced plant or animal species. In addition to these acute effects, however, there is also a mounting chronic pressure on many species owing to a combination of human factors that alter species' environments in ways that inhibit or interrupt reproduction, dispersal, and colonization of new sites and thus the establishment of new populations. Local or regional anthropogenic effects, such as the production and dispersal of ground-level ozone or acid precipitation, alter the chemical environment adversely for some species (witness the effects of acid rain on *Picea rubens* in New England, or the contribution of airborne sulfur compounds to Waldsterben in Germany; Schulze et al. 1989), killing or weakening individuals, thus rendering them more susceptible to pathogens, drought, or wind damage. Fragmentation of habitat can introduce changes in the biological and physical characteristics of a location that can accumulate dramatically over time (Bierregaard et al. 1992; Brothers and Spingarn 1992; Harris and Silva-Lopez 1992; Saunders et al. 1991). These changes can both cause the death of plants currently occurring there and prevent or largely inhibit the establishment of new populations, either by the creation of barriers to dispersal, by the local extinction of dispersers, or by the introduction of weedy species that compete with previously occurring species.

On a larger scale and over a longer period of time, global climate change, especially carbon dioxide (CO_2) enrichment of the atmosphere and attendant global warming, is likely to contribute as well to the cascade of plant extinctions, as the temperature and precipitation regimes render areas of the current distribution of many species inhospitable (Bazzaz 1996; Kutner and Morse 1996; Peters 1992). The rate of anthropogenic climate change currently projected (Houghton et al. 1996) would require an adjustment of species ranges at a rate higher than any known to have occurred during at least the past 10,000 years, and species often will not be able to migrate naturally across the human-fragmented landscape.

Rates of extinction of species across all five biological kingdoms are estimated by some to be as high as 0.5% per year worldwide (Wilson 1992; Woodwell 1990). Studies of local extinctions in areas in which human impacts such as habitat modification and fragmentation have been sustained over a long period are consistent with this estimate (Drayton and Primack 1996; Newmark 1991; Robinson et al. 1994; Turner et al. 1994). As much as one third or more of the native species have been eliminated from some small and high-impact conservation areas. In the face of the local and global threats to biological diversity, the basic conservation response has been site protection: setting aside habitat that is maintained relatively undisturbed, in order to allow threatened populations to survive with no further damage (Primack 1998).

This protection is necessary but probably not sufficient as a conservation strategy (Buttrick 1992; Falk and Olwell 1992; Pressey 1994). It can prevent further direct disturbance of a site, or the effects of overexploitation of the site or population. It does not, however, protect against the more subtle stressing effects of climate change or pollution. It also does not counteract the long-term impoverishing effects of habitat fragmentation, which inhibit or interdict the metapopulation dynamics necessary to the continued survival of a species at the local and regional scales—specifically the colonization of fresh suitable sites at a rate sufficient to offset the natural and human-induced extinction of local populations (Grubb 1977; Holsinger 1993; Hughes and Fahey 1988; Norton 1991; Peterken and Game 1984; White 1996).

Increasingly, *in situ* management includes the creation of new populations of taxa or the augmentation of existing populations (Falk et al. 1996; Primack 1996), despite some concerns about implications of the practice and the indifferent success of many programs. The restoration ecology and conservation biology literature now reports many projects in which plants are reintroduced to an area where they once occurred, or new populations are initiated near existing stands, or species are introduced at apparently suitable sites. This flush of reintroduction activity has opened up many areas of research both on the basic biology of the species under consideration (Drayton 1999; Primack 1996; Schemske et al. 1994), and on many aspects of technique that must be considered in relation to the biology: whether to undertake a reintroduction or augmentation plan (Gordon 1994), how to define success for a reintroduction (Pavlik 1996; Sutter 1996), how to select suitable sites (Fiedler and Laven 1996), and how to design the actual introduced "population" (Guerrant 1996; Havens 1998; Husband and Barrett 1996; Primack 1996). In addition, there is still much to be learned about which techniques are most effective in restoration and reintroduction, including the relative value of seeds versus propagated material for introduction, and the extent and nature of appropriate site preparation and aftercare.

Choosing material for reintroductions: Seeds or plants? Because the germination and seedling stages of growth are periods of high vulnerability and high mortality, and because rare plant material must often be used with great care and economy, the majority of reintroductions of perennials have proceeded by the propagation of plants *ex situ,* and then transplanting into the target site (Guerrant 1996). Transplants of material in forms such as seedlings, cuttings, or bulbs arrive at the target site already past the most vulnerable stage of life. Individuals translocated in these forms tend to survive at a higher rate than seedlings germinating *in situ* (Barkham 1992; De Mauro 1994; McEachern et al. 1994; Ray and Brown 1995; Rochefort and Gibbons 1992; Vora 1992) and initiate flowering or asexual reproduction faster than individuals propagated from seed (Seliskar 1995; Vasseur and Gagnon 1994). In cases where the site cannot be characterized quantitatively, transplants that survive provide evidence that the site is suitable for the species and that its absence there may be due to lack of dispersal (Barkham 1992; Lee 1993; Primack and Miao 1992).

Yet even when it seems feasible from a logistical point of view, transplanting does have inherent risks, since there can be significant trauma during the transplant. Plants grown *ex situ* by definition have not grown *in situ,* so that the change in environment may subject the transplants to stress that affects their viability or results in high levels of herbivory (Cavers and Harper 1967). Poor horticulture or adverse conditions such as unanticipated drought can result in high mortality in the field (Fahselt 1988). Further, introduction of plant materials may inadvertantly introduce pathogens as well (Given 1994).

Beyond the biological considerations, however, is the factor of the cost of such an approach, which must be weighed against potential higher rates of success as compared with the use of seeds to initiate the new populations (Danielson 1996; Given 1994). For example, the cost of establishment of a single individual of Texas Ebony by tranplanted seedling (raised *ex situ*) was about $1.25, while the cost of establishment by seed was around $0.39 per individual (Vora 1992).

Reintroductions by seed offer some important advantages over transplants. In the first place, seeds can often be collected in large numbers. Collection of seed can usually be accomplished without damage to the individuals in existing populations, and this is especially important when there are only a few individuals of a taxon remaining. For example, in the case of the threatened Prairie Fringed Orchid (*Platanthera leucophaea*), populations are scattered and declining to the point that pollination is inhibited in some parts of its range. Little is known about the cultivation requirements of this species, so transplanting of existing individuals entails an unacceptable risk of mortality. The use of seeds for the creation of new populations of this species is the most useful short-term strategy for increasing the number of populations or for augmenting existing populations (Packard 1991).

It is possible that in a suitable site the individuals that germinate and grow *in situ* have a better long-term chance of success on that site than plants not "selected" by the microenvironment of the site. In some cases, seedlings from seeds sown *in situ* may have a more rapid growth rate than seedlings transplanted from elsewhere (Vora 1992), and rapid growth rate can be important if light is the limiting medium so that the production of photosynthetic tissue is decisive for survival in the face of aboveground competition or litter-fall.

Seeds can be dispersed soon after collection, thus ensuring that the propagules used for reintroduction are arriving at the target site in synchrony with the natural dispersal process. Seeds are also amenable to several kinds of experimental plantings which may provide important information about the biology of the species under study. This may improve the effectiveness of recovery or mitigation plans. For example, it may be important to design an introduced population to have maximal genetic diversity (Dole and Sun 1992; Fenster and Dudash 1994; Jacobson et al. 1994). It is easier to introduce multiple populations and multiple genotypes by means of seed than by means of transplanted material. Another important concern is the density of the population, but the optimal density and spatial arrangement of individuals in a population is known for rather few species. Reintroduction by seed allows for a variety of planting arrangements and densities.

In the case of species for which abundant seed is available, one can even design restoration or reintroduction plans at a landscape level using mixtures of seeds and seeding techniques (e.g., Jacobson et al. 1994), though this is perhaps most likely for grassland habitats.

Site preparation and post-translocation care. The concept of "safe sites" for establishment (Harper 1977), or the "regeneration niche" (Grubb 1977), provides an important rationale for careful site selection for the reintroduction of a species. The rationale includes a range of criteria, including biological criteria (e.g., specific nutrient or water requirements), logistical criteria (e.g., is the site accessible enough to the researcher to enable the operation to proceed and to enable appropriate monitoring, with "after care" or maintenance activities?), and "defensive" criteria (e.g., is the area vulnerable to human disturbance? Have management policies resulted in a high density of deer that might eat the plants?; Fiedler and Laven 1996). In addition, there may be other evidence to consider, such as the historical presence of the species. The autecology of many species is not well understood. If time and resources permit, one can conduct the studies needed to ascertain the answers to critical questions. As this is not always possible, some surrogate measures of site suitability may be required. A common example is the use of indicator species, species whose occurrence is highly correlated with the occurrence of the target species.

Initial experiments on which this study is based used little in the way of site preparation (for a summary, see Primack 1996). There is a strong *a priori* rationale for this, since most plants disperse the bulk of their seeds onto unprepared sites. Further, for many species it is not known what kinds of "preparation" might favor establishment by seed or the survival of seeds once germinated. Studies of germination requirements are not reliable guides to the requirements for establishment, as the ideal conditions for germination may not be ideal for the new seedling (Grubb 1977). This is likely to be the reason that studies show high laboratory germination rates but very low seedling survivorship in the field (Vora 1992), or high seedling emergence and also high seedling mortality (Barkham 1992; Bazzaz 1996).

For species whose establishment biology is not well understood, some approximation can be attempted based on dispersal mechanisms (Robinson and Handel 1993), germination requirements known or conjectured (Baskin and Baskin 1998), and on what is known of the disturbance regime of the species' habitat. For example, desiccation is an important cause of mortality in emergent seedlings (Larcher 1995). Sites can be prepared with mulches (Jackson et al. 1990; Rochefort et al. 1992) or shaded with branches, litter, or screens (McChesney et al. 1995) to minimize drying of the top layer of soil. Bringing seeds' emergent radicles close to mineral soil may require the removal of litter or the mowing or removal of vegetation (Gordon 1996; Rochefort and Gibbons 1992; Vasseur and Gagnon 1994; Vora 1992; Watson et al. 1994). Removal of over-shadowing vegetation can improve the light supply for early rapid growth of seedlings and can impair root competition, significantly improving seedling survival (Danielson 1995; Pavlik et al. 1993). Cultivation of the soil can also reduce below-ground competition (a decisive factor in the mortality of seedlings in many systems; Bazzaz 1996), aerate the soil, and facilitate root growth (Bainbridge and Virginia 1990). The site may be irrigated or enriched by fertilizers to facilitate rapid growth (Doerr and Redente 1983). A fire regime may be instituted, which can remove above-ground competition, remove thatch or litter that may prevent seeds' reaching the soil, and provide a nutrient pulse (Gordon 1996; Pavlik et al 1993). Finally, some species may require protection against seed predators or herbivory on the emergent seedlings (Bainbridge et al. 1995; Barkham 1992; Chambers and MacMahon 1994; Primack and Drayton 1997).

Post-reintroduction care (''soft release'') may also be part of the reintroduction plan. Techniques reported from the literature include protection against seedling dessication with mulching, screening, or irrigation (Bainbridge and Virginia 1990; Doerr and Redente 1983; Jackson et al. 1990). Sites can be weeded (Jackson et al. 1990) or clipped (Danielson 1995; Gordon 1996) to continue to prevent competition during early growth.

Criteria for success of a reintroduction. Increasingly it has been recognized that a reintroduction effort must be evaluated with reference to its original goals, and that these will vary considerably from case to case (Pavlik 1996). These goals may specify an extension of a species' range by the creation of new populations or by increasing the size of existing populations in order, for example, to reach a threshold of attractiveness to pollinators. In most cases, success will be achieved stage-wise, first by the presence of individuals on the target site, then by their reaching reproductive stage, then by their dispersing viable seed, and perhaps finally by their establishing secondary populations. A longer-term goal may be a minimum viable population size, a target developed on the basis of demographic modelling.

Long-term monitoring of new populations or reintroductions can serve several critical purposes, yet systematic monitoring past the initial stages of establishment is a surprisingly rare feature of published reports on reintroductions. Measures of success are often expressed in terms of biomass (Doerr and Redente 1983; Shaw 1996), per cent cover (Jackson et al. 1990), or presence-absence (Packard 1991; Revel 1993).

Despite the large amount of attention that plant reintroduction has received in recent years, it is still possible for a leading researcher to state that there is no example of a taxon's having been conserved or brought to nonendangered status as a result of a restoration plan (Pavlik 1996). In part this statement can be explained by the length of time often needed to assess the outcome of a reintroduction, especially when working with perennials. In part the statement also reflects the state of our understanding of many aspects of the reintroduction process. In each section above, one sees open questions that require further research. The recent history of reintroduction work shows a swift development of understanding of the challenges facing such conservation work as researchers have attempted various approaches, developed criteria for assessing results, and collected results from a range of different studies and species.

The literature and examples of restoring populations of rare and endangered species have grown considerably over the last 10 years, but the development of general approaches has been inhibited by a variety of factors. First, most attempts to restore species are done with a single species, so it is unclear if the result would be applicable to another species of different growth form, family, or basic biology. Second, most attempts involve a single approach rather than conducting experiments in which several approaches are contrasted. Third, most attempts do not replicate the approach, so it is unknown how consistent the reported results are. Fourth, the results of many, if not most, such projects are never published, and in particular it is quite likely that most unsuccessful attempts to create new populations are never published at all. This may lead to literature biased in favor of successful and optimistic results. The purpose of the work presented here is to develop generalizations on the most effective way to establish new populations of rare, declining, and endangered species. We used many species, several techniques, and many replicates to develop generalizations that could be widely applicable. In this research we focused on perennial wildflower species, as many New England plant species are in this category, and our earlier research investigated annual species (Primack 1996; Primack and Miao 1992).

The present experiment was intended to answer the following questions with regard to eight native perennial species:

1. How frequent is the establishment of new populations of perennial species in relation to the number of propagules arriving on a site?
2. Is transplantation of seedlings and adults more or less effective than reintroduction by seed?
3. Does site preparation increase the success of reintroduction by seed?
4. Finally, is the establishment of new plant populations in the wild a realistic goal for perennial wildflower species?

MATERIALS AND METHODS

Starting in 1993, we identified eight perennial species that were not present but formerly attested, or whose distributions were highly restricted, in two conservation areas in the Boston area. None of these species was endangered or threatened in Massachusetts, but the number and population size of most of them appeared to have declined substantially over the last century. Such species may be of conservation interest in themselves—and thus the subject of reintroduction efforts—if the populations' distributions were shrinking so that (presumed) genetic diversity was diminishing, or if there were other biological, cultural, or aesthetic values to the species' continued presence in a particular locale (Hunter and Hutchinson 1994). In addition, such species can serve as model systems for the purpose of exploring the values and limits of conservation techniques before attempts are made to apply such techniques to endangered species.

The species used for this study were as follows (nomenclature follows Gleason and Cronquist 1991; geographic information from Seymour 1993): Marsh Marigold (*Caltha palustris*); Columbine (*Aquilegia canadensis*); Bloodroot (*Sanguinaria canadensis*); Early Saxifrage (*Saxifraga virginiensis*); Spikenard (*Aralia racemosa*); Cardinal Flower (*Lobelia cardinalis*); Sweet Cicely (*Osmorhiza claytonii*); Bluets (*Hedyotis caerulea*).

These species are well-known, even "characteristic," elements in the New England flora. All species were present in the Middlesex Fells, and all were uncommon except Bloodroot, Bluets, and Sweet Cicely. Only Marsh Marigold was present in the Hammond Woods, where it existed as a single large population. While each species has its distinct requirements, there are a few features that should be noted. Columbine and Cardinal Flower are hummingbird-pollinated, whereas the other species are insect-pollinated. Marsh Marigold and Cardinal Flower are wetland species, while the others grow in forests, fields, and disturbed areas.

Sources of plant material. In the summer and fall of 1994 seeds of all species were collected from populations in eastern Massachusetts, in most cases within 2 km of the experimental sites. Seeds to be sown on quadrats were collected at the time of natural dispersal, cleaned, counted, and placed on quadrats within a week of collecting; they were stored to ensure viability in the meantime (Baskin and Baskin 1998). In the winter of 1994, samples of the seeds of all species were sown in flats, cold-stratified at 4°C for 10 weeks, and germinated in growth chambers to test for viability and if necessary to provide material for transplantation. All species showed germination rates in the laboratory > 50%, except for *Saxifraga,* for which seeds germinated at a rate of approximately 10%.

Seedlings and adults for transplantation (see below) were obtained in the spring of 1995, when possible from wild populations in the area that were of sufficient size to allow removal of plants for transplanting (*Sanguinaria, Osmorhiza, Caltha, Saxifraga, Hedyotis* seedlings). In cases where this was not possible (*Lobelia, Hedyotis* adults, *Aquilegia, Aralia*), seeds were collected from naturally occurring sites in eastern Massachusetts and propagated first in the laboratory, then in suitable sheltered areas outside for hardening until transplantation.

Study sites. Experimental sites were established in the Hammond Woods (Newton, MA) and the Middlesex Fells (Medford, MA). The Hammond Woods is a conservation area approximately 80 ha in area. It comprises a mixture of deciduous woods, swamps, parking areas, meadows, ledges, and roads. The Middlesex Fells is approximately 800 ha in area, in two roughly equal sections isolated from each other by major highways; the reserve overlaps five municipalities. The park is dominated by mixed deciduous woods, but includes large and small bodies of water, stream courses, maintained and abandoned fields, gravel carriage roads, and hiking trails. It is used heavily for hiking, mountain biking, picnicking, and similar recreational purposes.

Sites within each area were selected on the basis of general topographical aspect by comparison with sites in which the species occurred naturally in their nearest populations. Criteria included degree of canopy closure, soil moisture, and co-occurring indicator species. For each species, apparently suitable habitat existed in these conservation areas, so that reasons for the absence or decline of populations are not known. A first hypothesis is that dispersal has limited the extent of occurrence. Further, human use of the areas may well have contributed to reduced dispersal (Drayton and Primack 1996 and references therein). Therefore, the design provided several useful kinds of information about the sites being explored: transplants that survived and seemed to establish well provided evidence that the site was suitable for the species, at least within the time frame of the study to date. Establishment of seedlings from seed provided evidence that dispersal may have been limiting. Relative success of individuals of different ages may also provide evidence about life-stages that are particularly vulnerable in these species, information that should be taken into account in designing a reintroduction plan (Schemske et al. 1994).

Experimental design. At each site, four quadrats were mapped and each marked with a numbered wooden stake in the summer and fall of 1994. Four treatments were used; one quadrat at each site was assigned randomly to each treatment; the number of quadrats (replicates) for each treatment for each species is shown in Table 1. The treatments were as follows:

Treatment 1: Seeds. A known number of seeds was sown di-

Table 1. Number of replicates (quadrats) of experimental design, number of seeds sown for treatments 1 and 2, and number of individuals transplanted for treatments 3 and 4. Treatments are described in Materials and Methods.

	# Replicates per Treatment	# Seeds Sown per Quadrat for Treatments 1 and 2	Total # Seeds Sown per Species	# Seedings and Older Plants per Quadrat for Treatments 3 and 4	Total # of Transplants
Species					
Aquilegia	24	100	4800	4	192
Sanguinaria	12	50	1200	4	96
Hedyotis	16	100	3200	5	160
Aralia	24	100	4800	6	288
Caltha	24	100	4800	4	192
Saxifraga	6	50	600	4	48
Lobelia	19	100	3600	4	144
Osmorhiza	24	100	4800	4	192
Total for all species	149		27,800		1312

rectly on the quadrat in the summer and fall of 1994 within a 25 cm radius of the marker. Nothing was done to disturb the site other than to introduce the marker.

Treatment 2: Dig and Seed. The quadrat was dug up within a 25 cm radius of the marker and to a depth of approximately 12 cm, removing possible competing herbaceous cover and superficial roots and exposing bare soil; then the same number of seeds as in treatment 1 was sown in 1994.

Treatment 3: Seedlings. Seedlings were transplanted onto the assigned quadrat in the spring of 1995, within a radius of 0.5 m of the marking stake, in holes prepared by trowel. The sites were not altered in any other way (e.g., by removal of overhanging vegetation). In the case of *Hedyotis,* seedlings were watered once soon after transplanting because of unusually dry conditions.

Treatment 4: Adults. Adult plants were transplanted into the assigned quadrat in the spring of 1995, within a radius of 0.5 m of the marking stake, in holes prepared by trowel. The sites were not altered in any other way. In the case of *Hedyotis,* adults were watered once soon after transplanting because of unusually dry conditions. For treatments 3 and 4, the same number of individuals (seedlings and adults) was used.

The number of replicates was determined by the number of seeds or potential transplants that were available. The number of seeds sown (for treatments 1 and 2) and of transplanted seedlings and adults is shown for each species in Table 1.

All sites were visited repeatedly during the growing seasons, and data were taken annually on:

- number of seedlings from seeds sown by researchers or dispersed by introduced individuals,
- number of survivors from transplants,
- number of plants flowering or setting seed in the summers of 1996 and 1997,
- number of fruits.

Although the seasons of 1996 and 1997 were quite dry in eastern Massachusetts, no transplants were watered, nor was there any other post-transplant care except as noted for the transplants of *Hedyotis* upon first planting in 1995.

Statistical analyses were performed using the Statsoft Statistica™ (Release 4.1) program and Microsoft Excel™ versions 4 and 5.

RESULTS

The success of a reintroduction can be assessed with reference to several questions. For perennials, these can be answered at least provisionally in chronological order. First, are individuals of the subject species present on any of the experimental sites? Second, what percentage of the original propagules have resulted in individuals surviving at the time of census? Third, are there any individuals reaching reproductive condition, and if so, are they setting seed? Fourth, is there evidence of a second generation at any site?

In overall terms, the results of this experiment emphasize the difficulty of successful reintroduction, the caution needed in generalization about methods, and the need for long-term monitoring. Transplanting material was by far the most reliable way to establish new populations when comparing the results for all species, but there was considerable variation among species in the rates of success as measured both by occupancy versus treatment and survivorship versus treatment.

Number of quadrats occupied. There was a total of 596 quadrats of all species, 149 per treatment (Table 1). Of these, by the end of the period here studied, there were 105 occupied by the subject species (Table 2), thus an overall rate of 19%. Of these, 87 (78%) were reintroductions by transplant, and 15 (22%) were by seed. The success rate of transplants was significantly greater than establishment by seeds (χ^2, $P < 0.001$; Table 3).

Although the values varied among the species in the study, for most species, transplants were clearly more successful than seeds in terms of survivorship. In three species, *Lobelia, Saxifraga,* and *Aquilegia,* no individuals from seed survived to 1997. By contrast, both *Sanguinaria* and *Osmorhiza* showed relatively large numbers of quadrats occupied by seedlings from introduced seeds: for *Sanguinaria,* 8 quadrats planted with seeds were occupied in 1997 (4 each for the two seed treatments); for *Osmorhiza,* 6 quadrats planted by seed were occupied in 1997. For *Hedyotis,* five quadrats planted by seed were occupied in 1997, which contrasts with the 8 quadrats occupied by transplants.

Table 2. Number of quadrats occupied in 1997, by species and treatment. Treatments are described in Materials and Methods.

Species	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Aquilegia	0	0	5	10
Sanguinaria	4	4	6	7
Hedyotis	2	3	7	1
Aralia	1	1	7	11
Caltha	1	1	2	18
Saxifraga	0	0	0	4
Lobelia	0	0	0	0
Osmorhiza	6	0	1	3
Total quadrats	14	9	28	54

Except for *Osmorhiza,* there seemed to be no significant difference in the success of seeds on prepared versus unprepared quadrats. This result in 1997 was surprising, because in the previous two years of the study for several species (*Sanguinaria, Hedyotis, Aquilegia*) the prepared quadrats showed higher numbers of individuals present. For example, in 1995 *Osmorhiza* showed seedlings at 63% of the prepared quadrats, versus 13% of unprepared quadrats. Although this was the largest disparity, emergence of seedlings from the first seed input on prepared quadrats was generally higher than on unprepared quadrats. Yet by 1997, this difference had diminished in all species (Figures 1 and 2). For *Osmorhiza,* in 1997 no prepared quadrats (treatment 2) were occupied, while six of the unprepared quadrats (treatment 1) had individuals on them. In 1996, three of the *Saxifraga* prepared quadrats (treatment 2) showed seedlings, as opposed to none of the unprepared quadrats, but in 1997 no quadrats sown with seeds showed any individuals present. For *Sanguinaria,* there were four occupied quadrats for each of the two "seed" treatments by 1997. The unprepared quadrats showed a significantly higher number of seedlings present in 1997; this reversed the situation of previous years. For *Hedyotis,* the prepared quadrats showed a significantly higher rate of occupancy in all years. Only prepared *Aralia* quadrats showed any individuals from seed present in any year. In general, the site preparation seemed to facilitate germination and initial establishment but not to affect longer-term persistence at a site.

With respect to the relative success of the two transplant methods, with mature versus younger plants, for most species more

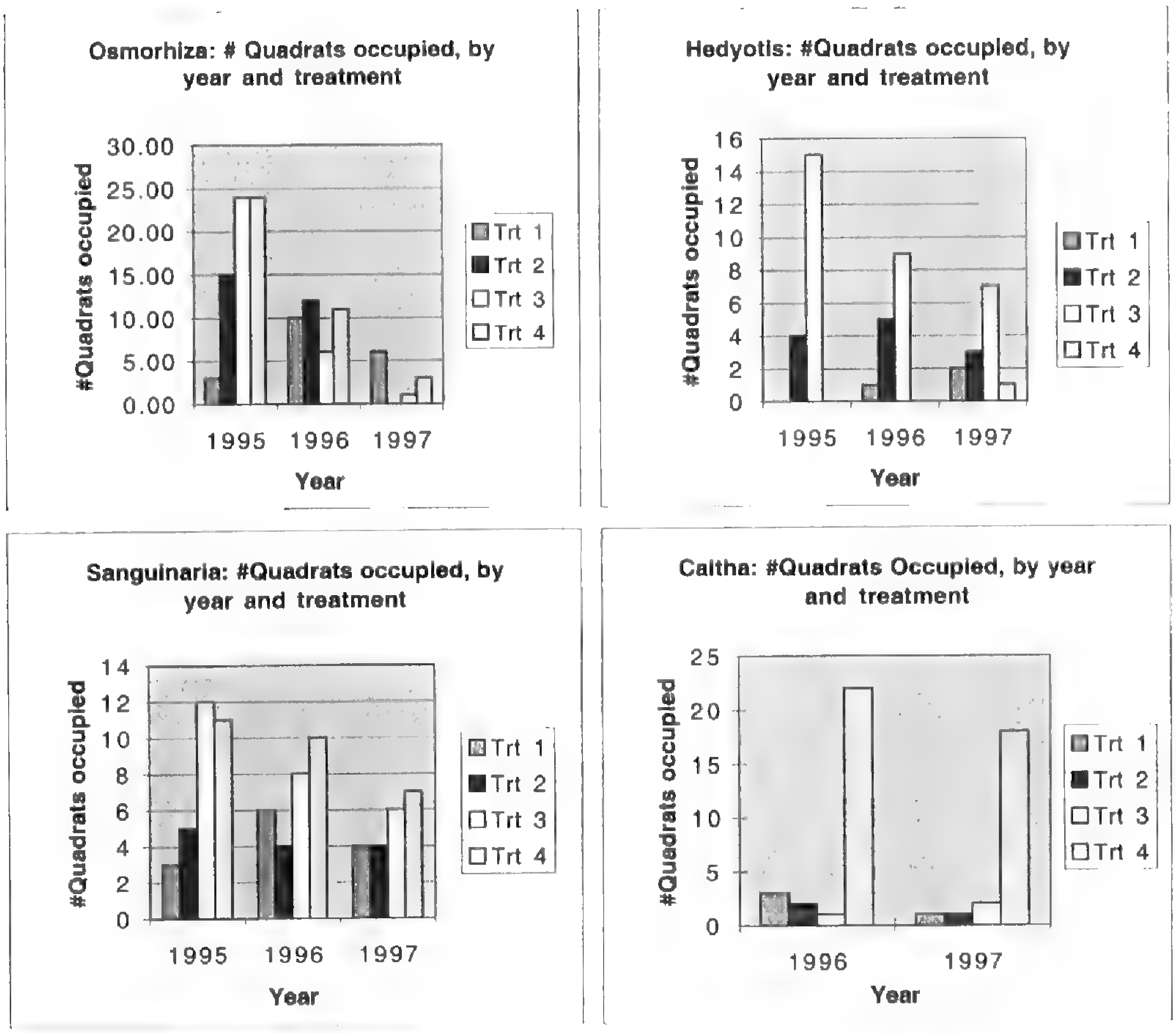

Figure 1. Number of quadrats occupied per year, by treatment, for *Osmorhiza, Hedyotis, Sanguinaria,* and *Caltha.* Treatments are described in Materials and Methods.

quadrats planted with mature plants were still occupied by 1997 than quadrats planted with seedlings (Figures 1 and 2). The advantage was most marked for *Caltha, Aquilegia,* and *Aralia,* with these differences statistically significant. For *Caltha,* 18 quadrats were occupied by mature transplants, while only 2 were occupied by seedlings. For *Aquilegia,* 10 quadrats were occupied by adults, 5 by seedling transplants. For *Aralia,* 11 quadrats were occupied by adults, 7 by seedlings. In one case, with *Hedyotis,* there was the opposite result with seedlings occupying more quadrats than mature plants in all years. For *Sanguinaria,* almost equal numbers of quadrats were occupied by plants: 6 seedling quadrats and 7 adult quadrats. For *Saxifraga* and *Lobelia,* only mature plants survived, and in the drought year of 1997, no *Lobelia* plants were found.

Rates of success per propagule. Overall, 27,800 seeds and

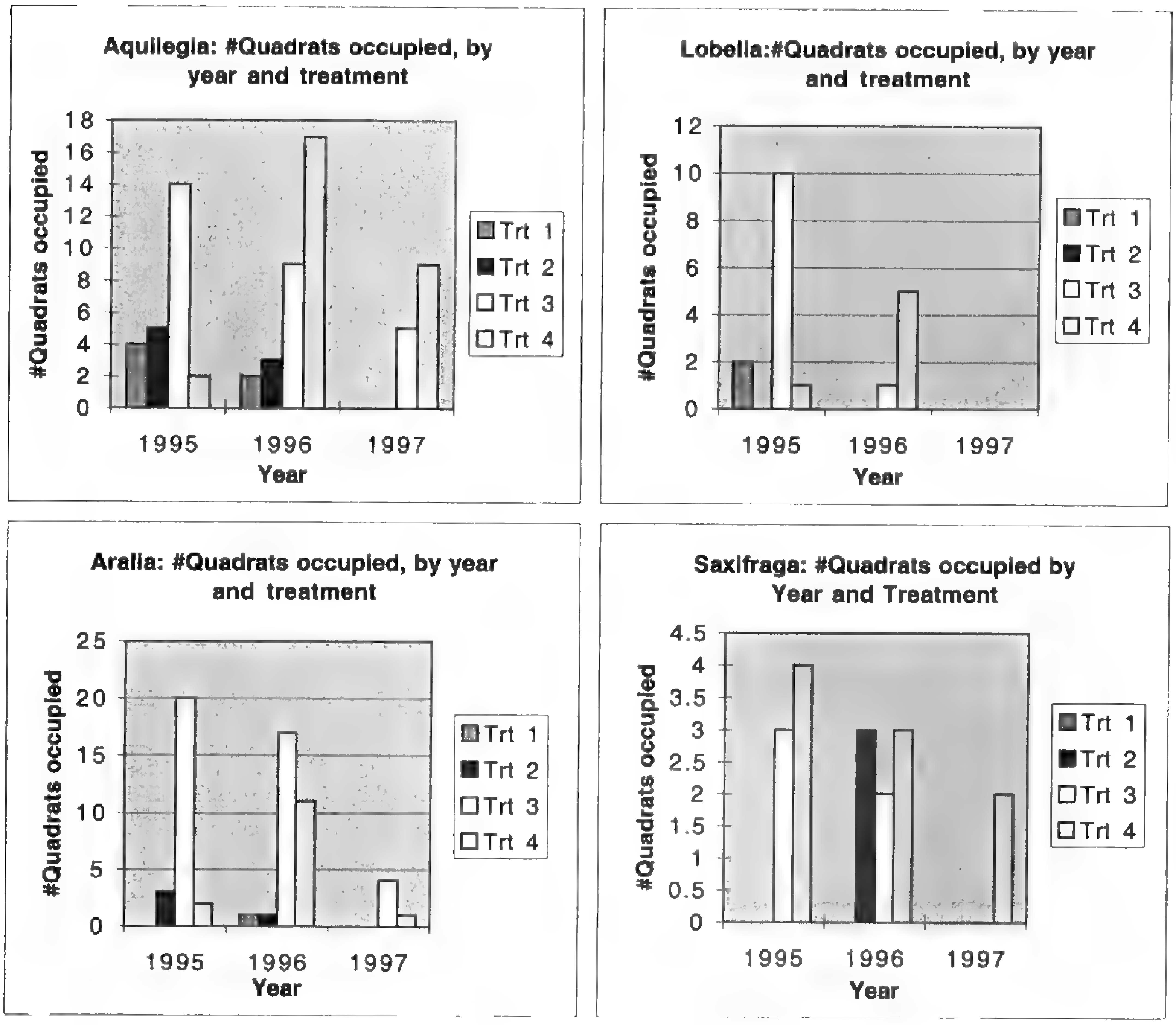

Figure 2. Number of quadrats occupied per year, by treatment, for *Aquilegia, Lobelia, Aralia,* and *Saxifraga.* Treatments are described in Materials and Methods.

1312 transplanted individuals (including both young and mature plants) were introduced on the experimental quadrats—half on prepared quadrats, half on unprepared. The rates of success per propagule introduced varied widely (Table 3) but in general they mirrored the results for rates of quadrat establishment. Thus the transplanting of material had a very much larger rate of success—that is, percentage of transplanted individuals surviving to 1997—than did introduction by seed. For all species, introduction by seeds (including both treatments) resulted in 131 individuals present for a success rate of 0.47%. Transplanted individuals fared better, with 23% of the 1312 transplants (including both seedlings and plants) surviving to 1997. Species differed in the relative rates of success, with *Sanguinaria* showing the most spread between seed treatments (about 4.5% for the two seed treatments) and transplants (about 44%); most species showed rates of estab-

Table 3. Number of 1997 survivors per treatment, and rates of survival per propagule in each category. Superscripts indicate values differing significantly by χ^2 test. Treatments are described in Materials and Methods.

	Treatment 1		Treatment 2		Treatment 3		Treatment 4	
Species	# Present 1997	% of Input	# Present 1997	% of Input	# Present 1997	% of Input	# Present 1997	% of Input
Aquilegia	0	0	0	0	9	9.4	8	18.8
Sanguinaria	35	5.8	20	3.3	19	39.6	23	47.9
Hedyotis	7	0.75	47	1.1	128	72.0	1	1.25
Aralia	1	0.042	1	0.042	20	13.8	20	13.8
Caltha	4	0.16	1	0.04	5	5.2	49	51.4
Saxifraga	0	0	0	0	4	8.3	4	8.33
Lobelia	0	0	0	0	0	3.9	0	9.2
Osmorhiza	13	1.0	0	0	3	3.0	4	4.0
Total for all species	60^{a}	0.43	69^{a}	0.5	188^{b}	28.0	109^{b}	16.6

lishment from seed at less than 1%, significantly less than rates by transplant. *Aquilegia* showed no individuals from seed present in 1997 but had a survival rate of 10% for seedling transplants and 19% for adults. *Aralia* showed survival rates of 0.04% for the seed treatments, and 14% for the transplant treatments. *Caltha* had a low survival rate from seed (0.16% and 0.04% for treatments 1 and 2, respectively), but 5% survival for seedlings and 51% for adult transplants. In the case of *Lobelia* and *Caltha,* the sites necessarily were near moving water, so it seems possible that many seeds were washed away from the experimental quadrats before germination. No seedlings of these species were noted downstream from the experimental sites, however.

Reproduction at experimental sites. The survival of introduced material is only the first level of success for a reintroduction effort, and the reintroduction can only be considered successful if some of the introduced individuals survive to reproduce and become a source of reproducing offspring in the target area. In the case of the present experiment, it is too early to assess this level of success with respect to individuals introduced by seed. In all cases except *Hedyotis,* which often flowers and sets seed during its first year, individuals of the perennial species in this study must reach a certain size, usually over several growing seasons, before they will reproduce. As these sizes are not defined in the literature so far as we can determine, this fact of life-history means that monitoring introduced populations must be a long-term effort.

In the case of introduced material, however, initial results can be reported. We recorded all instances of reproduction in 1996–97 (Table 4), and flowering individuals in 1996 (Table 5) and 1997 (Table 6). All but one species, *Aralia,* showed some reproducing individuals during the experiment to date. It appears that in the very dry conditions of 1996 and 1997 *Osmorhiza* was prevented from reproducing, even in the few sites where there were flowering transplants in 1995. However, in a few cases the seeds produced by those transplants did yield seedlings in 1996. *Lobelia* flowered in 1996 and two individuals set fruit (a total of 20 capsules between them), but no flowering individuals appeared in 1997. For *Caltha,* only the adult transplants flowered, but a high percentage did so (72% in 1996, with a total of 32 fruits on 47 flowering individuals; 70% in 1997, with a total of 42 fruits

Table 4. Number of quadrats with reproducing individuals, total number of fruits produced 1996–7, and presence/absence of second generation, i.e., seedlings from seeds dispersed by introduced material.

Species	# Quadrats	# Fruits	Second Generation?
Aquilegia	10	54	no
Sanguinaria	10	31	yes
Hedyotis	14	800	yes
Aralia	0	0	no
Caltha	19	263	no
Saxifraga	4	126	no
Lobelia	1	14	no
Osmorhiza	10	310	yes

on 33 flowering individuals). *Saxifraga* showed a high percentage of adult transplants flowering (89% in 1996, 100% of 2 individuals in 1997), and essentially all flowers matured fruit though no seedlings have appeared at these sites. *Sanguinaria* seedlings and adult transplants showed similar proportions of flowering individuals in both years (about 16% in 1996, around 50% in 1997), with a total of 31 fruits over those two years. *Aquilegia* showed increasing proportions of flowering individuals (12% of seedling transplants in 1996, 78% in 1997), but negligible fruit production until 1997 (22 fruits noted).

Hedyotis showed the most vigorous reproduction in both years although adult transplants showed only one flowering individual, in 1997. The individuals appearing from seeds sown on the prepared plots flowered starting in 1996 (83%) and continued in 1997 at a lower rate (21%). Seedling transplants flowered vig-

Table 5. Percentage of individuals per treatment flowering in 1996. Treatments are described in Materials and Methods. [1] Based on one individual.

Species	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Aquilegia	0	0	12.5	37.2
Sanguinaria	0	0	15.8	16.1
Hedyotis	100[1]	83	93.8	0
Aralia	0	0	0	0
Caltha	0	0	0	71.5
Saxifraga	0	0	33.3	88.9
Lobelia	0	0	100	42.9
Osmorhiza	0	0	0	0

Table 6. Percentage of individuals per treatment flowering in 1997. Treatments are described in Materials and Methods. [1] Based on one individual; [2] Based on two individuals.

Species	Treatment 1	Treatment 2	Treatment 3	Treatment 4
Aquilegia	0	0	77.8	33.3
Sanguinaria	0	0	47.8	57.9
Hedyotis	0	21.3	13.3	100[1]
Aralia	0	0	0	0
Caltha	0	0	0	69.8
Saxifraga	0	0	0	100[2]
Lobelia	0	0	0	0
Osmorhiza	0	0	0	0

orously in 1996 (94%), but less so in 1997 (13%). However, this lower proportion of flowering reflects the fact that there were more individuals present on these sites (58 in 1997 versus 16 in 1996). The increase apparently was largely due to the establishment of new seedlings from seeds dispersed the previous year. These seedlings were all very small and did not flower, but persisted through the growing season.

Table 4 summarizes the number of quadrats with reproducing individuals per species for 1996–97, the estimated number of fruits for those two years, and the presence or absence of seedlings from dispersed seeds (a "second generation"). As of the 1997 growing season, only *Sanguinaria* and *Hedyotis* showed quadrats with both mature flowering individuals and new seedlings present. The few *Osmorhiza* seedlings derived from 1995 flowering transplants did not appear to be of flowering size yet.

DISCUSSION

Plant reintroductions are considered an important tool in the work of plant conservation, but there remain many unanswered questions about techniques for reintroduction and the biology that underlies them (Allen 1994).

The present experiment, still in progress, reinforces previous work in which reintroduction by seed has shown very low rates of success in establishment of new populations at even the most basic definition of "success," that is, presence of individuals of the species. The rates reported here, ranging from 0% to about 6%, are similar to rates reported in a series of experiments by

Richard Primack for many species in eastern Massachusetts (Primack 1996; Primack and Miao 1992). In one set of experiments with annuals and perennials, out of 221 quadrats, a single population of an annual species and two populations of a perennial species survived to reproduce and disperse seeds. Those experiments showed short-lived appearances of seedlings, as reported here, but the passage of time saw these "populations" extinguished.

Similar experiments in quite different habitats have shown comparable results. For example, recruitment from seeds of 8 different species sown in the field in the semi-arid Rio Grande Valley ranged from 11% to less than 1%, except for a single species (Vora 1992), despite several steps taken to improve the chances for success both by site preparation and after-care. Vasseur and Gagnon (1994) reported emergence rates in their experiment with *Allium tricoccum* to vary widely from about 3% to 90%, but they did not provide data on the survival of recruits from seeds after germination. Barkham (1992) reported seedling survivorship of *Narcissus* sown in the field as "rapidly declining to zero." In the New England area, repeated attempts have been made to establish new individuals and new populations of the endangered perennial *Potentilla robbinsiana* in the White Mountains of New Hampshire (unpubl. report). Some success has been achieved using transplants of adults, but sowing seed in a variety of locations has had no success whatever.

There can be many reasons for this kind of result. Many plants need some kind of disturbance to establish successfully. Thus the "safe site" at which the propagule must arrive is not only a particular locale, but a place in time as well. Site suitability is not only a function of characteristics such as soil composition and the presence of competitors and predators, but also the interaction of these with temperature and precipitation conditions.

The work of David Foster and others (e.g., Foster and Boose 1992; Whitney and Foster 1988) has shown how, on an ecological time scale—from a few decades to a few centuries—an ecosystem is likely to experience recurrent though unpredictable major disturbances that may have important consequences for successional processes, including the establishment or extermination of populations of plant species. In New England, a prime example of such a disturbance is hurricanes, whose effects on northern hardwood forest systems have been studied now for some years. In light of this work, Primack (1996) extended his experiments to an area artificially disturbed to recreate some of the features of a hurricane disturbance. The radically altered light and temperature regimes of such a disturbance can enhance or trigger seed germination, and the removal of competing vegetation and the exposure of mineral soil might be expected to foster a flush of germinations. In the event, no such response was seen for 15 perennial species sown on the experimental site, suggesting that other factors besides, or in addition to, disturbance affect establishment.

The present experiment follows on from these, with a change in the site preparation, and the addition of a comparison with transplants of two different sizes. Seeds were sown in some quadrats with no preparation, this being the most common fate for the seeds of these species. This unprepared sowing was compared, however, with small-scale site preparation, which imitated in its effects a very common type of disturbance, the uprooting of a tree or sapling (Runkle 1985). A disturbance on this scale will not materially alter the radiation regime of a microsite, but will expose mineral soil and provide a site largely free from root competition in the upper soil layers, and from shading by plants nearby.

This level of site preparation may have some positive effect on the rate of emergence of seedlings, but in these experiments it had no discernible effect on longer-term presence on a site. Similar results are reported from a series of experiments with a different set of species in sandhill conifer forests of South Carolina (Primack and Walker, unpubl.), in which in addition to disturbance, site preparation included a nutrient pulse. From the Cape Cod area as well, attempts to create new populations of the endangered Sandplains Gerardia, *Gerardia acuta,* in grassland sandplains, are enhanced by a carefully timed program of mowing and burning (P. Somers, unpubl. data). Preliminary results suggest that in this very different biological system as well, local disturbance does enhance the emergence of seedlings, while fertilizer does not. The long-term consequences for survivorship remain to be seen.

In fact, the point made by Grubb (1977) that the "regeneration niche" is more than a good site for germination is quite apposite here. Germination is the first and essential condition for a new colonization event by seed, but the conditions must also be conducive to the survival of new seedlings, so that some reach the next period of dormancy in good enough condition to survive the winter. For a species that takes some years to reach reproductive maturity, this second stage of recruitment lasts through several growing seasons, with their attendant risks of adverse climatic conditions, herbivory, and disease. The length of this "probationary period" will vary with conditions and with the species. In the present study, *Hedyotis* was a species that flowered in its first or second year, but seedlings of the other species still have not reached reproductive size.

These experiments suggest that establishment of new populations of these species may be a very rare event, and thus successful human reintroduction by seed will also be rare. There is a need for more exploration of the biology of the particular species involved, which may lead to the specification both of dispersal conditions and of horticultural practices that could protect the seedlings that do emerge. Some species in this experiment, with a single input of seeds, performed better than others. The interaction between seed-colonist and the environment at the time of arrival means that performances are likely to differ from year to year (as seen in Vasseur and Gagnon 1994), and that both abiotic and biotic conditions, including competition with other species, are important factors (Berger 1993). It is clear in any case that, given the low percentage of emergence for most species in the field, reintroduction by seed requires the use of a large number of seeds and probably more than one year. The number of propagules used (assuming that the supply is plentiful) will depend in part upon the ultimate population size deemed desirable for viability in the reintroduction site. What size is sufficient for "viability" is a subject of current research, though it is safe to say that generalizations are perilous at the moment, since regardless of the definition of viability used, there remain major areas of uncertainty that can only be resolved by longitudinal studies. In any case, we can only conjecture how resilient a population will be, given all possible disturbances over any particular stretch of time (is the target 50 years? 500 years?; Howald 1996; Menges 1991; Pavlik 1996).

The present experiments show (over the course of three years' data collection) rates of "establishment" (in a limited sense) from seed dispersal ranging from about 6% to far less than 1%, with an average around 1%. Using that figure, if the goal is a population of 50 individuals, one would use 5000 seeds. This large number of seeds would only grow larger if one's target population was, for example, 500, as suggested by some researchers, in order to provide a population that might be resilient to disturbance and environmental stochasticity over some length of time. In fact, several of the species in this study were introduced in numbers approaching this figure. In the short term, only two species might be said to be present in the numbers desired (*Hedyotis* and *Sanguinaria*), but they are present not in one population but several.

This raises another design consideration that has entered the design of plant reintroduction plans only recently, that of metapopulation structure (McEachern et al. 1994). Metapopulation theory has formalized the insight that species often exist in populations of populations, patchy concentrations in the landscape at varying distances from each other, joined by gene flow in various forms at a low rate. It is thought that this structuring of a species' population provides resilience to disturbance not provided even by a very large single population. The appropriate size and placement of introduced populations or subpopulations is not only a matter of "distributing the risk" across varying habitats but also of ensuring that there are enough individuals to support cross-pollination when the species is not self-compatible. In the case of the species that have shown the most flowering success in this study (*Sanguinaria, Hedyotis*), the fact that they are pollinated by generalist pollinators may have promoted fruiting success, while *Aquilegia,* which showed good flowering but relatively poor fruit set in both years, may have been pollinator-limited in the areas in which the plants occurred, being too widely spaced to attract hummingbirds. In the Hammond Woods, the flowering individuals were widely separated, and there were no other stations of the species present. In the Middlesex Fells, *Aquilegia* did occur naturally, and it appears that fruit set was somewhat higher there, but further monitoring would be necessary to establish trends. The attraction of appropriate pollinators remains a critical factor for the success of introduced species that require animal or insect pollination vectors.

In the design of a reintroduced population, especially when site characterization may be approximate or missing some critical factor, a plan which disperses the reintroduced propagules in more than one site is an attempt to build in the resilience that the metapopulation may provide. In addition, the reintroduction does not risk all its resources on one or a few sites' viability at the time of reintroduction, thus "sampling" the landscape for a wider range of safe sites (Harper 1977). This assumes as part of the reintroduction plan that the multiple sites of introduction will show varying rates of success and persistence, as in any colonization beyond a population's area of concentration (Prince and Carter 1985; Prince et al. 1985). Despite the best efforts of trained ecologists, it may be difficult to identify the critical environmental factors that allow or prevent the establishment of new populations. Selecting several or many sites for initial attempts increases the chance that at least some will be successful. The sites that show initial promise can then become target sites for more extensive reintroduction efforts.

This raises another point, however, which is relevant to reintroduction efforts: the "sampling" of the topography of time as well as space. The strategy of very large inputs at one point in time is convenient in the construction of emergency rescue plans for threatened species, and for the creation of research programs for doctoral theses, but it may be well to structure reintroductions by seed to include the axis of time in the population structure. Thus, a particular *Hedyotis* or *Sanguinaria* individual may disperse at most two dozen seeds in a year. Perennials, however, are iteroparous, that is, they will under most conditions disperse seeds year after year. Thus their dispersal "shadow" will take into account the interactions of site with climate. The plant conservationist may well wish to do the same, thus adding repeated dispersals to the same sites over the course of several years. In this case, the 50 or 500 plants in the final target metapopulation would not be the result of a single dispersal of 5000 or 50,000 seeds, but of a smaller annual deposit continued for several years.

The experiments reported here, however, show that where transplantable material is available for use, one is much more likely to achieve success in a reintroduction by means of transplanting of individuals past the seedling stage. This is supported by the results of experiments with *Potentilla robbinsiana* mentioned earlier. As discussed in the introduction to this paper, there are important advantages to the use of seeds as the method of reintroduction. Nevertheless, success rates are generally much higher with established individuals than with seeds. The number of individuals required is smaller than the number of seeds, though the cost per individual is higher: to reach a population of

50 to 500, with a success rate of 25% (plausible, based on the results reported here), would require an input of 200 to 2000 individuals, again probably distributed over multiple sites. The higher rate of success per propagule makes it more possible to "structure" something like a metapopulation. With even as few as four individuals per quadrat, a series of 100 quadrats spread across a target location could produce several populations separated by enough distance to provide some protection against disturbance, but close enough for occasional long-distance seed dispersal or exchange of pollen. In the present experiments, sites were usually clustered, with three or four replicates of the experimental unit in one general area, separated by no more than 10 meters. The next experimental site was from 50 to 500 meters distant. In cases like *Caltha* or *Sanguinaria* where there were multiple occupied quadrats, the result in effect was a metapopulation.

Yet there is still the question of the definition of success. For these experiments, success cannot be determined as yet, because for these perennial species, time to reproductive maturity may be as much as five years or more. Thus individuals established from seed, or from the transplant of young plants, will not begin to reproduce for some time, if they survive. Even for reproducing individuals, though, the monitoring time must be on the order of a decade or more. This is in part because of the dormancy of seeds and in part because of the relatively small number of seeds dispersed per plant per year. If the locale is suitable for the species (as may be deduced prima facie from the survival and reproduction of transplants), it may not always be suitable for seedlings, as demonstrated by these same experiments. Thus if a *Sanguinaria* is dispersing 15 seeds per year, with a success rate of perhaps 6% it may take 2–5 years for these seeds to result in new seedlings that persist for more than a year or two. The need for a long time-horizon is emphasized by the attempts to create new populations of the endangered orchid, Small-whorled Pogonia (*Isotria medeoloides*) using wild-collected adult transplants (Brumback and Fyler 1996). While there was a good rate of survival for the first 5 years after the transplants, after 8 years virtually all plants had died out and the remaining plants were no longer in flower.

The experiment reported here suggests that a reintroduction program should include reintroduction by more than one method since, as argued above, reintroduction by seed and by transplant each has its advantages. Further, the reintroduction should be designed when possible to provide new information about the biology of the species under consideration. Although the species used in this study are common features of the New England flora, there is little information available about their population biology and demography, about the applicability of the metapopulation model to them, or about the frequency and conditions under which new populations arise. Finally, it is clear that given the numerous hurdles that a reintroduction effort may encounter, protection of existing populations remains the fundamental ingredient in any conservation plan (Falk 1991; Lesica and Allendorf 1992), and "mitigation" of habitats even with species that are not threatened should be done with caution. If attempts are made to create new populations, these attempts should involve examining multiple sites and methods over a period of years to increase the chances of success.

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THE MYTH OF THE RESILIENT FOREST: CASE STUDY OF THE INVASIVE NORWAY MAPLE (*ACER PLATANOIDES*)

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ABSTRACT. In a New Jersey *Quercus–Fagus–Acer saccharum* forest (Drew University Forest Preserve), the exotic tree Norway maple (*A. platanoides*) is a major and growing presence in all size classes. Norway maple, long one of North America's favorite shade trees, is invading nature preserves in New Jersey and elsewhere. Research in the Drew Forest Preserve shows that the forest is not a tight, resilient unit that repels invasions. Norway maple does not rely upon disturbance or edges. Norway maple seedlings are shade-tolerant and abundant, far outnumbering sugar maple and beech seedlings in the heart of the forest preserve. An analysis of population size and age structure shows that Norway maple trees date back to 1915 or earlier and are present in all subsequent age classes. Spatial studies show clumped distributions for Norway maples as for other plant species but show no restriction to edges. In the understory, species richness is significantly lower beneath Norway maple than under sugar maple or beech, and most stems under Norway maple are additional Norway maples. A restoration experiment (with tree removal plots and seedling removal plots) was begun in 1998 in a patch of 75-year-old sugar and Norway maples; this unusually simple two-species area will elucidate the competitive interaction over time. Other invasive species also penetrate relatively undisturbed forest; *Lonicera japonica, Alliaria petiolata, Berberis thunbergii,* and *Wisteria floribunda* are present alongside Norway maple in the Drew Forest Preserve. Nor is disturbance needed to admit exotic pathogens or insect pests that attack native trees. The threat to the eastern deciduous forest is grave. If the forest is not sufficiently resilient to weather the onslaught of intentional and accidental introductions, then intervention is urgently needed.

Key Words: *Acer platanoides, Acer saccharum,* biological invasions, forest ecology, New Jersey, northern hardwoods forest, succession

Invasive species pose one the greatest of all threats to forest integrity in eastern North America, especially in conjunction with other anthropogenic changes: forest fragmentation and climate change (Vitousek et al. 1997). The eastern deciduous forest has faced devastating invasions by introduced pathogens, particularly the chestnut blight and Dutch elm disease, which virtually eliminated host trees from the canopy. Invasive phytophagous insects have also exerted profound influence (Niemela and Mattson 1996), including the gypsy moth and the hemlock wooly adelgid (Orwig and Foster 1998).

When it comes to introduced plants, many ecosystems worldwide have been transformed by invasive plant species, for example, *Myrica fava* in Hawaii (Vitousek and Walker 1989; Vitousek et al. 1987; Walker and Vitousek 1991), *Melaleuca quinquenervia* and *Schinus terebinthifolius* in Florida (U.S. Congress 1993), several pines in South Africa (Richardson 1998; Richardson et al. 1994), and *Hieracium lepidulum* in New Zealand mountain beech forests (Wiser et al. 1998). Wetlands are under siege by invasive plants such as *Lythrum salicaria* (Hight and Drea 1991; Thompson 1991), *Phalaris arundinacea* (Apfelbaum and Sams 1987; Barnes 1999) and *Phragmites communis.* Since Elton's seminal book on the subject (Elton 1958), biological invasions have been studied by a growing number of scientists (compilations include Groves and Burdon 1986; Luken and Thieret 1997; Mooney and Drake 1986; U.S. Congress 1993).

The eastern deciduous forest has also begun to acquire a heavy, if geographically patchy, load of invasive shrubs, vines, and herbs: *Lonicera japonica* (Evans 1984), *L. maackia* (Luken 1988; Pringle 1973; Williams et al. 1992), *Berberis thunbergii* (Ehrenfeld 1997), *Rhamnus frangula* (Post et al. 1989), *Euonymus alatus* (Ebinger et al. 1984), *Elaeagnus* spp. (Randall and Marinelli 1996; Szafoni 1991), *Alliaria petiolata* (Baskin and Baskin 1992; Byers and Quinn 1998; McCarthy 1997; Nuzzo 1991), and many others (Randall and Marinelli 1996; U.S. Congress 1993).

Is the eastern deciduous forest also threatened by invasive trees, alongside these smaller plants? Many exotic trees thrive at forest margins (*Ailanthus altissima; Paulownia tomentosa* [Williams 1993]) and can be battled by minimizing forest fragmentation. Is this true for all invasive trees, or might some also invade the forest interior? When invasive plants move into the forest, what are the consequences for the community as a whole? Here we examine the invasion of Norway maple as a case study.

At first glance, the small forest preserve on Drew University's campus in New Jersey seemed a natural and intact forest ecosystem, a mixture of mature (though not old growth) oak, beech, and maple. However, closer inspection revealed that a large and growing proportion of the maples were not native sugar maples (*Acer saccharum*) but were instead an introduced species, the superficially similar Norway maple (*A. platanoides*; nomenclature follows Gleason and Cronquist 1991).

Norway maple can be distinguished from its native congener by its milky sap, glabrous lower leaf surface, early yellow-green flowers in erect corymbs, and schizocarp wings at an angle of 180° (vs. 120° in sugar maple). This native of continental Europe was introduced intentionally to Philadelphia around 1760 (Spongberg 1990). It is now among the top-selling shade trees in North America (Nowak and Rowntree 1990; Nowak and Sydnor 1992). While Norway maple is still planted along the streets of America, it is simultaneously removed, often with considerable difficulty and expense, from natural areas where it has spread, from New York's Central Park to Pennsylvania to Ontario. Unlike many horticultural plants, Norway maple has the capacity to reproduce and spread in diverse habitats. It is widely naturalized not only in North America but also in the British Isles (Streets 1962; Webb 1979).

Here we pose several questions about Norway maple as a potential threat to the eastern deciduous forest. The overriding conceptual issue is to what extent a forest resists invasion; the pragmatic issue is to what extent intervention is thus necessary to maintain or restore forest integrity.

1. Is Norway maple truly invasive or simply a modest and transient presence in the forest? Dendrochronology and population sampling shed light on the age structure and size structure of the Norway maple population.
2. Does Norway maple depend upon edges, as do many light-demanding plants, or is it successful in the heart of the forest? Spatial analysis helps test for any edge effects.
3. How does Norway maple influence the richness and structure of the forest? We compare the undergrowth beneath Norway maple with that beneath native trees.
4. How can Norway maple be removed from invaded forests, and with what consequences? A controlled restoration experiment will permit tracking of the effects of removals of both trees and seedlings.

STUDY AREAS

The Drew Forest Preserve encompasses approximately 18 ha in Madison, Morris County, New Jersey (40°46′N, 74°26′W), within the Loantaka terminal moraine of Wisconsin glaciation. Soils are a mosaic of well-drained and somewhat poorly-drained loamy soils derived from gneissic glacial outwash (Tedrow 1986). Outwash deposits are interspersed with steep dells of ice-block origin. More generally the Preserve lies within the Piedmont physiographic province, in the region classified by Braun (1950) as the central hardwoods area of the oak-chestnut region. The vegetation has characteristics of both Mixed Oak and Sugar Maple–Mixed Hardwoods (Collins and Anderson 1994; see Table 1). Historical perspectives on the region's forests are provided by Russell (1981a, 1981b) and Ehrenfeld (1982).

The three components of this research utilized different study areas. The first two projects focused on the most naturalized forest zone, the Forest Preserve Study Area, a second-growth forest dominated by oaks, beech, and the two maples; composition and age structure are detailed in "results." The original tree-ring plot (Tree Ring Study Area) was a 0.25 ha plot situated within the Forest Preserve Study Area (Webb and Kaunzinger 1993). The second project, the study of understory influence, included the Tree Ring Plot but also much more of the forest, for a total Forest Preserve Study Area measuring 3.52 ha; sampling covered 14% of this study area in randomly selected plots (Wyckoff and Webb 1996). Stand attributes are reported in Table 1.

The third project took place in the 1.8 ha Maple Study Area, a different forest community of younger, even-aged (75–80 year old) sugar and Norway maples with few trees of other species. The Maple Study Area was chosen for the study of spatial patterns and for the removal experiment because of its floristic simplicity. Seven other tree species were present but at very low densities in this study area: *Fagus grandifolia* (3.17% density), *Quercus rubra* (2.65%), *Acer rubrum* (0.38%), *Q. alba* (0.33%), *Q. velutina* (0.19%), *A. saccharinum* (0.8%), and *Q. prinus* (0.04%).

MATERIALS AND METHODS

Detailed methods for the tree ring and understory projects have been reported in Webb and Kaunzinger (1993) and Wyckoff and

Table 1. Forest composition and stand attributes, Drew University Forest Preserve Study Area (3.52 ha). Note that forest composition is somewhat different in the Maple Study Area; see text. Based on random sampling in circular plots with 10 m diameter. Includes trees with DBH ≥ 2.5 cm. (From Wyckoff and Webb 1996.)

Species	Density (#/ha)	Relative Density	Mean DBH (cm)	Basal Area (m^2/ha)	Relative Dominance
Acer platanoides	161	26.0%	8.5	2.14	7.3%
Acer saccharum	217	35.1%	14.2	7.38	25.5%
Fagus grandifolia	123	19.9%	22.1	6.94	24.0%
Ulmus americana	20	3.2%	24.0	1.29	4.4%
Prunus avium	20	3.2%	9.7	0.33	1.1%
Robinia pseudo-acacia	16	2.5%	40.3	1.47	5.1%
Quercus velutina	12	1.9%	47.1	2.16	7.4%
Fraxinus americana	10	1.6%	34.3	0.96	3.3%
Quercus alba	10	1.6%	51.5	2.35	8.1%
Acer saccharinum	8	1.3%	41.4	1.28	4.4%
Betula lenta	6	1.0%	50.2	1.20	4.1%
Quercus rubra	6	1.0%	41.4	0.82	2.8%
Acer rubrum	4	0.6%	17.8	0.11	0.3%
Cornus florida	2	0.3%	22.2	0.77	0.2%
Prunus pensylvanica	2	0.3%	2.5	<0.01	<0.1%
Liriodendron tulipifera	2	0.3%	48.4	0.37	1.3%

Webb (1996), respectively. In brief, the tree ring study censused and cored all sizable trees (DBH $\geq$ 5 cm) in 1988, within a 0.25 ha plot. Smaller stems were sampled in subplots. Increment cores from the diffuse-porous trees were soaked and sanded before counting. Thirteen of 74 tree cores were excluded from analysis because of missing centers due to heartrot. Estimated ages omit time before each tree reached the core-extraction height of 25 cm. Age distributions for the four major taxa were compared using the Komogorov-Smirnov statistical test (Sokal and Rohlf 1981).

To compare the understories of Norway maple with those beneath native trees, and also to extend our picture of the Norway maple invasion outside the dendrochronology plot, Wyckoff and Webb (1996) established a random sampling network in fall 1993, sampling a 3.5 ha area of the forest. Sixteen circular plots, each measuring 314 m^2, were centered on points at coordinates derived from a random number table. Plot centers within 20 m of the forest edge were rejected. All trees with DBH $\geq$ 2.5 cm were identified and measured for stand attributes.

Next, to assess the understory influence of Norway maple relative to that of native canopy trees, we sampled subplots under Norway maple, sugar maple, and beech canopy trees within the tree plots. In each tree plot, we examined up to six canopy trees by choosing the two individuals closest to the plot center for each of the three target species. Random coordinates were used to select additional trees for a total of 20 canopy trees for each species. At the base of each randomly chosen Norway maple, sugar maple, and beech tree, we laid out eight 1 m × 1 m subplots, for a total of 160 subplots under each canopy species. All rooted vascular plant stems, including nonwoody species, were identified and tabulated. For small individuals of the tree species, we distinguished between saplings (height $>$ 1 m, DBH $\leq$ 2.5 m) and seedlings (height $\leq$ 1 m). We used nested ANOVA (subplots nested within canopy trees) to avoid pseudoreplication (Hurlbert 1984) when testing each understory species for differences attributable to canopy species. Post-hoc LSD tests were applied for pairwise comparison of means when ANOVA indicated significance at $P < 0.05$. A broader understory sampling was added to better capture patterns among understory trees and saplings; we tabulated those trees and saplings that were 50% or more overtopped by each of the 60 randomly selected trees.

In fall 1997, two of us (Dwyer and Webb) began a third pro-

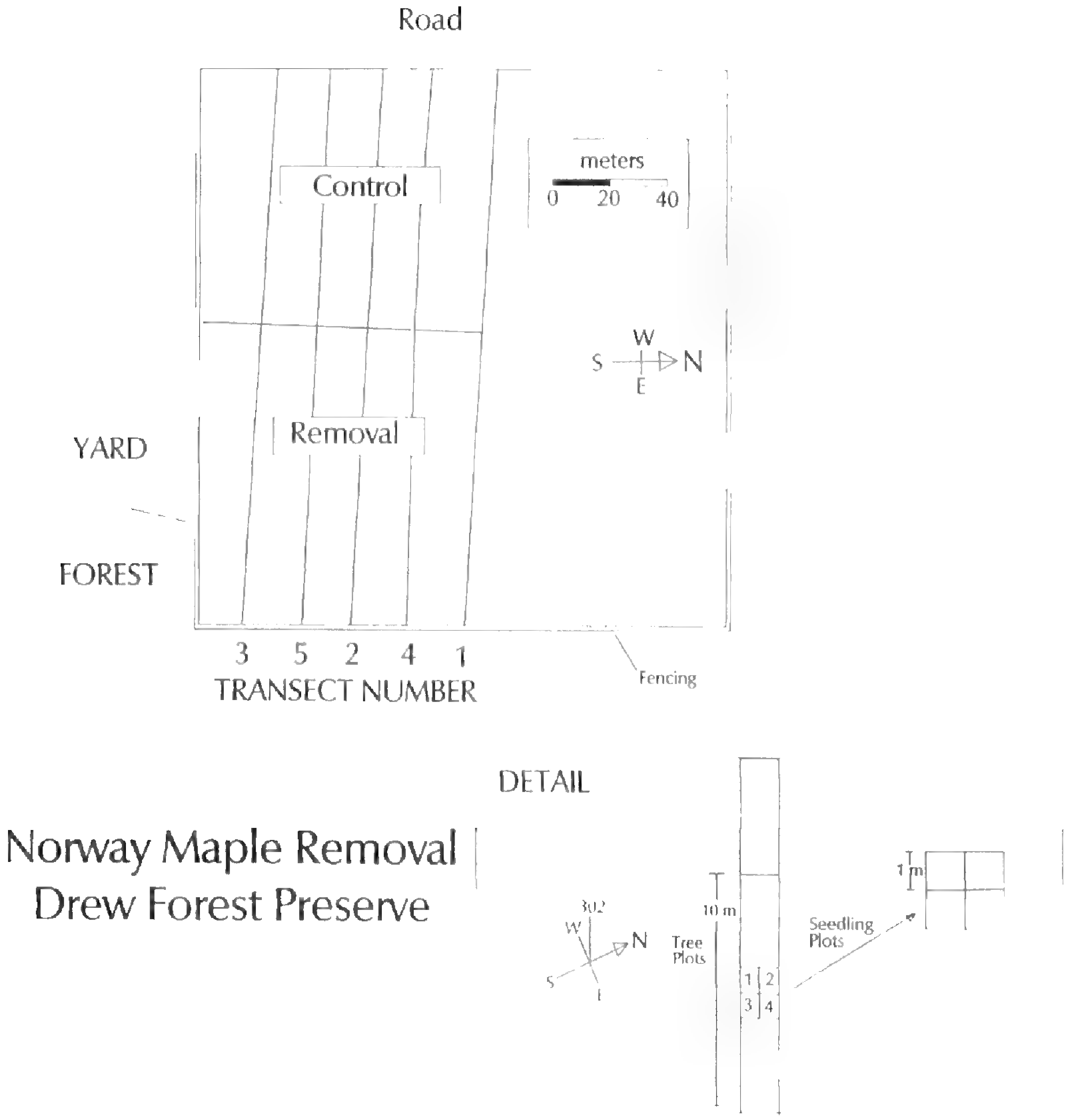

Figure 1. Sampling scheme and arrangement of permanent plots in the Maple Study Area, with Norway maple removal plot and control (nonremoval plot). Permanent plot markers are at centers of each 2 m × 10 m tree plot. Seedling plots measuring 2 m × 2 m are nested within tree plots for four of the five transects.

ject: an experiment in Norway maple removal and, ultimately, in forest restoration. The 1.84 ha Maple Study Area was bisected into a 0.914 ha removal plot and a 0.929 ha control plot (Figure 1); asymmetry resulted from old fencing being used to delineate the area. Before trees and seedlings were removed, trees and seedlings were sampled in detail.

Five evenly-spaced transects were partitioned into 20 adjacent linear plots measuring 2 m wide by 10 m long (the westernmost plot in each transect was 7 m long; Figure 1). The plot centers were permanently marked by rebar stakes with labeled metal caps. In each plot, all woody stems with height $\geq$ 1.5 m were identified and measured. Thus this "tree" category includes smaller stems than the "tree" categories used in the above studies of tree-ring and understory influence. This partial sampling of trees, necessary to assess spatial patterns and statistical relationships, was supplemented by a complete census of trees in both removal and control areas. Norway maples were flagged during sampling within the removal plot.

Seedlings (height $<$ 0.5 m) were also sampled, using subplots nested within the tree plots, for four of the five tree transects. Seedling plots measured 2 m × 2 m and were centered on the permanent markers within tree plots to facilitate future resampling. Patterns were analyzed with regression using SPSS (Norusis 1993) and with tests of dispersion (Krebs 1999).

The removal component of this study included both trees and seedlings. For trees, 428 flagged Norway maples were cut down or girdled in January 1998. Machetes were used on small stems, while 29 trees were too large for this method and were either girdled or felled by chain saw. A total of 1430 Norway maple seedlings were pulled up by the roots, as they were tabulated, in two of the four transects, in 40 subplots with total area of 160 m^2. Seedling removal and seedling control (nonremoval) subplots were situated in both tree removal and tree control plots, so that the interaction between seedling and tree removal can be examined in the future.

RESULTS

Norway maple population age structure. Norway maple was present within the Drew Forest Preserve by 1915. It has been a major component of all age classes since then, with especially heavy recruitment in the 1940s and subsequent decades (see Webb and Kaunzinger 1993 for details). Figure 2 shows age distributions for trees with interpretable cores. The Norway maple age distribution is not significantly different from those of sugar maple or American beech (Kolmogorov-Smirnov test, $P > 0.05$), though it is different from the age distribution profile for the oaks. Note that apparent shortages of trees in younger age classes simply reflect the lower diameter limit for coring (10 cm in this study). Size profiles for each tree population fill in the smaller

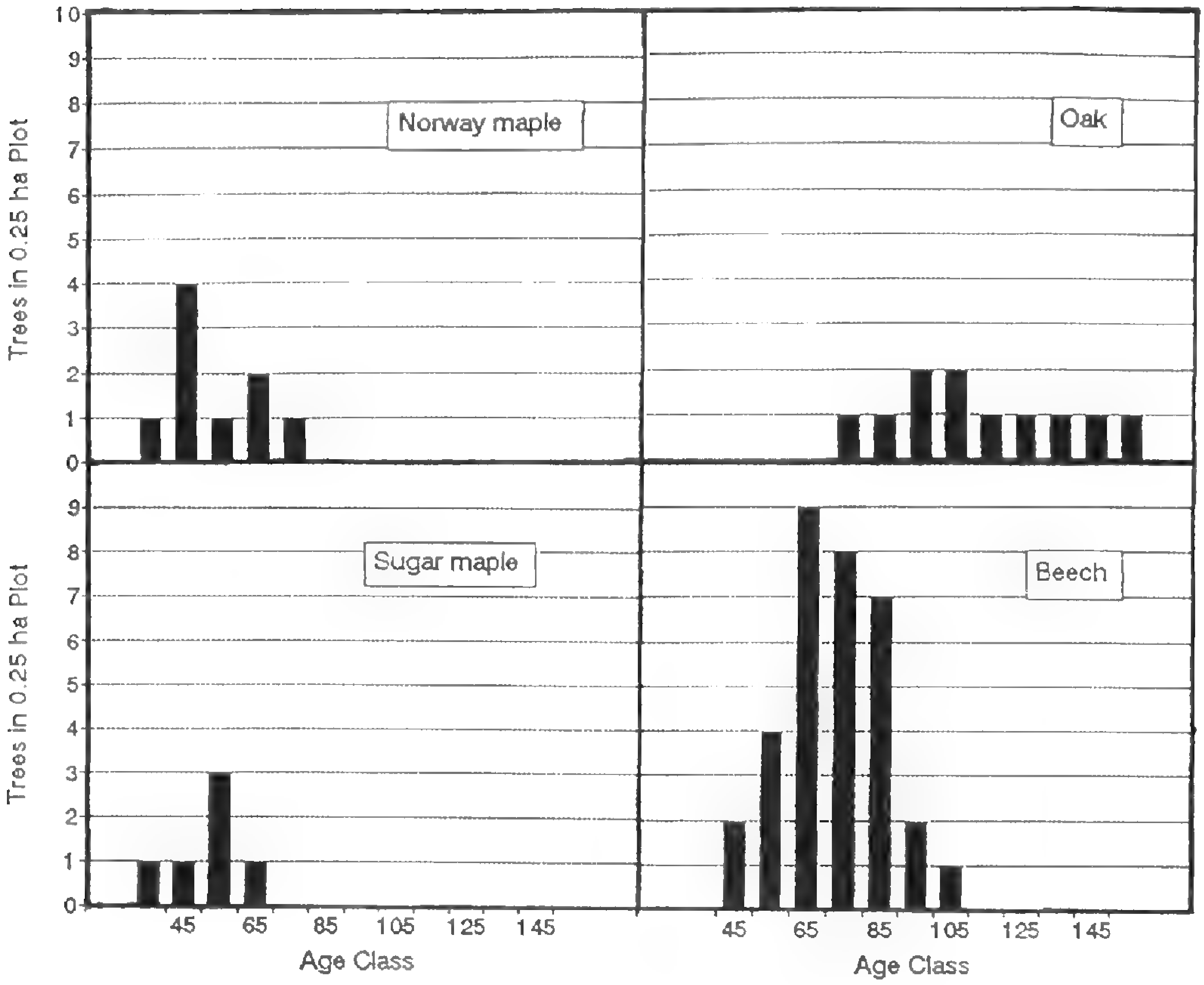

Figure 2. Age distribution for the four major taxa in the Tree Ring Plot. The "oak" category combines *Quercus velutina, Q. alba, and Q. rubra.* Apparent shortages of younger trees reflect lower diameter limit for coring (10 cm); compare with Figure 3. Age distribution of Norway maple was significantly different from that of oaks but not from beech or sugar maple (Kolmogorov-Smirnov test). From Webb and Kaunzinger (1993).

trees but otherwise parallel age profiles (Figure 3). American beech was present by 1890 and sugar maple by 1920; like Norway maple, both of these shade-tolerant species have been reproducing ever since.

The overall picture of forest age structure suggests that Norway maple appeared just as the forest became too closed for further oak reproduction. The oldest and largest trees were oaks: *Quercus velutina, Q. alba,* and *Q. rubra,* with estimated ages of 79–154 years (origins between 1835 and 1910; Webb and Kaunzinger 1993), and with open-grown crown morphology reflecting establishment when the site was still open pasture. The ongoing ability of Norway maple trees to establish since forest closure attests to its shade tolerance and ability to invade beyond disturbed ground and sunny edges.

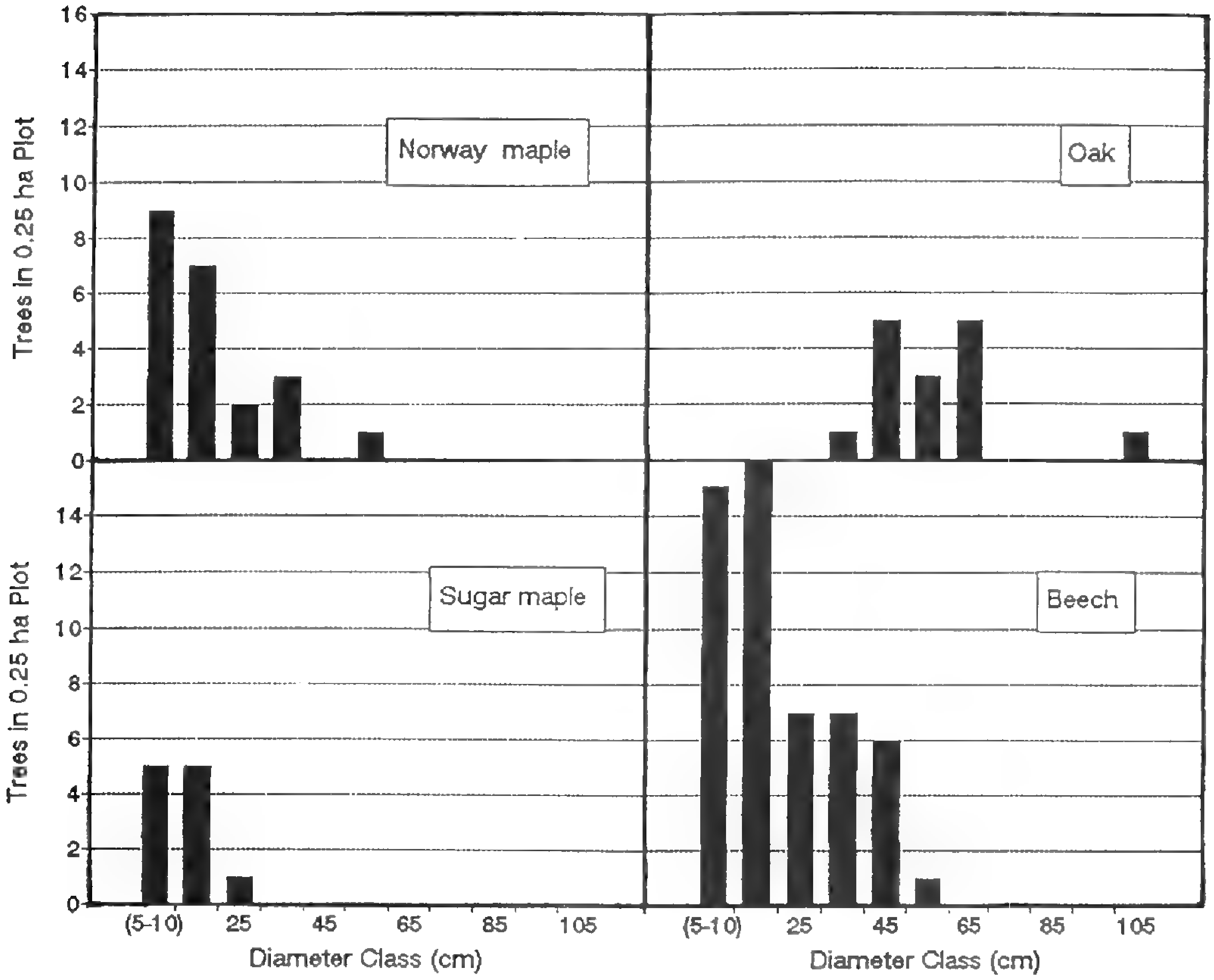

Figure 3. Size distribution graphs for the four major taxa in the Tree Ring Plot, including all trees with DBH > 5 cm. From Webb and Kaunzinger (1993).

Additional tree-age data are also available for the very different Maple Study Area, the mixed stand of sugar and Norway maples. Here, canopy trees were mostly even-aged at 75–80 years (in 1997). Both maple species were represented by abundant seedlings and saplings too small to core, demonstrating once again their tolerance of shady, competitive environments.

Norway maple abundance, dominance, and reproduction. The abundance and size distributions for Norway maple varied between study areas but in all localities showed an influential role for this species. Norway maple trees (DBH > 5 cm) ranked second in abundance (17.2% relative density) behind beech, among 13 tree species present in the Tree Ring Plot (Webb and Kaunzinger 1993). In the larger Forest Preserve Study Area (Wyckoff and Webb 1996), Norway maple also ranked second in abundance (26%) but was outranked by sugar maple rather than beech (Table 1). In the younger Maple Study Area, Norway maple and sugar maple were nearly even in tree density (46.5% and 45.4% of stems); note that tabulations for this study area included saplings as well as trees (all stems with height > 1.5 m).

Norway maple's youth relative to oaks and beeches in the Drew Forest gave it somewhat lower rankings for dominance, an estimate of biomass based upon tree diameters (Table 1). In the Tree Ring Plot, Norway maple was fourth in dominance (8.2% of basal area, behind black oak, beech, and white oak; Webb and Kaunzinger 1993); in the larger Forest Preserve Study Area, it ranked fifth in dominance (7.3%, behind the same three species and sugar maple). In the Maple Study Area, Norway maple ranked second in dominance (20.6%) behind sugar maple (52.4%); *Quercus rubra* ranked third (12.43%) with a few (2.65% of density) very sizable trees; none of six other tree species had more than 1.5% relative dominance.

Perhaps most revealing about the future of the forest are seedling and sapling data. In these small size classes, Norway maple showed an extremely strong presence in all study areas. In the Tree Ring Plot, Norway maple accounted for nearly 60% of all seedlings (DBH < 5 cm), with over 2000 stems per ha, or one per five square meters (Webb and Kaunzinger 1993). In the younger Maple Study Area, dense carpets of very small maple seedlings (counting only stems with height < 1.5 m) comprised a 50:50 mixture of Norway and sugar maple seedlings, with an average of 50 Norway maple seedlings per five square meters.

Spatial patterns and edge effects. Norway maple was not restricted to forest margins; all size classes were abundant throughout the forest interior. Both trees and seedlings of Norway maple exhibited clumped dispersion patterns, but this was also true for the native sugar maple (in Maple Study Area, for both Morisita's Index and the Variance-to-Mean Ratio; Krebs 1999; Sokal and Rohlf 1981).

The Maple Study Area had two edges whose influence differed sharply. The first edge was a major two-lane roadway toward the west (Figure 1); surprisingly, Norway maple dominance (as basal area) decreased significantly toward this edge (regression, $P = 0.038$). A row of planted sugar maples along this roadway suggests that the proximity of seed sources or perhaps some competitive effect was at work; physical aspects of the edge itself did not promote Norway maple growth in this case. Beyond this dom-

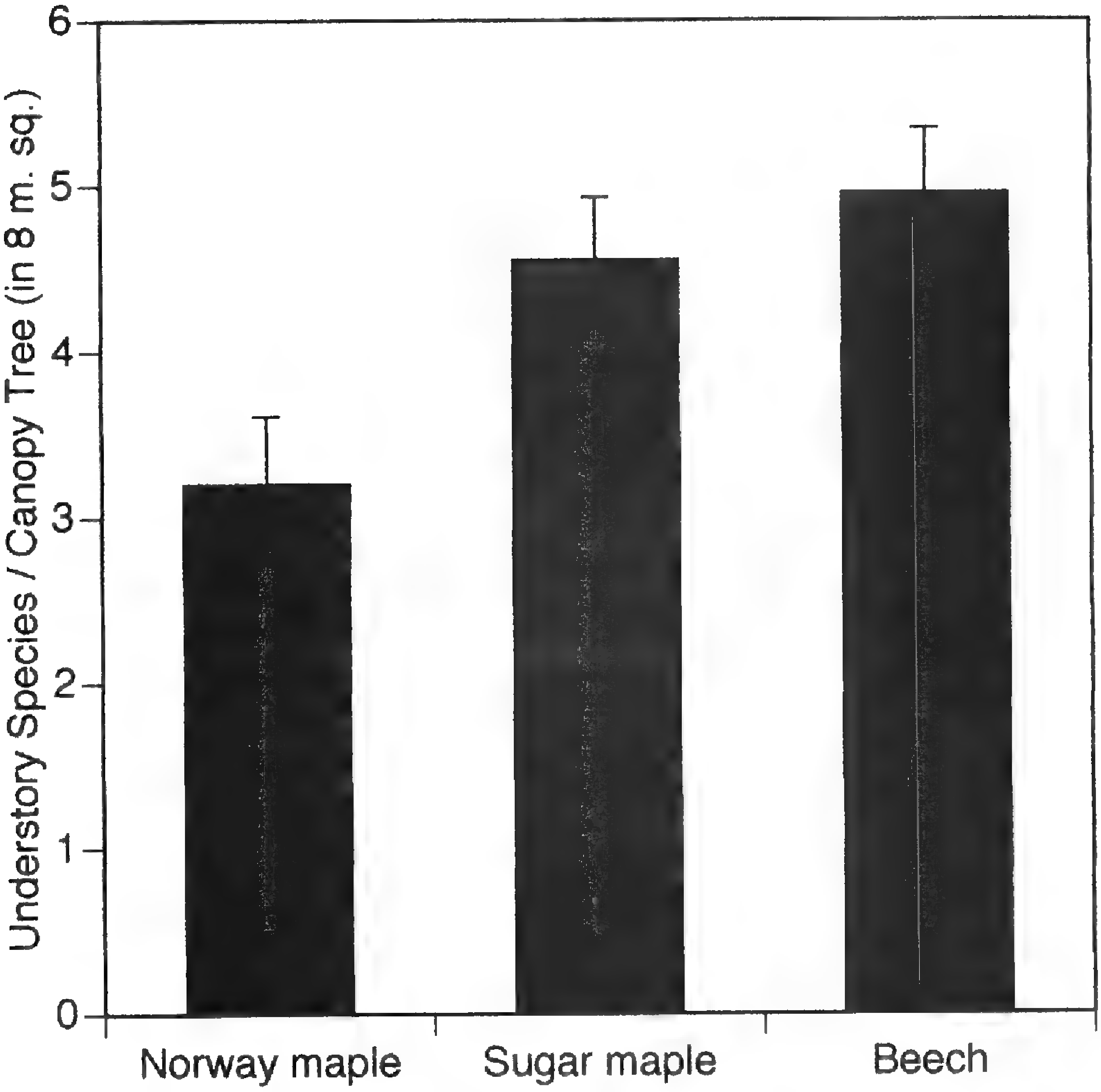

Figure 4. Understory species richness beneath Norway maple as compared with sugar maple and beech. Bars show average number of species in subplots measuring 8 m^2. Species richness was significantly lower beneath Norway maple. Bars indicate one standard error. From Wyckoff and Webb (1996).

inance response, distance from this edge did not influence density of Norway maple trees or seedlings, nor density or dominance of sugar maple trees or seedlings.

The second edge was a residential yard to the south of the Maple Study Area (Figure 1). In contrast to the roadway, this yard edge fostered significantly higher densities of Norway maple seedlings (height < 1.5 m; regression, $P = 0.040$) without a similar effect on sugar maple seedlings. Seed source again seemed to play a more influential role than edge microclimate or light levels. The residential yard had a dozen mature Norway maples adjacent to the forest before the residents removed most over the

Table 2. Plant species in understory plots of the Drew Forest Preserve Study Area, with mean densities under each canopy type (per 8 m^2). Significant differences are reported in the last column, based on Fisher LSD ($P < 0.05$). B = beech, SM = sugar maple, NM = Norway maple.

Understory Species	Canopy Type NM	Canopy Type SM	Canopy Type B	P (ANOVA)	Differences ($P < 0.05$)
Trees					
Acer platanoides (yearling)	54.95	16.5	22.30	0.0111	B = SM < NM
Acer platanoides (older seedling)	12.15	7.80	6.70	0.3365	
Acer platanoides (sapling)	3.00	1.05	1.55	0.2592	
Acer saccharum (yearling)	0.20	1.30	1.60	0.2729	
Acer saccharum (older seedling)	1.15	3.00	3.50	0.3925	
Acer saccharum (sapling)	0.00	0.95	0.10	0.0039	B = NM < SM
Fagus grandifolia (seedling)	0.05	0.25	0.95	0.0264	NM = SM < B
Fagus grandifolia (sapling)	0.00	0.40	0.20	0.4075	
Shrubs, Vines, and Forbs					
Actaea rubra	0.05	0.00	0.05	0.6092	
Aster divaricatus	0.45	0.95	1.60	0.7470	
Epifagus virginiana	0.15	8.75	33.15	0.0064	NM = SM < B
Fraxinus americana	0.50	1.00	1.35	0.7433	
Ilex verticillata	0.40	0.70	0.85	0.6493	
Lindera benzoin	0.60	2.95	0.05	0.0308	B = NM < SM
Lonicera japonica	4.25	7.80	0.05	0.1607	
Maianthemum canadense	0.00	2.60	0.00	0.3742	
Mitchella repens	0.00	1.90	0.00	0.3742	
Parthenocissus quinquefolia	0.05	3.70	0.25	0.6505	
Polygonatum pubescens	2.00	0.70	2.65	0.1823	
Polygonium virginiana	0.05	0.00	0.00	0.3742	

Table 2. Continued.

Understory Species	Canopy Type			P	Differences
	NM	SM	B	(ANOVA)	($P < 0.05$)
Robinia pseudoacacia	0.00	0.05	0.00	0.3742	
Sassafras albidum	0.00	0.05	0.00	0.3742	
Toxicodendron radicans	0.75	0.25	0.20	0.5465	
Uvularia sessilifolia	0.00	0.00	0.05	0.3742	
Vaccinium corymbosum	0.25	0.30	0.00	0.3286	
Viburnum acerifolium	3.55	3.85	3.70	0.9940	
Total Richness	16	18	15		

past decade. A clump of sizable Norway maples was also found within the forest near this edge. Even more telling: when seedling density was regressed on both dominance (basal area of Norway maple) and on distance from the edge, the distance factor lost its significance ($P = 0.874$) while dominance, as a proxy for large trees, more fully explained the pattern ($P = 0.004$).

While seed sources and competitive effects thus seemed to influence Norway maple, it is important to note the lack of a spatial relationship between trees and seedlings, either presence or abundance, on the finer spatial scale within the forest. For neither Norway maple nor sugar maple seedlings was it necessary to have mature conspecific trees within 10 m or more.

Norway maple influence on undergrowth. The understory beneath Norway maple was distinctive in its low diversity and in its preponderance of Norway maple seedlings. Understory richness was significantly lower beneath the average Norway maple ($\bar{x} = 3.20$ species/8 m^2) than beneath sugar maple ($\bar{x} = 4.55$ species/8 m^2) or beneath beech ($\bar{x} = 4.95$ species/8 m^2; Figure 4; ANOVA, $P = 0.0074$). Of 21 understory species present (Table 2), most were found under all three canopy species: 16 beneath Norway maple, 18 beneath sugar maple, and 15 beneath beech. Sugar maple supported the most distinctive assemblage, on average, with slightly more *Lindera benzoin, Parthenocissus quinquefolia, Maianthemum canadense, Mitchella repens,* and *Lonicera japonica;* however, only differences in abundance of *Lindera benzoin* were statistically significant at the level of the individual species (Table 2).

The Norway maple understory was typically a carpet of Norway maple seedlings, which comprised 83% of stems and 98% of all woody seedlings beneath Norway maple trees. Paradoxically, Norway maple understories had slightly higher densities of understory stems (84.65 stems/8 m^2) than beech (80.40) or sugar maple (63.85; Figure 5). However, when we excluded Norway maple stems from the totals, this pattern was reversed, as shown by the filled bars in Figure 5, in a statistical trend toward lower densities of non-Norway maple stems (ANOVA, $P = 0.0881$).

While Norway maple seems likely to replace itself in future generations, it also promises to replace most beech and sugar maple trees as well, if seedling and sapling survivorship continues at current rates. Norway maple accounted for 81% of all woody

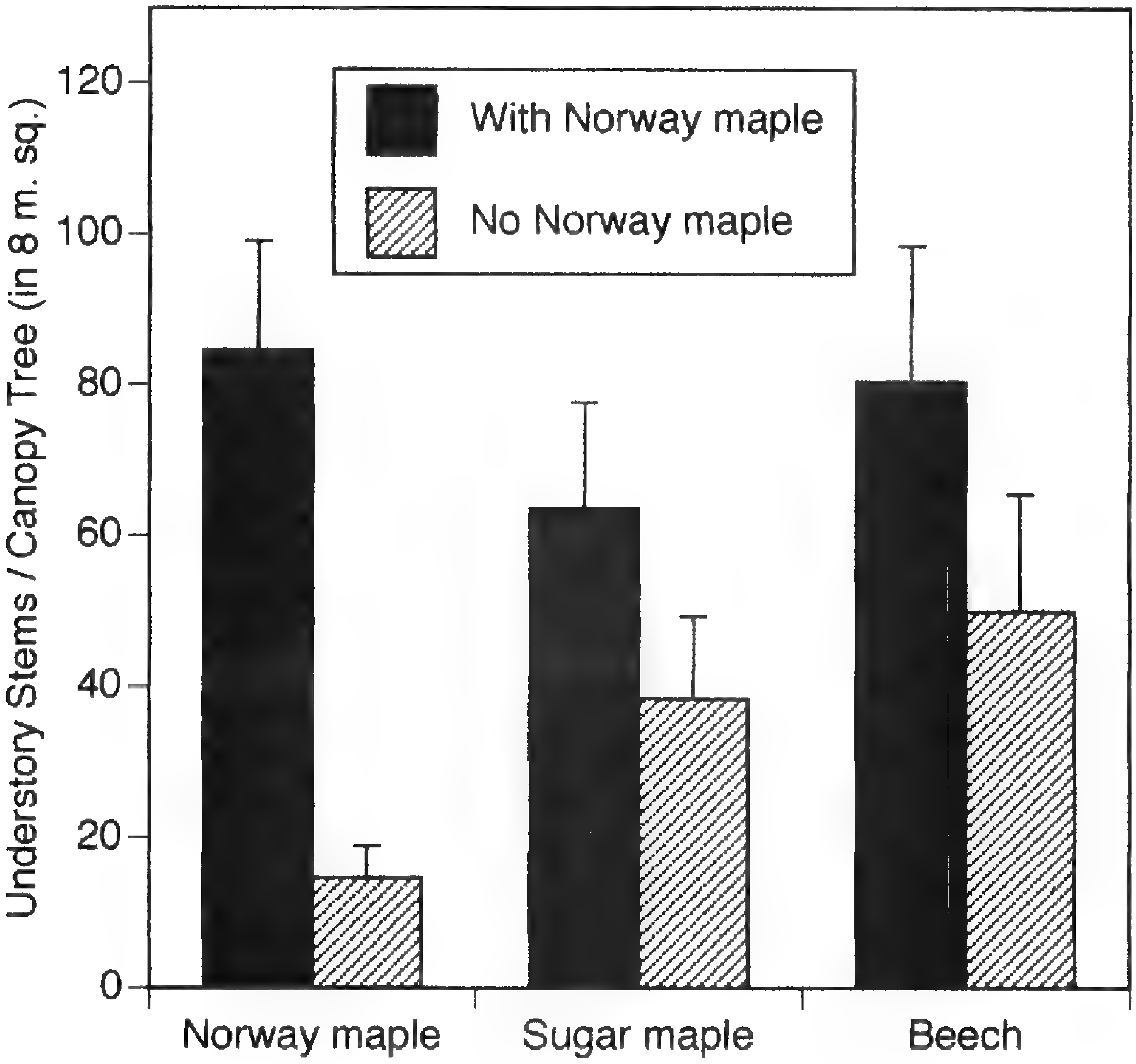

Figure 5. Understory stem densities beneath Norway maple, sugar maple, and beech. Bars show average number of vascular plant stems within 8 m^2 plots. Understory stems of Norway maple are included in filled bars but excluded from shaded bars. From Wyckoff and Webb (1996).

seedlings beneath sugar maples and 80% beneath beech (Figure 6). Only under sugar maple was there much prospect for future canopy trees that were not Norway maples. Amongst larger saplings and understory trees, the pattern was somewhat different than for seedlings: sugar maples sometimes equaled Norway maple saplings in abundance beneath sugar maple trees (Wyckoff and Webb 1996). Elsewhere the numerical dominance of Norway maple suggests an increasing role in the future and a concomitant decline in native wildflowers and shrubs throughout the preserve.

Effects of Norway maple removal. Results of the removal experiment initiated in 1997–98 must obviously await the passage of time and future resampling of permanent plots. The baseline

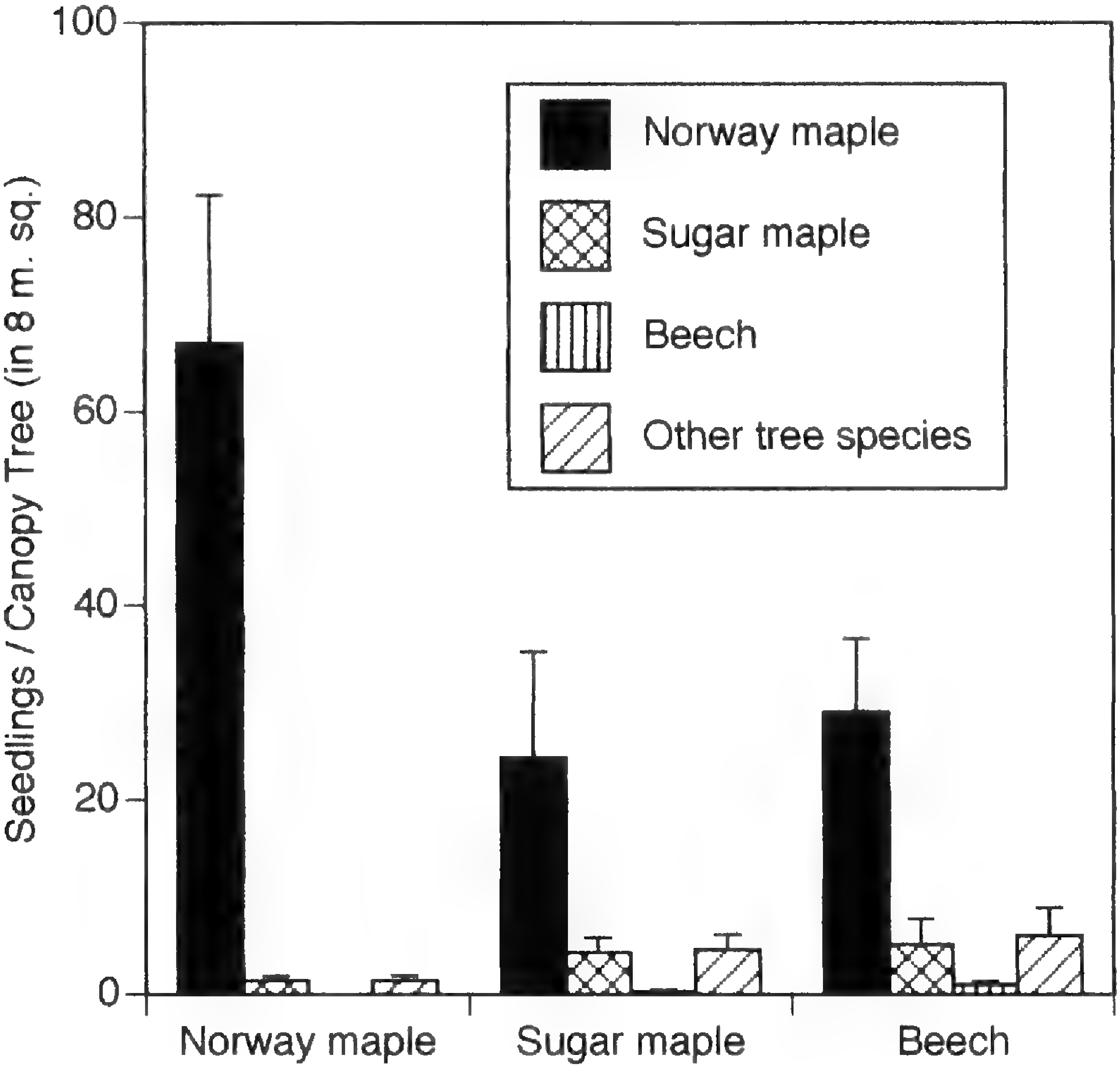

Figure 6. Differences in assemblages of tree seedlings under Norway maple, sugar maple, and beech canopies. Bars show mean seedling densities per 8 m^2 plot. Note that Norway maple seedlings were dominant under all three canopy species.

sampling of the Maple Study Area provided insights into the questions outlined above, specifically about population structure and edge effects on Norway maple. Early observations showed that most Norway maples had resprouted and would require additional treatment to control. Light levels were greatly elevated in the 0.88 ha experimental removal plot, where 399 small Norway maples and 29 large Norway maples were cut down. The abundant seedlings of both sugar and Norway maple in this Maple Study Area were exhibiting a rapid growth response to the new openings. For the seedling removal plots, the future replenishment of the maple seedling bank is of great interest for both maple species.

DISCUSSION

This case study of the Norway maple invasion depicts a species that is highly successful at penetrating an intact second-growth forest. Norway maple is shade-tolerant, a good competitor for conditions in forest interiors, as evidenced by its presence in all age and size classes throughout the forest (Webb and Kaunzinger 1993). Its dominance will almost certainly increase in the future. Forest edges are not essential for Norway maple. However, edges coupled with adjacent landscape plantings help accelerate its spread by increasing the seedling bank. Large tracts of unfragmented forest might be invaded more slowly. Norway maple has advantageous physiological mechanisms besides its tolerance of shade, including early leaf expansion and late leaf drop for a longer growth season than is seen for sugar maple (Kloeppel and Abrams 1995). Seeds are produced abundantly and dispersed widely (Matlack 1987).

The ability of Norway maple to depress species richness (Wyckoff and Webb 1996) raises concerns about preserving forest integrity. Negative consequences are likely, both for populations of native wildflowers and shrubs and for the future of native trees with which Norway maple competes in the canopy.

The vulnerability of our forests to this tree and to other new arrivals, such as the chestnut blight (Good 1968), the hemlock woolly adelgid (*Adelges tsugae*; Orwig and Foster 1998), and Japanese barberry (*Berberis thunbergii*; Ehrenfeld 1997), challenges the myth of the resilient forest. These examples call into question the common generalizations that invasions are most likely following disturbance or in insular habitats. A theoretical framework on biological invasions continues to elude us because efforts to predict invasiveness have not been generally successful.

An expectation that forests will eventually recover from damage derives in part from outdated equilibrial views of nature and in part from the regional experience in northeastern North America where most abandoned fields and clear-cuts do indeed return to a forested state. Several lines of evidence challenge this complacent view. Recent research has shown that apparent recovery from clear-cutting does not include return of the entire herbaceous flora (Bratton 1994; Duffy 1993; Duffer and Meier 1992; Matlack 1994). Foster (2000) has shown that the second-growth forest does not exhibit the presettlement forest's topographic patterning of tree species. Thus forests need not follow a rapid trajectory to some original steady state following perturbation. Indeed, such recovery is unlikely in the face of complex interactions among anthropogenic impacts: forest fragmentation, global warming, and introduction of invasive species.

The Norway maple population explosion and the onslaught of other invasive species together suggest that we are asking the wrong question when we wonder why introduced species become invasive. The real question is, "Why not?" What prevents some species from becoming invasive, and what keeps in check those species like Norway maple that seem capable of more widespread colonization? What causes an invasive species to shift over time from an occasional presence in the wild to a community-transforming dominant?

The future of the New England forest, and of the eastern deciduous forest as a whole, is very much at a crossroads. If exotic species continue to enter the region and if invasive species are not deterred, the result will be dramatic shifts in forest composition, structure, and function.

To protect and restore the eastern forest will take hard work and creativity. Three distinct steps must be taken. First, invasive species must be forcibly removed from natural areas and surrounding lands (Randall and Marinelli 1996; Sauer 1998). Land managers, conservation organizations, and volunteers already have taken up this daunting charge, although much more is needed. The second step is prevention of further invasions. Legal action is essential to restrict intentional plantings of invasive species. However, to achieve this aim also requires a cultural shift by which native plants become desirable and even fashionable choices in horticulture and landscaping. Local native plant organizations have had some success in promoting native plants. An important element of success is availability and affordability of diverse native plant materials. The third front in the war on invasives is restoration: replacing the lost plants and providing environments in which they can thrive (Drayton and Primack 2000). For highly disturbed or heavily invaded sites, research in herbaria and in historical archives may be needed to reconstruct in detail which species once grew in which habitats. Paleoecological records provide insights into tree assemblages of the past, but offer little insight into the nonarboreal flora. In addition, survival of replanted wildflowers is compromised by deer, whose populations are elevated by human interference (Alverson et al. 1988, 1994). There is little hope that forests can maintain or recover their diversity without active intervention from *Homo sapiens,* the species that has posed so many challenges to forest integrity.

ACKNOWLEDGMENTS. We are very grateful to members of the Drew University grounds crew and especially grounds manager Michael Virzi for their invaluable work on the Norway maple removal project. We thank Raegan O'Lone for help with recent field work, and countless other students and friends for past assistance with the project. We also thank neighbors and friends of the Drew Forest Preserve for their vigilance and concern: Greg Leuser, Chris Hepburn, Mirelle Bessin, and Rolf Bessin.

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CLOSING REMARKS

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When I spoke to the New England Botanical Club (NEBC) last year about a naturalist's perspective on science education, I approached the task with a bit of trepidation, for I have been working outside of a formal academic institution for nearly 20 years. Providing the epilogue for today's symposium is slightly more daunting.

A word for those who may be new to the NEBC: the NEBC has been around a long time. This is a wonderful association of academic and amateur botanists who have been sharing their work and experiences on the first Friday of the month since 1896. David Barrington, a professional, academic botanist, and Les Eastman, a self-trained amateur, introduced me to the NEBC 23 years ago this month. I clearly remember Friday evenings in the room at the top of this building, participants packed between glass-topped cases of Richard Evans Shultes' ethnobotanical collections to listen to a young man named Michael Donoghue talk about *Acer* and *Viburnum* in the mountains of Mexico. Or, a similar crowd listening to Les tell stories of searching for orchids in cedar swamps of Aroostook County, Maine, with George Newman and some eager student by the name of Les Mehrhoff in tow. So when the committee asked me to wrap up this day, I looked back there for some inspiration.

If you read through the early numbers of *Rhodora,* you will find reports of expeditions, explorations, and investigations that provided some of the academic foundations for the reports that you listened to today. Certainly that is the case for the paleoecological investigations of George Jacobson and Ray Spear, which elucidate dramatic changes in the structure of the forests, upper elevational limits of species, shifts in treeline, and linkages of these changes to fluctuations in temperature and other measures of climate. Ray Spear's work in the mountains, in particular, could be a page right out of Fernald's work, had he lived to be 130.

Notable for those of us who love to think about the mountains, the 700 year period during the Younger Dryas, when average annual temperatures are estimated to have changed 5–10°C, must have wrecked havoc on the prior (relative) stability of the post-glacial alpine tundra vegetation and its associated mega-herbivores. During the last 20,000 years our New England flora has been transformed through the utter devastation of an ice age and the somewhat more subtle influences of human commerce—not only with axes and skidders in the 19th and 20th centuries, but schooners and a thirst for riches that sent (mostly) northern European people around the globe at a frantic pace in the 16th, 17th, and 18th centuries, with microbes, pathogens, plant propagules, rats, and pigs in tow (Crosby 1986).

Notable among their contributions, Charlie Cogbill, David Foster, and Les Mehrhoff have shown us the irrefutable value of the written human record for elucidating the presettlement and early colonial forests and associated vegetation of this region. I admit a great affection for studies that combine evidence gleaned from multiple disciplines, and today's presentations fit the bill. Our modern-day concerns about rapid plant migrations, and the extraordinary loss of populations and whole species to both habitat destruction and displacement by aggressive intruders, takes on a whole new hue when we consider that it is just the most recent wave of the biological expansion. *Trifolium repens* was an early scout, now found on every continent. Sara Webb's studies of *Acer platanoides* show us just how aggressive are some of these relative newcomers to our flora.

The work presented today represents hundreds (if not thousands) of years of collective inquiry, investigation, and analysis. I know for certain that at least one of our speakers has years of unfinished work stretched out before him—am I not right, Charlie (Charles V. Cogbill)? I owe him notes and descriptions of vegetation for at least two remote mountain peaks in Maine before he can complete his exhaustive survey of alpine vegetation in northern New England and New York.

In the remaining few minutes of this celebratory symposium, I offer a few thoughts and an announcement about future botanical explorations—what you and your students ought to be thinking about for work in the coming century. I offer these thoughts with that certain trepidation that comes before telling someone with more experience what they ought to be doing with their life, but . . . why not?

Many of you know that I have been railing for years that the science of our late 20th century is a fragmented discipline. Students and the general public are poorly prepared to solve problems, not knowing where to begin to address landscape-scale issues in botany, zoology, or ecology, let alone contribute to discussions affecting public policy and the stewardship of natural resources.

Thought # 1: Teach. Or, inspire learning! The numbers wouldn't mean too much, but I'll wager that the general public knows less of the world of (whole) plants in 1999 than they did in 1899. There are certainly fewer botany or plant science majors on most campuses that still support the discipline than there were in 1900 or 1950 or even 1975. Please correct me where I may go wrong here. We're all smart enough to do something about that, but it means creating a working environment that invites participation by the sheer energy and high quality of its intellectual inquiry.

Notably, Richard Primack's efforts in restoration ecology have provided a touchstone for the residents of Newton, and I imagine that his particular botanical genius has already infected a generation of future botanists. Community members experience the exhilaration of having "made a difference," and I'd wager that Richard gets a real lift by sharing in that enthusiasm. And, as a result, we know a lot more about the establishment of perennial plants in new environments.

You know I love to explore, most recently on Baffin Island in Nunavut, so the next thought should come as no surprise.

Thought # 2: Travel and explore with students and friends. As the stationary tools and aids to learning continue to amaze and distract us, so I think we need to redouble our effort to get teams of collaborative learners and teachers into the field, if for no other reason than to avoid William Morton Wheeler's "dry rot of academic biology." You may not have read Wheeler's humorous analysis of the state of biology, delivered in Boston 75 years ago, as the Presidential Address to the American Society of Naturalists (Wheeler 1923). He said that we suffered then from an academic form of *Merulius lacrymans*, or the dry-rot fungus:

> "Undoubtedly the best culture medium for the academic dry-rot fungus consists of about equal parts of narrow, un-

> sympathetic specialization and normal precocious senile abstraction."

In his own fight against the tyranny of specialization, Wheeler preferred "natural history" to "ecology," then a young branch of our life sciences. He stated:

> "History shows that throughout the centuries, from Aristotle and Pliny to the present day, natural history constitutes the perennial root-stock or stolon of biological science and that it retains this character because it satisfies some of our most fundamental and vital interests in organisms as living individuals more or less like ourselves."

Herb Wagner's poignant review of the past 50 years of botanical research, and especially the merciless tug-of-war on the psyche of the field and herbarium worker, is telling, particularly in light of Wheeler's earlier comments. Modern systematists have had to adapt to increasingly more frequent changes in techniques and tools, from the early population studies of the likes of Greg Anderson and Charlie Heiser, through the era of numerical taxonomy, countless chemical analyses, to sizing gels and power supplies. These days our work spaces resemble a forensic lab and not an herbarium.

A couple of years ago, I attended a conference in St. Charles, Illinois, sponsored by a world-wide business consulting firm, Arthur Andersen, for both school people and business people. Our presenters predicted some significant changes to the structure of our primary and secondary schools across the country by 2050. A few of those predictions:

- No school building with more than 150 students
- Multi-age classrooms and learning groups
- Teachers as facilitators of learning not dispensers of "the truth"

If anecdotes are worth anything, more and more matriculating freshmen have experienced the positive jolt to learning of well-guided independent study years before entering our hallowed halls. We risk losing them to more stimulating alternative experiences unless we help them take the reins for their learning at the earliest possible age. Many of the graduates of the Maine Coast Semester at the Chewonki Foundation, all of whom are attending or have graduated from places like this (Harvard University), still tell me years later that their 16 weeks on the coast of Maine surpassed everything else for an academic experience . . . "I learned more, etc."

Back at work we are embarking on a new project with the Smithsonian's Arctic Studies Center, the Quebec/Labrador Foundation, and the Center for Northern Studies. The ultimate goal is to put college-aged students in the field with experienced professionals like yourselves, helping to establish local, community-based archaeological, historical, ecological, economic, and environmental projects in the Great Northern Peninsula of Newfoundland, along the Labrador Straits, and north, past Nain, to the Torngats.

We are making a deliberate effort to practice E. O. Wilson's concilience (Wilson 1998). At the risk of repeating myself, I'll pitch that idea again this year. You will recall that Wilson lamented the lack of interest in "the big picture" and urged us to find consilience, literally a "jumping together" of knowledge, between our many and fragmented disciplines of science and the humanities. He said:

> "A balanced perspective cannot be acquired by studying disciplines in pieces: the concilience among them must be pursued. Intellectually it rings true, and it gratifies impulses that arise from the admirable side of human nature. To the extent that the gaps between the branches of learning can be narrowed, diversity and depth of knowledge will increase. They will do so because of, not despite, the underlying cohesion achieved. The enterprise is important for yet another reason: It gives purpose to intellect. It promises that order, not chaos, lies beyond the horizon. Inevitably, . . . we will accept the adventure, go there, and find what we need to know." (p. 62)

As most of you know, the coast of Labrador looks and feels like the top of Katahdin or Mt. Washington. Places like this will "bring 'em in," believe me. I'll wager that four weeks in Labrador will do more to sink the hook in a larval botanist, archaeologist, or even a post-industrial economist than four years hanging around the usual haunts with the usual suspects. But, I digress! Back to the business at hand.

Many of us have more than a mild interest in questions about plant migrations in a world facing some potentially dramatic shifts in climate during the coming century. How will our plant and animal communities respond to predicted increases in annual mean temperature? What might we expect to see or measure in our New England mountains, or farther north along the coast of Labrador? When the Baxter State Park Advisory Committee asked me a dozen years ago what effect the reintroduction of caribou might have on the Tableland of Katahdin, I shrugged and said that, "Whatever the change, we would never really get the measure of it." Beyond a plant list, there was precious little information in the record on the structure of plant communities on that summit—no baseline data.

Thought # 3: Take good notes, the world may be changing fast! If you haven't established some long-term study plots to re-visit in your retirement, this summer is not too late. Take great care to collect good specimens with exquisite notes and details for the labels.

Thought # 4: Share what you and your students are learning. Or, put another way, publish in *Rhodora*!

To that end, it gives me the greatest pleasure to be able to announce this afternoon the establishment of a special award, offered by the New England Botanical Club, named for the most prolific contributor to our journal, the "boss" himself. The Merritt Lyndon Fernald Award will be presented each year to the author or authors of the paper published in *Rhodora* judged best to exemplify the goals and objectives of the journal (and the NEBC) to promote our knowledge and understanding of the world of plants.

So, there you have it. Inspire learning. Get yourself and your students into the field, perhaps with colleagues from neighboring, or even distant disciplines. Improve your data collection, and establish some permanent plots for long-term study; the world is changing fast. Make collections, pay attention to preserving the record, and publish regularly in *Rhodora*.

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NOTE

CALLERY PEAR (*PYRUS CALLERYANA*—ROSACEAE) NATURALIZED IN NORTH CAROLINA

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The Callery pear is noted by Kartesz (1999) to occur in North Carolina, based on an undesignated specimen of *Pyrus calleryana* Decne. in the NCU herbarium. The specimen referred to by Kartesz (*Larke 1649,* cited below) was taken from a tree growing in a natural habitat in the North Carolina Botanical Garden, but there is a probability that it was planted there. The current report provides documentation for the North Carolina Botanical Garden specimen as well as a clear example of incipient naturalization of the same species in North Carolina.

VOUCHER SPECIMENS: NORTH CAROLINA: Orange Co., Chapel Hill, north side of Morgan Creek in North Carolina Botanical Garden, near spring in Hunt's garden area, Grid 14, Aspect F, pine–hardwood bottomland, 23 Sep 1990, *Larke 1649* (NCU)—identified on the label as "*Pyrus* sp. (F3 hybrid—Bradford × LeConte)"; Chapel Hill, Heritage Hills subdivision in southeast corner of county, numerous seedlings and saplings as volunteers in several yards along Concord Drive, apparently from fruits from a single, large, cultivated tree (apparently cv. "Aristocrat") at 106 Concord, 31 Oct 1999, *Nesom NC99-10-1* (BRIT, NCU, TEX, US, to be distributed).

Each of the vouchers of *Nesom NC99-10-1* consists of a fruiting branch of the parent tree and a full plant of one of the young, deeply taprooted progeny. Most of the young plants range 3–12 dm tall at about 1–4 years old; one of them is 2.2 m tall and may be older. Some of youngest individuals have lobed leaves, a feature not seen on mature trees. The parent tree, which was probably planted in the 1970s or early 1980s, judging from its size and the history of the neighborhood, is about 12 m tall and has a relatively loose, elongate-oblong crown with sharply upturned branches, compared to the tighter, nearly globose crowns of the shorter cultivars currently so commonly planted in urban landscapes.

Everett (1981) noted that "nearly all pears are self-sterile." Zielinski (1965) observed that within the genus, "*Pyrus fauriei* appears to be unique in producing seeded fruits upon self-pollination. All other species studied are self-incompatible." The abundant fruits on the parent tree in Orange County (*NC99-10-1*) presumably are from flowers outcrossed to a different clone (see Ackerman and Creech 1966), although it seems remarkable that there apparently are no other reproductive individuals of *P. calleryana* within a radius of 0.4 kilometers of this one. From the parent tree, 30 fruits ranged 11–27 mm in diameter and produced an average of 1.6 mature seeds per fruit (range 1–4). Haserodt and Sydnor (1983, p. 162) noted that "fruiting of this cultivar [cv. "Aristocrat," as the tree is identified here] appears to be heavier than for other cultivars." None of the progeny of *NC99-10-1* observed here (as seedlings and saplings) have matured enough to become reproductive. All are growing within about a 40-meter radius of the parent tree. The parent tree also has produced numerous root sprouts within a 3-meter radius of its base—these are similar in morphology to the young, independent seedlings and saplings.

Russell (1999) also notes that *Pyrus calleryana* is "beginning to naturalize locally in North Carolina and the mid-Atlantic states." By 1983, it was observed to be naturalized in Maryland "on a wide variety of sites around the U.S. Plant Introduction Station" in Glenn Dale (Santamour and McArdle 1983). Stewart (1999) has observed "tremendous numbers" of young wild trees of Callery pear in vacant lots along Route 450 in Bowie, Maryland, and along roadsides of the Capital Beltway around Washington, D.C. At one spot in Bowie, he counted "over one hundred trees in a stretch of neglected ground about 100 ft. long and 50 ft. wide. They were so thick that in places the individual young trees grew only a foot or two apart." Stewart notes that "we seem to have a new horticultural plague on our hands in Maryland, a plague of pears." The sources of these naturalized plants are urban landscapes in the United States, where "the tree is now approaching epidemic proportions" because of overplanting (Dirr 1990, p. 680; also see Anonymous 1986).

The Bradford pear was introduced in the eastern United States through plantings about 1950, although the name was not published until later (see Jacobson 1996). In the last 30 years, many other cultivars of *Pyrus calleryana* have been selected and widely planted (Dirr 1990; Huxley et al. 1992; Jacobson 1996; Santamour and McArdle 1983)—although these apparently are all sometimes informally referred to as "Bradford," technically they should be described by other cultivar names or else generally referred to as "Callery pear." Trees of this species naturalizing in North Carolina and other areas of the southeastern United States apparently represent a range of different cultivars.

The original cultivar of *Pyrus calleryana,* the "Bradford pear," was developed at the U.S. Plant Introduction Station in Glenn Dale, Maryland from seeds collected from northern China (Whitehouse et al. 1963). The native range of *P. calleryana* includes "11 provinces of eastern China, south of the 37th parallel," where it grows in mixed forests on slopes and in swamps (Santamour and McArdle 1983). A closely related entity from Korea, *P. fauriei* Schneider, has sometimes been treated as a variety within *P. calleryana* but is distinct in a number of respects (Zielinski 1965). A naturally occurring hybrid between *P. calleryana* and *P. betulifolia* Bunge has been reported from Illinois (Wandell 1997).

ACKNOWLEDGMENTS. Jeff Beam and Bill Burk (University of North Carolina Couch Botanical Library) and John Kartesz and Amy Farstad (Biota of North America Program) helped in acquiring literature.

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NEW ENGLAND NOTE

SNOW ALGAE IN THE NORTHEASTERN U.S.: PHOTOMICROGRAPHS, OBSERVATIONS, AND DISTRIBUTION OF *CHLOROMONAS* SPP. (CHLOROPHYTA)

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Each spring the waters of melting snowpacks revive a unique consortium of microbes and small invertebrates that thrive within this cold oligotrophic environment. While bacteria, fungi, protists, rotifers, tartigrades, and small insects such as Collembola (springtails) all inhabit springtime melting snow (Hoham et al. 1993), snow algae are generally the most conspicuous inhabitants. Populations of snow algae generally manifest as a red, orange, or green color within several centimeters of the snow surface (Hoham 1980; Kol 1968), and they may exceed 10^6 cells ml^{-1} of liquid meltwater (Hoham 1987). In high alpine regions such as in the western United States and in polar regions, expansive blooms of snow algae have been documented and studied extensively with regard to their adaptive capacity to withstand extreme environments (Bidigare et al. 1993; Hoham and Blinn 1979; Hoham and Ling 2000; Thomas 1972; Thomas and Duval 1995). While most studies from North America report snow algae from high alpine areas in the Sierra Nevada, Cascade, and the Rocky mountains, there are relatively few studies that have focused on snow algae from the northeastern United States and Canada (Duval 1993; Dybas 1998; Hoham et al. 1989, 1993).

Snow algae have been described from the White Mountains

(New Hampshire), Green Mountains (Vermont), and the Sunday River ski area and Mt. Katahdin (Maine), as well as the Adirondacks and Tughill Plateau of upstate New York (Duval 1993; Hoham et al. 1993). Snow algae have also been described from the Laurentian Mountains, Quebec (Hoham et al. 1989; Jones 1991), and from southern Ontario (Gerrath and Nicholls 1974), and probably occur in other parts of eastern Canada but have yet to be discovered. In Massachusetts, their occurrence is spotty, limited to the higher elevations of the Berkshire Hills and Wachusett Mountain where there are higher yearly snowfalls or man-made snow (Hoham et al. 1993). There are no reports of snow algae from southern New England or the middle or southern Appalachian ranges. A reconnaissance to the West Virginia highlands found no evidence of snow algae in melting spring snow (Duval, unpubl. data).

From our studies between 1972–1998, we plotted locations where snow algae were and were not found in the northeastern United States. These findings were compared to a snowfall accumulation map compiled by the Northeast Regional Climate Center (Cember and Wilks 1993), and the results are shown in Figure 1. The snow depth lines are for an "average winter," i.e., in the 50th percentile. Our records show that in the northeastern United States, areas with greater than 200 cm (80 in.) of annual snowfall are more likely to have snow algae than areas that receive lesser snowfall amounts. However, contrary to this generalization is a lack of positive snow algal findings from West Virginia, many parts of the central plateau of New York State, and wooded areas near the city of Syracuse, all of which receive greater than 200 cm of snowfall annually. Thus, snow algal distribution probably involves other factors in addition to snowfall accumulation such as vegetative habitat, the rate at which snowpacks melt, or physio-chemical aspects that affect snow on a regional level (Hoham et al. 1989; Jones 1991).

In the northeastern United States, populations of green snow algae (Figure 2), are typically found in the shaded coniferous fir and spruce forests at high elevations (Hoham et al. 1989). Here, to avoid misnaming the species shown in Figure 3, earlier described as *Scotiella cryophila* and later as a resting spore of *Chloromonas nivalis,* we refer to the spindle-shaped resting spore as *Chloromonas* sp.-A. We hope that a later explanation and Latin

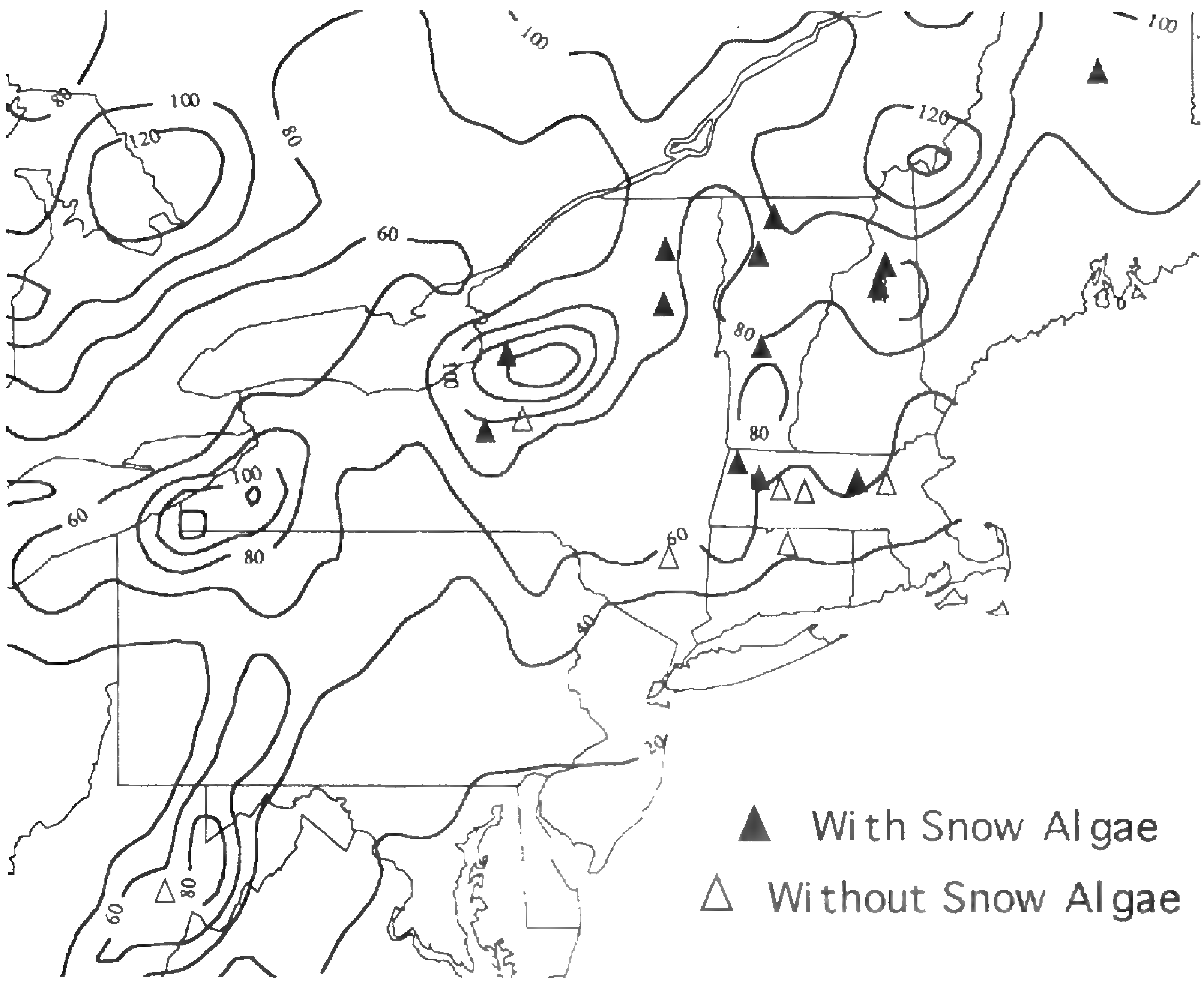
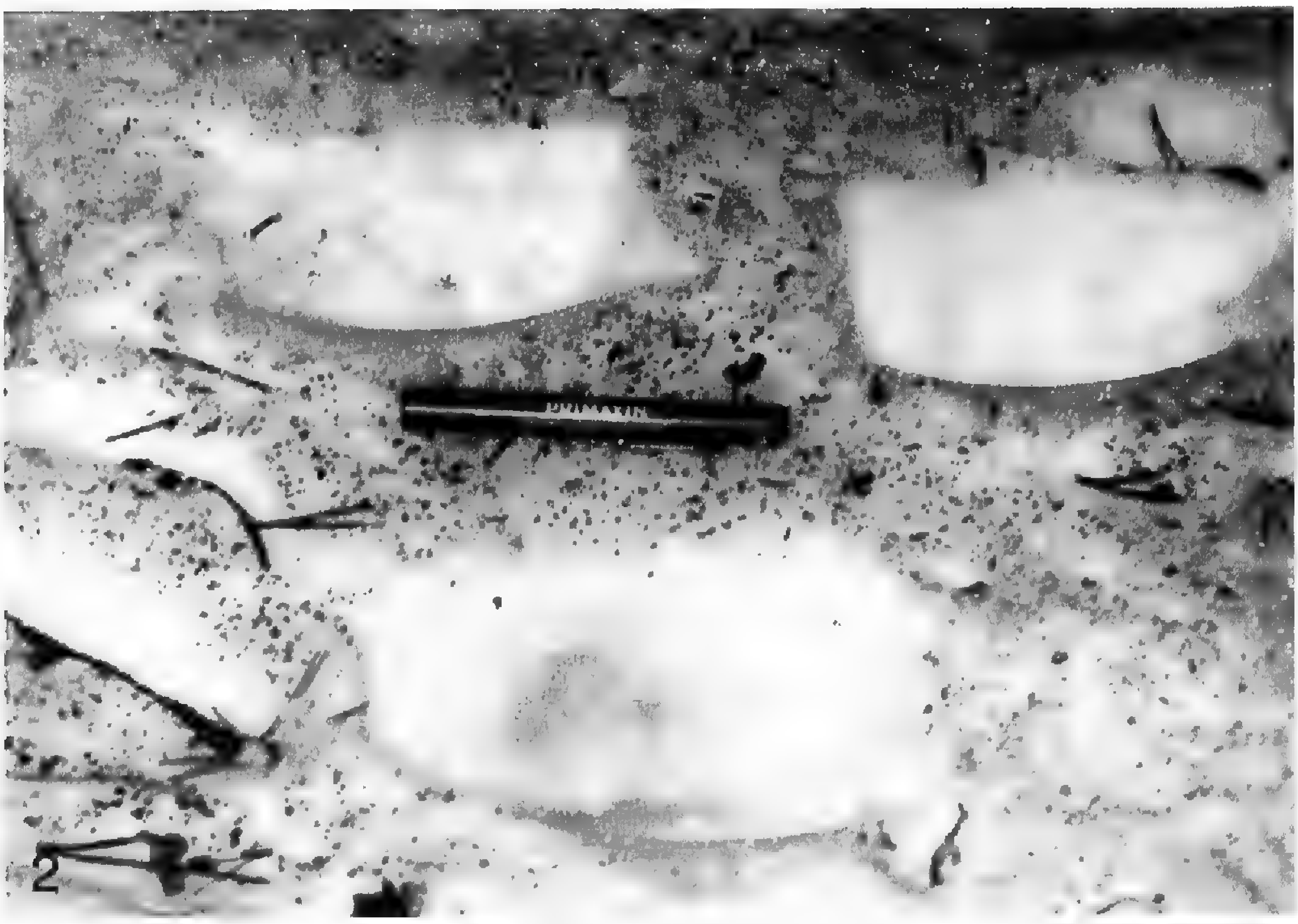


Figure 1. Map of snow algal distribution in the northeastern United States shown with average yearly snowfall accumulation.

description will help clarify the confusion surrounding the name of this snow alga.

Additionally, we have observed a species of salmon-orange colored snow alga in open areas from several New England ski areas (Duval 1993; Hoham et al. 1993). Since we have observed only a few biflagellate cells that appear to belong to *Chloromonas*, we designated the species as *Chloromonas* sp.-B until further observations are made (Hoham et al. 1993). We have found *Chloromonas* sp.-B to inhabit snow at four disjunct ski areas in New England and have not observed this alga in natural alpine snow. This has led us to propose that one of the mechanisms of this snow alga's dispersal might involve transport of resting spores on the bottom of skis (Dybas 1998; Hoham et al. 1993).

Morphologically, the resting stage of *Chloromonas* sp.-B is oval to rounded, ranges in size between 10–25 μm in diameter (Figure 4), has an outer wall about 1 μm thick (Figure 5), and resembles resting stages reported for other species of *Chloromonas* (Hoham 1975; Hoham and Mullet 1978; Hoham et al.



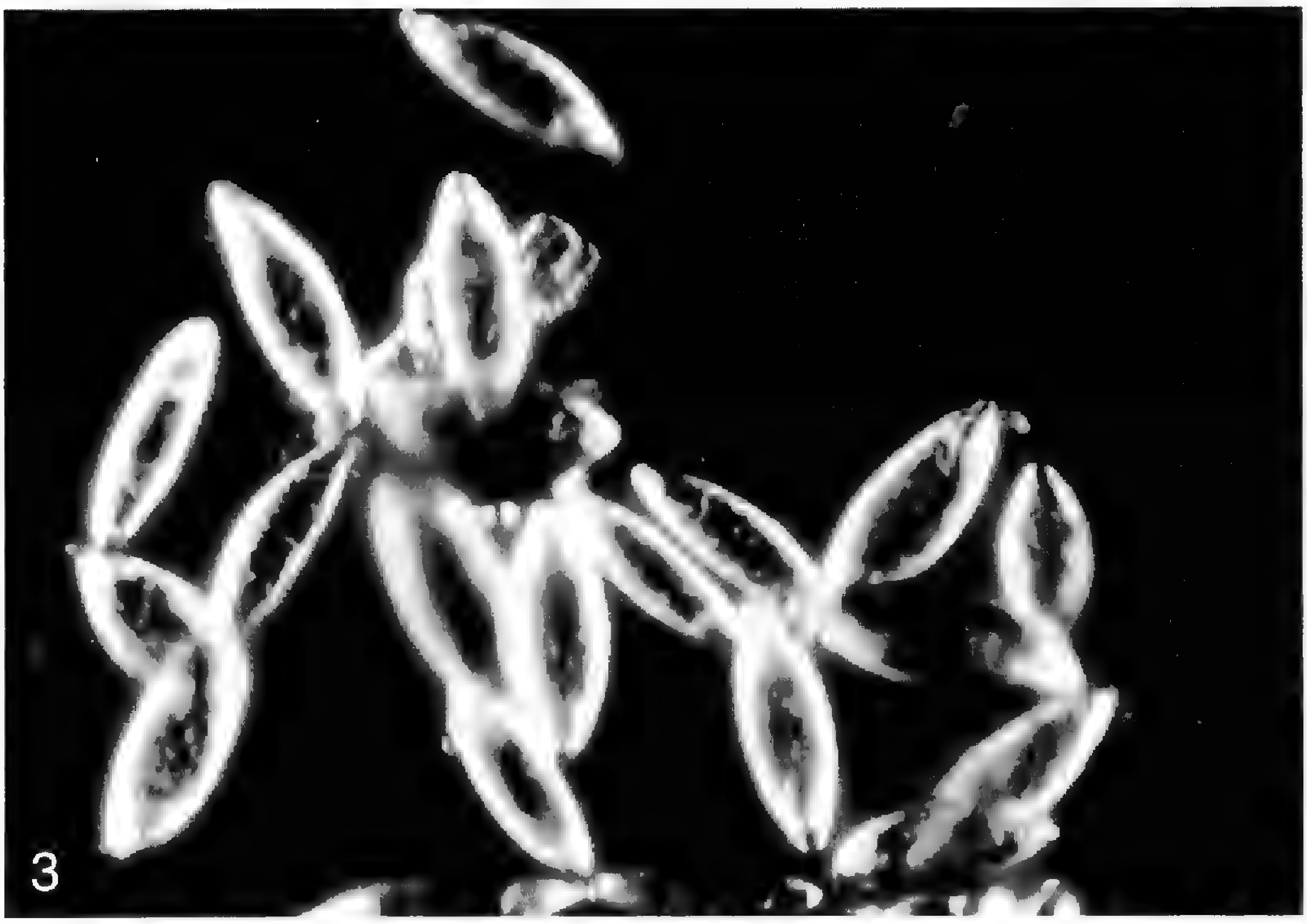
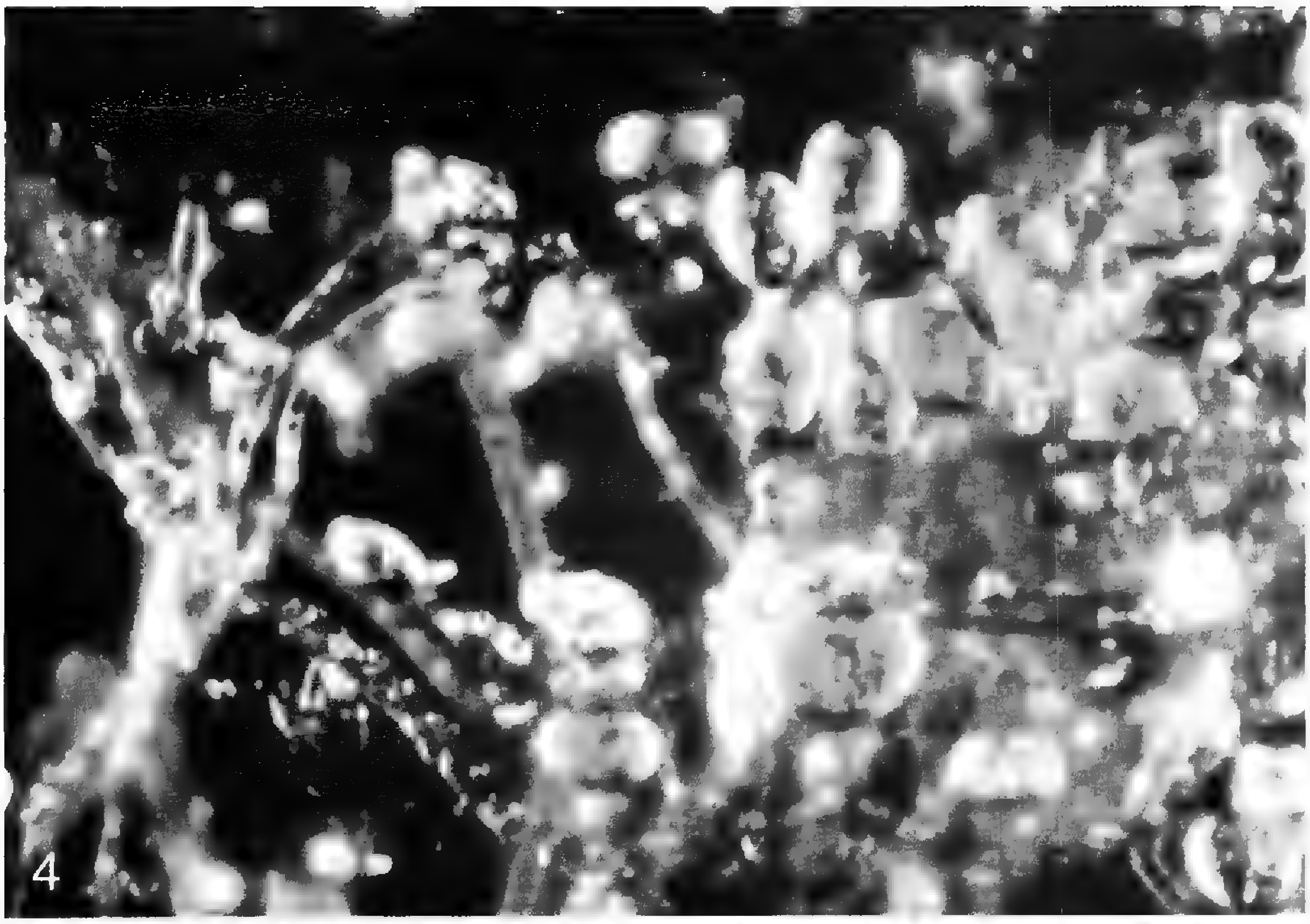


Figure 2. A green population of *Chloromonas* snow algae from Mt. Washington, New Hampshire. In North America, populations of green snow algae are found near the snow surface in shaded areas such as in coniferous forests.

Figure 3. Spindle-shaped asexual resting spores of *Chloromonas* sp.-A green snow algae found in the New York Adirondacks and New England, photographed at 400 × magnification using Nomarski interference contrast optics (DIC). These algae are from a population collected from the Berkshire Hills, Massachusetts.



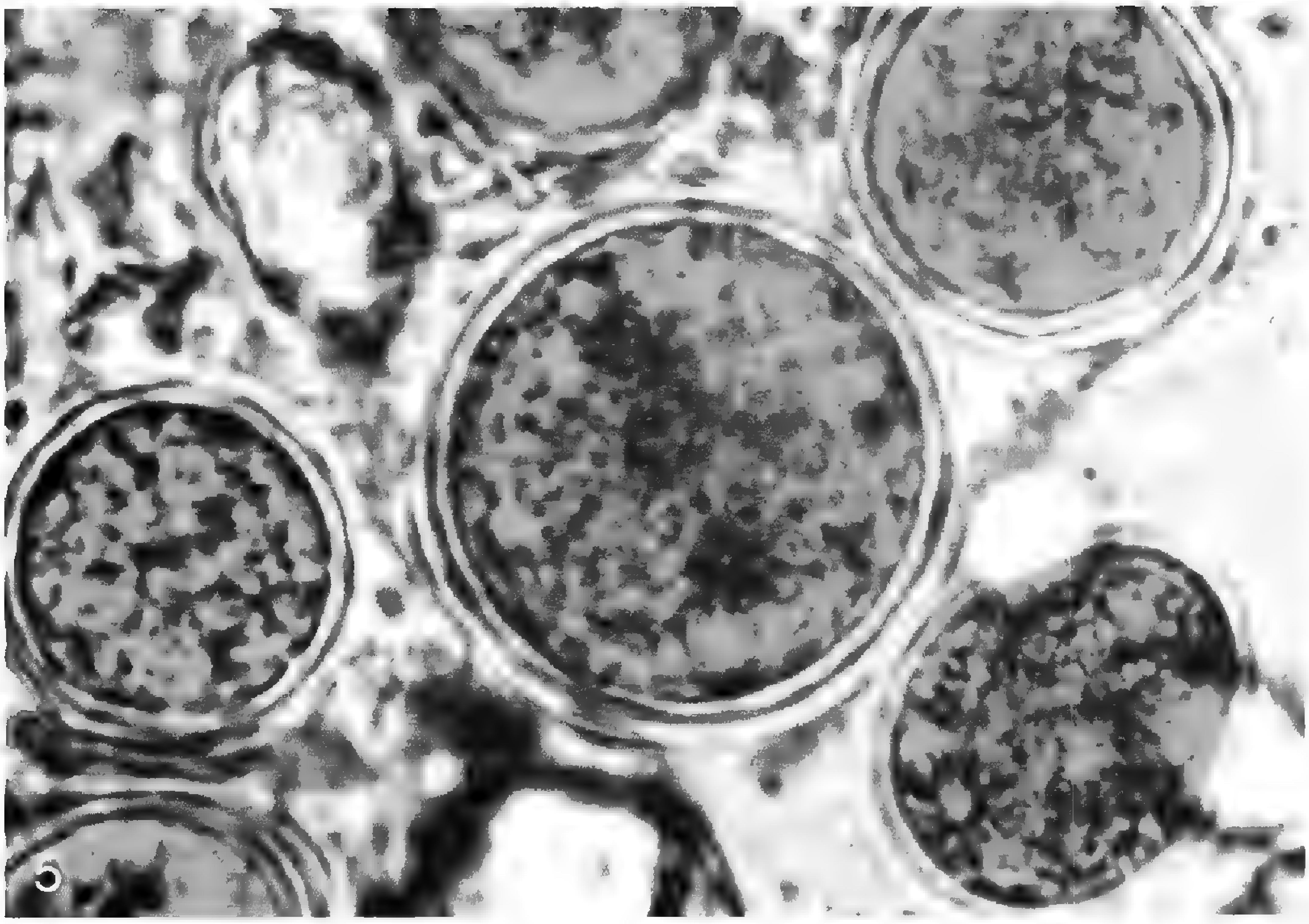


Figure 4. The salmon-orange colored snow alga designated as *Chloromonas* sp.-B (Hoham et al. 1993) collected from the ski area at Killington Peak, Vermont. Filamentous fungi are generally in close proximity to, or in contact with the algae (200 ×).

Figure 5. *Chloromonas* sp.-B snow algal resting spores at 1000 × magnification. Note the differences in cell size, shape, and the 1 μm thick wall that envelopes each cell.

1983). *Chloromonas* sp.-B is generally observed with filamentous fungi and often appears to be in contact with them. However, while fungi and snow algae are generally observed together in snow samples, it is not clear if there is any exchange of nutrients or other symbiosis-like relationship between the two microbial types.

The difference in habitat between species of snow algae, i.e., the green *Chloromonas* sp.-A under forest canopy and the orange pigmented *Chloromonas* sp.-B found in open areas, has previously been observed and attributed to variations in light intensity (Fukushima 1963). *Chloromonas* sp.-B is orange in color due to intracellular carotenoids and other pigments that may serve as photoprotectants toward biologically harmful ultraviolet radiation (Bidigare et al. 1993; Czygan 1970; Thomas and Duval 1995). Indeed, the absorption spectra from solvent extractions of this alga show absorption in the visible wavelength regions typical of chlorophylls and carotenoids, as well as in the ultraviolet regions (Duval 1993).

Chloromonas sp.-B is often observed at the snow surface near shoots of sprouting *Cornus* sp. (dogwood), *Acer pensylvanicum* (striped maple), and *Betula alleghaniensis* (yellow birch), and occasionally it is found at a depth of 5–10 cm, coloring the snow salmon-orange. This species and other snow algae consistently appear at the end of the snow melt period (April–May) in areas where deep snow tends to accumulate from year to year. It is interesting to note that at lower elevations (Tughill Plateau and Georgetown Hill, New York), snow algae have been found in ravines where enough snow accumulates to allow for a deeper snowpack. *Chloromonas* sp.-B generally appears near the snow surface in late April and May, but has been collected as late as July from Tuckerman Ravine, Mt. Washington, New Hampshire. Algal predators such as rotifers and ciliated protists are often observed within snow samples and are members of the snowpack ecosystem that can support several levels of microbial diversity (Hoham and Duval 2000; Hoham et al. 1993).

It is our intention to stimulate the amateur microbial ecologist through the photographs presented here to investigate melting snowpacks, which provide an ephemeral microbial ecosystem within their cold meltwaters.

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RHODORA, Vol. 102, No. 911, pp. 373–379, 2000

NEBC MEETING NEWS

February 2000. Michele Dionne, an aquatic ecologist and Research Director at the Wells National Estuarine Research Reserve in Wells, Maine, spoke on the topic: "Is the tide turning for salt-marsh ecology and restoration in the Gulf of Maine?" The presentation centered on ecological research and habitat restoration efforts at the Wells Reserve, one of 25 federally designated coastal research reserves, and a few other salt-marsh locations in the Gulf of Maine. Describing salt-marshes as "New England's native grasslands," Dr. Dionne highlighted some of their functions and values. Ecologically, they contribute to shoreline anchoring, storm surge buffering, water quality, and habitat for wildlife, fish, and shellfish. For our human society, she noted that there are recreational, commercial, aesthetic, educational, and historical values. In the Gulf of Maine salt-marshes, where mean tide ranges are typically 8–10 ft., there is a close relationship between elevation and vegetational zones, as one might expect. Here one finds *Spartina patens,* salt-marsh hay, dominating high marshes and the taller *S. alterniflora,* which has the capability of exuding salt from specialized cells on its leaf blades, in the low marshes. She described the niches of some of the other plants of the salt-marshes as well, including *Phragmites australis* and *Typha angustifolia,* which occupy the high edges of the salt-marshes and often take over when the hydrologic regime is altered. Dionne described several types of salt-marshes in Maine: (1) back barrier marshes, the typical coastal marsh; (2) fringing marsh, the narrow bands of salt-marsh lining miles of major rivers like the Kennebec and Penobscot, and (3) finger marshes, those found in "drowned valleys" associated with coves and bays.

The oldest salt-marshes in New England are reported to be about 5000 years old. Despite changing sea-levels during this time, they have persisted through accretion of new peat that builds up in response to new sediments brought in by the tides. Dionne emphasized that, conversely, natural events or human activities, such as the construction of roads, beach barriers, jetties, or stream control gates, can interfere with this accretion, causing rapid erosion of salt-marsh habitat. Tidal restriction can lead to such events as subsidence from oxidation of peat, restricted fish passage, less exchange of nutrients and organic matter, water freshening, encroachment by invasive species, and incremental development. The Little River at the Wells Reserve is one of the few rivers and salt-marsh systems that is minimally impacted in the above ways. The Drakes Island marsh system on the southern edge of the Wells Reserve, on the other hand, has been impacted by a number of things including a road built on a berm across the marsh's north end. A water control gate was installed where the Webhannet River went under the road, thus preventing spring tides from entering the marsh from the estuarine lagoon to the east. The gate fell off this structure in 1988, partially restoring the tidal influence. In 1991, scientists began monitoring the changes to the upper marsh (above the gate) where three feet of elevation had been lost from years of abuse. Salt-tolerant plants and marine fish quickly returned to the area, and by 1998, soils were stabilized and a low marsh vegetation dominated by *Spartina alterniflora* was well established in the area. In 1999, *S. patens* was observed colonizing upper edges despite the marsh still being lower than normal. A return to a high marsh is presumed to be many years away yet. In contrast, researchers found a much more rapid restoration of Mill Brook Marsh, located near the mouth of the Squamscott River which flows into Great Bay in Stratham, New Hampshire. It had a somewhat similar history of road impact and gating in 1970 followed by flow restoration in fall 1993. Before restoration, purple loosestrife had become a dominant species in the upstream marsh. Five years after removal of the tide gate and installation of a large culvert, the purple loosestrife was gone and a salt-marsh with three taxa of *Spartina* had been restored.

"Have we stemmed the tide?" Dionne asked rhetorically at the end. Her answer is that we are returning the tide to historical salt-marsh communities in many cases but that many obstacles still exist to maintaining their normal function. There is much concern about development along beaches and upland edges, for instance. Also, there are concerns about predation by the introduced green crab on soft shell clams, an important indigenous species in the marsh ecosystem. It appears that the Wells Reserve is key to research and education on these issues for Gulf of Maine towns where salt-marsh restoration is needed and maintenance is forever.

—PAUL SOMERS, Recording Secretary.

March 2000. The evening's speaker was outgoing President David Conant, whose talk was entitled "The Biology of Tree Ferns." David traced his love of the ferns and field biology to an afternoon foray to New Hampshire's Bear Mountain with mentor Albion Hodgdon. Assaulted by yellow jackets, Hodgdon tumbled one hundred feet, head over heels, down a rocky slope and into the crook of a tree. Fearing the worst, David hurried to Albion's side. Notwithstanding the bites of dozens of yellow jackets, Albion rose to his feet to continue the plant hunt down the mountain. During refreshments at the bottom, David thought, "This is all right!" He happily cast his lot with Albion Hodgdon. A couple of false starts with the ferns of New Hampshire and flora of Sullivan County preceded David's introduction to the tree ferns, and he has been a student of the group since the mid-1970s.

David traced, through the 1980s, the emergence of the use of tools like electrophoresis and analysis of chloroplast DNAs in analyzing relationships among the ferns. Notably, the work of Japanese botanist Haseke has confirmed many of the assumptions of our narrative phylogenies for the ferns with his analysis of the gene for the enzyme (rbcL) that plucks CO_2 from the air to build glucose in the dark reactions of photosynthesis. He confirmed the ancient lineage of primitive ferns like the Osmundaceae, and sorted out the higher leptosporangiate ferns, just as do the narrative phylogenies. As an aside, David said, if we are to recognize many orders of the "younger" flowering plants, this modern work with the ferns underscores abandonment of a single order, Filicales, for all the ferns. For his part, David took his work with the tree fern genus *Alsophila,* begun with Rolla Tryon in 1976, into the modern laboratory. The days of plant collecting with the aid of a converted mail van were followed by collaborations in biochemistry with Gillian Cooper-Driver of Boston University and Gus Dimaggio of Dartmouth College. Analyses of flavonoid pigments and storage proteins were helpful, but not absolutely conclusive in sorting out the tree ferns. Together with Diana Stein of Mount Holyoke College, David moved next to analysis of chloroplast DNAs. David jetted all over the New and Old World tropics to collect the ferns, shipping them back to Diana within two days for grinding. Countless southern blots later, David recounted the horrible experience of trying to make sense of it all, "like trying to put Humpty Dumpty back together again." The two scientists struggled with a number of molecular probes of the collected chloroplast DNAs, settling on ones derived from Christmas ferns to retrieve the clearest set of data.

After years of work, David and Diana produced a fresh picture of the tree ferns as three major groups centered on *Alsophila, Cyathea,* and *Sphaeropteris.* The *Cyathea* clade is not restricted to the New World tropics as previously believed, but linked through geological time to ferns found in Western Queensland and the Pacific. It appears that the Greater Antilles group of *Alsophila* is the most derived of the tree ferns.

David ended his presentation with striking images of hand-prepared sections of fern stems, produced with the help of his students at Lyndon State College. David declared that there is "a lot to learn beyond who they (*sic* the ferns) are!"—a refreshing perspective on teaching and learning, indeed.

April 2000. Dr. Paul Godfrey of the University of Massachusetts at Amherst spoke on "Biodiversity of Medicinal Plants in Northwestern Thailand." Dr. Godfrey has spent the large part of his career investigating aspects of coastal ecology along the Atlantic seaboard. Richard Evans Shultes, who once surprised an NEBC audience by firing a blowgun dart across a crowded hall, inspired Paul's interest in ethnobotany. At this juncture of his introduction, Paul reached for a small bamboo bow and fired its bamboo arrow across the crowded hall. He had our attention.

Paul was asked some years ago by Linda A. Swift of Hartwick College to lend his ecological expertise to an ethnobotanical investigation of plant utilization by an Akha hill tribe village of northwestern Thailand. Thai hill tribes have long used small-scale swidden and crop rotation for maize and rice production. Such swidden-based tropical agriculture is often linked with the loss of biodiversity, though it is critical to the survival of the hill tribes. The long-term studies of forest utilization and plant use around Pakhasukjai Village were designed to measure the impacts of wood gathering, agriculture, medicinal, and spiritual activities on diversity. Drs. Godfrey and Swift expected to find the lowest diversity in disturbed forests close to the village and the highest in undisturbed forests further away. They selected a group of native gingers (Zingiberaceae) to investigate, gathering data on the abundance and distribution of species within three discreet study areas near Pakhasukjai Village in order to evaluate modified importance values and biodiversity indices.

Paul was pleased to find J. F. Maxwell at Chaing Mai University during his first season in northern Thailand. As it turns out, Dr. Maxwell has contributed the largest part of northwest Thai plant specimens to the Harvard University Herbaria during the past several decades. Dr. Maxwell offered his considerable expertise by acquainting Paul and his colleagues with the fine points of collection and identification of the gingers *in situ*. The ethnobotanical team was supported at Pakhasukjai Village by the Hill Area Development Foundation, which provided space and facilities in its rustic center.

The Akha of Pakhasukjai Village are forest dwellers who are spiritually bound to their surroundings. They find both good and bad spirits in the forest. The forests provide both wood and medicines. Paul and his colleagues had great difficulty in learning the uses of medicinal plants, in particular. Two layers of interpretation are needed to get from the native language to Thai, then to English-mediated interviews. Add to the linguistic hurdles the certain possibility of deliberate deception on the part of the shaman, and the team had its work cut out. Ten species of ginger in 7 genera were of particular interest. The list included *Alpinia galanga* (for stomach ache and diarrhea); *Amomum repoense* (for multiple medicinal uses from appetite stimulant to pain reliever); *Boesenbergia rotunda* (similar medicinal uses as *Amomum*); *Costus speciosus* (stimulant, aphrodisiac, or for relief of back pain); *Curcuma longa* (leaf poultice for cuts and bites); *Kaempferia parviflora* (poultice to stop bleeding cuts); and three species of *Zingiber* (for headache, stomach ache, diarrhea, or a stimulant for breast milk production).

Paul devised an ecological sampling plan for three forest sites, each of which had been substantially cleared nearly 50 years earlier. On the first day out, the shaman lead the team by a tortuous and turning path to a very sacred site, the Cemetery Forest. It turned out to be the closest to the village. Diversity of gingers was relatively low here, and greatest within a more heavily exploited site dubbed the Shrine Forest. Several of the gingers appear to respond to changes on the landscape as early successional types. The light and regular disturbance by the Akha may contribute to this increase in overall diversity.

Paul ended his presentation with a personal testimonial. He had learned that a local *Eupatorium* was effective for stanching blood flow. One errant blow of the machete and Paul was able to put the plant to the test. The wound healed nearly overnight.

—Don Hudson, Recording Secretary.

May 2000. Vice President Paul Somers introduced the evening's speaker, Dr. Avril de la Cretaz, of the Department of Natural Resources Conservation at UMass Amherst. She spoke on her doctoral thesis research topic, "Understory Restoration in a Watershed Degraded by Deer Browsing and Fern Invasion," and won the Club's award for "best performance under adverse circumstances" by giving an outstanding summary of her research despite a balky slide projector.

The Quabbin Reservoir is a 120,000-acre tract of land and water of which 64% is administered by the Metropolitan District Commission (MDC) to protect the Metropolitan Boston water supply. Many of the upland areas of the Quabbin, farmland before being incorporated in the watershed protection area, were planted in white or red pine plantations to protect water quality. Deer hunting was banned in the Quabbin from 1940 to 1991 (originally because of fear of sabotage during WWII), resulting in a deer population of 40–60 deer per square mile. This resulted in intensive browsing on understory vegetation, essentially eliminating tree seedling regeneration from large areas of the Quabbin watershed. The MDC is now interested in restoring a natural forested community to the Quabbin. However, large areas of the watershed, including many of the pine plantations, have a dense monoculture of hay-scented fern (*Dennstaedtia punctilobula*) with essentially no tree regeneration, even after the deer population has been substantially reduced. Dr. de la Cretaz investigated the mechanism by which hay-scented fern influences tree regeneration and mechanical means of control that may allow forest managers to restore the forest. Hay-scented fern, although a native, behaves like many exotic invasives in the landscape by creating mono-dominant stands and altering the natural community diversity and dynamics. Although some studies alleged that hay-scented fern dominance was because of allelopathy, more recent work has shown that these ferns are not necessarily allelopathic. The fern's effect on other species seems to be because of competition for resources, particularly space in the thick root mat and light that is blocked by the fern fronds.

Avril also compared the ability of different tree species to become established in hay-scented fern communities. She found that only white pine and black birch were capable of developing into saplings in a dense fern stand, because the leaves of these species develop and expand before the fern fronds expand in the spring and are therefore able to compete for light. White ash and oak seedling leaves expand after the fern and thus are not as competitive.

In the final stage of her research, Dr. de la Cretaz compared three mechanical treatments to control fern growth and promote tree regeneration: root mat removal (''scalping''), mixing root mat and mineral soil (''scarification''), and clipping (mowing). Herbicide treatments are not allowed in the watershed forest. She found that scarification actually increased the growth and dominance of hay-scented fern. Root mat removal resulted in the greatest germination response of tree seedlings, but also graminoid dominance (sedges, especially *Carex debilis,* established in high densities from the soil seed bank in the first two treatments). Clipping, particularly if done repeatedly during the growing season, resulted in the highest tree seed germination and seedling growth and the lowest fern and graminoid dominance. She hypothesized that clipping is the most effective treatment for tree seedlings because there are fewer graminoid competitors and a higher nutrient availability. The root mat of the ferns may interfere with seed germination, but this effect is outweighed by the increased light available without the dense fern frond canopy.

In summary, Avril's studies showed that the lack of tree regeneration is a result of deer browsing following overstory thinning. Browsing eliminates tree seedlings and depletes the seedbank, while increased understory light accelerates the growth rates of existing fern colonies and increases spore production. This results in the dominance of hay-scented fern: the fern's root mat inhibits germination of any remaining seeds, and the fronds block the light and inhibit growth of any seeds that do germinate. In dense fern stands, trees will not regenerate without intervention, and mowing is a promising mechanical treatment that may be effective for understory restoration.

—LISA STANDLEY, Recording Secretary *pro tempore.*

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 2001. This award is made annually to stimulate and encourage botanical research on the New England flora, and to make possible visits to the New England region by those who would not otherwise be able to do so. It is anticipated that two awards will be given, although the actual number and amount of awards will depend on the proposals received.

The award will be given to the graduate student submitting the best research proposal dealing with systematic botany, biosystematics, plant ecology, or plant conservation biology. Papers based on the research funded must acknowledge the NEBC's support. Submission of manuscripts to the Club's journal, *Rhodora,* is strongly encouraged.

Applicants must submit three copies of each of the following: a proposal of no more than three double-spaced pages, a budget, and a curriculum vitae. Two letters in support of the proposed research, one from the student's thesis advisor, should be sent directly to the Awards Committee by sponsors. All materials should be sent to: Awards Committee, The New England Botanical Club, 22 Divinity Avenue, Cambridge, MA 02138–2020. Proposals and supporting letters must be received no later than March 1, 2001. The recipient(s) will be notified by April 30, 2001.

This year the Graduate Awards Committee is pleased to announce two recipients of the Graduate Student Research Awards. Dirk Albach of the Universitat Wien (University of Vienna, Austria) received support for his proposal entitled "Evolution, biogeography, and genetic diversity in *Veronica alpina* L. and related taxa." Also chosen for an award was Michael Booth of Yale University, for his proposal entitled "Material flows across ectomycorrhizal networks and plant diversity in New England forests." For more details on these research proposals and a listing of the awards from 1985 to the present, consult the Club's web page (http://www.herbaria.harvard.edu/nebc/).

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

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FLORAS AND TAXONOMIC TREATMENTS: Specimen citation should be selected critically, especially for common species of broad

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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 102nd 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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RHODORA

Journal of the
New England Botanical Club

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A NEW SPECIES, A NEW COMBINATION, AND NEW SYNONYMY FOR SOUTH AMERICAN *JALTOMATA* (SOLANACEAE)

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ABSTRACT. *Jaltomata hunzikeri,* a rare shrub of the coast of the department of Lima, Peru, is described and shown in a photograph. *Hebecladus sinuosus,* transferred as *J. sinuosa,* is a shrub that is widely distributed in the Andes. *Saracha lobata* and *S. sordideviolacea* are placed in synonymy with *J. dentata.*

Key Words: edible fruit, *Hebecladus, Jaltomata, Saracha,* Solanaceae

In the process of taxonomic revision of the genus *Jaltomata* we have found it necessary to describe a new species, make a new combination, and place two binomials in synonymy with another.

Jaltomata hunzikeri Mione, *sp. nov.* TYPE: PERU. Dept. Lima: Prov. Barranca, 5 km north of Barranca, lomas of Pativilca, 300 m, sandy hillside, 18 Sep 1938, *Stork, Horton, and Vargas C. 9228* (HOLOTYPE: GH; ISOTYPE: G, K, MO). Figure 1.

Planta fruticosa ad 1 m altitudine; axes juvenes, petioli, pedunculi, pedicelli, facies abaxialis calycis villosa, pilis uniserialibus, non ramosis, erectis, apice glandiferentibus; inflorescentia floribus 10 ut maximum; corolla breviter tubulosa, limbo 16–17 mm diametro, quinque lobis triangularibus, alba, annulo azureo prope extremum tubi; stamina 4.8–7 mm longitudine, filamenta villosa secus proximales 45–60 partes per centum longitudinis; stylus 6.0–7.7 mm longitudine.

Figure 1. *Jaltomata hunzikeri* Mione, in flower, *Stork, Horton, and Vargas 9228*, (HOLOTYPE: GH). Photo by S. J. H.

Shrub to 1 m high. Young axes, petioles, peduncles, pedicels, and abaxial face of calyx villous, the hairs uniseriate, unbranched (finger-type), erect and gland-tipped. Young axes with raised longitudinal ridges (an artifact of drying?). Older axes to 1.5 cm in diameter, terete and glabrate. Leaves alternate, often geminate, the blades ovate, to 8 × 5.5 cm, with 3–4 pairs of primary veins, the apex acute, the base somewhat truncate and often oblique, the younger blades densely pubescent, the older sparsely pubescent, the margin dentate or erose-dentate or repand and ciliate with gland-tipped hairs 0.12–0.42 mm long; petioles to 3 cm long. Inflorescences axillary or sometimes arising from branch dichotomies, umbellate, to 10-flowered including buds. Peduncle 4–9 mm long; pedicel 8.6–11.3 mm long. Calyx green at anthesis, stellate, the lobes triangular and 4.0–5.9 mm from pedicel to tip, 1.9–3.2 mm from pedicel to sinus, the margin ciliate with finger hairs 0.3–0.6 mm long, abaxially with both finger hairs 0.3–0.8 mm long and glands 55–70 μm long having multicellular heads and unicellular stalks (illustrated in Mione and Serazo 1999); calyx 10 mm in diameter with fruit (mature?). Corolla short-tubular (the tube not evident after pressing, but mentioned by collectors on label), the limb crateriform or broadly infundibular or rotate, 16–17 mm in diameter, white with blue ring near end of tube, with 5 triangular lobes, 6.2–11.0 mm from flower center to tip of corolla lobe, 4.0–7.3 mm from center to sinus, the margin ciliate with finger hairs 0.1–0.5 mm long. Stamens 4.8–7.0 mm long, the filaments villous on proximal 45–60% of the length, the finger hairs 1.0–1.5 mm long; anthers 1.3–1.5 × 0.7–0.9 mm, some basally sagittate. Pollen grains (stained 30 minutes in "cotton blue") 26.25–31.25 μm in diameter (average 28.5 μm, n = 24). Style and ovary glabrous. Style 6.0–7.7 mm long, 0.1–0.2 mm wide at midlength; stigma capitate, not bilobed, 0.24–0.6 mm wide perpendicular to style, exserted 0–1 mm beyond dehisced anthers. Berry (mature?) 5 mm across, and very likely subspherical and orange or red at maturity.

PARATYPE: **Peru.** Dept. LIMA: Prov. Barranca, 5 km north of Barranca, talus slope of hill rising abruptly from low, narrow, coastal plain, 80 m, 5 Sep 1938, *Morrison and Beetle 9099* (GH).

The specimens (the type and paratype) of this species were treated as *Saracha villosa* (Zuccagni) G. Don by Macbride (1962). We do not agree, based on study of: 1) photos of the type of *S. villosa* (G-DC, F neg. 6880, NY), 2) description of the hairs of the type of *S. villosa* (provided by G), and 3) the translation to English (by N. R. S.) of the Latin description within the protologue of *Atropa villosa* Zuccagni, basionym of *S. villosa.*

Jaltomata hunzikeri is similar to *J. cajacayensis* S. Leiva & Mione and *J. propinqua* (Miers) Mione & M. Nee, of the departments of Ancash and Lima, Peru, respectively; all three shrubs bear gland-tipped hairs and have a short-tubular corolla with a much broader limb. *Jaltomata hunzikeri* lacks corolla lobules, the stigma is at approximately the same height as the dehisced anthers, and grows at 80–300 m in the fog-dependent, coastal lomas habitat. The other two species have corolla lobules alternating with the larger lobes, have stigmas exserted several mm beyond the anthers, and grow above 1,800 m (Mione et al. 2000).

The specific epithet was chosen to honor Armando T. Hunziker, eminent Solanaceae taxonomist.

Jaltomata sinuosa (Miers) Mione, *comb. nov.*

Hebecladus sinuosus Miers, London J. Bot. 7: 352. 1848. Miers, Ill. S. Amer. Pl. 1: 151–2. 1850. TYPE: PERU. Dept. Amazonas: Chachapoyas, *Mathews s.n.* (HOLOTYPE: BM; ISOTYPE: G two sheets, K). *Saracha sinuosa* (Miers) Bitter, Repert. Spec. Nov. Regni Veg. 18: 101. 1922.

Saracha glandulosa Miers, Ann. Mag. Nat. Hist., ser. 2, 3: 450. 1849. TYPE: COLOMBIA. La Peña: Bogota, *Goudot s.n.* (HOLOTYPE: P, F neg. 39250; ISOTYPE: F). *Witheringia glandulosa* (Miers) Miers, Ann. Mag. Nat. Hist., ser. 2, 11: 92. 1853. Miers, Ill. S. Amer. Pl. 2: 20. 1857, t. 39a. *Jaltomata glandulosa* (Miers) Castillo & R. E. Schult., Rhodora 88: 292. 1986.

Saracha vestita Miers, Ann. Mag. Nat. Hist., ser. 2, 3: 449. 1849. TYPE: ECUADOR. "Minasurcu prope Quito" on types ("Minashuaicu" is the Defense Mapping Agency [1987] spelling), *Hartweg 1292* (HOLOTYPE: K; ISOTYPE: LD). *Witheringia vestita* (Miers) Miers, Ann. Mag. Nat. Hist., ser. 2, 11: 92. 1853. *Jaltomata vestita* (Miers) Castillo & R. E. Schult., Rhodora 88: 292. 1986.

Jaltomata whalenii S. Knapp, T. Mione & Sagást., Brittonia 43: 181. 1991. TYPE: PERU, Dept. Cajamarca: Prov. Contumazá, lecho de Río San Benito, alrededores de San Benito, 1300 m, *Sagástegui, Leiva, and Sagástegui 12471* (HOLOTYPE: HUT; ISOTYPES: IBE, MO, NY).

Jaltomata sinuosa is superficially similar to *J. sanctae-martae* (Bitter) Benítez of Colombia and Venezuela. Both species are shrubs, are villous with gland-tipped finger hairs, and bear rotate corollas. *Jaltomata sinuosa* has 3–5 flowers per inflorescence, flowers 2.5–3.8 cm in diameter, and orange berries while *J. sanctae-martae* has up to 10 flowers per inflorescence, flowers to 1.8 cm in diameter, and according to Benítez de Rojas (1980), red berries.

DISTRIBUTION, HABITAT, USES, LOCAL NAMES. *Jaltomata sinuosa* occurs in disturbed habitats in the Andes from western Venezuela to Bolivia. The fruits are eaten (*Dillon et al. 6193*; *Leiva et al. 2042*; *Mione et al. 672*) and the local names include "tomatillo" (*Hawkes and García-Barriga 100*) and "uvilla de monte" (*Mione and McQueen 468, 469*).

REPRESENTATIVE SPECIMENS: **Venezuela.** MÉRIDA: Vicinity of El Royal, near La Toma, 2440 m, 4 Nov 1978, *Luteyn et al. 6181* (MO, NY).

Colombia. CUNDINAMARCA: Cordillera Oriental, Monserrate, Valle del Río San Francisco, 2700–2900 m, 18 Jun 1948, *Hawkes and García-Barriga 100* (K, US); Cordillera Oriental, western slopes, 20 km from Bogotá, via Salto de Tequendama-El Colegio road, 2470 m, 13 Jan 1976, *Luteyn et al. 4817* (K, MO, NY).

Ecuador. IMBABURA: on road from Otavalo to Selva Alegre, 29.4 km from junction of Panamerican Hwy, 2900 m, 28 May 1991, *Spooner et al. 5113* (CONN). PICHINCHA: canton Quito, Parroquia Nanegalito, quebrada Santa Rosa, steep slopes SW of Río Pichán, 2000 m, 12 Jan 1995, *Webster and Rhode 31234* (DAV). TUNGURAHUA: vicinity of Ambato, Feb 1919, *Pachano 138* (GH, NY, US). CHIMBORAZO: highway to Pallatanga from just S of Cajabamba, 32.1 km in from Panamerican Hwy, 3000 m, 10 Jan 1990, *Mione and McQueen 468, 469* (CONN, NY). CAÑAR: outskirts of Asorgues, 2897 m, 27 Jun 1939, *Balls B7327* (K, US). LOJA: road to La Toma on slopes of Cerro Villonaco, ca. 10 km W of Loja, 2440 m, 7 Mar 1965, *Knight 583* (WIS).

Peru. AMAZONAS: 2 kms along road W of Chachapoyas, 2195 m, 13 Jan 1983, *King and Bishop 9179* (G, K, MO, US); Mendoza, 1400–1500 m, 19 Aug 1963, *Woytkowski 8153* (MO, NY). PIURA: Huancabamba, alrededores de Sapalache, 2400 m, 9 Jun 1997, *Leiva et al. 2042* (CONN, HAO); Ayabaca, alrededor de Yacupampa (Ayabaca–Cuyas), 2702 m, 21 Sep 1996, *Leiva et al. 1867* (CONN, HAO). CAJAMARCA: Cutervo, garden in village of San Andrés de Cutervo, 2050 m, 6 Nov 1990, *Dillon et al. 6193* (F); Chota, 6° 33′ 54″ S, 78° 38′ 42″ W, 2300 m, 19 Jun 1999, *Leiva 2374* and *Mione 672* (CONN, HAO); Santa Cruz, ruta Chorro Blanco–Monteseco, 1750 m, 21 Jan 1996, *Leiva et al. 1756* (HAO); Hualgayoc, entre Hualgayoc y Bambamarca, 2850 m, 11 Mar 1994, *Sánchez 6868* (F); Celendín, desvío a Sorochuco, bajando Tahuan, 2900 m, 27 Dec 1988, *Sánchez 4943* (F); San Miguel, 7° 00′ 02″ S, 78° 50′ 41″ W, 18 Jun 1999, *Leiva 2369* and *Mione 668* (CONN, HAO); Contumazá, alrededores de San Benito, 1300 m, 28 Mar 1985, *Sagastegui and Leiva 12548* (BH, NY). LAMBAYEQUE: Ferreñafe, Cañaris, 2600 m, 24 Jun 1989, *Llatas 2486* (F). CUZCO: Acomayo, 2900 m, Feb 1937, *Vargas 201* (F, GH, MO); Machu Picchu, 2134 m, 2 Feb 1938, *Stafford 1224* (K). APURÍMAC: Grau, Mancahuara, Oropeza Valley, 3000 m, 23 Jan 1939 *Vargas 9798* (G, K).

Bolivia. LA PAZ: Prov. Bautista Saavadra, Charazani, 20 kms hacia Apolo, 2400 m, 5 Aug 1985, *Beck 11396* (NY); Prov. Larecaja, Sorata, Challapampa, ca. 2600 m, Jul–Aug 1863, *Mandon 429* (G two sheets).

The type specimens of *Saracha lobata* Bitter and *S. sordideviolacea* Bitter were both collected in Peru, department of Lima, province of Huarochirí, near Matucana. Both types were destroyed in Berlin; only photos are available for study. It was evident that these species belong to the genus *Jaltomata,* but given only photos of the types we were not able to decide whether these should be placed in synonymy with *Jaltomata* species, or transferred to *Jaltomata.* To solve this problem T. M., S. L. G., and L. Yacher visited Matucana in 1998 and collected specimens that match the photos. In the same region, at the type locality of *J. dentata* (R. & P.) Benítez, we collected conspecific specimens we identified as *J. dentata.* We conclude that *S. lobata* and *S. sordideviolacea* are synonyms of *J. dentata.*

Jaltomata dentata (R. & P.) Benítez, Rev. Fac. Agron. (Maracay), 9(1): 91. 1976. Basionym: *Saracha dentata* R. & P., Fl. Peruv. 2: 43. 1797, t. 179b. *Atropa dentata* (R. & P.) Spreng., Syst. Veg. 1: 699. 1815. *Bellina dentata* (R. & P.) Roem. & Schult., Syst. Veg. 4: 689. 1819. *Witheringia dentata* (R. & P.) Miers, Ann. Mag. Nat. Hist., ser. 2, 11: 92. 1853. TYPE: PERU. Dept. Lima: Prov. Canta, Obrajillo, 2732 m, *Ruiz s.n.* (LECTOTYPE: MA, not seen; ISOTYPE: G).

Saracha lobata Bitter, Repert. Spec. Nov. Regni Veg. 18: 103. 1922. TYPE: PERU. Lima–Oroya road, southwest of Matucana, 3,000 m, *Weberbauer 206* (HOLOTYPE: B, destroyed, F neg. 2553).

Saracha sordideviolacea Bitter, Repert. Spec. Nov. Regni Veg. 18: 104. 1922. TYPE. PERU. Lima–Oroya road, Matucana, 2,600 m, *Weberbauer 5258* (HOLOTYPE: B, destroyed, F neg. 2556).

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BIRDS, POLLINATION RELIABILITY, AND GREEN FLOWERS IN AN ENDEMIC ISLAND SHRUB, *PAVONIA BAHAMENSIS* (MALVACEAE)

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ABSTRACT. *Pavonia bahamensis* (Malvaceae) is a shrub that is endemic to the southeastern Bahama Islands. Here I present the first detailed description of its pollination biology. On San Salvador Island, *P. bahamensis* appears to be pollinated exclusively by two bird species, Bananaquits and Bahama Woodstars. This pollination dependence was dramatically demonstrated in one season when hurricanes decimated these bird populations, and pollen deposition and fruit set of *P. bahamensis* was significantly reduced. However, the lack of pollination limitation of fruit set during two other flowering seasons and the relatively low pollen/ovule ratio (607) suggests that pollination of *P. bahamensis* by these birds is generally reliable. Flowers show traits typical for a bird pollination syndrome, except that the corolla is green. Flowers are held horizontally on the shrub, rather than vertically, suggesting that passerine birds (Bananaquits) rather than hummingbirds have been the most effective pollinator and major selective agent for the floral traits in this species. Individual Bahama Woodstars are ineffective pollinators, depositing few or no pollen grains on stigmas per visit; however, they maintained pollination in one season when visits by Bananaquits were infrequent, and they contributed to the reliability of pollination for this endemic species.

Key Words: bird pollination, breeding system, endemic plant pollination, flowering phenology, fruit set, green flowers, hummingbird pollination, island pollination, nectar production, passerine pollination, pollen/ovule ratio, pollen deposition, pollination limitation, pollination syndrome

Islands typically have fewer pollinator species than mainlands (Barrett 1996; Carlquist 1974; Elmqvist et al. 1992; Feinsinger et al. 1982; Inoue 1993; Spears 1987; Woodell 1979). As a consequence, many island plant species are generalized for pollination and have inconspicuous flowers (Carlquist 1974). Plants that are specialized for a pollinator type, such as hummingbirds, can be especially vulnerable to pollination limitation if only one or a few pollinating species are present (Rathcke 1988a, 1988b, 1998; Rathcke and Jules 1993; Wolf and Stiles 1989), unless those pollinators are abundant and predictable. Visitation to flowers has been demonstrated to be lower on islands for some species (Feinsinger et al. 1982; Spears 1987), but pollination limitation has not been measured. Many island plant species reduce or avoid pollination limitation by auto-pollination and selfing (Baker 1955; Barrett 1996; Carlquist 1974).

If plants have only a few, similar pollinating species, they could experience stronger, directional selection for a specific pollination syndrome (i.e., a suite of predictable floral traits adapted to the most effective pollinator type, such as butterflies or birds; Faegri and van der Pijl 1979; Stebbins 1970). For example, hummingbird-pollinated flowers in western North America are typically red and tubular with large amounts of nectar and no fragrance (Brown and Kodric-Brown 1979; Grant and Grant 1976). Recently, the concept of the pollination syndrome has been criticized for being limited and misleading because flowering species often have many different pollinators that vary over space and time (Herrera 1996; Ollerton 1996; Waser et al.1996). Studies show that flowers categorized in one pollination syndrome may be pollinated effectively by other types of pollinators (Baker et al. 1971; Feinsinger 1987; Schemske 1983; Schemske and Horvitz 1984; Waser 1983). As a consequence, selection on floral traits may be weak or inconsistent (Ollerton 1996; Waser et al. 1996). In contrast, an island plant with few pollinator species may be more likely to exhibit a floral syndrome that accurately predicts its pollinator type. Species on islands have been found to evolve different pollination syndromes from their mainland ancestors (Carlquist 1974; Inoue 1993), but the reliability of pollination and pollination limitation has seldom been quantified for island species.

In this study I present the first detailed description of the pollination and reproductive biology of an endemic island shrub, *Pavonia bahamensis* Hitchc. (Malvaceae; Bahama swamp-bush), growing on San Salvador Island, Bahamas. The pollination of *P. bahamensis* has only recently been described in brief reports, and it appears to be pollinated exclusively by birds on San Salvador (Rathcke 1998, 2000; Rathcke et al. 1996). I describe the breeding system and the floral traits of *P. bahamensis.* I compare the pollen/ovule ratio of *P. bahamensis* to the ratios categorized by Cruden (1977) for plants with different breeding systems and different probabilities of pollination. I compare the floral traits with those predicted for a classic bird pollination syndrome, and I discuss the traits associated with passerine versus hummingbird pollination.

Reliability of pollination may be especially crucial for this endemic island species. *Pavonia bahamensis* grows only on the southeastern islands of the Bahamas in limited habitats near mangroves (Correll and Correll 1982). Populations tend to be relatively small and isolated, which may make this species especially sensitive to changes in pollinator species or behavior (Rathcke 1998, 2000; Rathcke and Jules 1993). In general, species on islands may be vulnerable to environmental changes such as global warming, habitat destruction, or introduced species (Loope and Mueller-Dombois 1989; but see Simberloff 1995). Species on small islands such as San Salvador, which is only 150 km^2, may be especially vulnerable to environmental changes (Eshbaugh and Wilson 1996). Therefore, documentation of the pollination biology and the reliability of pollination may be valuable in providing baseline data for future comparisons, as was found in Hawaii for lobeliad plant species after the extinction of the Hawaiian Honeycreeper (Smith et al. 1995).

STUDY SPECIES

Pavonia is in the family Malvaceae (the mallow family), which has about 1800 species throughout the world (Fryxell 1999). *Pavonia* is the largest genus in the tribe Malvavisceae and has an estimated 100 to over 200 species that are mostly subtropical and tropical (Fryxell 1999). The species are most diverse in South America, but species are also found in Africa and other parts of the Old World and in the West Indies, Central America, and Mexico, reaching the southern United States (Fryxell 1999; Howard 1989).

Pavonia bahamensis is endemic to the Bahamas and is found only on the southeastern islands (i.e., San Salvador, Long Cay, Crooked Island, Acklins Islands, and the Turks and Caicos; Correll and Correll 1982). The northernmost limit is San Salvador Island. *Pavonia bahamensis* was first described by Hitchcock in 1893 from a specimen collected in 1890 on Fortune Island (now called Long Cay) in the Bahamas (Hitchcock 1893). It is a shrub or small tree that grows in rocky coastal thickets (Correll and Correll 1982) and inland adjacent to mangroves (Rathcke et al. 1996; Smith 1993). Its pollination and reproductive biology have been only recently briefly described (Rathcke 1998; Rathcke et al. 1996). Little is known about the pollination biology of any *Pavonia* species (Fryxell 1999).

SAN SALVADOR ISLAND

San Salvador is one of the easternmost islands in the Bahama Archipelago (24°05′N, 74°30′W; Shaklee 1996), and it lies about 600 km east southeast of Miami, Florida and 340 km north of Cuba (Smith 1993). San Salvador is a low, carbonate island, about 19 km long and 10 km wide (Smith 1993). Although many of the Bahama islands have been isolated and reconnected with the fall and rise of the ocean during the glacials and interglacials of the Pleistocene (Sealey 1994), San Salvador has remained separated by a deep ocean trench (Carew and Mylroie 1997).

Total annual mean rainfall on San Salvador is 1007 mm (Shaklee 1996), with a rainy season from August to November (the hurricane season) and a lesser rainy season in May and June (Smith 1993). Annual temperature variation is 6°C (Shaklee 1996) with the coolest months averaging 22°C (January–February) and the warmest months averaging 28°C (July–August; Shaklee 1996). The major vegetation of San Salvador is a scrubland or coppice (Smith 1993). *Pavonia bahamensis* grows in a zone between the scrubland and the mangroves that line the inland hypersaline lakes and the tidal basin of Pigeon Creek (Smith 1993). San Salvador has about 440 species of vascular plants that are native or naturalized, and 6–8% of these species are endemic to the Bahamas (Smith 1993).

MATERIALS AND METHODS

I studied *Pavonia bahamensis* near the Bahamian Field Station at the northeastern end of San Salvador Island. Most data were collected on shrubs growing adjacent to mangroves on the southern edge of Reckley Hill Pond about 500 m southeast of the field station. Most of the flowering shrubs along the path are permanently tagged and studied. These shrubs included most of the local population in this area. Studies were done during three winter flowering seasons (December–January) during the following dates: December 23, 1994 to January 2, 1995; December 17, 1995 to January 4, 1996; and December 17, 1996 to January 5, 1997.

This period encompasses the major flowering period on San Salvador.

All animals observed visiting flowers of *Pavonia bahamensis* were recorded throughout each study period over three winter flowering seasons. I typically spent 2–6 hours a day in the local site during most days for the entire research visit. Flower dimensions, such as corolla length and stigma–anther distances, were measured in the field using a metric ruler. Stigma–anther distances were measured from the bottom edge of the lowest lobe of a stigma to the upper surface of the nearest anther. The age or developmental stage of each flower was recorded to determine if measurements changed over time. Individual flower phenology was documented by marking and following flowers daily over their life span, and their developmental stages were categorized. Both unbagged, naturally-pollinated flowers and bagged, unpollinated flowers were observed to determine if pollination-induced floral senescence occurred.

The flowering phenology of shrubs was quantified by counting the numbers of open flowers per day per shrub. Total fruit set per shrub was censused in June 1995 by counting fruit or enlarged, dried peduncles remaining on each shrub. Seeds (mericarps) were counted in fruits that had not dehisced. Ovaries that were developing one week after pollination typically matured fruit. Therefore, fruit set data are based on ovary development after a minimum of one week. Ambiguous cases have been excluded, so estimates of fruit set are conservative. A flower can produce a maximum of five seeds, and most fruits sampled had five seeds ($\bar{x}$ = 4.6, SD = 0.62, n = 25 fruits; 4 plants). Therefore, most of the variation in seed production was due to fruit set, and those values are reported here.

Nectar production reported here is based on the amount of nectar in open flowers (standing crop) in 1996/97, because pollinator visitation was so rare that nectar was seldom removed. These nectar volume values are similar or even higher than those recorded previously for bagged flowers (Rathcke 1998; Rathcke et al. 1996). Measurements were not included if nectar had overflowed the corolla. Nectar removals did not appear to stimulate nectar production. To determine if nectar could be resorbed, nectar was also measured in bagged flowers, which never had nectar removed until the end of their floral life (day 3 or 4). Sugar concentrations of nectar were measured using a Bellingham refractometer. Sugar concentrations are estimated as sucrose equivalents and calculated from Brix values according to Bolten et al. (1979).

To determine the breeding system, large flower buds were tagged and given one of the following four pollination treatments: 1) bagged with no subsequent hand-pollination, 2) bagged with self-pollen added, 3) open and augmented with cross-pollen from at least two other individual shrubs, and 4) open and exposed for natural pollination. The pollen-ovule ratio was calculated based on the average number of anthers and the average number of pollen grains per anther. Pollen numbers in upper and lower anthers were measured but were not significantly different.

Pollination limitation of fruit set was tested by augmenting flowers with cross-pollen from at least two other shrubs and by comparing this subsequent fruit set with the fruit set of naturally pollinated flowers. Results of the pollination treatments are reported in detail in Rathcke (2000). Pollination limitation (PL) was estimated using a relative index based on fruit sets (FS—fruit per flower) of pollen-augmented flowers (P+) and naturally pollinated flowers (NP) using the following equation:

$$\%\mathrm{PL} = 100\,\frac{(\%\mathrm{FS\ of\ P+}) - (\%\mathrm{FS\ of\ NP})}{(\%\mathrm{FS\ of\ P+})}$$

If the percentages of fruit set of naturally pollinated flowers and augmented flowers were equal, then PL = 0%. If fruit set was zero for naturally-pollinated flowers and 100% for pollen-augmented flowers, then % PL would equal 100% (Rathcke 2000).

The number of pollen grains necessary for maximum fruit set was determined by comparing fruit set in bagged flowers that had a known number of pollen grains deposited by hand on the stigmas. Cross-pollen from at least two other plants was used for each flower. Pollen grains deposited by pollinators on exposed stigmas by the end of floral life were counted in the field using a 10× hand lens.

The effectiveness per flower visit of Bahama Woodstars was measured by counting the number of pollen grains deposited per individual visit to virgin flowers in 1995. Because overall pollinator effectiveness is determined by the frequency of visits as well as by the amount of pollen transferred by a single visit, overall effectiveness of the two bird pollinators was also based on average pollen loads on stigmas and pollination limitation of fruit set over the three years.

Statistical analyses were done using SYSTAT ver. 5.01. Nonparametric tests (Mann-Whitney U or Kruskal-Wallis tests) were used due to small sample sizes and because the data were nonnormally distributed. These tests are conservative. Sample sizes were based on the averages per plant unless otherwise noted, but the total number of flowers is also shown for each sample. Most flowers in the population were tagged and studied, so the data nearly comprise the entire available flower population.

RESULTS

Pollinators. During three winter flowering periods, two bird species were the only major pollinators seen visiting *Pavonia bahamensis* flowers: Bananaquits (*Coereba flaveola*; Emberizidae, Coerebinae), also called the Bahama Honeycreeper, and Bahama Woodstars (*Calliphlox evelynae*; Trochilidae; Rathcke 1998). Bananaquits are resident birds and are common flower visitors to many plants (White 1991). The Bahama Woodstar is the only hummingbird on San Salvador, and it is also a resident (White 1991). I observed a single foraging bout by a Bahama Mockingbird (*Mimus gundlachii*; Mimidae) in January 1997. I saw a single visit by a wasp in 1996, but it visited between the petals to collect nectar and did not effect pollination.

Flower visitation. Flower visitation by bird pollinators decreased greatly between 1994/95 and 1996/97. In 1994/95, Bananaquits were the most common visitors to *Pavonia bahamensis* flowers. They were in small flocks of 5–7 birds and appeared to remain in the local area, visiting flowers continuously throughout every day during 10 research days in 1994/95. Bahama Woodstars were seen visiting flowers several times each day. In 1995/96, Bananaquits were infrequently seen or heard in the site, but Bahama Woodstars appeared to visit about as frequently as in 1994/95. In 1996/97 after the severe Hurricane Lili, I never observed either Bananaquits or Bahama Woodstars visiting flowers (see also Rathcke 1998, 2000).

Description of flowers and fruits. Because of the apparent specialization for bird pollination, I compared the observed floral

Table 1. Floral traits of *Pavonia bahamensis* on San Salvador Island, Bahamas, compared to those considered typical for a bird-pollination syndrome, including passerine vs. hummingbird pollinators (based on Howe and Westley 1988 and see discussion in text); * denotes non-matching traits. Table modified from Rathcke 2000.

	"Typical" Bird Flower	*P. bahamensis*
Corolla		
Color	*vivid; red	*green; yellow anthers
Odor	none	none
Shape	tubular corolla	tubelike corolla, 18.1 mm
Orientation	horizontal (passerine) *vertical (hummingbird)	horizontal
Anthesis	diurnal	diurnal
Phenology	steady-state	seasonal steady-state
Nectar	ample	ample (>100 μl/flw/day)
Concentration	20% sucrose	20% sucrose
Volume	>100 μl/flw/day	>100 μl/flw/day
Secretion	continuous	continuous

traits of *Pavonia bahamensis* with those predicted for a bird pollination syndrome (based on Howe and Westley 1988; Table 1; see Figure 1). In contrast to the classic bird pollination syndrome, the corolla and calyx of these flowers are green (see also Correll and Correll 1982) and blend into the leaves, but the exserted anthers with yellow pollen are highly visible (Figure 1). Other traits appear to fit a bird pollination syndrome. Flowers have no detectable odor. Flowers have five separate petals joined to the staminal column. The calyx and corolla form a cup that retains large amounts of nectar (Table 1). Although the petals are not fused, they remain somewhat closed and form a tubelike corolla that was 18.1 mm (SD = 1.74, n = 12 plants; 50 flowers) from the edge of the corolla to the base for flowers measured in this study. The average total length of the flower from the base to the upper surface of the exserted stigma at maximum exsertion was 31.1 mm (SD = 3.15, n = 11 plants; 42 flowers). Correll and Correll (1982) reported that petals were about 2 cm long and the stamen column was 3 cm or more.

Flowers are perfect. The style typically had 10 stigmas on short branches (n = 5 plants; 5 flowers). Anthers are located on the stamen column that surrounds the style, and flowers I observed had an average of 41 anthers (SD = 0.19, n = 14 plants; 26 flowers). On average, each anther contained 74 pollen grains (SD

Figure 1. Flower of *Pavonia bahamensis* on San Salvador Island, Bahamas.

= 17.5, n = 7 plants; 13 flowers, 24 anthers). The number of pollen grains per anther did not vary significantly with location on the stamen column (upper versus lower). Although the anthers encircle the stamen column, the filaments on the underside of the column curve upward causing the anthers to be arranged on the upper side of the stamen column (Figure 1). This arrangement of the anthers probably ensures more effective transfer of pollen to the body of a visiting bird (Figure 1).

Flowers exhibit herkogamy (spatial separation of male and female parts). On average, for the flowers I sampled, the uppermost anther was separated from the nearest stigma lobe by 4.6 mm (SD = 1.88, range = 1–10 mm, n = 8 plants; 85 flowers). However, occasionally flowers showed distances of 1 mm or less (2% of flowers, n = 85). Even in this case, however, the few pollen grains that could be transferred would not be sufficient alone to promote fruit set where usually around 20 grains are needed (see below). Pollen grains are large, spiny, and sticky and are not easily moved by wind or by other movements. Typically pollen must be transferred by a visitor.

Flowers are solitary and are displayed singly on branches (see also Correll and Correll 1982). The flowers are oriented horizontally or at a slight upward angle (Figure 1).

Fruits (schizocarps) are dry, and the mericarps (each with one seed) separate for dispersal. Each fruit has a maximum of five mericarps. Most intact mature fruits had 4 or 5 seeds ($\bar{x}$ = 4.6, SD = 0.62, n = 25 fruits on 4 plants). No mature fruits had 1 or 2 seeds and only 6% had 3 seeds. Total fruit production censused in June 1995 ranged from 0–44 fruits per shrub ($\bar{x}$ = 16, SD = 16.8, n = 8 plants; 130 fruits). Based on these averages, each shrub produced 74 seeds in June 1995. I never saw any evidence of pre-dispersal seed predation. Fruits have spongy tissue and can float for two weeks or more in the lab in fresh water.

Individual flower phenology. Flowers open throughout the day, and stigmas are receptive for 2–3 days. Flowers are partially protogynous (i.e., the stigma is receptive before the anthers dehisce and remains receptive until all the anthers have dehisced). Stages of flower development are described below (based on 15 flowers on 5 plants; see also Rathcke et al. 1996). Day 1 (Stage 1): The stigma emerges through the closed corolla and gradually the stigma lobes open and spread. Flowers are occasionally visited at this point and may have pollen deposited on the stigma. Next, the corolla begins to open, the stigmas become exserted beyond the corolla to their maximum length and the many anthers on the upper half of the style sheath begin to emerge beyond the corolla. Day 1–2 (Stage 2): The upper anthers begin to dehisce. Day 2–3 (Stage 3): The lower anthers begin to dehisce. Later, the stigma lobes begin to contract and move close together. Day 3–4 (Stage 4): All anthers are dehisced, the stigma lobes contract, the style starts to retract into the corolla, and the corolla begins to close. The stigma remains exserted beyond the corolla. Day 4–5: The corolla and the stamen column fall. The style becomes withered and brown. Subsequently the ovary either stays green and begins to enlarge in size, or the ovary, sepals, and calyx turn yellow and abscise, usually within about 10 days. Pollination does not induce floral senescence.

Flowering and fruiting phenologies. The major flowering of *Pavonia bahamensis* occurred in winter, November through January, on San Salvador. Other flowering during the year ap-

Table 2. Nectar production of different flower stages of *Pavonia bahamensis* in December 1996. Microliters of nectar per flower per day and mg sucrose-equivalents per ml are shown with means and standard deviations. n = number of flowers from 7 tagged plants.

Stage (days of age)	n	Secretion Rate µl/day	Sugar Concentration mg/ml sucrose
Stage 1 (day 1)	19	72 ± 90.9	1.30 ± 1.646
Stage 2 (day 1–2)	6	162 ± 129.9	3.00 ± 2.665
Stage 3 (day 2–3)	7	184 ± 82.5	3.35 ± 1.495
Stage 4 (day 3–4)	4	33 ± 35.7	0.66 ± 0.731

peared to be minor and I only saw a few flowers at other times. However, Correll and Correll (1982) have reported flowering throughout the year in the Bahamas.

Flowering showed a seasonal steady-state pattern (after Gentry 1974). Most individual shrubs had only 1–3 flowers open each day during the major flowering season ($\bar{x}$ = 2.3, SD = 2.42, n = 3 years; 9 plants). Flowering of each shrub lasted for more than a month, and new buds were produced as flowering continued.

Fruits developed from flowers produced in November–February were dispersing mericarps 5–6 months later in June.

Nectar production. Nectar was relatively dilute, with average sucrose concentration equal to 19.5% or 0.195 mg/ml (SD = 0.048, n = 7 plants; 43 flowers; Brix = 18.1 ± 4.1; measured in winter 1996/97). Nectar tasted sweet and had no other noticeable flavor.

Nectar production was highest for Stage 3 (day 2–3) flowers when it averaged 184 µl per flower (Table 2). Average lifetime nectar production per flower was 458 µl. Nectar production was continuous throughout the day and accumulated over the night to high levels in the morning. Nectar in old flowers could be resorbed. Bagged flowers in which nectar was never collected each had no nectar or less than one microliter of nectar each (6 plants; 11 flowers) at the end of floral life. There was no evidence that nectar removal stimulated nectar production.

Breeding system and pollen-ovule ratio. *Pavonia bahamensis* plants depended upon birds for fruit set. Plants did not autopollinate, and they were self-incompatible or weakly self-com-

Table 3. Breeding system of *Pavonia bahamensis* on San Salvador Island, Bahamas. Average fruit set is shown for bagged flowers with no hand-pollination, bagged flowers augmented with self-pollen, open flowers augmented with cross-pollen, and naturally pollinated flowers. % Fruit set equals 100 (fruits/flowers). [1] Pollen was not augmented by hand but pollen grains were counted on naturally pollinated flowers. [2] Two of five flowers on one plant produced fruit. Means within each season with different superscript letters are significantly different; Mann-Whitney U tests, * $P < 0.10$.

Treatment	Number		% Fruit Set
	Plants	Flowers	$\bar{x} \pm$ SD
1994/95			
Bagged, no hand-pollination	5	7	0
Bagged, self-pollen	5	11	0
Abundant pollen, >50 grains[1]	5	18	93 ± 13.4^{a}
Natural pollination	6	22	82 ± 30.9^{a}
1995/96			
Bagged, self-pollen	4	6	0
Augmented cross-pollen	11	47	51 ± 50.5^{b}
Natural pollination	11	67	40 ± 49.4^{b}
1996/97			
Bagged, self-pollen	4	16	$10 \pm 20.0^{c*}$
Augmented cross-pollen	7	31	$43 \pm 46.5^{d*}$
Natural pollination	7	64	$11 \pm 17.9^{c*}$

patible (Table 3). Bagged flowers typically produced no fruit if pollen was not deposited on the stigmas by hand. Flowers hand-pollinated with self-pollen did not set fruit in 1994/95 or 1995/96 (and see Rathcke 1998; Rathcke et al. 1996). However, in 1996/97 two flowers on one shrub produced fruit in the treatment with added self-pollen (Table 3).

The pollen-ovule ratio for *Pavonia bahamensis* was estimated to be 607. This was based on the following measurements: Flowers had an average of 41 anthers (SD = 0.19, n = 14 plants; 26 flowers). Each anther contained an average of 74 pollen grains (SD = 17.5, n = 7 plants; 13 flowers, 24 anthers). Using these two averages, I estimated that flowers had an average of 3034 pollen grains. Flowers typically had five ovules.

Pollination limitation and pollen deposition. Fruit set was not significantly pollination limited in either 1994/95 or in 1995/96 (Table 3; Rathcke 2000). Fruit set of naturally pollinated flowers and that of pollen-augmented flowers were not statistically different (Rathcke 2000). However, fruit set was strongly pollination limited in 1996/97 after Hurricane Lili when populations of the two bird pollinators were decimated (Murphy et al. 1998; Rathcke 1998, 2000). Using the equation given in the methods, percent pollination limitation = (43% − 11%) / 43% = 74% (see also Rathcke 2000). Pollen deposition on stigmas was also much lower in 1996/97 than in the previous two years (Rathcke 2000).

Effectiveness of pollinators. Pollination effectiveness of a flower visitor reflects both pollen transfer by an individual pollinator per visit and the frequency of visits. Bahama Woodstars were not very effective as pollinators of *Pavonia bahamensis,* both because individuals transferred little or no pollen to stigmas and because they were relatively infrequent visitors. Because Bahama Woodstars have long bills, and because they could probe through the sides of the flowers between the petals, these birds could access nectar without touching either the stigma or the anthers. In 1995/96, no pollen was transferred by individuals in 27% of the visits to flowers (n = 11). For the visits that did transfer pollen, the majority of visits (73%) transferred < 20 pollen grains ($\bar{x}$ = 16, SD = 19.5, n = 11). A minimum of ca. 20 pollen grains is needed for maximum high fruit set (Rathcke 2000). In 1995/96 when Bananaquits were rare and Bahama Woodstars were the most frequent flower visitors, both pollen deposition and fruit set were lower than in 1994/95, although flowers were not significantly pollination limited (Table 3; Rathcke 2000). Bahama Woodstars were relatively infrequent visitors to flowers. During a day, typically only one or two birds were observed visiting flowers in 1994/95 and 1995/96. In 1996/97, no birds were seen or heard in the site.

Bananaquits appeared to be effective pollinators, although the effectiveness of single visits was not quantified. Bananaquits probed flowers in two different ways; most often they probed with their heads up so that the anthers contacted their breasts but occasionally they probed with their heads upside down so the anthers contacted their foreheads. The bright yellow *Pavonia bahamensis* pollen was often evident on the foreheads of these birds but was less obvious on their yellow breasts. Very rarely, birds probed through the side of the flower between the petals and did not transfer or collect pollen. Bananaquits tended to remain in small flocks and to visit flowers throughout the day. In 1994/95 when Bananaquits frequently visited flowers, pollen deposition on stigmas was high and fruit set was not pollination limited (Table 3).

Although I observed one Bahama Mockingbird visit flowers, this occurred in 1996/97 when nectar was overflowing and dripping from the flowers. It is unlikely these mockingbirds could reach the nectar when other birds were removing it to low levels in the flowers. The mockingbird had pollen covering its chest and it is possible that it could have transferred some pollen. However, pollen deposition in this winter period (1996/97) was low (51% of the flowers had no pollen deposition by the end of flower life) and fruit set was low and pollen-limited (Table 3; Rathcke 2000). Therefore, Bahama Mockingbirds were not considered effective pollinators, possibly because they rarely visited flowers and/or were poor at transferring pollen.

DISCUSSION

As is common for many island plants, *Pavonia bahamensis* has few pollinator species; its pollination appears to depend totally on two bird species, Bananaquits and Bahama Woodstars. Perhaps because it has only bird pollinators, the floral traits of *P. bahamensis* closely fit those predicted by the bird pollination syndrome, except for corolla color (Table 1). The corolla is green and is neither vivid nor red as is typical for hummingbird-pollinated flowers in western North America (Grant and Grant 1976; Howe and Westley 1988; Raven 1972; Stiles 1976).

The red color of flowers that is typical for hummingbirds in western North America is apparently not preferred by hummingbirds, but red is conspicuous to them and not to insect pollinators, which may explain its selective advantage (Melendez-Ackerman et al. 1997; Raven 1972). Because red is conspicuous, it has been hypothesized that there is an advantage for plants to converge on this single, distinctive flower color to attract migrating hummingbirds (Raven 1972). This color convergence would not be necessary for plants on San Salvador where nectarivorous birds are non-migratory. In fact, flowers visited by short-billed hummingbirds, like the Bahama Woodstar, in Central and South America and the West Indies often show a diversity of colors (Feinsinger 1987) although green is highly unusual. For *Pavonia bahamensis*, the yellow pollen of the exserted anthers may provide the vivid visual cue rather than the corolla. It is also possible that the flowers exhibit an attractive color in the ultraviolet (Bleiweiss 1994; Goldsmith 1980), but this was not tested for this species. Green or greenish-yellow flowers are also found in three close relatives of *P. bahamensis* (*P. paludicola, P. troyana, and P. rhizophorae*) (Fryxell 1999), so green is not an unusual color in this lineage. However, the maintenance of the green color may also reflect a lack of selection for more vivid colors in areas where birds are not migratory. Green corollas may also have an adaptive advantage because they can contribute to photosynthesis and reduce resource limitation of fruit set (Bazzaz et al. 1979; Jurik 1983).

Other characteristics of *Pavonia bahamensis* flowers are typical of a bird pollination syndrome (Grant and Grant 1976; Howe and Westley 1988; Table 1). Flowers have no detectable odor. The calyx and corolla form a tube where nectar collects. Nectar per flower is ample (> 100 microliters per day) with a sugar concentration of 20%, which is typical of bird-pollinated species (Baker 1975; Bolten and Feinsinger 1978; Feinsinger 1983; Feinsinger et al. 1985; Hainsworth and Wolf 1976; Opler 1983). Insects can access nectar by forcing their way between the petals, as one wasp was observed to do. However, during three winter flowering periods, only this single wasp individual was ever observed to visit the flowers. This lack of visitation may support the hypothesis that the dilute nectar deters bees and wasps, which may need higher rewards (Bolten and Feinsinger 1978). Although ants fed on the nectar when flowers were placed on the ground, they were never seen in the flowers on the plant.

Pavonia bahamensis plants show a seasonal steady-state flowering pattern, which is a common flowering pattern for plants that support long-lived pollinators such as birds (Gentry 1974). Different flowers continued to open throughout the day, and nectar was secreted throughout the day as is characteristic of many bird-pollinated species (Howe and Westley 1988).

The pollinator specialization of *Pavonia bahamensis* is partly enforced by pollinator availability: Bananaquits and Bahama Woodstars are the only nectarivorous birds on San Salvador (Murphy et al. 1998; White 1991). However, other bird species, especially migratory warblers, occasionally visited the flowers of other nearby species (see also Murphy et al. 1998). Insects, especially wasps and butterflies, can be common flower visitors to other plant species (Rathcke et al. 1996; pers. obs.). However, these species were never seen visiting the flowers of *P. bahamensis*, with two exceptions. I saw a single wasp visit one flower by pushing its way between the petals into the corolla tube; it appeared to access nectar as it stayed for some time. I observed one foraging bout by a Bahama Mockingbird feeding at flowers overflowing with nectar during winter 1996/97 when the main bird pollinators were scarce (Rathcke 1998, 2000). This bird had yellow pollen on its breast and head and may have transferred pollen. However, it is unlikely it could have reached the nectar if nectar removal was at the levels seen in the previous two winters (Rathcke 1998, 2000). Generalist pollinator species can provide compensatory pollination for plants, especially when nectar accumulates in flowers and becomes available to more species, and prevent or reduce pollination limitation (Wolf and Stiles 1989), but this was not the case for *P. bahamensis.* When populations of two bird pollinators, Bananaquits and Bahama Woodstars, were decimated by the severe Hurricane Lili in October 1994, the fruit set of *P. bahamensis* was strongly pollination limited the following December–January (Rathcke 1998, 2000). This species has no "fail-safe" mechanism (Wolf and Stiles 1989) to maintain pollination if these two bird species decline, and as such, it is highly vulnerable to changes in their behavior or population densities (Rathcke 1998, 2000).

Bird pollination is generally reliable for *Pavonia bahamensis* when either Bananaquits or Bahama Woodstars are present, as evidenced by the lack of pollination limitation in the two years before Hurricane Lili decimated their populations in 1996 (Murphy et al. 1998; Rathcke 1998; 2000). Hurricane Lili was a Category 2 storm with winds up to 105 miles per hour (Rathcke 2000). In September 1999 an even more intense, Category 4 hurricane, Hurricane Floyd, passed directly over San Salvador with winds up to 150 miles per hour (Bahamian Field Station records), but nectarivorous bird populations did not seem to be reduced; both Bananaquits and Bahama Woodstars appeared to be at typical population levels (M. Murphy, pers. comm.; pers. obs.). Although hurricanes affect San Salvador about every three years on average (Shaklee 1996), few hurricanes may be severe enough to reduce the nectarivorous bird populations. The strong pollination limitation seen in 1996/97 may seldom occur. However, pollination limitation could also occur if birds are unreliable pollinators for other reasons. For example, in 1995/96 Bananaquits rarely visited although they were common on the island (Murphy et al. 1998; Rathcke 2000). In that year Bahama Woodstars appeared to be sufficiently effective to prevent pollination limitation although pollen deposition and fruit set were lower. It is possible that this island species usually has reliable pollination despite its specialization, in contrast to some other island plants where pollination is less certain with fewer pollinators (Feinsinger et al. 1982; Spears 1987).

The low pollen-ovule ratio (P/O) of 607 also suggests that pollination by these two bird species is generally reliable. The value of 607 is similar to the average ratio reported for plant species with facultative xenogamy ($\bar{x}$ = 797) whereas the pollen-ovule ratio for plants with obligate xenogamy (i.e., obligate outcrossers) is much higher (P/O = 5860; Cruden 1977). Facultatively xenogamous species have more certainty of pollination than obligate xenogamous species because they typically can auto-pollinate and are self-compatible, although some species require pollinators (Cruden 1977). Given that *Pavonia bahamensis* could be classified as an obligate outcrosser, the low pollen-ovule ratio suggests that this species may have unusually reliable pollination. Flowers are unlikely to self-pollinate and outcrossing is usually required for fruit set. The production of fruit by two selfed flowers in 1996/97 may represent the breakdown of the compatibility system when cross-pollination is low, or it may reflect pollen contamination.

What is the evidence that either Bahama Woodstars or Bananaquits is the "most effective pollinator" and hence the stronger selective agent molding the pollination syndrome (Stebbins 1970)? The morphological match of bill and floral tube lengths suggests that the Bahama Woodstar was the more effective pollinator. The tube-like corolla was 18.1 mm and the bill length of the Bahama Woodstar is ca. 17 mm (based on one museum male specimen collected on New Providence in 1949 and deposited in the Museum of Zoology at the University of Michigan). In contrast, the average length of Bananaquit bills measured from nares to tip was 10.8 mm (SD = 0.902, min = 7.95, max = 13.47, n = 221; M. Murphy, unpub. data). Tongue lengths would also determine morphological matching, but data are unavailable. A visual estimation of tongue length in Bananaquits from a slide indicated that tongues could extend 1.2–1.4 × beyond the bill length (ca. 13–15 mm long or a total of 24–26 mm; Bruce Hallett, pers. comm.).

Regardless of the morphological matching between bills and tongues and corolla lengths, Bahama Woodstars were not effective as individual pollinators because they typically visited the flowers through the side of the corolla and usually transferred little or no pollen per visit. They were also relatively infrequent visitors to flowers compared to Bananaquits, which foraged in small flocks. Other evidence suggests that Bananaquits are more effective pollinators than Bahama Woodstars. Bananaquits commonly had dense pollen loads on their foreheads and breasts and they usually contacted the stigma and anthers when visiting flowers. Pollen deposition was especially high when Bananaquits were the major flower visitors in 1994/95 (Rathcke 2000) although it is not known if this occurred because they transferred more pollen per visit or because they were very frequent visitors. Bananaquits usually visited the flowers so that pollen was deposited on their chests, but they occasionally visited flowers while hanging upside down so that pollen was deposited on their foreheads. In either case, pollen could be easily transferred to the extended stigma if the bird retained the same position during other floral visits. *Pavonia bahamensis* appears to be an important floral resource for Bananaquits on San Salvador (Murphy et al. 1998), and Bananaquits may be reliable pollinators over years. However, relatively few were seen in 1995/96 and the reason for this is not clear, suggesting that their foraging patterns may change and pollination reliability over years may vary.

A second line of evidence also suggests that Bananaquits are more effective pollinators than Bahama Woodstars. The horizontal flower orientation in *Pavonia bahamensis* supports the syndrome for passerine pollination, rather than hummingbird pollination. Flowers that are held horizontally, rather than vertically, allow passerine birds to perch on nearby branches while feeding (Bruneau 1997; Cruden and Toledo 1977). Another test for passerine versus hummingbird pollination would be to examine sugars in the nectar, but this remains to be done. Nectars of passerine-pollinated species tend to have low sucrose/hexose ratios ($<$ 0.499) whereas hummingbird-pollinated species tend to have high sucrose/hexose ratios (Baker and Baker 1983; Bruneau 1997).

Bird pollination of *Pavonia bahamensis* may be relatively unusual for the genus *Pavonia*. Most species of *Pavonia* are thought to have relatively generalized pollination (Fryxell 1999). However, hummingbirds are reported to be pollinators for several species that have tubular corollas and exserted stigma and anthers, including *P. schrankii* with a yellow corolla (Gottsberger 1972), *P. viscosa* (as *P. montana*) and *P. malvaviscoides* with red flowers (Sazima 1981), and *P. dasypetala* (McDade and Davidar 1984; Roubik 1982; see also Porsch 1929). The green flowers of *P. bahamensis* are unusual for a bird-pollinated flower. The three closely related species (*P. paludicola, P. troyana, and P. rhizophorae*) all have green or greenish-yellow flowers (Fryxell 1999). Whether these species will also prove to be pollinated by birds, or specifically by passerines or hummingbirds, remains to be determined. Among these four species, *P. bahamensis* is unique in having single flowers displayed among the leaves; the other three species have racemose inflorescences that rise above the leaves. If they are bird-pollinated, the more vertical, racemose inflorescence may reflect hummingbird pollination rather than passerine pollination (see Cruden and Toledo 1977).

For *Pavonia bahamensis,* a species of passerine bird (Bananaquits) may be a more effective pollinator than hummingbirds, but whether Bananaquits are more reliable over the long term remains to be determined. Although Bahama Woodstars are ineffective at transferring pollen, they maintained pollination one flowering season when Bananaquits were infrequent visitors. Having two pollinator species increased pollination reliability for *P. bahamensis,* although it still incurs a risk of pollination limitation if these two species decline or change their foraging patterns (Rathcke 1998, 2000).

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NOMENCLATURAL PROPOSALS IN *ATRIPLEX* (CHENOPODIACEAE)

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ABSTRACT. This article includes a report of nomenclatural novelties in the genus *Atriplex,* which were determined as appropriate following preparation of a summary revision of the genus for the Flora of North America Project. Subgeneric novelties include: *Atriplex* subgen. *Obione, stat. nov.* and *Atriplex* subgen. *Pterochiton, stat. nov.* Sectional or subsectional taxa are: *Atriplex* subgen. *Obione* sect. *Pleianthae, sect. nov.*; *Atriplex* sect. *Obione* subsect. *Graciliflorae, stat. nov.*; *Atriplex* sect. *Obione* subsect. *Saccariae, stat. nov.*; *Atriplex* sect. *Obione* subsect. *Argenteae,* stat. nov.; *Atriplex* sect. *Obione* subsect. *Truncatae, comb. nov.*; *Atriplex* sect. *Obione* subsect. *Wolfianae, comb. nov.*; *Atriplex* sect. *Obione* subsect. *Pusillae, comb. nov.*; *Atriplex* sect. *Obione* subsect. *Arenariae, comb. nov.*; *Atriplex* sect. *Obione* subsect. *Leucophyllae, comb. nov.*; *Atriplex* sect. *Obione* subsect. *Californicae, comb. nov.*; *Atriplex* sect. *Phyllostegiae, comb. nov.*; and *Atriplex* sect. *Covilleiae, sect. nov.* New varietal combinations are: *Atriplex gmelinii* var. *alaskensis, comb. nov.*; *A. glabriuscula* var. *acadiensis, comb. nov.*; *A. glabriuscula* var. *franktonii, comb. nov.*; *A. saccaria* var. *cornuta, comb. nov.; A. saccaria* var. *asterocarpa, comb. nov.; A. argentea* var. *longitrichoma, comb. nov.; A. argentea* var. *rydbergii, comb. nov.; A. powellii* var. *minuticarpa, comb. nov.; A. wolfii* var. *tenuissima, comb. nov.; A. parishii* var. *minuscula, comb. nov.; A. parishii* var. *depressa, comb. nov.; A. parishii* var. *subtilis, comb. nov.; A. parishii* var. *persistens, comb. nov.; A. cordulata* var. *erecticaulis, comb. nov.*; and *A. coronata* var. *vallicola, comb. nov*

Key Words: *Atriplex,* nomenclature

The proposals presented herein are preliminary to publication of a summary revision of the genus *Atriplex* L. for North America. The main body of the article will be published as a part of the Flora of North America Project, and is to be presented in prepublication form, possibly through the internet system. Thus it is deemed necessary to present the proposals to the scientific community in standard form prior to that event.

Interpretations of the genus and its included taxa in North America have undergone modifications since the first attempts at revision of the genus by Sereno Watson (1874) and by Paul C. Standley (1916). The work of Hall and Clements (1923) presented a then revolutionary treatment in which species were enlarged to include complexes of related taxa under a trinomial or quadrinomial system. Since 1923 most workers chose to follow the work of Hall and Clements in provincial treatments, but as more information became available the large groupings of Hall and Clements were dissected again (Bassett et al. 1983; Taschereau 1972). Other papers have dealt with portions of the genus or have added new taxa (Stutz and Chu 1993a, 1993b, 1997a, 1997b; Stutz et al. 1975, 1990, 1993, 1994, 1997, 1998; Stutz and Sanderson 1983, 1998).

The present author (Welsh 1993, 1995, unpubl. ms.) has attempted to strike a balance between the complex, and often unnatural, groupings as interpreted by Hall and Clements, and the more natural arrangement of individualized taxa of the later authors. He has also attempted to examine all original descriptions (see included list of references) and the type specimens of all names involved in the genus in North America. Still, when taxa were apparently closely allied and of the same general morphological conformation, they have been united in the present work as varieties under an inclusive species. This is the case with most of the nomenclatural novelties given below.

Many of the names treated herein were formally proposed by Standley (1916), but with the taxonomic rank not designated. They serve as basionyms for many of the infrageneric proposals presented in this paper.

Atriplex gmelinii C. A. Mey. ex Bong., Mem. Acad. St. Petersb. VI. 2: 160 (Observ. Veg. Sitcha 41). 1838.

var. **alaskensis** (S. Watson) S. L. Welsh, *comb. nov.*, based on: *Atriplex alaskensis* S. Watson, Proc. Amer. Acad. Arts 9: 108. 1874.

Bassett et al. (1983) distinguish var. *alaskensis* at the rank of species from the closely allied *Atriplex gmelinii* by the sizes of brown seeds (i.e., 1.7–2.7 mm wide in *A. gmelinii* and 2.8–3.7 mm wide in *A. alaskensis*). However, some seeds of *A. gmelinii* measure as much as 3 mm wide, so the distinction in seed size is not absolute. Also, *A. gmelinii* occasionally bears black shiny seeds, which have not been observed in specimens of var. *alaskensis*. It appears that mainly juvenile plants have been collected, those which lack mature fruiting bracteoles and seeds. The *alaskensis* phase occurs completely within the range of *A. gmelinii*, and it might represent no more than a growth phase of the latter species. Certainly there is considerable ecologically induced variation within the *gmelinii* complex. Plants that grow within the littoral, where they are inundated by high tide, show a completely different series of facies than do those that are immediately above the tidal zone. Leaves vary from linear to oblong, oval, and various other shapes within what has been traditionally regarded as *A. gmelinii* in a strict sense (*A. patula* var. *obtusa, sensu* various authors). The two entities, *gmelinii* and *alaskensis* are treated herein as belonging to an inclusive *A. gmelinii.*

Atriplex glabriuscula Edmondston, Fl. Shetland 39. 1845.
var. **acadiensis** (Tascher.) S. L. Welsh, *comb. nov.*, based on: *Atriplex acadiensis* Tascher., Canad. J. Bot. 50: 1577–1579. 1972.

Historically, this taxon has been thought to be closely allied to the ruderal weed, *Atriplex patula* L. (with which it is often sympatric, and with which it was synonymized by Gleason and Cronquist 1991:101), but from which it differs in some aspects (shorter, stockier, rarely over 4 dm tall; bracteoles ovate-triangular and joined only at the base, not rhombic-triangular with margins united almost to the middle). The variety, like *A. glabriuscula, sensu lato*, appears to be confined mainly to native habitats in saline marshes, and apparently is not, or is seldom, a ruderal weed as is the case with *A. patula.* It grows occasionally with the indigenous *A. dioica* Raf., which has elliptic (not round) seeds.

Plants examined from New Brunswick typically have at least half of the nodes opposite, and with opposite branches of unequal size. The plants still seem to be closely allied to, and perhaps not always separable from the largely sympatric *Atriplex glabriuscula.* Bassett et al. (1983: 12) indicate that *A. acadiensis* formed spontaneous hybrids with *A. glabriuscula* in the Botanic Garden at Manchester England, noting further that these "presumably sterile triploid hybrids exhibited marked heterosis."

var. **franktonii** (Tascher.) S. L. Welsh, *comb. nov.*, based on: *Atriplex franktonii* Tascher., Canad. J. Bot. 50: 1586–1589. 1972.

This taxon has been placed in synonymy of *Atriplex hastata* L. (i.e., *A. prostrata* Boucher ex DC.) by Gleason and Cronquist (1991: 102), but is clearly more nearly allied to *A. glabriuscula* within whose range it is completely submersed. It is likewise evidently confined to indigenous salt marsh habitats, unlike the clearly ruderal weedy status of the evidently introduced *A. prostrata.*

Atriplex subgen. *Obione* (Gaertn.) S. L. Welsh, *stat. nov.*, based on: *Obione* Gaertn., Fruct. II. 198. t. 126. 1791; subgen. *Obione* [autonym created by subgen. *Pterochiton* (Torr. & Frem.) Ulbr., *in* Engl. & Prantl, Nat. Pflanzenfam, ed. 2. 16c: 509. 1934]; sect. *Obione* (Gaertn.) Rchb., Consp. Regn. Veg. 164. 1828; C. A. Mey. *in* Ledeb., Fl. Altaic. 4: 315. 1833.

Plants monoecious to subdioecious or less commonly dioecious annuals or perennials, the leaves (typically) with or (uncommonly) without Kranz anatomy. Staminate flowers with calyx lobes crested or not. Pistillate flowers bibracteolate, lacking or rarely with a perianth (in *Atriplex covillei, A. pleiantha,* and *A. suckleyi*). Bracteoles cuneate to ovate or obovate united at least to the middle; the faces with tubercles or crests or smooth; the seeds erect; the radicle typically superior (except in *A. pleiantha*), erect, the tip adjacent to styles.

TYPE species: *Atriplex muriculata* Gaertn. (*nom. illeg.*) = *A. sibirica* L.

The subgenus is comprised of numerous, indigenous North American species and some Old World ones as well.

Atriplex subgen. *Obione* sect. *Pleianthae* S. L. Welsh, *sect. nov.* TYPE: *Atriplex pleiantha* W. Weber, Madroño 10: 189. 1950; *Proatriplex* (W. Weber) Stutz & G. L. Chu, Amer. J. Bot. 77: 366. 1990; *Atriplex* subgenus *Proatriplex* W. Weber, Madroño 10: 188. 1950.

Similis subgeno *Obione* secti *Endolepe* Torr. sed in bracteolis multifloribus habentibus, sepalis staminata noncristatis et radicula inferiore absimilis.

Plants monoecious annuals, the leaves with normal (non-Kranz) anatomy. Staminate flowers with calyx lobes not crested. Pistillate flowers bibracteolate, enclosing 2–5 flowers, these typically with a 5-lobed perianth. Bracteoles triangular-ovate united to the middle or above, the faces lacking tubercles, the seeds erect, the radicle lateral, declined (the tip at opposite end from the styles).

TYPE species: *Atriplex pleiantha* W. Weber.

The section is monotypic, with distribution as noted below. The relationship of the solitary included taxon, *Atriplex pleiantha,* with other species of *Atriplex* in the Colorado Plateau is illusory. Great weight has been given to the presence of apparently primitive inflorescences within the flowering bracteoles, but that feature is probably derived, and not primitive. The linear, pale, perianth segments subtending the 3–5 flowers are not unlike those within both *A. phyllostegia* and *A. suckleyi,* both of which also lack Kranz anatomy in their leaves, but from which they are otherwise grossly dissimilar. Rather than representing primitive features, the presence of the perianth and in the case of *A. pleiantha,* multiple flowers, these striking and seductively attractive features appear to represent independent, derived occurrences within the highly variable genus *Atriplex.* If any of them are to be segregated within separate genera, then each should be so treated. The radicle placement in seeds of section *Pleianthae* is inferior (with the tip of the radicle at a point diametrically opposed to the styles), possibly pointing to a relationship divergent from the other species with perianth scales subtending the ovary in pistillate flowers. Because of the radicle position, the section might well have been placed within subgenus *Atriplex.* However, the radicle position might also be a derived condition, at least in some cases. If so, the relationship could well lie with other members currently treated within the subgenus *Obione.* It is anomalous wherever it is placed.

Atriplex sect. *Obione* subsect. *Graciliflorae* (Standl.) S. L. Welsh, *stat. nov.*, based on: *Atriplex* VI. *Graciliflorae* Standl., N. Amer. Fl. 21: 34, 45. 1916.

Leaves short-petiolate, the blades often subcordate, entire. Staminate flowers in paniculate glomerules, the panicles soon deciduous. Fruiting bracteoles pedicellate, suborbicular (samara-like), united, entire or nearly so, the faces lacking tubercles.

TYPE species: *Atriplex graciliflora* M. E. Jones, Proc. Calif. Acad. Sci. II. 5: 717. 1895.

The subsection is monotypic, with the solitary species endemic to saline clays and silts of southeastern Utah.

Atriplex sect. *Obione* subsect. *Saccariae* (Standl.) S. L. Welsh, *stat. nov.*, based on: *Atriplex* VII. *Saccariae* Standl., N. Amer. Fl. 21: 34, 45. 1916.

The leaves short-petiolate; the blades mostly cordate or ovate, entire. Staminate flowers in spicate or paniculate glomerules; the inflorescence soon deciduous. Fruiting bracteoles typically (but not always) dimorphic; some large, pedicellate and the faces mostly tuberculate, the others small, cuneate and unappendaged, or lacking.

TYPE species: *Atriplex saccaria* S. Watson, Proc. Amer. Acad. Arts 9: 112. 1874.

The subsection consists of a single species with three varieties, all distributed from Wyoming and Utah south to Arizona, New Mexico, and Texas.

Members of the subsection *Saccariae* are closely allied with, and morphologically similar to, members of subsection *Argenteae,* and differing in the usually dimorphic fruiting bracteoles, with the smaller sessile bracteoles mainly lacking surficial appendages, but with radiating appendages on the larger stipitate bracteoles, or where the mainly stipitate bracteoles are monomorphic, by the appendages radiating from the globular surface. The alliance of this complex with the *argentea* assemblage is suggested by intermediacy of even the main diagnostic features. It seems probable that the sessile, smooth-faced bracteole might have been derived from some *argentea* type ancestor. Certainly the two complexes are closely allied both taxonomically and geographically.

Atriplex saccaria S. Watson, Proc. Amer. Acad. 9: 112. 1874.

var. **cornuta** (M. E. Jones) S. L. Welsh, *comb.* et *stat. nov.,* based on: *Atriplex cornuta* M. E. Jones, Proc. Calif. Acad. Sci. II. 5: 718. 1895.

var. **asterocarpa** (Stutz, G. L. Chu & S. C. Sand.) S. L. Welsh, *comb.* et *stat. nov.*, based on: *Atriplex asterocarpa* Stutz, G. L. Chu & S. C. Sand., Madroño 41: 199. 1994.

The species consists of three infraspecific taxa. It is, in a broad sense, a taxon with great variability, and is confined to the American West from Wyoming south to the Four-Corners portion of Colorado, New Mexico, Arizona, and Utah.

Atriplex sect. *Obione* subsect. *Argenteae* (Standl.) S. L. Welsh, *stat. nov.*, based on: *Atriplex* VIII. *Argenteae* Standl., N. Amer. Fl. 21: 34, 46. 1916. Synonym: *Atriplex* IX. *Powellianae* Standl., N. Amer. Fl. 21: 34, 46. 1916.

Leaves petiolate or sessile, alternate or the lowermost opposite, the blades typically broadest near the base, entire or dentate, often hastate. Staminate flowers in axillary glomerules, or the glomerules paniculate. Fruiting bracteoles monomorphic, sessile or pedicellate, usually broadest at or above the middle, the faces tuberculate or smooth.

TYPE (LECTOTYPE: vide McNeill et al., Agric. Canada Monogr. 31: 17. 1983) species: *Atriplex argentea* Nutt., Gen. N. Amer. Pl. 1: 198. 1818.

The subsection consists of three (more or less) polymorphic species, some of which are further subdivided into varieties, distributed from British Columbia east to Manitoba and south to California, Arizona, New Mexico, and Texas.

Atriplex argentea Nutt., Gen. N. Amer. Pl. 1: 198. 1818.

var. **longitrichoma** (Stutz, G. L. Chu & S. C. Sand.) S. L. Welsh, *comb.* et *stat. nov.*, based on: *Atriplex longitrichoma* Stutz, G. L. Chu & S. C. Sand., Madroño 45: 128. 1998.

var. **rydbergii** (Standl.) S. L. Welsh, *comb.* et *stat. nov.*, based on: *Atriplex rydbergii* Standl., N. Amer. Fl. 21: 47. 1916. Synonym: *A. pachypoda* Stutz & G. L. Chu, Madroño 44: 277. 1997.

The species is widely distributed over much of the American West and exhibits a great variety of morphological subunits, some of which are geographically correlated. The two combinations proposed herein represent taxa with such correlations.

Atriplex powellii S. Watson, Proc. Amer. Acad. Arts 9: 114. 1874.

var. *minuticarpa* (Stutz & G. L. Chu) S. L. Welsh, *stat. nov.*, based on: *Atriplex minuticarpa* Stutz & G. L. Chu, Madroño 40: 161. 1993.

This taxon, which occurs entirely within the geographical area of the species proper, is a local endemic on fine-textured saline substrates in eastern Utah.

Atriplex sect. *Obione* subsect. *Truncatae* (Standl.) S. L. Welsh, *stat. nov.*, based on: *Atriplex* X. *Truncatae* Standl., N. Amer. Fl. 21: 34, 49. 1916.

Leaves petiolate or the uppermost sessile, alternate, the blades typically broadest near the base, entire or nearly so. Staminate flowers in axillary glomerules. Fruiting bracteoles monomorphic, sessile or short-pedicellate, broadly cuneate, dentate at the truncate apex, the faces typically smooth.

TYPE (LECTOTYPE: vide McNeill et al., Agric. Canada Monogr. 31: 17. 1983) species: *Obione truncata* Torr. *ex* S. Watson = *Atriplex truncata* (Torr. *ex* S. Watson) A. Gray, Proc. Amer. Acad. Arts 8: 398. 1872.

The subsection is monotypic, with distribution rather broad in the American West.

Atriplex sect. *Obione* subsect. *Wolfianae* (Standl.) S. L. Welsh, *stat. nov.*, based on: *Atriplex* XI. *Wolfianae* Standl., N. Amer. Fl. 21: 34, 49. 1916.

Leaves sessile, alternate, the blades linear, entire. Staminate flowers in axillary glomerules. Fruiting bracteoles monomorphic, sessile or subsessile, cuneate, entire, the faces typically short-tuberculate.

TYPE species: *Atriplex wolfii* S. Watson, Proc. Amer. Acad. Arts 9: 112. 1874.

The subsection is monotypic, the solitary species with two geographical races separated herein as varieties; their distributions include southern Wyoming, Colorado, and Utah.

Atriplex wolfii S. Watson, Proc. Amer. Acad. Arts 9: 112. 1874.
var. **tenuissima** (A. Nelson) S. L. Welsh, *comb.* et *stat. nov.*, based on: *A. tenuissima* A. Nelson, Bot. Gaz. 34: 359. 1902.

This variety is known from southwest Wyoming, north-central and western Colorado, and central to northeastern Utah.

Atriplex sect. *Obione* subsect. *Pusillae* (Standl.) S. L. Welsh, *stat. nov.*, based on: *Atriplex* XII. *Pusillae* Standl., N. Amer. Fl. 21: 50. 1916.

Sometimes villous as well as scurfy; the leaves opposite or alternate, sessile, small, ovate to linear, entire. Staminate flowers in axillary glomerules. Fruiting bracteoles monomorphic, sessile or subsessile, typically ovate or hastate, broadest at or near the base, entire or denticulate, the faces tuberculate or smooth.

TYPE species: *Obione pusilla* Torr. = *Atriplex pusilla* (Torr.) S. Watson, Proc. Amer. Acad. Arts 9: 110. 1874.

The subsection is comprised of five species, some of them with two or more constituent varieties. In large part, they are distributed in the Great Valley of California, with extensions to the coastal region of southern California and to western Nevada and southeastern Oregon. The members of the subsection are characterized by its small leaves and tiny fruiting bracteoles.

Atriplex parishii S. Watson, Proc. Amer. Acad. Arts 17: 377. 1882.

var. **minuscula** (Standl.) S. L. Welsh, *comb.* et *stat. nov.*, based on: *Atriplex minuscula* Standl., Fl. N. Amer. 21: 51. 1916.

var. **depressa** (Jeps.) S. L. Welsh, *comb.* et *stat. nov.*, based on: *Atriplex depressa* Jeps., Pittonia 2: 304. 1892.

var. **subtilis** (Stutz & G. L. Chu) S. L. Welsh, *comb.* et *stat. nov.*, based on: *Atriplex subtilis* Stutz & G. L. Chu, Madroño 44: 184. 1997.

var. **persistens** (Stutz & G. L. Chu) S. L. Welsh, *comb.* et *stat. nov.*, based on: *Atriplex persistens* Stutz & G. L. Chu, Madroño 40: 211. 1993.

The *parishii* complex consists of a series of subordinate, small-leaved taxa with distribution mainly in the Great Valley of California. They differ from other in subtle but evidently consistent ways.

Atriplex cordulata Jeps., Pittonia 2: 304. 1892.

var. **erecticaulis** (Stutz, G. L. Chu & S. C. Sand.) S. L. Welsh, *comb.* et *stat. nov.*, based on: *Atriplex erecticaulis* Stutz, G. L. Chu & S. C. Sand., Madroño 44: 89. 1997.

This is yet another of the minor variants of species in the Central Valley of California.

Atriplex coronata S. Watson, Proc. Amer. Acad. Arts 9: 114. 1874.

var. **vallicola** (Hoover) S. L. Welsh, *comb.* et *stat. nov.*, based on: *Atriplex vallicola* Hoover, Leafl. W. Bot. 2: 130. 1938.

This is another variant of a species with distribution in the Great Central Valley of California.

Atriplex sect. *Obione* subsect. *Arenariae* (Standl.) S. L. Welsh, *stat. nov.*, based on: *Atriplex* XIV. *Arenariae* Standl., N. Amer. Fl. 21: 34, 52. 1916.

Erect or decumbent-ascending, monoecious annuals or perennials. Leaves with Kranz type anatomy, alternate, short-petiolate or sessile, the blades typically widest at or above the middle, entire or dentate. Staminate flowers in axillary glomerules or these in paniculate spikes. Fruiting bracteoles monomorphic, sessile or subsessile, broadest near or above the base, dentate, the faces smooth or tuberculate.

TYPE species: *Atriplex arenaria* Nutt. = *A. mucronata* Raf., Amer. Monthly Mag. & Crit. Rev. 2: 119. 1817.

The subsection is comprised of more than a dozen species, eight of which occur in or near coastal regions from the eastern U.S. to the south and west along the Gulf coast, and along the coast of California.

Atriplex sect. *Obione* subsect. *Leucophyllae* (Standl.) S. L. Welsh, *stat. nov.*, based on: *Atriplex* XVI. *Leucophyllae* Standl., N. Amer. Fl. 21: 34, 58. 1916.

Erect or prostrate, monoecious perennials. Leaves with Kranz anatomy, alternate, sessile, the blades typically widest at or near the middle, entire. Staminate flowers in axillary glomerules or these in short spikes. Fruiting bracteoles monomorphic, sessile, rotund-ovate and spongy-thickened, entire or dentate, the faces tuberculate.

TYPE species: *Obione leucophylla* Moq. = *Atriplex leucophylla* (Moq.) D. Dietr., Syn. Pl. 5: 536. 1852.

The subsection is monotypic, with distribution in coastal California and Baja.

Atriplex sect. *Obione* subsect. *Californicae* (Standl.) S. L. Welsh, *stat. nov.*, based on: *Atriplex* V. *Californicae* Standl., N. Amer. Fl. 21: 34, 44. 1916.

Prostrate, monoecious or dioecious perennials. Leaves typically with Kranz anatomy, alternate or opposite, sessile, the blades widest from below to above the middle, entire. Staminate flowers in axillary glomerules. Fruiting bracteoles monomorphic, sessile or short-stipitate, ovate, entire or dentate, the faces unappendaged.

TYPE species: *Atriplex californica* Moq., Prodr. 13(2): 98. 1849.

The subsection is comprised of three disparate but subtly comparable species, two of them from along the sea beaches and cliffs of the California coast, the other from southwestern Texas and adjacent Mexico.

Atriplex subgen *Obione* sect. *Phyllostegiae* (Standl.) S. L. Welsh, *stat. nov.*, based on: *Atriplex* XXVII. *Phyllostegiae* Standl., N. Amer. Fl. 16: 34, 69. 1916.

Plants monoecious or subdioecious glabrate annuals. Leaves with Kranz anatomy, alternate, petiolate, the blades variously rhombic-triangular, oval or lanceolate, entire or subhastate. Staminate flowers in axillary glomerules or in naked terminal spikes. Fruiting bracteoles sessile or stipitate, sharply hastate and often sharply cristate as well, united to above the middle, the enclosed pistillate flower lacking a perianth.

TYPE species: *Obione phyllostegia* Torr. *ex* S. Watson = *Atriplex phyllostegia* (Torr. *ex* S. Watson) S. Watson, Proc. Amer. Acad. Arts 9: 108. 1874.

Atriplex subgen. *Obione* sect. *Covilleiae* S. L. Welsh, *sect. nov.*

Folliis alternis sessilibus vel subsessilibus floribus staminatis axillaribus vel in racemes terminales bracteolis omnibus similis.

Plants monoecious or subdioecious glabrate annuals. Leaves without typical Kranz anatomy, alternate, petiolate, the blades sharply triangular-hastate or less commonly some of them entire, the overall shape ovate to lanceolate or elliptic. Staminate flowers in axillary glomerules or in naked terminal spikes. Fruiting bracteoles sessile or stipitate, mostly 3-lobed, the lateral lobes rounded, united only at the base, the enclosed pistillate flower with a calyx of 3 (1–5) segments.

TYPE species: *Endolepis covillei* Standl. = *Atriplex covillei* (Standl.) J. F. Macbr., Contr. Gray Herb. II. 53: 11. 1918.

The section is monotypic, with distribution in southeastern Oregon, western Nevada, and California.

The pattern of venation is very similar to that of the closely comparable *Atriplex phyllostegia,* even though the veins lack the associated C-4 arrangement of chloroplast bearing cells in contact with the veins. The plants differ otherwise as noted in the descriptions. Placement of this species within the segregate genus *Endolepis* by various workers is based on two morphological characteristics considered to be of fundamental importance (i.e., the lack of Kranz leaf anatomy and the presence of sepals subtending the ovary within the fruiting bracteoles). However, sepals of staminate flowers in *A. covillei* lack the distinctive crests present in *A. [Endolepis] suckleyi,* a feature on which the genus *Endelopis* was based. The placement of *A. covillei* within *Endolepis,* while convenient, does not take into account the overall similarity of this species to the evidently related *A. phyllostegia.*

Neither does it take into account the potential for recurrence of sepals subtending the ovaries as possibly derived features.

Atriplex subgen. *Pterochiton* (Torr. & Frem.) S. L. Welsh, *stat. nov.*, based on: *Pterochiton* Torr. & Frem., *in* Frem., Rep. Exped. Rocky Mts. 318. 1845. [*Obione* subgen. *Pterochiton* (Torr. & Frem.) Ulbr. *in* Engl. & Prantl, Nat. Pflanzenfam, ed. 2 16c: 509. 1934; *Obione* sect. *Deserticola* Ulbr. *in* Engl. & Prantl, Nat. Pflanzenfam, ed. 2 16c: 508. 1934; *Atriplex* sect. *Deserticola* (Ulbr.) McNeill, Bassett, Crompton & Tascher., Agric. Canada Monogr. 31: 17. 1983; *Atriplex* XXVI. *Nuttallianae* Standl., N. Amer. Fl. 21: 66. 1916; *Atriplex* XXVIII. *Confertifoliae* Standl., N. Amer Fl. 21: 70. 1916; *Atriplex* XXIX. *Canescentes* Standl., N. Amer. Fl. 21: 70. 1916.]

The subgenus consists of dioecious or subdioecious shrubs of western American distribution. The leaves possess Kranz anatomy, and the radical position is typically superior. That they are closely allied is indicated by the propensity of all or most of the included taxa forming hybrids when they are in geographical contact.

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SYSTEMATIC NOTES ON THE OLD WORLD FERN GENUS *OLEANDRA*

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ABSTRACT. A classification and key to Asian, Australian, and Pacific *Oleandra* is presented to complement studies of Pichi-Sermolli (Africa) and Tryon (the Americas). Six species are recognized in this large area. Many species that have been proposed are evidently local variants and not recognized here.

Key Words: Southeast Asia, Australia, Pacific, Oleandraceae, *Oleandra*, fern

Oleandra is one of the most distinctive genera of the Polypodiaceae (*sensu lato*). Its characters have been noted by Copeland (1947), Kramer (1990), Nayar and Bajpai (1976), Pichi-Sermolli (1965), Tryon (1997), and Tryon and Tryon (1982). Among the especially noteworthy characters of the genus are the long, parallel and simple veins (branched, if at all, at their base), the occurrence of rhizophores (or unusual roots), the peltate stem scales, and the articulated petiole. The glaucous coating on the stem of nearly all of the specimens needs to be chemically studied.

The relationship of *Oleandra* is rather obscure in spite of several reports that have considered this: Nayar and Bajpai (1976), Ogura (1938), Sen and Sen (1973), Seong (1977), Tryon and Lugardon (1991), Hasabe et al. (1995), and Pichi-Sermolli (1965), who noted: "*Oleandra* differs from the other genera of the Filicidae in many features and this is the reason why its taxonomical position is debated."

There are about 35 accepted species in the region concerned, while only six are recognized in this study. Some general commentaries concerning the conservative assessment of species in *Oleandra* are pertinent here. The characters of a species must be those of a population, or of a series of populations, not of single plants. The characters must be distinctive over a significant geographic area. Minor variations may develop in *Oleandra* in isolated areas. Copeland (1958) notes under *O. columbrina*, "The

Palawan specimen is fairly typical. Otherwise, each region or mountain has its own recognizable strain." Plants may also have some morphological features that relate to different environments. Pichi-Sermolli (1965) remarked on the variable African species *O. distenta*: "This polymorphism is probably the result of great ecological plasticity of the species which may grow in very dissimilar habitats." Minor variants may deserve some kind of recognition, but not at the rank of species. Characters such as the shape of the apex or base of the lamina and the distribution and density of trichomes on the lamina are not sufficient to warrant the recognition of species.

This study has involved ca. 400 collections from the wide region concerned. It is based on the collections at the Harvard University Herbaria (HUH) and the New York Botanical Garden (NY). It is not concerned with the details of distribution, or nomenclature, or of taxonomy within the six species recognized. The sequence of species has no evolutionary implications except as the key may illustrate affinities; synonyms are listed only where there is relative certainty of their status.

This treatment may serve as a prodromus that may be amplified or revised by a study of holotypes and of populations in the field.

Oleandra Cav., Anal. Hist. Nat. 1: 115. 1799. Type and sole species: *Oleandra neriformis* (= *O. neriiformis*).

Neuronia D. Don, Prod. Fl. Nepal. 6. 1825. Type and sole species: *Neuronia asplenioides* D. Don (= *Oleandra Wallichii*).

Ophiopteris Reinw., Syll. Pl. Nov. 2: 3. 1825. Type and sole species: *Ophiopteris verticillata* Reinw. (= *Oleandra neriiformis*).

Aspidium subgenus *Oleandra* (Cav.) Splitg., Tidjs. Nat. Gesch. 7: 411. 1848.

KEY TO ASIAN, AUSTRALIAN, AND PACIFIC SPECIES

1. Leaves and phyllopodia borne on all sides of the aerial stem and its branches, often in clusters (i.e., pseudowhorls); the aerial stem with few or no rhizophores; a long internode of the aerial stem a straight continuation, or nearly so, of the long internode below . . . . (2)
    2. Leaves monomorphic or nearly so; sori ca. halfway between the costa and the margin of the lamina, or closer to the costa . . . . 1. *O. neriiformis*

2. Leaves strongly dimorphic; the fertile lamina much narrower than the sterile, 3–7 mm wide in the middle (rarely more), and also usually much longer; sori near the margin of the lamina, the indusia often extending beyond the margin . . . . 2. *O. Werneri*

1. Leaves and phyllopodia borne only on the upper side of the aerial stem, well-spaced or in clusters (pseudowhorls); aerial stem with rhizophores on the lower side; the aerial stem often arcuate beyond the leaf-bearing region, divergent in orientation from the long internode below. (see Fig. 4) . . . . (3)

3. Stem scales closely imbricate and usually appressed, concealing the stem, bicolorous (marginate) beyond the point of attachment . . . . (4)

4. Phyllopodia mostly less than 1 cm long (sometimes almost absent), often concealed by scales; lamina more than 5 times as long as the petiole, often 10 times as long or more . . . . (5)

5. Stem with the scales mostly straight and appressed . . . . 3. *O. musifolia*

5. Stem more or less squarrose-paleaceous, scales then with a reflexed tip . . . . 4. *O. Wallichii*

4. Phyllopodia mostly over 1 cm long, often 5 cm long or more, not concealed by scales; lamina up to 5 times as long as the petiole . . . . 5. *O. undulata*

3. Stem with the scales irregularly patent, somewhat thinly investing the visible stem, concolorous or nearly so and light brown to reddish brown beyond the point of attachment . . . . 6. *O. Sibbaldii*

1. Oleandra neriiformis Cav., originally as *neriformis*
Figures 1, 2.

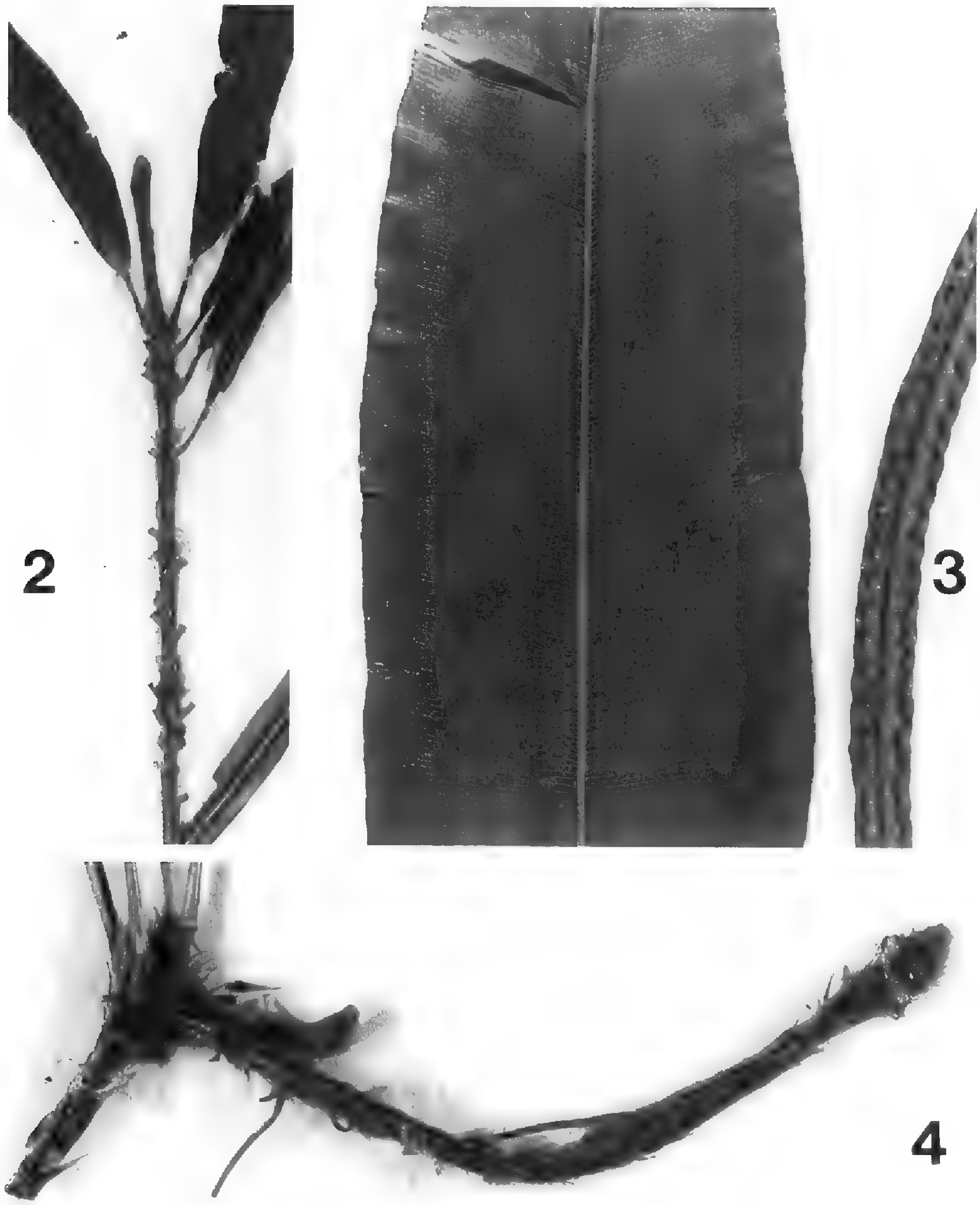
Aspidium bantamense Blume, *A. pistillare* Swartz, *Blechnum colubrinum* Blanco, *Oleandra angusta* Copel., *O. Archbaldii* Copel., *O. bantamense* (Blume) Kunze, *O. ciliata* Kuhn, *O. Clemensiae* Copel., *O. colubrina* (Blanco) Copel., *O. cuspidata* Baker, *O. Herrei* Copel., *O. hirtella* Kunze, *O. lanceolata* Copel., *O. maquilingensis* Copel., *O. mollis* C. Presl, *O. nitida* (Copel.) Copel., *O. Parksii* Copel., *O. pistillaris* (Sw.) C. Chr., *O. platybasis* Copel., and *Ophiopteris verticillata* Reinw.

The application of the earliest name remained in doubt until

1

Figure 1. Habit of *Oleandra neriiformis,* terminal portion of erect stem, × ca. 1/4, adapted from *Kalkman 4005* (A), New Guinea.

Christensen (1937) published on the original material at Madrid. This is the most abundant and most widely distributed species among those treated. Distinctive characters are the radially symmetrical aerial stem, the monomorphic leaves, and the sori that are borne away from the margin. Merrill (1918) and Price (1973)



Figures 2–4. 2. Portion of a stem of *Oleandra neriiformis,* with many phyllopodia, × 1/2, *Webster 14181* (GH), Fiji. 3. *Oleandra Werneri,* portion of sterile lamina (left) and fertile lamina (right), both × 1, *Brass 12841* (A), New Guinea. 4. Arcuate internode of *O. musifolia,* base of petioles (above, at left), × 1, *Molesworth-Allen 2418* (A), Sumatra.

both treated *Blechnum colubrinum* (*Oleandra colubrina*) as a synonym of *O. neriiformis.*

Oleandra cuspidata was considered a valid species by Copeland (1940) who noted characters of the species as: "indusium small and fugacious" and "minute and fugative, not to be detected on most specimens in the herbarium." The material is probably not exindusiate, the size and persistence varies, and a small fugacious indusium may be undetected among the mature sporangia as Copeland indicated.

The above synonymy mostly involves the species of Copeland, mainly because he tended to recognize minor variants. This rationale may have value in evolutionary studies, but not in taxonomic studies. In his Samoa study, Christensen (1943) rightly indicated, "After a careful examination of numerous specimens I find the differences between the forms, briefly characterized below, rather insignificant and inconstant, and I do not hesitate to refer them all to *Oleandra neriiformis* and to refer Copeland's three Fijian species to the same. The forms run together and even a grouping of the forms is difficult."

Among the specimens of *Oleandra neriiformis* that I have seen, the following are variants toward *O. Werneri*: *Brass 5466,* New Guinea (GH, NY); *Brass 31002,* New Guinea (GH); Rosenstock Exssic. *132,* New Guinea (GH, NY); and *Kajewski 537,* New Hebrides (GH).

The species is usually terrestrial or epiphytic, but sometimes lithophytic. When terrestrial, the erect aerial stems may grow to 2 m in height although they are usually 1–1.5 m tall, and they have a shrublike habit. The habit of the species when it grows as an epiphyte is uncertain. It grows from 50–2200 m, mostly above 1000 m, in northern India and southwest China (Yunnan), Burma, Vietnam, Malaysia and through Indonesia to the Philippine Islands and to New Guinea, and in the Pacific to American Samoa.

2. Oleandra Werneri Rosenst. Figure 3.

Oleandra dimorpha Copel. and *O. subdimorpha* Copel.

The strongly dimorphic leaves and the very narrow, long and falcate fertile leaves make this a distinctive species. The radially symmetrical aerial stem (and presumably the creeping underground stem) link this species with *Oleandra neriiformis.* The fertile lamina is usually more than twice as long as the sterile one. Sometimes the indusia project beyond the sterile tissue, which may be reduced, especially toward the base of the fertile lamina.

The specimen *Van Royen 3644* (A), from New Guinea, has only several fertile leaves, the sori are somewhat back of the margin, and the fertile lamina is shorter and broader than usual in this species. In the latter two characters this resembles *Oleandra subdimorpha.* This specimen and some others with aberrant fertile leaves: *Brass 2916,* Solomon Islands (GH) and *Brass 6886, 11870,* both New Guinea (GH), may represent hybrids with *O. neriiformis* or, more likely represent variants of *O. Werneri.*

The species is epiphytic, rarely terrestrial, and it grows from ca. 50–1800 m, usually above 1200 m, in New Guinea, New Ireland, New Britain, and San Cristoval (Solomon Islands).

3. Oleandra musifolia (Blume) Kunze, originally as *musaefolia.* Figure 4.

Aspidium Moritzii Kunze, *A. musifolium* Blume, *Oleandra benguetensis* Copel., *O. hainanensis* Ching and Wang, *O. Moritzii* (Kunze) Kunze, *O. scandens* Copel., and *O. Wangii* Ching.

The species is characterized by the long and arcuate, dorsiventral aerial stems with their scales straight and fully appressed, and by the short phyllopodia that are usually concealed by the scales. Relations, based on the dorsiventral stems, seem to be with *Oleandra Wallichii,* a species often of higher altitudes. Similarity is also shown with *O. undulata,* a terrestrial species also with dorsiventral stems. *Oleandra musifolia* may possibly be a progenitor of these two.

The species is usually lithophytic, but sometimes terrestrial or epiphytic. It grows from 250–1800 m in northwestern India and Nepal, southeastern China, to southern India and Sri Lanka (Ceylon), through Indonesia (Sumatra to Timor), also the Philippine Islands, Thailand (Siam), and northeastern Australia (Queensland).

4. Oleandra Wallichii (Hooker) C. Presl Figure 5.

Aspidium Wallichianum Bory ex Bérlanger, Voy. Bot. 2: 56. 1833 (*nom. superfl.* for *A. Wallichii* and with the same type; the illustration, Pl. 5, is clearly *Oleandra neriiformis*; not Sprengel, 1827). *Aspidium Wallichii* Hooker, *Neuronia asplenioides* D. Don (*nom. superfl.* for *A. wallichii* and with the same type).

This species has few synonyms, perhaps because it was described and figured early and the type material (*Wallich,* Nepal) was widely distributed. It is found at elevations nearly 1000 m higher than other species. The squarrose-paleaceous stems are

Figures 5–7. 5. Portion of squarrous-paleaceous stem of *Oleandra Wallichii*, *Feng 3307* (A), China. 6. Long phyllopodia of *O. undulata*, one phyllopodium at extreme right, one at left, others with part of the petiole, × 1, *Rock 2026* (NY), Burma. 7. Portion of stem of *O. Sibbaldii*, × 1, *Brass 29706* (A), New Guinea.

diagnostic for this species among its relations that have a dorsiventral stem.

Oleandra Wallichii grows as an epiphyte or a lithophyte at relatively high altitudes, 1100–3300 m, in the Himalayas of northern India and China (Yunnan), to Assam, in the mountains of northern Vietnam, and in Taiwan.

5. Oleandra undulata (Willd.) Ching Figure 6.

Oleandra Cumingii J. Sm., *O. intermedia* Ching, *O. macrocarpa* C. Presl, *O. pubescens* Copel., and *Polypodium undulatum* Willd.

The application of the name follows Ching (1933), although it seems that the holotype, consisting of two sterile leaves, is not clearly identifiable. This taxon is tentatively kept at the rank of species with the expectation that as more material becomes available it can be distinguished more clearly from *Oleandra Wallichii.* The most distinctive form of *O. undulata* has a short, coriaceous lamina; the sori are near the costa; the base of the lamina is cuneate; and the phyllopodia are long. However, it is difficult to distinguish some variants that resemble *O. Wallichii.* The undulate margin of the leaf is not a useful character because the wavy condition is not uniform along the margin, and the character also occurs in other species. Holttum (1968) has clarified the identity of *Cuming 60* (PRC). This material is a mixture; a fertile leaf with immature sori is clearly *O. Cumingii,* while a fertile leaf with large mature sori is *O. macrocarpa.* The creeping, terrestrial habit of this species may be derived from *O. musifolia.*

The species is usually terrestrial, but sometimes it is a lithophyte or rarely an epiphyte. It occurs from 100–1100 m in China (Yunnan) to southern India, and eastward in Thailand (Siam), Laos and Malaysia, to the Philippine Islands.

6. Oleandra Sibbaldii Greville Figure 7.

Oleandra crassipes Copel., *O. gracilis* Copel., *O. vulpina* C. Chr., and *O. Whitmeei* Baker, originally as *Whitmei.*

This distinctive species is recognized by the light brown to reddish brown stem scales that are not appressed. Many of the scales are deciduous so that the stem surface may be exposed in some places. The species resembles *Oleandra Bradei* of Costa Rica in the deciduous character of the scales. Although *O. vulpina* has been considered as a possibly exindusiate species, it is treated here as a synonym of the indusiate *O. Sibbaldii.* A small, fugacious indusium may be undetected among mature sporangia. The sheet of *Craven and Schodde 1123* (A) probably represents a hybrid with *O. Werneri* as shown by the sori near the margin and the fertile leaves longer than the sterile ones.

Plants are usually epiphytic, or rarely terrestrial, from 950–2450 m, mostly above 1200 m. It is found in the Philippine Islands, Celebes (Sulawesi), Borneo Island, New Guinea, and eastward in the Pacific to Tahiti and the Marquesas.

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FLORISTIC INVENTORY OF THE WACCASASSA BAY STATE PRESERVE, LEVY COUNTY, FLORIDA

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ABSTRACT. A floristic inventory of the Waccasassa Bay State Preserve in southwestern Levy County, Florida was conducted from April 1996 to December 1997. The 12,488 ha (30,849 acres) Preserve yielded vouchers for a total of 2 charophytes, 24 liverworts, 29 mosses, 43 macrolichens, and 576 vascular plants. Of the vascular plants, there is 1 lycopsid, 12 ferns, 1 cycad, 4 conifers, and 555 angiosperms, 178 of which are monocots. Sixty-nine species are nonindigenous, and 73 species are recorded for the first time from Levy County. Seventy-two species are at or near their northern or southern limits, 18 species have disjunct distributions or very restricted ranges in Florida, and 16 species are Florida endemics or near-endemics. Five natural plant communities, as well as ruderal areas, were recognized based on field observations: tidal marsh, coastal hydric hammock, freshwater pools, basin swamp, and mesic to scrubby flatwoods. Treatment of the coastal hydric hammock as a single highly variable community, as opposed to a mosaic of intermixed communities, was supported by a limited quantitative analysis.

Key Words: Waccasassa Bay, Levy County, floristics, phytogeography, plant communities, Florida

Waccasassa Bay State Preserve is located within the Gulf Hammock in southwestern Levy County, Florida (Figure 1). The Gulf Hammock area, at the southern end of the Big Bend region of Florida, is one of the largest, relatively undeveloped, continuous forests remaining in the state. Gulf Hammock abuts the Gulf of Mexico and is roughly bounded on the north by S.R. 24 and on the east by U.S. 19, with the southern boundary running somewhat parallel to and just north of the Withlacoochee River. The Waccasassa Bay State Preserve is a relatively thin strip that occupies most of the coast of the Gulf Hammock region, with 56 km (35 mi.) of indented shoreline (WBSPR 1997). Tidal marsh and coastal hydric hammock dominate the 9745 ha (24,070 acres) of the terrestrial portion of the Preserve (Figure 2). An additional 2743 ha (6775 acres) are submerged almost entirely by brackish salt water, for a total of 12,488 ha (30,849 acres) in the Preserve

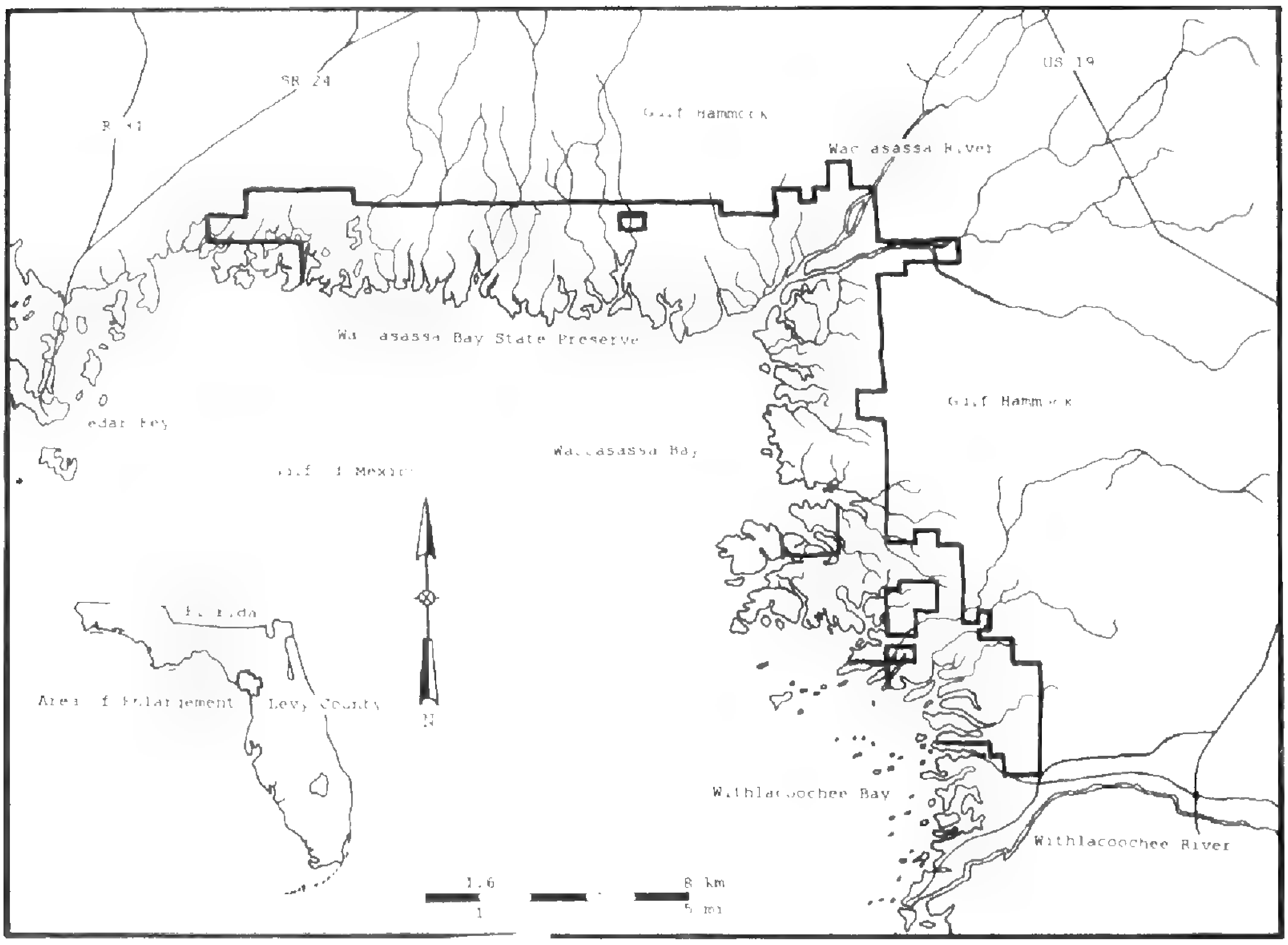

Figure 1. Map of Waccasassa Bay State Preserve and the Gulf Hammock region in southwestern Levy County, Florida.

(WBSPR 1997). During this study, an additional 24 ha (60 acres) at the southern end of the Preserve were purchased. Several additional parcels of land that are slated for purchase would greatly contribute to the extent and diversity of the more inland plant communities (WBSPR 1997).

The Gulf Hammock Wildlife Management Area was established in 1948 (Swindell 1949) and included the area of the more recently established Waccasassa Bay State Preserve. The Preserve was opened in 1972 from land purchased in 1971. Most of the Preserve is surrounded by various hunt clubs on land leased from Georgia-Pacific Railroad, the largest landholder in the Gulf Hammock. A few private inholdings remain within the Preserve. Numerous undeveloped roads transect the Gulf Hammock area, with some of them providing access to gates along the inland boundary of the Waccasassa Bay State Preserve. Public access into the Preserve, however, is legal only by water.

The Florida Department of Environmental Protection (DEP), Division of Recreation and Parks, District 2, manages the Preserve with the principal mission of protecting natural habitat to

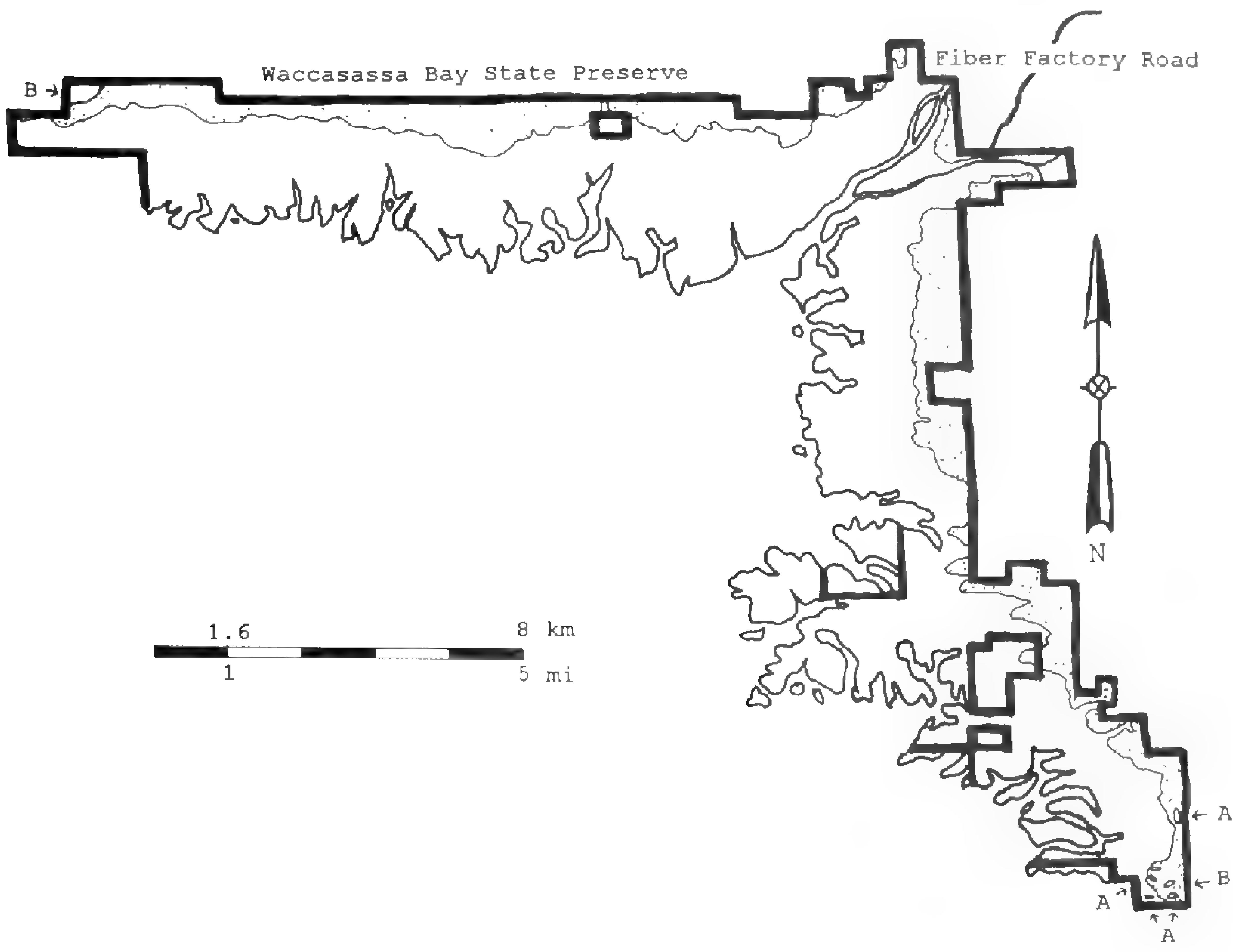

Figure 2. Map of Waccasassa Bay State Preserve, with delimited plant communities. Thick lines within outer boundaries mark private inholdings. White areas are tidal marsh, stippled areas are coastal hydric hammock, "A" represents mesic to scrubby flatwoods, and "B" represents basin swamp.

ensure the survival of rare and endangered plants and animals. The objectives of this floristic study were to document the current flora with representative voucher specimens, to describe the variation and distribution of the plant communities, and to provide a baseline of botanical information for management and field use by DEP personnel and other researchers.

Soils, geology, and physiography. Florida's land area is the highest portion of a plateau that is mostly submerged in the Atlantic Ocean and the Gulf of Mexico. Past sea level fluctuations have variously covered or exposed parts of the Floridian plateau, which is of volcanic origin and now has a deep limestone foundation underlying much of the shallow surface soil (Matter 1990).

The Gulf Hammock region has a low-energy coastal environment without adequate sand to sustain beaches or dunes (Burnson et al. 1984). Very poorly drained, frequently flooded, strongly saline soils of the Tidewater and Cracker series support tidal marsh throughout the Preserve. These mucky soils were formed in loamy and clayey marine sediments underlain by limestone (Slabaugh et al. 1996). Soils of the Wekiva, Demory, and Waccasassa series occur throughout the nontidal Preserve. These poorly drained soils are shallow to moderately deep and were formed in sandy and loamy marine sediments underlain by limestone (Slabaugh et al. 1996).

Inland, the depth of the sandy soil mantle varies in thickness over short distances, related to irregularities in the underlying limestone (Rupert 1988). Field observations by the first author suggest that there may be a trend for the areas of thickest sand to support mesic to scrubby flatwoods, but there is no correlation between this community and areas demarcated on the soil maps of Slabaugh et al. (1996).

Geological formations underlying the uppermost surface Pamlico formation deposits (Pleistocene), in descending order, are the Ocala Group, Avon Park and Lake City Limestones (all Eocene), and Cedar Key Limestone (Paleocene; WBSPR 1997). The Pamlico Terrace is highly varied, due largely to depositional and later erosional patterns, and includes irregular patches of sand or sandy clay illuvium, brackish-water clay or sand and marl; pasty, sandy, nonfossiliferous limestone; and sandy, coquina marl and locally dolomitized marly sand (WBSPR 1997). Rock outcrops, primarily of the uppermost Ocala member of the Ocala group of limestones, are common in the Preserve.

Physiographically, the north peninsular Gulf coast of Florida lies within the Terraced Coastal Lowlands, a broad, flat, topographical subdivision of the Coastal Plain, that comprises sandy, Pleistocene shoreline deposits and erosional, Eocene limestone surfaces (Vernon 1951). Alternatively, the area also is seen as part of the Gulf Coastal Lowlands of the Mid-peninsular Physiographic Zone (Rupert 1988). Following Vernon (1951), the Preserve is entirely within the Pamlico Terrace, an ancient coastline roughly demarcated by the 8 m (25 ft.) elevation line. According to Swindell (1949), the Pamlico Terrace is not recognizable in the Gulf Hammock, and there is no corresponding change in vegetation as it intergrades with the Talbot Terrace, an even older coastline with elevations up to about 30 m. Vernon (1951) further recognized the Preserve area as part of the Coastal Marsh Belt, with a Limestone Shelf and Forested Hammocks zone along the inland edge. Rupert (1988) included the Pamlico Terrace in his more broadly defined Limestone Shelf and Hammocks zone, although he still recognized a Coastal Marsh Belt.

In the Preserve, the coast is often rocky, but marshy, with numerous bays and inlets. Scattered islands dot the shoreline in and near the Preserve. These are not true barrier islands, but were formed as the Gulf of Mexico inundated the coastline, cutting off relic Pleistocene sand dunes and isolating elevated areas from the mainland.

Terrain within the Preserve grades slowly from sea level to about 1.5 m (5 ft.) in places along the inland boundary (WBSPR 1997). Especially near the coast, there are superficial rock beds that are much-eroded and pitted by solution. This karst topography, derived from porous Eocene marine limestones, is an important part of the present-day continental shelf of Florida. Two large springs in the Waccasassa River Basin and scattered small sink-holes provide evidence of the importance of karst topography in the hydrology of the region.

Hydrology. Salt water and coastal climate influences are probably the most important elements that define the floristic communities in the Waccasassa Bay State Preserve. However, most, if not all, truly marine areas lie outside the legal boundaries of the Preserve, which does not include coastal waters. There are numerous inlets which may harbor pockets of marine communities interspersed with estuarine communities. The distinction between marine and estuarine communities relies on the amount of dilution by fresh water, so there is obviously no sharp line of differentiation. There are three sources of fresh water within the Waccasassa Bay State Preserve: rainfall, the Floridan aquifer, and several streams and rivers that all eventually drain into the Waccasassa Bay estuary or Withlacoochee Bay at the southern end of the Preserve.

The Floridan aquifer is a regionally unconfined water table diffused throughout pockets in porous Eocene limestones. Since the uppermost layer of the aquifer, the Ocala Group deposits, are locally exposed, the water table is also at or near the surface throughout the area (Conover et al. 1984). This high water table, in conjunction with the flat terrain, leads to quick soil saturation and surface flooding, which can take weeks to drain after a major storm (Suwannee River Water Management District [SRWMD] 1991). Numerous freshwater pools and wet depressions throughout the forested Preserve are maintained by rainfall. Discharge from the aquifer and rainfall can lead to sheet flow of water across much of the forested Preserve. In the Preserve and in the Gulf Hammock area, the water table discharges via seepage, and it is recharged through direct infiltration of rainwater (Rupert 1988). As suggested by Williams et al. (1997), it is possible that this aquifer discharge is, in part, responsible for locally reducing salinity and maintaining islands of nonhalophytic species in scattered areas near the inland edge of the Preserve's tidal marsh.

All streams north of the Waccasassa River, and a few associated tributaries to the south, are within the jurisdiction of the Suwannee River Water Management District (Burnson et al. 1984). Streams in the southernmost portion of the Preserve lie within the Southwest Florida Water Management District (Waldron et al. 1984). There are 44 named streams and rivers that occur entirely or partially within the Preserve (WBSPR 1997). The most important of these, because of its large drainage basin, is the Waccasassa River, which drains a total of 2424 km^2 (936 mi.^{2}; SRWMD 1991). The Waccasassa River begins as a poorly defined channel connecting swamps and ponds in the Waccasassa Flats of Gilchrist and Alachua Counties and becomes a recognizable channel west of Bronson, well into Levy County. Generally, the Waccasassa River flows to the southwest, where it is fed by Blue Springs and joined by Wekiva Creek, which is fed by Wekiva Springs. Otter Creek and Cow Creek, which is joined by Ten Mile Creek, also flow into the Waccasassa River. Numerous other freshwater creeks and tidal channels drain the western and southern portions of the Preserve.

Estuarine conditions prevail along the north peninsular Gulf coast of Florida due to shallow coastal waters with abundant freshwater discharge from shore. The Waccasassa River and numerous small drainages are the primary sources of fresh water within the Preserve boundary. Cedar Key and nearby islands roughly mark the western limit of the Preserve, but actually have the Suwannee River as the main factor controlling their estuarine habitats (Wolfe 1990). The Withlacoochee River, although barely south of the Preserve, has its entire drainage outside the Preserve, and its freshwater discharge affects only the southernmost portion of the Preserve.

The Waccasassa Bay system is an estuary at the mouth of the Waccasassa River, the largest source of freshwater in the Gulf

Hammock. The bay has an average depth of less than 1 m (3 ft.) at mean low tide. Both the Waccasassa Bay and the Withlacoochee Bay often have a depth of less than 1.5 m (5 ft.) for many miles away from the coast, although there are deeper channels that reflect old stream courses (Swindell 1949). There is no distinct line of separation between the Waccasassa Bay and the Withlacoochee Bay, and both are part of the Big Bend Seagrasses Aquatic Preserve. Tides are primarily diurnal, with a mean range of 0.8 m (2.6 ft.; Hine and Belknap 1986). Tidal influence extends several miles inland along creeks, which support tidal marsh species rather than forested riverine swamp throughout the Preserve.

Coastal waters are multi-use areas and can be negatively impacted by waste discharge, urban runoff, shoreline development, and marine traffic. In the Waccasassa Bay, there are 18,949 ha. (46,800 acres) of approved shellfish harvesting waters, with oyster species offshore and in subtidal and intertidal areas (Gunter et al. 1992). Numerous homes and small developments are present in the Gulf Hammock area, but most are far from inland shorelines along rivers and streams because of the expansive swampy areas. Primary waterfront developments include Williams Camp on the Waccasassa River, Lebanon Station on Ten Mile Creek, and Gulf Hammock on the Wekiva River and Mule Creek. Otter Creek, Bronson, and Usher are in the Waccasassa River drainage basin but not near surface waters (Gunter et al. 1992). Other small towns in the region that serve as possible sources of pollution and disturbance include Cedar Key, Ellzey, Inglis, Rosewood, Sumner, and Yankeetown. The most probable major source of pollution and disturbance near the Preserve comes from extensive logging in the adjacent Gulf Hammock. Clear-cutting could potentially alter surface water flow or lead to contamination via surface runoff, and possible impact should be closely monitored.

Climate. Levy County is at the southern limit of the continental temperate zone, and has a peninsular subtropical climate in coastal areas (Jordan 1984). Summers are long, warm, and humid, while winters are mostly warm but with invasions of cool air from the north (Slabaugh et al. 1996). Relative humidity is often high, with an annual mean of 78% (Swindell 1949). Average relative humidity varies from about 55% in mid-afternoon to about 90% at dawn (Slabaugh et al. 1996). During the summer season, humid breezes from the Gulf of Mexico lead to frequent summer convection storms of high intensity, short duration, and limited extent. Although lightning is a frequent component of these summer storms, the hydrology and the sparse understory contribute to the virtual nonexistence of wildfires in the area (Swindell 1949). From November to February there are prevailing northwesterly to northern winds which bring frontal systems into the area, with precipitation of low intensity, long duration, and wide coverage (Chen and Gerber 1990).

Levy County had an average annual rainfall of 127 cm (50 in.) from 1841 to 1949 (Swindell 1949). During the same time period, at Cedar Key, just west of the Preserve, the average annual rainfall was 119.4 cm (47 in.), but it varied from 68.6 cm (27 in.) to 210.8 cm (83 in.; Swindell 1949). These extremes are similar to those more recently reported for the region, namely, 78.7 cm (31 in.) and 222.3 cm (87.5 in.; Jordan 1984). Within the Waccasassa River Basin, the average annual rainfall from 1977–1989 was 158.8 cm (62.5 in.; SRWMD 1991). These data support the broadly generalized maps of Jordan (1984) and Tanner (1996), which showed several different patterns of rainfall in the Gulf Hammock region. Thus, on average, the westernmost portion of the northern Preserve may receive up to 20 cm (8 in.) less rain annually than the easternmost inland portion of the Preserve. Ironically, it is in this westernmost corner of the northern Preserve that the most well-developed and extensive swamps occur. This surely must reflect drainage patterns and not the direct rainfall patterns.

For the entire region, there is a pronounced rainy season from June to September, during which time 50–60% of the mean annual rainfall occurs. Up to a third of the average annual rainfall often comes in September alone, in conjunction with tropical storms and hurricanes (Jordan 1984). The national record for the most rainfall in a 24 hour period occurred at the southern end of the Preserve in Yankeetown on 5–6 September 1950, with 98.3 cm (38.7 in.). Less than 25% of the yearly rainfall occurs from December to March (Jordan 1984). Relatively severe drought occurs in the spring every 8–10 years on average, infrequently lasting into the early summer (Burnson et al. 1984). The impact of occasional dry spells is probably less defining for the area than the frequent periods of inundation.

At Cedar Key, the average annual temperature is 22.2°C (72°F;

Burnson et al. 1984). From 1841–1949, the average January temperature was 14.7°C (58.4°F), with an extreme low of −9.4°C (15°F; Swindell 1949). During the most severe cold snap in this century, on 21–22 January 1985, temperatures dropped as low as −12.2°C (10°F) in the area (Tanner 1996). The average July temperature at Cedar Key was 27.7°C (81.8°F), with an extreme high of 38.3°C (101°F; Swindell 1949). On average, 100–150 days a year reach a maximum of 35.6°C (88°F) or higher (Tanner 1996). Freezing temperatures, on average, occur 29 days per year (Slabaugh et al. 1996). Frost-free seasons were noted for 6 of 34 years of data from Cedar Key (Swindell 1949).

Average climatic patterns may typify an area, somewhat determining the vegetation, but extremes of hydrology and climate are probably more important for determining actual species composition. Major disturbances, such as hurricanes, though rare, are also important in defining plant community structure and often eventually lead to environmental heterogeneity and increased species richness. Hurricanes occur mostly in the fall, from August to October, with strong winds and often with torrential rains. Sometimes two or three major storms hit or pass near the Preserve in a single year, but usually there are many years between hurricanes that severely impact the area (Matter 1990). Only five hurricanes have hit the coast near Cedar Key since 1871 (Ho and Tracey 1975). A weak tropical storm that hit Cedar Key in October 1941, produced 89 cm (35 in.) of rain inland in just 48 hours (Tanner 1996). Frontal systems in the winter and spring can also lead to dramatic flooding and tidal surges. Given the flat terrain, the high water table, and the far-reaching impact of tidal surges, even a relatively minor storm can flood the area or carry salt water relatively far inland, thus affecting species composition.

Gulf of Mexico currents reportedly moderate the coastal climate, leading to slightly warmer winters and slightly cooler summers along the coast, on average, than are found inland (e.g., Jordan 1984). The depth of inland penetration and the full extent of this current-related climate moderation are questionable, and such moderation must be highly variable locally. Several subtropical plant species at their northern limit are present on coastal islands in the area, while they are absent inland. The dynamic interactions in the area between varying hydrological and climatic extremes contribute to the confusing mosaic of ecotonal plant associations that dominate much of the forested Preserve.

HISTORY

The Waccasassa Bay State Preserve was created in 1972. The Preserve is south of the Suwannee River, well north of Tampa Bay, and just east of Cedar Key, three well-known areas with long histories of human occupation. Historical detail can be found elsewhere [see especially Gannon (1993, 1996), George (1989), Jennings (1951), Milanich (1994, 1995), Swindell (1949), Tebeau (1971), and Webb (1990)], and is summarized in Abbott (1998).

The Gulf Hammock Wildlife Management Area (ca. 40,470 ha. or almost 100,000 acres) was created in 1948, and included all of the land now considered part of the Waccasassa Bay State Preserve. Prior to the Civil War, there was a sugar cane plantation 2 miles south of the community of Gulf Hammock and another on the south bank of Ten Mile Creek. Both of these plantations were just east of the current Waccasassa Bay State Preserve, and both were abandoned at the end of the Civil War, although the latter area had minor farming until around 1900. In the late 1940s, Swindell (1949) found the farmed area to be indistinguishable from surrounding forested areas, suggesting rapid regeneration.

Traditionally, people in the Gulf Hammock area mainly had small gardens and free-ranging livestock. Agriculture has been little-practiced due to the region's poor drainage and shallow soils underlain by limestone. Cattle and hogs were found throughout the area, even well into salt marsh (Swindell 1949). There were large herds of cattle in the area even before 1900. Cattle grazing and hog disturbance, while still common in the Gulf Hammock proper, have been somewhat controlled by fences along much of the boundary of the Waccasassa Bay State Preserve. Signs of hog-rooting were observed only in one part of the northern Preserve, and cows were seen to have breached the fence only in an area south of the Waccasassa River.

Records exist of as many as 20 different lumber companies in the Gulf Hammock area, but specific details are poor or lacking. Some evidence does exist of the impact, as compiled by Swindell (1949) and Jennings (1951), based primarily on oral interviews and old aerial photographs. Bald cypress was logged from swamps shortly after the Civil War. Almost all of the coastal hammock was cut over for southern red cedar and cabbage palm. Red cedar was cut, especially for pencils, from 1875 until about 1920, with mills at Cedar Key and along the coast. Cabbage palms were cut for fiber made from the bud, starting around 1900 and still ongoing as late as 1949. There was a fiber mill on Cow Creek around 1900. During the peak activity, an estimated 100,000 plants were being cut a year. Hardwood logging started later, and probably peaked in the 1920s after most of the cypress and cedar were gone. Numerous logging roads were established in the early 1950s in the areas of driest, firmest soil. Mesic hammocks were more severely affected by logging than were hydric hammocks due to the larger number of suitable timber trees. Swamp trees were rarely cut in the early 1950s since cypress, ash, and swamp tupelo were already largely gone. Logging in Gulf Hammock continues to the present, with logging in the area of the current Preserve possibly into the 1940s or 1950s. Remnants of old logging roads can still be seen, but there is virtually no overland vehicular access within the Preserve now. Presently, many pine stands within the Preserve are being cut in an effort to control a southern pine beetle infestation (*Dendroctonus frontalis*). This disturbance will undoubtedly have a profound impact on plant community structure in the affected areas.

Human activity is by no means the only kind of disturbance that affects plant community composition in the area. Root systems are shallow due to the thin soil underlain by limestone, and heavy winds and storms often blow down large numbers of trees. As mentioned previously, hurricanes sometimes hit the area and, occasionally, severe northern frontal systems come through during the winter or spring. The aftermath of one such storm was witnessed in the spring of 1996 when the first author saw numerous large treefall areas and debris as high as 2 m throughout much of the forest just inland from the salt marsh. One local resident reported an 8 ft. water surge at his house over a mile from the coast.

Despite the relatively recent development (in the last 3000 years) of the current mesic habitats in the Preserve area, the coastal hydric hammock found in the Gulf Hammock area contains virtually all of the diversity and variation known in hydric hammocks found elsewhere in Florida (Vince et al. 1989). It is possible that the area served as a refugium of sorts, as there are a few regionally endemic (or near endemic) animals and plants: *Elaphe obsoleta williamsi,* a type of rat snake described from Gulf Hammock; *Microtus pennsylvanicus dukecampbelli,* the Florida salt marsh vole known only from one location just west of the Preserve (SRWMD 1991); *Pseudobranchus striatus lustricolus,* a subspecies of salamander described from Gulf Hammock, in stagnant mucky water (Neill 1951); and *Spigelia loganioides, Phaseolus smilacifolius,* and *Phyllanthus liebmannianus* ssp. *platylepis.* Additionally, at least two other plant species uncommon in Florida are present in great abundance within the region, namely, *Leitneria floridana* and *Ulmus crassifolia.*

PLANT COMMUNITIES

"Unlike the rest of Florida, much of the north peninsular coastline has not been ditched, diked, graded, filled, or otherwise altered by modern development, giving us a glimpse of what a soggy place the Gulf coast of Florida used to be" (Milanich 1994, p. 210).

An excellent, detailed, ecological characterization of Florida's northern peninsular Gulf coast region was provided by Wolfe (1990). Thompson (1980) described the forest vegetation in the northern Gulf Hammock. Plant communities within the Gulf Hammock area, of which the Waccasassa Bay State Preserve is a part, were described in detail by Jennings (1951), Pearson (1951), and Swindell (1949). Although their studies were zoological in nature and some of their plant identifications, unfortunately unvouchered, are certainly questionable, our own observations largely support their plant community descriptions, which were mostly of areas further inland than the Preserve. Much of the Gulf Hammock floods regularly, altering the species composition somewhat from that typically found in standard community descriptions used elsewhere in the state. Nonetheless, all of the above Gulf Hammock workers described separate coastal, mesic, and hydric forested communities, recognizing that they usually occurred as a mosaic of poorly defined, intermixed small patches. Jennings (1951) captured the essence of the first author's early attempts to understand the vegetation when she wrote that there was "a multiplicity of ecotones, succession stages, and other confusing plant aggregations in the area." As Swindell (1949) pointed out, the size of the area precludes complete field-reconnaissance, and it is almost impossible to distinguish similar communities in the area using aerial photos. Thus, it is likely that undiscovered pockets of vegetation may vary in composition from the descriptions provided here.

In order to make our work maximally useful to other workers in Florida, we followed the community types outlined by the Florida Natural Areas Inventory and Florida Department of Natural Resources (FNAI and FDNR 1990), with one exception as noted later. Our emphasis was on the recognition of plant communities that are discernable based on species composition and not based on potential differences in hydrology related to microtopographical variances.

Five natural communities, in addition to ruderal areas, are here recognized within the Waccasassa Bay State Preserve: tidal marsh, coastal hydric hammock, freshwater pools, basin swamp, and mesic to scrubby flatwoods (Figures 3 and 4). Tidal marsh is the only floral-based group in the Preserve within the combined FNAI marine-estuarine categories. Seagrass beds exist just outside the coastal boundary and are described here as they reportedly occur in scattered localities within the many shore inlets (SRWMD 1991). In the FNAI palustrine category, the basin wetlands group is represented by basin swamp, and the wet flatlands group is represented by a type of hydric hammock. Here, we deviate from the FNAI community description and recognize coastal hydric hammock, following Vince et al. (1989). The term hammock, used primarily on the coastal plain of the southeastern United States, refers to an area of hardwood trees, often in an otherwise treeless or pine-dominated area. Scattered throughout the hydric hammock were numerous freshwater pools not assignable to an FNAI community, yet they were ecologically and floristically distinctive. Finally, in the FNAI terrestrial category, the mesic flatlands group was represented by a mixture of mesic and scrubby flatwoods. Upland mixed forest (synonym: mesic hammock) was frequent just outside of the inland Preserve boundary and is described here since small patches of vegetation transitional to upland mixed forest occur along the inland margin of the Preserve. Ruderal areas can occur within any of the communities but are recognized by their "weedy" aspect, often with signs of human disturbance and nonindigenous plant species.

Even FNAI and FDNR (1990) admit that "FNAI classification is perhaps more often useful . . . in potential natural vegetation rather than existing vegetation" and that community lines are often obscure in the field. As explained below, several other FNAI communities could possibly be recognized within the Preserve, but it is our judgement that the area is best described as a


A
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relatively thin coastal strip, predominantly with tidal marsh zones in nonforested areas and highly variable coastal hydric hammock in forested areas. The lack of several distinctive forest communities, as described by others in the Gulf Hammock area, though at first confusing, was eventually understood as a reminder of the arbitrariness of plant community delimitation and of the continuum that often exists between different communities.

All of the FNAI marine-estuarine communities were present along the coastal edge of the Preserve, but the mineral and faunal based community groups were outside the scope of this study, as were algal beds. Tidal swamp (synonym: mangrove forest) did not exist per se, but there were several coastal island areas in the southern portion of the Preserve where black mangrove (*Avicennia germinans*) could be found.

The difference between terrestrial and palustrine systems is that palustrine systems have soil that is inundated or saturated for more than 10% of the growing season, resulting in plant communities that are adapted to regular periods of anaerobic soil conditions (FNAI and FDNR 1990). As mentioned earlier, much of the Preserve and adjacent Gulf Hammock flooded regularly, and the species composition was different from that typically found in similar communities elsewhere in the state. Thus, in an area like the Preserve where widespread inundation followed every storm and heavy rain, the distinction between terrestrial and palustrine systems may not be real or meaningful. Nonetheless, flatwoods and swamp are here recognized as they appeared to be more or less distinct from coastal hydric hammock in a few areas within the Waccasassa Bay State Preserve.

Following terminology of the Florida Natural Areas Inventory, the forested Preserve could be described as an inseparable complex mosaic of northern maritime hammock (synonym: coastal

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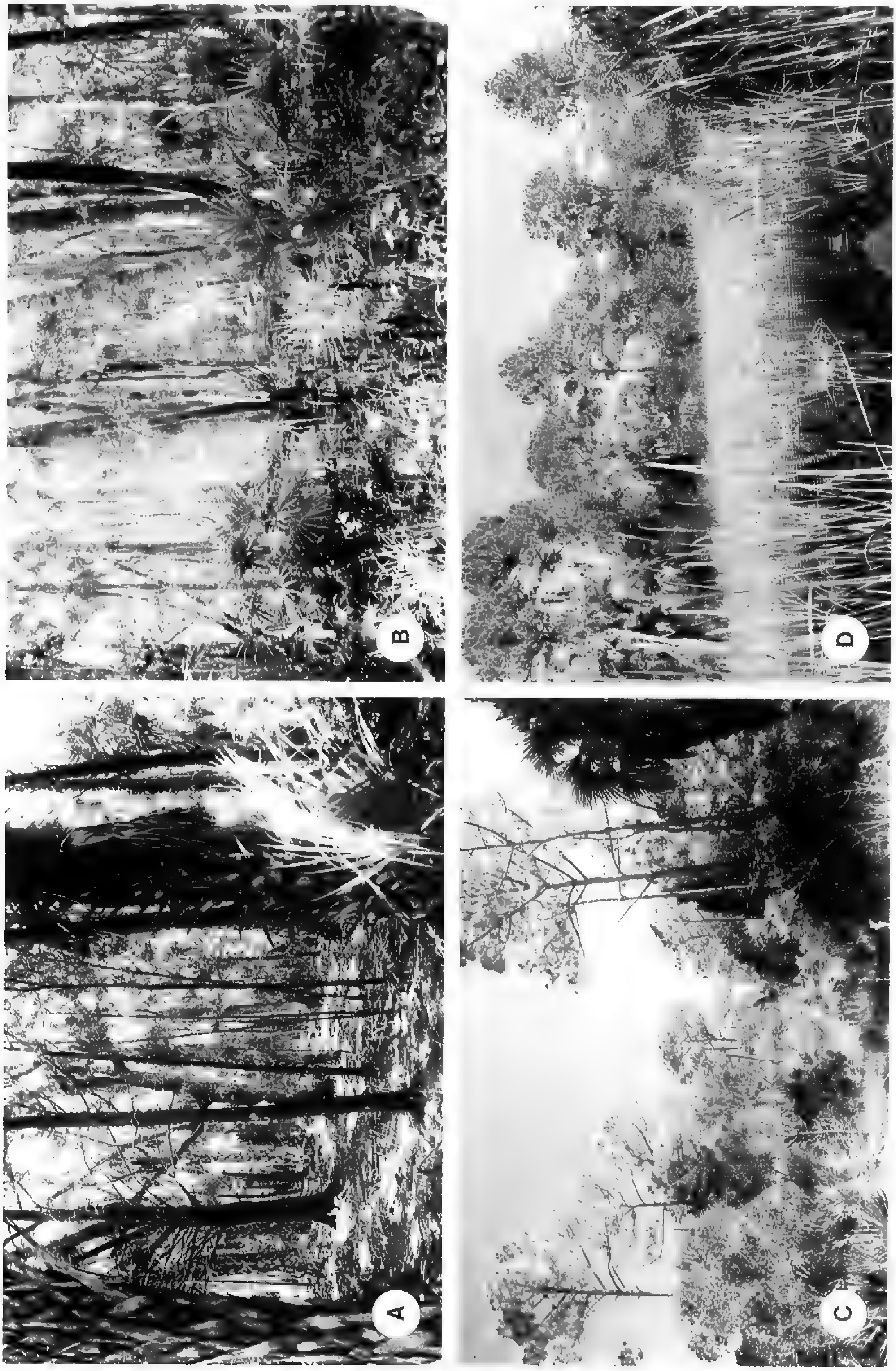
Figure 3. Plant communities nearest the coast. A. Tidal marsh abutting coastal hydric hammock near Turtle Creek, dominated by *Juncus roemerianus*; low foreground with *Batis maritima* and *Salicornia perennis*. B. Tidal marsh in southern Preserve, showing tidal channel and *Avicennia germinans*. C. Waccasassa River, banks dominated by *Juniperus virginiana* and *Sabal palmetto*. D. Brackish water pool in southern Preserve; banks dominated by *Juncus roemerianus*, with *Claduim jamaicense*; background shrubs are *Baccharis halmifolia*; background trees are *Pinus taeda*.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hammock), mesic hammock, hydric hammock, basin swamp, and several other terrestrial and palustrine communities. In a study of the ecology of hydric hammocks throughout Florida, Vince et al. (1989) recognized the Gulf Hammock region as having its own distinctive variant of hydric forest and called it coastal hydric hammock, including much of the variation described as separate intermixed communities by Jennings (1951), Pearson (1951), and Swindell (1949). The first author quantitatively investigated the variance in this plant community and concluded that the majority of the forested Preserve is best treated as coastal hydric hammock, a highly variable plant community where species typical of many different FNAI communities can be found growing in intermixed patches related to microtopography, hydrology, and past disturbance.

Seagrass beds. In areas west and south of the mouth of the Waccasassa River, which had an unconsolidated mud bottom, sparse to dense seagrass beds occurred. No seagrass species were documented within the Preserve boundary during this study, but it is very likely that at least a few populations occurred within the many coastal inlets. The SRWMD (1991) reported the inshore presence of *Halodule wrightii* and *Halophila engelmanni*, although no vouchers have been seen. A total of five species of seagrass have been reported from the general area, with four of them present between the Cedar Key area and the Withlacoochee River (Iverson and Bittaker 1986). *Thalassia testudinum* (turtlegrass) was reportedly the dominant bed-forming species. *Syringodium filiforme* (manatee-grass), *Halodule wrightii* (shoal-

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Figure 4. Plant communites farther inland. A. Coastal hydric hammock near Turtle Creek; dominated by *Juniperus virginiana* and *Sabal palmetto*; understory very sparse, here with scattered *Chasmanthium* spp. and *Panicum* spp. B. Basin swamp in northwestern corner of Preserve; mixed hardwoods as dominants, here with *Liquidambar styraciflua, Fraxinus caroliniana, Quercus laurifolia,* and *Magnolia virginiana*, with *Taxodium distichum*; note the standing water, cypress knees, and an understory with *Rhapidophyllum hystrix*. C. Scrubby flatwoods along boundary trail off Dewey Allan Park Road; canopy of *Pinus taeda*, with sparse *Sabal palmetto*; understory with *Serenoa repens, Ilex glabra, Quercus myrtifolia, Myrica cerifera, Andropogon* spp., *Rhynchospora* spp., and *Liatris* spp. D. Freshwater pool in southern Preserve; dominated by *Typha domingensis*, with *Pinus taeda* in the background.

grass), and *Halophila engelmanni* were also reportedly present, usually in intermixed beds. *Ruppia maritima* (widgeon-grass), a freshwater to estuarine species, was observed by the first author in the bay near the mouth of the Waccasassa River.

Tidal marsh. Coastal areas frequently inundated by salt water and dominated by salt tolerant herbs are known as tidal marsh (synonyms: salt marsh, coastal marsh, brackish marsh). Tidal marsh here is alluvium-poor, with numerous karst features such as creek channels, circular depression ponds, and limestone outcrops. A mosaic of marshes and coastal hammocks has been created by the low-energy karstic coastline, where small changes in elevation, tidal inundation, soil characteristics, and fresh water flow all control vegetation patterns (Wolfe 1990). In the area, there is usually a very broad continuum from near-marine conditions to near-freshwater conditions. The community was often around 1.5 km wide, although it could be up to 5 km wide in areas, due to the very gradually sloping continental shelf. Numerous tidal creeks with oyster reefs and unvegetated intertidal flats interlace with tidal marsh and support it inland along waterways throughout the width of the Preserve. The following description of variation in tidal marsh is based on the first author's personal observations within the Preserve.

The seaward edge of tidal marsh often consisted of *Spartina alterniflora* (saltmarsh cordgrass) stands. Extensive stands of *Juncus roemerianus* (needle rush) dominated most of the area. Other plants in the *Juncus* stands were sporadic and were most frequently *Aster tenuifolius* and *Solidago sempervirens,* with *Lythrum lineare* locally abundant in a few places. Along the edges of needle rush stands, which sometimes occurred in relatively inland habitats, most of the species mentioned below could also be found.

Open flat depressions, often with exposed limestone, are scattered throughout the tidal marsh. These depressions could be completely bare or have mixed to nearly monospecific stands of the following halophytic species: *Salicornia perennis, Batis maritima, Borrichia frutescens,* and *Distichlis spicata,* or less commonly, *Salicornia bigelovii, Sporobolus virginicus, Sesuvium portulacastrum,* and *Blutaparon vermiculare.* Similar areas, when forming stands just seaward of coastal hammocks, are referred to by FNAI as coastal grassland (synonyms: salt flat, overwash plain, coastal savannah). Reportedly, these areas were historically burned by ranchers to promote better grazing conditions (Pearson 1951). In addition to all of the species found in the depressional flats, these more inland areas usually had *Triglochin striata, Limonium carolinianum, Spartina patens,* and *Agalinis maritima,* often in association with a more or less shrubby transition zone frequently composed of *Iva frutescens, Baccharis halimifolia,* and *Lycium carolinianum,* and occasionally with *Baccharis glomeruliflora, B. angustifolia,* and diminutive *Forestiera segregata.* Areas that appeared to be less saline often had a mixture that could include all of the above species, plus some of the following: *Fimbristylis spadicea, Ipomoea sagittifolia, Bacopa monnieri, Cynanchum* spp., *Eleocharis* spp., *Cladium jamaicense,* and sometimes *Rayjacksonia phyllocephala, Flaveria linearis,* and *Eustoma exaltatum.* All of the above areas frequently occurred adjacent to or intermixed with stands of *Sabal palmetto* (cabbage palm), *Juniperus virginiana* var. *silicicola* (southern red cedar), and *Quercus virginiana* (live oak).

The least brackish areas, not necessarily always the farthest inland (depending on topography), were often dominated by *Cladium jamaicense* and, in a few areas, *Typha domingensis,* often with pockets of *Juncus roemerianus.* Most of the above species could still be found as associates, with the addition of *Acrostichum danaefolium, Crinum americanum,* and *Samolus* spp. The most prevalent submerged plant in inland brackish water was *Ruppia maritima. Myriophyllum pinnatum* occurred in the least brackish areas.

The FNAI beach dune community (synonym: coastal strand), is essentially nonexistent in the area, but two small coastal islands were seen with thin sand deposits. Both areas were bordered by coastal hydric hammock and tidal marsh. One had *Ipomoea pes-caprae, Sesuvium portulacastrum, Cyperus esculentus, Cenchrus echinatus,* and *Heliotropium curassavicum.* The other had *Cakile lanceolata, Atriplex pentandra,* and *Chenopodium berlandieri,* with *Sideroxylon celastrinum* nearby. A separate, thin, elongated, raised sandy area parallel to the shore supported a dense stand of giant *Amaranthus australis,* bordered by *Spartina alterniflora* and *Scirpus robustus* on the seaward side and *Juncus roemerianus* on the inland side. Perhaps this area could be considered a poorly developed example of an FNAI coastal berm (synonym: coastal levee).

Numerous slightly elevated islands occur throughout the tidal marsh, with vegetation varying from scrubby flatwoods (only a very few in the southernmost portion of the Preserve) to coastal hydric hammock to entirely herbaceous associations (as described above). The abundant islands of coastal hydric hammock were dominated by *Sabal palmetto* and *Juniperus virginiana* var. *silicicola,* frequently with *Quercus virginiana, Ilex vomitoria, Iva frutescens, Baccharis halimifolia,* and *Opuntia stricta.* Occasional associates included *Pinus taeda, Quercus laurifolia, Forestiera segregata, Yucca aloifolia, Zamia floridana,* and *Stenotaphrum secundatum.* Rarely, almost any of the coastal hydric hammock species, and most individuals of more tropical species, such as *Maytenus phyllanthoides* and *Eugenia axillaris,* could be found on islands. Interestingly, *Persea borbonia,* which is entirely replaced by *P. palustris* inland, seemed restricted in the area to coastal islands. Islands of tall cabbage palms and live oaks in the midst of marsh communities are considered prairie hammocks by FNAI in other parts of Florida, but they are clearly just relict coastal hammock outliers in the Preserve. The inland spread of salt water inundation due to rising sea levels, studied by Williams et al. (1997), has resulted in the die-off of terrestrial species, with relict individuals of cabbage palm, southern red cedar, and live oak. Cabbage palm, *S. palmetto,* is usually the last species to succumb, and scattered clumps, individuals, and standing dead trunks could be found throughout tidal marsh.

Coastal hydric hammock. Hydric hammock is a community virtually restricted to Florida. The most extensive stands of hydric hammock in Florida occur along the Gulf Coast, often forming a belt just inland of salt marsh, and were referred to as coastal hydric hammock by Vince et al. (1989). Throughout the state, hydric hammock varies from nearly monospecific stands of *Sabal palmetto* to mixed stands of *S. palmetto* and *Juniperus virginiana,* or dense hardwood stands with highly variable species composition. Statewide, hydric hammock often has a broadleaf evergreen appearance and is typically dominated by *S. palmetto, J. virginiana, Quercus virginiana,* and/or *Q. laurifolia* (laurel oak), and often also has *Liquidambar styraciflua* (sweetgum) and *Carpinus caroliniana* (hornbeam). Gulf Hammock is the largest contiguous stand of hydric hammock in Florida and includes almost all of the variation in structure and composition found in hydric hammocks throughout the state. Along inland edges of the Gulf Hammock, coastal hydric hammock is usually intermediate with other community types, such as swamps and mesic hammock (Vince et al. 1989). Almost all of the species known to occur in hydric hammock in Florida can be found in the Gulf Hammock (Vince et al. 1989), including relatively rare trees such as *Prunus americana* and *Ulmus crassifolia,* and rare herbs such as *Spigelia loganioides,* all of which were found within the Waccasassa Bay State Preserve. The following descriptions of coastal hydric hammock are based entirely on field observations by the first author.

Areas closest to salt marsh often contained near-pure stands of *Sabal palmetto* and *Juniperus virginiana,* often with an understory of *Iva frutescens, Lycium carolinianum, Baccharis halimifolia,* and *Yucca aloifolia.* Frequently, *Quercus virginiana* also was present in the canopy, with an understory of *Ilex vomitoria, Myrica cerifera, B. halimifolia, Viburnum obovatum,* and often *Forestiera segregata.* This coastal-most forest was the only type of canopy cover included as coastal hammock by authors such as Pearson (1951). This area is reportedly very similar to hydric hammock bordering marshes along the St. Johns and Myakka Rivers (Vince et al. 1989). Occasionally, especially adjacent to inland fingers of tidal marsh, *Pinus taeda, Ulmus* spp., and *Fraxinus* spp. could be locally abundant in the canopy. Lianas were rare in the most coastal areas, which mostly had only *Smilax bona-nox* and *Toxicodendron radicans*; these species increased in abundance with distance inland. Herbs were usually infrequent or lacking in the most coastal areas, and were predominantly represented by scattered salt marsh species and grasses, especially *Chasmanthium* spp. and *Panicum* spp. With increasing distance from the salt marsh, *S. palmetto* and *J. virginiana* decreased in abundance while mixed hardwoods increased. However, within the Preserve, which occupies a narrow coastal strip, there were virtually no areas where *S. palmetto* and *J. virginiana* were not important canopy members.

Inland, trees characteristic of FNAI mesic to hydric hammocks and swamps (i.e., mixed hardwoods) became more common, though rarely did more than two or three of these species occur together. Most such species had a scattered distribution. The following abundance estimates are based on the first author's observations over the entire area of coastal hydric hammock. Frequent woody additions inland were *Pinus taeda, Quercus lauri-*

folia, Ulmus alata, U. crassifolia, U. americana, Acer saccharum ssp. *floridanum,* and *Persea palustris.* Mostly along the inland boundaries, one occasionally found *Carpinus caroliniana, Carya glabra, Diospyros virginiana, Liquidambar styraciflua, Celtis laevigata, Gleditsia triacanthos, Tilia americana, Quercus shumardii, Erythrina herbacea,* and *Sabal minor.* Infrequent woody plants were *Forestiera ligustrina, Morus rubra, Ptelea trifoliata, Rapanea punctata, Sapindus saponaria,* and *Zanthoxylum clava-hercules.* The rarest of the intermixed woody mesic species were *Cercis canadensis, Crataegus aestivalis, Prunus americana, Aesculus pavia, Osmanthus americanus, Viburnum dentatum, Quercus michauxii, Q. nigra, Sideroxylon lanuginosum, Aralia spinosa,* and *Symphoricarpos orbiculatus.* In wet depressions and in areas transitional to swamps, *Fraxinus caroliniana, F. pennsylvanica, Acer rubrum, Magnolia grandiflora,* and rarely *Cornus foemina, Carya aquatica, Nyssa biflora,* and *Ilex cassine,* could be found. Areas transitional to flatwoods had a greater abundance of *Pinus taeda,* but there were also numerous isolated stands of *Pinus taeda* scattered elsewhere through the forest.

Frequent inland lianas were *Vitis* spp., *Smilax bona-nox,* and *Toxicodendron radicans.* Occasional lianas were *Sageretia minutiflora, Smilax auriculata, S. tamnoides,* and *Campsis radicans. Berchemia scandens, Matelea gonocarpos, Bignonia capreolata, Chiococca alba, Parthenocissus quinquefolia, Gelsemium sempervirens, Ampelopsis arborea,* and *Lonicera sempervirens* were infrequent. Rare lianas and vines were *Phaseolus smilacifolius, Smilax smallii, S. laurifolia, Cocculus carolinus, Clematis crispa, C. catesbyana,* and *Dioscorea floridana.*

The ground layer was often bare or with sparse, patchy herbs, such as *Chasmanthium* spp., *Panicum* spp., *Elephantopus elatus,* and *Ruellia caroliniensis.* In the areas that flooded least, a relatively thick ground cover of the same species could develop, along with *Zamia floridana.* Additional woodland herbs that could be found scattered or in patches included numerous sedges and grasses, along with *Salvia lyrata, Galium hispidulum, Rubus* spp., *Elytraria caroliniensis, Dyschoriste humistrata,* and *Sanicula canadensis.* In a few scattered areas grew *Spigelia loganioides, Phyllanthus liebmannianus* ssp. *platylepis, Trepocarpus aethusae, Euphorbia commutata,* and *Lithospermum carolinense.* Bare areas often had a scattering of wetland herbs, described below under freshwater ponds. In many areas, there were thick, lawn-like stands, mostly of *Stenotaphrum secundatum,* with a few areas of *Axonopus furcatus.* Both of these are native grasses, but their growth pattern often seemed unnatural and perhaps reflects remnant areas of old logging roads.

Freshwater pools. Included here are shallow rainwater depressions, relatively deep isolated pools, and isolated inland channels. Most of the areas likely flood with salt water during extreme tidal surges in connection with major storms, but sheet flow of surface rainwater may serve to dilute them sufficiently to maintain their freshwater vegetation. The Florida Natural Areas Inventory does not have a community type that corresponds to the freshwater pools in the Preserve. Since many of them are ephemeral and in depressions, they could be treated as variants of depression marsh (synonyms: isolated wetland, ephemeral pond), but the FNAI habitat description and species lists show nothing in common with these areas. A couple of the deepest ponds (ca. 1.5 m deep) are similar to miniature sinkhole lakes, and could perhaps be treated as versions of them, since they are karstic in origin. But, rather than forcing several ill-fitting FNAI names here that have highly overlapping species compositions, we chose just to describe the variation, without recognizing the pools as a distinct FNAI community, since most of the pools are nothing more than wet depressions whose species are mostly scattered in saturated soil in areas throughout the coastal hydric hammock and basin swamp communities.

Shallow rainwater depressions are common throughout the Preserve. Many of the depressions are ephemeral, and presumably, saturated soil conditions are responsible for supporting wetland plants when there is no surface water. Many depressions were devoid of vegetation or have only two or three species growing in them. *Leitneria floridana* was frequent overall, usually forming dense shrubby stands, often with nearby *Fraxinus* spp. and *Salix caroliniana* in semi-permanently flooded areas. The largest of these depressional areas with long-standing water often appeared very similar to small patches of swamp forest. Most commonly, *Hydrocotyle umbellata, Samolus ebracteatus, S. valerandi, Bacopa monnieri, Sabatia calycina, Lippia nodiflora, Crinum americanum, Cardamine pensylvanica, Pluchea* spp., *Asclepias perennis,* and *Iris hexagona* were found. *Saururus cernuus, Centella* *asiatica, Polygonum hydropiperoides,* and *Ammania latifolia* were also occasionally found in these areas.

Areas of deeply pooled fresh water are uncommon within the Preserve. Only three such areas were seen by the first author. One of them actually had the estuarine *Juncus roemerianus, Spartina patens,* and *Ruppia maritima* in association with *Cladium jamaicense, Leitneria floridana, Hibiscus coccineus,* and *Thalia geniculata.* The other two pools were bordered by *Cladium, Leitneria, Hibiscus,* and *Panicum* spp. One of them also had *Hibiscus grandiflorus* and was filled with submerged and floating mats of *Bacopa monnieri* with *Nitella capillata.* The other pool was more diverse, with a dense stand of *Typha domingensis* in the middle and with *Nymphaea odorata, N. elegans, Chara zeylanica, Myriophyllum pinnatum, Echinodorus berteroi, Sagittaria graminea,* and *Polygonum hydropiperoides* along the edges. This latter pool was highly dynamic during the period of study. The above-listed species were the dominants in the beginning. During a final visit to the area, the first author found *Lemna obscura* and *Ceratophyllum echinatum* to be the dominants, with the original species virtually absent. Closer inspection revealed that the water level had risen by at least half a meter and that many of the original species were still present as small plants along the bottom in about one meter of water. Dozens of other deep pools were seen, with a strong estuarine influence, as indicated by the salt marsh vegetation and brackish water, with only one submerged or floating aquatic, *Ruppia maritima.*

Numerous inland channels were also seen, mostly with an obvious or seasonally intermittent continuity with tidal marsh. In several areas, however, the inland boundary trail cuts across fingers of elongate depressions that appear to be isolated portions of predominantly freshwater creek channels. Vegetation included species found near the depression pools, though it was usually dominated by *Leitneria floridana* and *Hibiscus coccineus.* Additionally, *Sagittaria lancifolia, Kosteletzkya virginica, Rumex verticillatus,* and several graminoids were found primarily along a few of these freshwater channels.

Basin swamp. Basin swamp (synonyms: cypress swamp, hardwood swamp, mixed swamp) occupies low areas that are flooded more frequently for longer periods of time and to a greater depth than hydric hammock (Vince et al. 1989). Only two distinct swamp areas were found within the Preserve, totaling perhaps 15 ha., although several small forest patches in scattered localities had standing water and trees such as *Carya aquatica, Acer rubrum,* and *Fraxinus caroliniana.* Much of the largest swamp area was actually very similar to adjacent coastal hydric hammock and perhaps could have been considered as just another variant form of hydric hammock. But the diminution in abundance of *Sabal palmetto* and *Juniperus virginiana* was distinctive, as was the hydrology, especially in conjunction with the presence of *Taxodium distichum,* which is considered very rare in hydric hammock (Vince et al. 1989). Swamps were also characterized here by the abundance of *Acer rubrum, Nyssa biflora, Fraxinus pennsylvanica, F. caroliniana,* and *Magnolia virginiana*; and by the rare presence of orchids such as *Malaxis spicata, Hexalectris spicata,* and *Habenaria floribunda,* of ferns and allies such as *Selaginella apoda, Thelypteris palustris, T. kunthii,* abundant *Acrostichum danaefolium,* and of other noteworthy plants such as *Lobelia cardinalis* and abundant *Rhapidophyllum hystrix.*

Mesic to scrubby flatwoods. Mesic to scrubby flatwoods (synonym: intermediate pine flatwoods) are typically dominated by *Pinus taeda* (loblolly pine) and *Sabal palmetto.* Hydric hammock species are intermixed, which is not characteristic for mesic or scrubby flatwoods. These areas within the Preserve are not typical for well-developed flatwoods elsewhere in the state. Thus, most of the flatwoods-like areas in the Preserve could easily be seen as just another variant form of a broadly defined hydric hammock plant community. Patches of *P. taeda* occur naturally throughout the Preserve, but along the boundaries of the southern portion, these patches likely reflect past logging, as clear-cut areas were widely replanted with *P. taeda* according to Vince et al. (1989). Aerial photos from the 1950s indicate that many of the areas considered here had been severely logged. Even though these areas would, perhaps, best be treated as a transitional variation of coastal hydric hammock, they are mostly very distinctive in the field and are here recognized as pine-dominated areas with a characteristic assembly of understory species in the southern portion of the Preserve, totaling perhaps 11 ha.

Flatwoods in Florida have poor drainage and low topography, which is true for most of these areas. Fires, usually every 10–20 years, are important in maintaining species composition in flatwoods. Only one area near the coast showed signs of having burned within the last few years, and it had an extremely dense stand of *Serenoa repens* (saw palmetto). *Pinus taeda* (loblolly) is one of the least fire-adapted pines in Florida, but several of these pine-dominated areas in the Preserve did have a little intermixed *P. elliottii* (slash pine), a typical flatwoods species. The preponderance of loblolly and the admixture of species more typical of well-drained sandy areas probably reflect the effects of fire exclusion and human disturbance in the area. The rareness of species typical of scrub suggests that the area most likely was not originally scrub, but an area of flatwoods that has been invaded by scrub species, perhaps due to fire exclusion.

Within the Preserve, canopy members were frequently *Pinus taeda* and *Sabal palmetto,* occasionally with *Juniperus virginiana, Quercus virginiana, Q. laurifolia,* and *Persea palustris.* Rarely, *Magnolia grandiflora, Osmanthus americanus, Q. geminata, Prunus serotina, Carya glabra,* and *Tilia americana* were intermixed. Some of these areas were notably poorly drained and had an understory of *Serenoa repens* and *Myrica cerifera* with scattered *Ilex glabra, Vaccinium arboreum, Lyonia fruticosa,* and *L. lucida.* Dense tangles of *Smilax* spp. were frequent. Other similar areas also had *Hypericum tetrapetalum, H. hypericoides, Carphephorus odoratissimus, Vaccinium myrsinites, Bejaria racemosa,* and *Liatris* spp. Additional rare indicative herbs included *Aster tortifolius, Penstemon multiflorus, Silphium astericus, Lechea mucronata, Bulbostylis stenophylla, Cyperus retrorsus, Buchnera americana, Piriqueta caroliniana,* and *Galactia elliottii.* The most scrubby-looking areas, oddly on sandy pockets adjacent to tidal marsh, also contained *Q. myrtifolia, Asimina longifolia, Myrica cerifera* var. *pumila, Xyris* spp., and *Polygala* spp.

Upland mixed forest. There are no pure stands of upland mixed forest (synonym: mesic hammock) large enough to consider as distinct within the Preserve boundary. Tiny patches along slightly elevated ridges within hydric hammock do approach upland mixed forest, as described by the FNAI and FDNR(1990) and as differentiated by Vince et al. (1989). We include this brief description here since much of the adjacent Gulf Hammock has been described by past workers (e.g., Swindell 1949) as mesic hammock and there may be a few undiscovered areas within the Preserve that would best be treated as mesic hammock.

Pearson (1951) found that even in the Gulf Hammock, mesic hammocks are usually along ridges or islands of better drained soils, without forming large continuous tracts. Although they are a major portion of the overall hammock, an extensive network of lower drainage areas separates the mesic hammock patches. Historically, the mesic hammocks had a very sparse understory with visibility of several hundred meters. Jennings (1951) reported that mesic hammocks can be inundated for several hours after heavy rains to several days after major storms due to poor drainage in the Gulf Hammock. Most of the species reported by Jennings (1951), Pearson (1951), and Swindell (1949) as typical of mesic hammock were found within the Preserve, but they were rarely together in groups of more than 2 or 3 species and occurred primarily along the inland boundaries.

As described in the adjacent Gulf Hammock area (Swindell 1949; Vince et al. 1989), characteristic canopy trees were *Magnolia grandiflora, Quercus michauxii,* and *Acer saccharum* var. *floridanum,* often with *Ostrya virginiana, Tilia americana, Cercis canadensis, Ilex opaca,* and *Pinus taeda.* Other common species that were more widespread, and thus less indicative, were *Carpinus caroliniana, Quercus virginiana, Q. nigra, Liquidambar styraciflua, Sabal palmetto, Juniperus virginiana, Persea palustris, Celtis laevigata, Ulmus alata, Acer negundo,* and *Aralia spinosa.* Common shrubs were *Ilex vomitoria, Serenoa repens, Vaccinium arboreum, Viburnum dentatum, Callicarpa americana, Sageretia minutiflora, Euonymus americana,* and *Myrica cerifera.* Less common shrubs were *Zanthoxylum americanum, Ptelea trifoliata,* and *Rhamnus caroliniana.* Common vines included *Toxicodendron radicans, Ampelopsis arborea, Vitis rotundifolia, Campsis radicans, Parthenocissus quinquefolia, Bignonia capreolata, Gelsemium sempervirens,* and *Smilax bona-nox.* Herbs included *Panicum commutatum, Oplismenus setarius, Elephantopus* spp., *Sanicula canadensis, Mikania scandens, Salvia lyrata, Dioscorea floridana, Melothria pendula,* and *Mitchella repens.*

Ruderal areas. Ruderal, human-created, open areas are very infrequent in the Waccasassa Bay State Preserve, largely due to the lack of roads and legal public access by land. In the Preserve, most ruderal areas would be virtually impossible to distinguish from areas of natural disturbance without the nearby fences and tire ruts, because ruderal areas usually were dominated by native species characteristic of the adjacent communities, a testament to the relatively pristine nature of the Gulf Hammock. Nonetheless, virtually every species documented from the Preserve can be found along or near a trail or road somewhere, so the emphasis here is to point out areas where nonindigenous species are found. Native species restricted to ruderal areas in the Preserve have been marked accordingly in the species list. In accordance with the Preserve's policy for control of exotic species, non-native species were eliminated, when found, in all localities except Fiber Factory Road where sheer numbers made it unfeasible. Undoubtedly, propagules in the soil and re-introduction will maintain the presence of most of the documented species.

The forested boundary has been mowed at least once in the past twenty years for much of the Preserve, creating an open and, in areas, somewhat disturbed trail up to a few meters wide. While the boundary is typically dominated by species native to forest gaps and wet depressions, a few nonindigenous plants rarely were found (e.g., *Apium leptophyllum, Conyza bonariensis, Hyptis mutabilis, Medicago lupulina, Murdannia nudiflora, Paspalum notatum, P. urvillei, Richardia brasiliensis,* and *Spermacoce prostrata*).

There are a few areas where old access roads still exist or where illegal entrance and use have created undeveloped roads into the Preserve. One such road near Turtle Creek had a few individuals of *Medicago lupulina, Mitracarpus hirtus,* and *Secale cereale,* with occasional *Plantago major* and *Youngia japonica.* A few illegal entrance roads at scattered localities were found with *Lindernia crustacea* forming small patches in wet depressions. *Echinochloa crusgalli* and *Polypogon monspeliensis* were found in scattered wet pools. *Stenotaphrum secundatum* is a native species, but its robustness and dense growth along old roadways suggest that the triploid cultivar form may have been introduced in areas.

One public gravel road, Dewey Allen Park Road, actually cuts across tidal marsh in the southwestern-most boundary of the Preserve. Exotics along this road were *Crotalaria spectabilis, Hyptis mutabilis, Lantana camara, Medicago lupulina, Melilotus alba, M. indica, Paspalum urvillei,* and *Verbena brasiliensis,* all of them occasional.

An area known as the Northcut Property is a recent acquisition in the southern end of the Preserve. The area was a homesite, with an undeveloped road transecting it. In this area occurred a single *Albizia julibrissin,* dense *Eremochloa ophiuroides,* infrequent *Medicago lupulina* and *Verbena braziliensis,* and rare *Sphagneticola trilobata.*

Around 4 km (2.5 mi.) of Fiber Factory Road, an undeveloped access road and its right-of-way, are owned by the state and are included in this study, though they are not within the main body of the Preserve. This roughly eight-meter swath cuts through a wide variety of areas on its way to the coast, and perhaps a third or more of the documented species could be found at some point along this road. Just outside the right-of-way, was a large *Melia azedarach,* but no seedlings were seen. Cows were abundant in this area, and several feeders were along the road, with exotic plants concentrated near them. It is in this area that signs of grazing could also be seen inside the Preserve. Exotics here, most of which were only in one or a few small areas, were *Amaranthus spinosus, Arenaria serpyllifolia, Cerastium glomeratum, Conyza bonariensis, Coronopus didymus, Cynodon dactylon, Eleusine indica, Hedyotis corymbosa, Hyptis mutabilis, Kummerowia striata, Kyllinga brevifolia, Lamium amplexicaule, Lindernia crustacea, Medicago lupulina, Murdannia nudiflora, Paspalum dilatatum, P. notatum, Pavonia hastata, Phyllanthus urinaria, Poa annua, Portulaca amilis, Raphanus raphanistrum, Senna obtusifolia, Sonchus asper, Sporobolus indicus, Stellaria media, Trifolium campestre, Verbena brasiliensis, Veronica arvensis, Vicia sativa,* and *Youngia japonica.* Within the Preserve itself, the road continued, locally with dense carpets of *Eremochloa ophiuroides,* with rare intermixed *Cyperus rotundus, Desmodium triflorum,* and *Sisyrinchium rosulatum,* and occasional *Kyllinga pumila, Medicago lupulina, Murdannia nudiflora,* and *Phyllanthus urinaria.* Near this access point, and at two other localities in the forested Preserve, the first author found *Citrus aurantium.*

Along the inland edge of tidal marsh, where piles of wrack accrued after tidal surges, three small plants of *Schinus terebinthifolius* were found. This species was observed in great abundance outside the Preserve on Cedar Key and Seahorse Key. Disseminules are likely to continue to be brought in from numerous other coastal locations as well. One coastal island had a diffuse population of *Cyperus esculentus.* Another island had *Tetragonia tetragonioides* along the salt marsh edge.

Rather extensive logging, though scattered over the last century, has undoubtedly affected species composition in the Waccasassa Bay State Preserve, and has left its mark in the form of old access roads, which mostly have been revegetated by forest species. During the course of this study, there was a southern pine beetle (*Dendroctonus frontalis*) outbreak that necessitated road construction and logging. The full impact of this disturbance remains to be seen. Probably the single most important factor that will shape the future plant communities in the Preserve, however, is the rising sea level. It can be expected that more and more of the Preserve will be inundated and that the plant communities will shift inland.

QUANTITATIVE FLORISTICS: VARIATION WITHIN COASTAL HYDRIC HAMMOCK

When the first author began this floristic inventory, much of the forested Preserve appeared to be a confusing array of possibly distinct plant communities, at least based on canopy dominants. Eventually, he realized that there were areas with distinctive swamp forest and mesic to scrubby flatwoods, but in most of the forested Preserve, here treated as coastal hydric hammock, three canopy extremes were seen, although all shared occasional to abundant *Sabal palmetto* and *Juniperus virginiana*. Many areas, especially those closest to the coast, were dominated by just *S. palmetto* and *J. virginiana* with only a few scattered hardwoods, primarily *Quercus virginiana* and *Q. laurifolia*. Previous workers in the region have called these juniper and *Sabal*-dominated areas coastal hammock (e.g., Swindell 1949). Some areas had a canopy codominated by several mixed hardwoods, including trees such as *Acer rubrum, A. saccharum, Fraxinus caroliniana, F. pennsylvanica, Liquidambar styraciflua,* and several *Quercus* species. These areas with mixed hardwoods seemed similar to mesic hammock and, in places, swamp forest. Other areas had a canopy with abundant *Pinus taeda* and seemed to be a possible variant of flatwoods. We decided to investigate whether the highly variable coastal hydric hammock (according to Vince et al. 1989) might be better treated as a mosaic of intermixed, yet distinctive, plant communities.

A general outline of our approach is as follows. Scattered patches of the three extreme canopy types were located throughout the Preserve. The Preserve was divided into roughly equal northern and southern portions, separated by the Waccasassa River. Using available access points along the Preserve boundaries, aerial photos, a compass, and a hand-held global positioning unit, the first author attempted to ensure that at least one of every three map sections (U.S. Geological Survey topographical quadrangle maps, 7.5 minute series) had a plot placed within it, so that half the plots were scattered over the northern Preserve and half over the southern Preserve. Typically, no more than two plots were placed within an area of 2.6 km^2 (1 $mi.^2$), roughly the amount of area covered by an aerial photo map (Florida Department of Transportation; scale 1 in. = 400 ft.). A plot was placed in each of 26 forest patches. In each plot, the presence of all understory species was recorded. Coefficient of community values (Whittaker 1975), essentially modified percent similarity values, were calculated, comparing all three of the canopy extremes to each other. For comparison, coefficient of community values were calculated between each pair of communities recognized within the Preserve and also between each pair of communities recognized in several other floristic studies in north-central Florida (Abbott 1998). By comparing coefficient of community values of our coastal hydric hammock plots to those of our communities and of communities recognized elsewhere in the state, quantitative support may be found either for recognizing the plots as different floristically-based plant communities or for treating the plots as part of one highly variable community.

Most of the Preserve was found to be transitional, without any one of the canopy extremes, although the juniper and *Sabal*-dominated canopy type was most abundant. By the time eight good patches of the coastal hammock had been found, only a few of the other canopy types had been found. In the end, then, the first author searched for pine-dominated and mixed hardwood-dominated areas until roughly equal numbers of each had been found.

The 26 areas into which plots were placed had to meet specific canopy cover criteria. Coastal hammock areas had to have only *Juniperus virginiana* and *Sabal palmetto* forming over 90% of the canopy cover as determined by site inspection. Pine-dominated and mixed hardwood areas had to have pines or mixed hardwoods comprising over half the canopy cover. Any forested areas with infrequent to absent *J. virginiana* and *S. palmetto* were excluded from this portion of the study, as these areas usually represented swamp forest or mesic to scrubby flatwoods.

Once the plots were placed within the 26 subjectively chosen forest patches, a random number of paces along a random heading was used to establish the center point of a 100 m^2 plot, a circle with a 5.6 m radius. Every vascular plant species present in each plot was recorded (for raw data see Abbott 1998).

Since we already had chosen to follow FNAI community classification, we decided to just compare the similarity between our plant communities with the similarity between communities recognized by other workers in north-central Florida (Amoroso and Judd 1995; Easley and Judd 1993; Herring and Judd 1995; Tan and Judd 1995). This comparison would provide an estimate of the consistency between our community delimitations and those of other workers.

A comparative reference of similarity was created using coefficient of community values (Whittaker 1975) to quantify the floristic similarity between pairs of communities in our study, and between communities in other studies. The coefficient of community value was derived by doubling the number of species shared between two communities, then dividing by the following sum: twice the number of shared species plus the number of species present in each of the communities that is not shared with the second community. Ignoring any abiotic factors involved, this phenetic approach simply gave a measure of overall similarity based on a modification of the percentage of species shared between any two plant communities.

Even though the categorization of the plots was based on dominance of the canopy species, the plots within each canopy-type category were hardly identical in canopy composition. Seventeen canopy species were encountered: 16 in mixed hardwood areas, 7 in coastal hammock areas, and 6 in pine-dominated areas (see annotated list below). In calculating coefficient of community values for the plots, we noticed that some of the plots did not contain the characteristic canopy species. These small areas were just coincidental gaps in forest patches defined by the surrounding canopy. For example, a few mixed hardwood and pine-dominated plots actually lacked juniper and *Sabal,* although they were present nearby. *Quercus laurifolia* and *Q. vir-*

giniana were scattered throughout all of the canopy categories. Their massive size often conveyed an impression of dominance, but only along inland boundaries did they occur in stands with more than a few individuals. A few of the mixed hardwood areas were codominated by several individuals of only one or two hardwood species, but usually there were a few different species, with no single species appearing dominant. Areas dominated by pure stands of juniper and *Sabal* were extensive only nearest the coast. Inland, pine stands or scattered hardwoods could usually be seen nearby. Pines were almost never found as an understory member of areas not dominated by pines, although mature, relic pines were often found as isolated clumps of emergent trees in an otherwise non-pine-dominated canopy. Patches of pine-dominated canopy were only rarely found in the northern Preserve, and they were most common in the southernmost end of the southern Preserve.

Many understory species were found only under certain canopy extremes. A total of 124 understory species was documented in the 26 plots: 89 species in mixed hardwood areas, 40 of which were found only there; 53 species in coastal hammock areas, 10 of which were found only there; and 49 species in pine-dominated areas, 22 of which were found only there. Areas with mixed hardwoods, then, typically had a greater species richness than other areas, possibly reflecting the rarity or infrequency of flooding by salt water in these areas. Pine-dominated areas, although they had twice as many restricted understory species as coastal hammock areas, were roughly comparable to coastal hydric hammock in total species richness. Fifteen understory species were found under all three canopy types. Presumably, these species represent the most versatile and adaptive species. Nine species were found only in the mixed hardwood and pine-dominated areas, likely a reflection of salt intolerance. Twenty-five species were shared by mixed hardwood and coastal hammock areas, while only three species were shared by both coastal hammock and pine-dominated areas.

Species richness in an area was often related to factors not reflected by canopy differences. That is, environmental heterogeneity often affected the understory in ways not detectable in the canopy. Field observations while collecting these data indicated that several of the species were actually restricted to wet depressions, usually with standing water: 13 species in mixed hardwood areas, 11 in mixed hardwood and coastal hammock areas, and 5 in coastal hammock areas. Thus, in the mixed hardwood and coastal hammock areas, species richness was enhanced by environmental heterogeneity due to scattered freshwater pools. Field observations also indicated that some of the coastal pine-dominated areas had been invaded by salt marsh species. Nine salt marsh species were present in association with what appeared to be a relict canopy, with little or no regeneration of canopy species. This situation is very similar to the pattern described by Williams et al. (1997) for relict patches of *Sabal palmetto* and *Juniperus virginiana.*

Seventy-two of the total 124 understory species were restricted to just one canopy extreme in this study, suggesting a possible association between various understory species and different canopy types. However, 97 species were present in three or fewer plots, with 51 species present in one plot only. This reflects the patchy nature of the Preserve's forest and the relative scarcity of most plant species. This high number of species restricted to only one (to three) plot(s) resulted in an inadequate sample size for determining whether or not there was a significant correlation between the different understory species and the different canopy extremes. Given the vast area of the Preserve, the amount of area covered by the plots was extemely small. Thus, any patterns in species distribution should not be considered as necessarily reflective of all of the Preserve's coastal hydric hammock.

The level of distinctiveness between plant communities recognized in this study corresponded to that of most communities recognized by other workers (Table 1; Abbott 1998). All of the plant communities in this study had coefficient of community values (× 100) less than 30, as did almost all of the plant communities recognized by others.

The coastal hydric hammock plots were all more similar to each other than our plant communities were to each other (i.e., they had higher coefficient of community values than were found between any of the plant communities recognized herein; Abbott 1998). These similarity data support the decision to treat the plots as variants of a single broadly defined community, coastal hydric hammock. Since there were no readily discernable differences in hydrology, microtopography, or soil depth or type between the plot areas, there was also no reason to recognize the canopy variants as nonfloristically based plant communities.

Table 1. Coefficient of community values (× 100) calculated for the Waccasassa Bay State Preserve, an estimate of similarity based on shared plant species. A. Plots in all communities. B. Plots in Coastal Hydric Hammock. C. Plots in Coastal Hydric Hammock, factoring out the Wet Depression species and Tidal Marsh species.

	FL	CH	SW	FP
A.				
Mesic to Scrubby Flatwoods (FL)				
Coastal Hydric Hammock (CH)	26			
Basin Swamp (SW)	20	29		
Freshwater Pools and Wet Depressions (FP)	7	10	19	
Tidal Marsh (TM)	10	15	14	20

	PC	JC
B.		
Pine-dominated Canopy (PC)		
Juniper & *Sabal*-dominated Canopy (JC)	39	
Mixed Hardwood-dominated Canopy (MC)	38	60

	PC	JC
C.		
Pine-dominated Canopy (PC)		
Juniper & *Sabal*-dominated Canopy (JC)	49	
Mixed Hardwood-dominated Canopy (MC)	49	62

FLORISTIC METHODS AND RESULTS

Field work was conducted by the first author in the Waccasassa Bay State Preserve from April 1996 to December 1997. Topographic maps, soil maps, and aerial photos were used to ensure adequate, representative coverage of plant community variation. A compass and a handheld global positioning unit greatly facilitated field-efficiency and accuracy, especially given the lack of trails, the large area, and the relative inaccessibility of much of the Preserve. Since species richness was generally greatest away from the coast, it was often convenient and most informative to walk the inland boundaries, when marked, making occasional transects toward the coast. On two occasions, an airboat was used to survey the outer limits of the tidal marsh and island hammocks. Several canoe trips were also made into the tidal marsh, in addition to numerous visits on foot.

Representative vouchers were deposited in the University of Florida Herbarium (FLAS), and a partial duplicate set at Selby

Botanical Gardens Herbarium (SEL). The primary references used for identification of vascular plants were Wunderlin (1982) and Clewell (1985), although Cronquist (1980), Godfrey and Wooten (1979, 1981), Hall (1978), Isely (1990), and Long and Lakela (1976) were also used. Current taxonomic revisions were consulted whenever possible, as cited on the species list.

A total of 576 vascular species and subspecific taxa was documented from 353 genera and 116 families. There was 1 lycopsid, 12 ferns, 1 cycad, 4 conifers, and 555 angiosperms, 178 of which were monocots. Sixty-nine nonindigenous species were documented from the Preserve, most of them from a single right-of-way access road, Fiber Factory Road. Seventy-three plants were Levy County records, having never been documented previously in the county according to Wunderlin et al. (1997). Given that larger numbers of species have been found in much smaller areas in Florida (e.g., Herring and Judd 1995), and that many of the Preserve's species have actually only been found in the very limited ruderal areas, it seems rather clear that the Preserve is not very species-rich. This is likely a reflection of its position as an extreme coastal strip.

The families with the greatest representation, followed by number of species, are Asteraceae (77), Poaceae (75), Cyperaceae (49), Fabaceae (36), Scrophulariaceae (14), Apiaceae (11), Polypodiaceae (10), Rubiaceae (10), Malvaceae (10), and Lamiaceae (9). The largest genera are *Cyperus* (15), *Panicum* (11), *Carex* (10), *Juncus* (8), *Paspalum* (8), *Eupatorium* (7), *Quercus* (7), *Smilax* (7), *Ipomoea* (6), *Rhynchospora* (6), and *Solidago* (6).

No vouchers were found for any of the previous studies, principally zoological, in the Gulf Hammock area (Jennings 1951; Pearson 1951; Swindell 1949), although most of their reported plant species, once nomenclature is updated, are documented herein or are to be expected in the area. There are also no vouchers from most of the limited, previous botanical work in the Waccasassa Bay State Preserve, although an unpublished species list exists for the Preserve. This unofficial list, on file at the office of the Division of Recreation and Parks, District 2, in Gainesville, Florida, was largely based on field identifications during 1986 and 1987 by Dr. David Hall. According to letters on file at the district office, several of his determinations were actually made in the FLAS herbarium from material sent in by Don Younker, a district employee at that time.

Personal communication with both D. Hall and D. Younker has convinced us that they were always aware of being within the Preserve boundaries and that the identifications were rarely in doubt. We believe that the species not recollected by us were in the Preserve and may still be there in rare tiny pockets, mostly in scrubby flatwoods at the southern end of the Preserve. Thus, for completeness and for future reference, any species whose name was clearly traceable to the work of David Hall, yet was not collected by us (41 species total), was included in the species list but was not used in any other way in the analyses or descriptions. Any species on the previous unofficial list from the Preserve that was not documented by us, or listed in the Hall and Younker correspondences on file, was excluded, since, in addition to the lack of vouchers, there was no indication from where or from whom the name came. The only vascular plant specimens found from previous work in the Preserve are those of the second author, who made a couple of casual collecting trips into the area in 1980 and 1994. All of the species found by him were found again by the first author during the course of this study.

Species of special concern or interest. Many species are of interest in the area as they are either at or near the limit of their natural ranges in Florida (72 spp.), are notably disjunct (13 spp.), have a very restricted range in Florida (5 spp.), are endemic or nearly endemic to Florida (16 spp.), or are listed as commercially exploited, of special concern, rare, threatened, or endangered in Florida (23 spp.). An on-line atlas of the vascular flora of Florida was used for determining species ranges (Wunderlin et al. 1997). For our purposes, species at their distributional limit reach Levy County from the north or south but do not extend any farther. Species near their distributional limit do not extend beyond two counties along the Gulf coast to the north or south of Levy County. A listing of species at or near their distributional limits is available in Abbott (1998). The five species with very restricted ranges in Florida found in the Preserve are *Leitneria floridana, Phaseolus smilacifolius, Phyllanthus liebmannianus* ssp. *platylepis, Spigelia loganioides,* and *Ulmus crassifolia.* Sixteen Florida endemics or near-endemics were documented in the Preserve: *Aristida patula, Berlandiera subacaulis, Campanula floridana, Carex vexans, Coreopsis leavenworthii, Eupatorium mikanioides, Lobelia feayana, Pluchea longifolia, Rhynchosia michauxii, Scutel-*

laria arenicola, and *Vicia floridana* are endemic, while *Ageratina jucunda* and *Panicum dichotomum* var. *breve* are nearly endemic to Florida (Muller et al. 1989).

Twenty-three species were found that have been listed as either commercially exploited, of special concern, rare, threatened, or endangered in Florida (Table 2) by Coile (1993), Kral (1983), and Ward (1979). Many of the listed bromeliads, ferns, and orchids are actually quite common in Florida. Perhaps some of these species would be better treated as potentially commercially exploited, if protection is indeed necessary. No federally-listed protected species were found within the Waccasassa Bay State Preserve (Wood 1996).

ANNOTATED LIST OF VASCULAR PLANTS

The vascular plant species inventoried for Waccasassa Bay State Preserve are listed in Appendix 1. Some angiosperm family names and/or circumscriptions here deviate from Wunderlin (1982); in such cases references are provided and the traditional family names are still included and are cross-referenced to facilitate use of the species list.

The species list is arranged alphabetically by family, genus, and species, within the context of the larger monophyletic groups of lycopsids, ferns, cycads, conifers, and angiosperms. Nomenclature follows Wunderlin (1982, 1998), unless otherwise indicated in the species list, and Wunderlin (1998) was used for determining exotic status. Forty-one species not found by the first author but reported by David Hall during the 1980s are also listed here. Most of Hall's taxa were reportedly seen in the southernmost portion of the Preserve, and, if still present, can be considered rare.

The plant communities in which the species occurred are tidal marsh, coastal hydric hammock, basin swamp, mesic to scrubby flatwoods, freshwater pools and wet depressions, and ruderal areas. There are obviously many transitional areas, and most species, especially the more abundant ones, can be found along the edges of, or in isolated patches within, adjacent communities. Such transitional areas are not reflected in the species list. Rather, multiple communities are listed only when a species was observed to occur as a distinctive element in several communities. For example, *Juncus roemerianus*, typically a salt marsh species,

Table 2. Status classification of vascular plants in the Waccasassa Bay State Preserve that are listed as commercially exploited (CE), of special concern (S), rare (R), threatened (T), or endangered (E) in Florida (Coile 1993; Kral 1983; Ward 1979).

	Status and Reference		
Species	Kral	Coile	Ward
Acrostichum danaefolium		T	
Asplenium platyneuron		T	
Avicennia germinans			S
Dryopteris ludoviciana		T	
Epidendrum conopseum		T	
Hexalectris spicata		E	
Ilex cassine		CE	
Leitneria floridana		T	R
Lobelia cardinalis		T	
Malaxis spicata		T	
Osmunda cinnamomea		CE	
Phyllanthus liebmannianus ssp. *platylepis*		E	R
Rhapidophyllum hystrix		CE	T
Sabal minor		T	
Sageretia minutiflora	E		
Selaginella apoda		T	
Smilax smallii			T
Spigelia loganioides		E	R
Thelypteris kunthii		T	
Thelypteris palustris		T	
Tillandsia bartramii		T	
Ulmus crassifolia			R
Zamia floridana		CE	T

could sometimes be found inland. Mostly this was in association with other typical salt marsh species, and such sites were considered as transitional patches of tidal marsh. In a few areas, however, *J. roemerianus* occurred in association with more freshwater species, without associated salt marsh species. In these areas, *J. roemerianus* was treated as a distinctive element of the freshwater pools. Finally, essentially every species within the Preserve could be found along or near a ruderal area. Our attempt here was to indicate only the species restricted to ruderal areas and the species that usually occurred in clearings or forest gaps of adjacent communities, as well as ruderal areas.

As pointed out by Amoroso and Judd (1995), the relative abundance of a plant is subject to its reproductive status, seasonal variation, population changes from year to year, and the judgement and acuity of the researcher. Thus, abundance values reflect the first author's subjective estimate of a plant's frequency, especially in comparison to associated species or related species. This is especially true for the basin swamp and mesic to scrubby flatwoods communities, because both are rare within the Preserve, occupying only a very few small areas, and any plant restricted to either of these communities is automatically rare in the whole Preserve. For all the other communities, a numerical scale (Appendix 1; modified from Thompson and Wade 1991) was used as a guide for abundance values.

LIST OF CHAROPHYTES, LIVERWORTS, MOSSES, AND MACROLICHENS

Two charophytes, 24 liverworts, 29 mosses, and 43 macrolichens were documented from the Waccasassa Bay State Preserve (Appendix 2). Numerous other mosses and macrolichens have been reported for Levy County and may eventually be found within the Preserve (see Amoroso and Judd 1995; Breen 1963; Moore 1968; also collections at FLAS). In the list of taxa, charophytes, liverworts, mosses, and macrolichens are presented separately, and within each list, taxa are arranged alphabetically by family and species.

Although bryophyte family relationships have been recently investigated by Buck and Vitt (1986) we simply followed the classification schemes used by the authors of the following keys and floras. Charophytes were identified using Wood (1967). Breil (1970) was used to identify liverworts, except for *Frullania cobrensis* (Griffin and Breil 1982). Breen (1963) and Crum and Anderson (1981) were used to identify mosses, with nomenclature following the latter, unless otherwise indicated. Macrolichens were identified using Moore (1968), Hale (1979), and Harris (1995), although nomenclature follows Esslinger and Egan (1995). Crustose lichens were not included in this inventory, although one or more crustose lichens are present in virtually all of the lichen voucher specimens. Some of the more distinctive crustose genera, *Haematomma, Pertusaria, Buellia*-like, and *Graphis*-like entities, were observed to be very common in the Preserve, especially on small branches in open sunny areas.

Bryophytes and macrolichens respond to microhabitat features on a scale much smaller than that of vascular plant communities.

Moisture and light intensity are undoubtedly the most important factors controlling bryophyte and lichen distribution within the landscape. Thus, a water-loving moss like *Fissidens cristatus* may be most abundant in the wettest plant community, such as swamp, but it can also be found in the drier flatwoods community, given a suitable moisture regime, such as in a crevice at the shaded base of a tree trunk. Lichens, such as many *Cladonia* spp., that are typically soil-dwelling, can be found on tree trunks under favorable conditions.

In general, mesic inland portions of the Preserve supported the greatest number of bryophytes, with a reduction in species richness and abundance towards the coast. The most common and widespread bryophytes were: *Cheilolejeunea* spp., *Fissidens cristatus, Isopterygium tenerum, Lejeunea* spp., *Leucobryum albidum,* and *Syrrhopodon incompletus.* The only bryophyte found in tidal marsh was *Frullania kunzei,* on bare branches of *Lycium carolinianum.* Soil-dwelling bryophytes were uncommon in the Preserve and were largely restricted to open sand in flatwoods (e.g., *Bryum pseudocapillare, Ditrichum pallidum*), a few raised hummocks in swamps (e.g., *Aneura pinguis, Odontoschisma prostratum, Pallavicinia lyellii*), and raised areas near the base of trees (most taxa, at least in places). Frequent flooding in the Preserve likely limits the ground diversity, as well as impacting species composition on fallen branches, logs, and tree bases. The only bryophytes consistently found on moist limestone rocks were *Barbula agraria, B. cancellata,* and *Marchantia domingensis.* Typically, in other areas, a succession of different suites of species are associated with the transition from living trunks to fallen logs to decomposing debris, but no strong successional patterns were seen by the first author within the Preserve. Certain species, such as *Leucobryum albidum, Octoblepharum albidum,* and *Syrrhopodon incompletus* were almost always restricted to erect *Sabal palmetto* trunks. Other species, such as *Cryphaea glomerata, Forsstroemia trichomitria, Leucodon julaceus,* and *Radula australis,* as well as most Frullaniaceae and Lejeuneaceae, were found primarily on living hardwood and juniper trunks. Most of the remaining bryophyte species seemed to grow anywhere that was moist enough: bark, fallen branches, logs, and soil.

Of the lichens, *Leptogium, Parmotrema* (and other similar-looking *Parmelia* segregates), and *Usnea* species were the most visually dominant and abundant. In shaded forests, lichens such as *Collema, Leptogium,* and *Pseudoparmelia,* could be found on bark and over bryophytes, but most lichens were growing on trunks in open areas or on canopy branches.

Both of the charophytes were submerged aquatics, with the only other true aquatic being the floating liverwort, *Riccia fluitans.*

Although no specific numerical values were assigned, largely due to identification uncertainty in the field, subjective abundance values were used to indicate relative frequency of each charophyte and bryophyte species. Rare species (R) were not seen more than once or twice. Infrequent species (I) were seen a few times, while occasional species (O) were seen several times. Frequent species (F) were scattered throughout the Preserve, but were not consistently common. Abundant species (A) were very common throughout the forested Preserve. Bryophytes that are difficult to identify in the field were very likely more common than indicated here (i.e., the accuracy of abundance values here is a function of how distinctive the species were in the field). There was definitely a pronounced bias toward bryophytes within two meters of the ground. No abundance values are given here for macrolichens, as accurate species determinations were only had once detailed laboratory inspection and chemical tests were carried out. Of the lichens, only some individuals of the *Cladonia* species were occasionally found on the ground. All other lichens were found on tree trunks and branches.

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APPENDIX 1

ANNOTATED LIST OF VASCULAR PLANTS OF WACASASSA BAY STATE PRESERVE

For each species, codes for the communities in which it occurs are listed, followed by an abundance code (sometimes with supplemental habitat or abundance information), and collection number(s) of J. R. Abbott, unless otherwise noted. Voucher specimens are housed in FLAS, with a partial duplicate set at SEL. Species that have "*Hall NV*" in place of the collection number were reported by D. Hall during the 1980s. The communities in which these species are most likely to be expected are listed. Levy County records, based on Wunderlin et al. (1997), are indicated by the word "new" after the collection number(s). An asterisk (*) denotes non-native species.

The communities are: tidal marsh (TM), coastal hydric hammock (CH), basin swamp (SW), mesic to shrubby flatwood (FL), freshwater ponds and wet depressions (FP), and ruderal areas (RU). Abundance categories are: Rare (R), 1–4 occurrences; Infrequent (I), 5–9 occurences; Occasional (O), 10–24 occurrences; Frequent (F), ≥ 25 occurrences; and Abundant (A) for continuous occurrence. Abundance values reflect subjective estimates of species' frequencies.

See text for detailed information on this list.

LYCOPSIDA

SELAGINELLACEAE

Selaginella apoda (L.) Fern. – SW R, on raised hummock; *9981*

FILICOPSIDA

OPHIOGLOSSACEAE

Botrychium biternatum (Sav.) Underw. – TM; *Hall NV*

OSMUNDACEAE

Osmunda cinnamomea L. – SW R; *10400*

POLYPODIACEAE *sensu lato* (see Pryer et al. 1995)

Acrostichum danaefolium Langsd. & Fisch. – CH I, SW & FP F; *9684*
Asplenium platyneuron (L.) Britt. et al. – CH I; *9935*
Dryopteris ludoviciana (Kunze) Small – SW R; *10929*

Phlebodium aureum (L.) J. Sm. – CH & SW O, epiphytic on *Sabal palmetto*; *9526, 9662*

Pleopeltis polypodioides (L.) E. G. Andrews & Windham var. *michauxiana* (Weath.) E. G. Andrews & Windham – CH, SW & FL F, usually epiphytic; *11095* [= *Polypodium polypodioides* (L.) Watt; Andrews and Windham 1993; Windham 1993]

Pteridium aquilinum (L.) Kuhn – FL I; *9107*; new

**Pteris vittata* L. – RU R, on limestone outcrops; *9707*

Thelypteris hispidula (Decne.) C. F. Reed – CH; *Hall NV*

T. kunthii (Desv.) C. V. Morton – CH & SW I, locally A; *8955, 9153, 9927, 10179, 10921*

T. palustris Schott – SW R; *9129*

Vittaria lineata (L.) Sm. – CH & SW R, epiphytic; *9660*

Woodwardia virginica (L.) Sm. – SW; *Hall NV*

SCHIZAEACEAE

**Lygodium japonicum* (Thunb.) Sw. – RU R, near old homesite; *9155*; new

CYCADOPSIDA

ZAMIACEAE

Zamia floridana A. DC. – CH F; FL I; *8372* [but see Eckenwalder (1980), Landry (1993), Stevenson (1991), and Ward (1979) for different interpretations of the correct name]

CONIFEROPSIDA

CUPRESSACEAE (incl. TAXODIACEAE; Eckenwalder 1976; Hart 1987; Hart and Price 1990)

Juniperus virginiana L. var. *silicicola* (Small) Bailey – CH A; SW I; FL O; *8162* (Adams 1986)

Taxodium distichum (L.) Rich. – SW O; *9787*

PINACEAE

Pinus elliottii Englem. – FL R; *11131*

P. taeda L. – CH & FL F, locally A; *9181, 10018*

ANGIOSPERMAE

ACANTHACEAE

Dicliptera brachiata (Pursh) Spreng. – CH R; *9440*

Dyschoriste humistrata (Michx.) Kuntze – CH I; *10161, 10349*

D. oblongifolia (Michx.) Kuntze – CH R; *10560*

Elytraria caroliniensis (J. F. Gmel.) Pers. – CH O; *9168*

Ruellia caroliniensis (J. F. Gmel.) Steud. – CH F; SW R; *9439, 10160*

ACERACEAE (see SAPINDACEAE)

ADOXACEAE (incl. part of CAPRIFOLIACEAE; Judd et al. 1994)

Sambucus canadensis L. – FP R; *10163*
Viburnum dentatum L. – CH R; *9216, 10162*
V. obovatum Walt. – CH F, locally A; FL I; *9180, 9438, 9449, 9936, 10401*

AGAVACEAE

**Yucca aloifolia* L. – CH O, especially on or near coastal islands; *8411* (status as native or introduced is problematic)

AIZOACEAE (incl. TETRAGONIACEAE)

Sesuvium portulacastrum (L.) L. – TM O; *9130*
**Tetragonia tetragonioides* (Pall.) Kuntze – TM R; *10546*; new

ALISMATACEAE

Echinodorus berteroi (Spreng.) Fassett – FP R; *9481, 9555* [= *E. rostratus* (Nutt.) Engelm.]
Sagittaria graminea Michx. – FP R; *9453*
S. lancifolia L. – FP R; *9035*
S. subulata (L.) Buch. – FP R; *9452, 9482*; new

ALLIACEAE (Dahlgren et al. 1985; Fay and Chase 1996)

Nothoscordum bivalve (L.) Britt. – RU R, boundary trails; *8384, 10009*

AMARANTHACEAE

Amaranthus australis (A. Gray) J. D. Sauer – TM, SW & FP R *9188*
**A. spinosus* L. – RU R; *9233*; new
Atriplex pentandra (Jacq.) Standl. – TM R; *10539*; new
Blutaparon vermiculare (L.) Mears – TM R; *9849*
Chenopodium berlandieri Moq. – TM R; *10540*
Iresine diffusa Humb. & Bonpl. ex Willd. – CH R; *11096*
Salicornia bigelovii Torr. – TM F; *8929*
S. perennis Mill. – TM A; *8400* (= *S. virginica* L. of most authors; Clemants 1992)
Suaeda linearis (Ell.) Moq. – TM F; *9507*

AMARYLLIDACEAE (excl. ALLIACEAE and HYPOXIDACEAE)

Crinum americanum L. – SW & FP F; *10561*

ANACARDIACEAE

Rhus copallinum L. – CH & RU R; *9463*
**Schinus terebinthifolius* Raddi – TM R; *9933*
Toxicodendron radicans (L.) Kuntze – CH, SW & FL F; *8398, 9099*

ANNONACEAE

Asimina longifolia Kral – FL R; *9108* (= *A. angustifolia* Raf.; Kral 1997)

APIACEAE (= UMBELLIFERAE; incl. ARALIACEAE; Judd et al. 1994; Thorne 1983)

Apium leptophyllum (Pers.) F. Muell. – RU R; *9961*; new
Aralia spinosa L. – CH R; *10393*
Centella asiatica (L.) Urban – TM R; CH, BS, FL, FP & RU F, open wet areas; *9022*
Cicuta maculata L. – SW R; *10931*
Eryngium baldwini Spreng. – RU R; *9143*
Hydrocotyle umbellata L. – FP I; *9248*
H. verticillata Thunb. – TM R; CH, BS, FL, FP & RU F, open wet areas; *8951, 9247*
Oxypolis filiformis (Walt.) Britt. var. *filiformis* – RU R; *10983*
Ptilimnium capillaceum (Michx.) Raf. – FP I; *9176, 10363*
Sanicula canadensis L. – CH I; *9135*
Trepocarpus aethusae Nutt. ex DC. – CH I; *8907, 8954, 10395*

APOCYNACEAE (incl. ASCLEPIADACEAE; Endress et al. 1996; Judd et al. 1994)

Amsonia tabernaemontana Walt. – CH & FP R; *10190* (= *A. rigida* Shuttlew.)
Asclepias lanceolata Walt. – FP R; *9020*
A. perennis Walt. – CH & FP O; *8903, 9208*
Cynanchum angustifolium Pers. – TM & FL I; *8934, 10733*
C. scoparium Nutt. – TM R; CH F; FL I; *9520*
Matelea gonocarpos (Walt.) Shinners – CH O; *9184, 10189, 10481*

AQUIFOLIACEAE

Ilex cassine L. – SW R; *9093, 9655*
I. glabra (L.) A. Gray – FL I; *9697, 10737*
I. vomitoria Ait. – CH A; FL O; *9433*

ARACEAE (incl. LEMNACEAE, e.g., French et al. 1995; Mayo et al. 1995)

Lemna obscura (Austin) Daubs – FP R; *9554, 10098*
Peltandra virginica (L.) Schott & Endl. – SW R; *10925*; new

ARALIACEAE (see APIACEAE)

ARECACEAE (= PALMAE)

Rhapidophyllum hystrix (Pursh) H. Wendl. & Drude ex Drude – SW R, locally A; *9924*
Sabal minor (Jacq.) Pers. – CH I; *8900, 9411*
S. palmetto (Walt.) Lodd. ex Schultes & Schultes f. – TM, CH, SW, FL & FP A; *10538*
Serenoa repens (W. Bartr.) Small – CH R; FL O; *9613*

ASCLEPIADACEAE (see APOCYNACEAE)

ASTERACEAE (= COMPOSITAE)

Acmella oppositifolia (Lam.) R. K. Jansen var. *repens* (Walt.) R. K. Jansen – FP I; *9486* [= *Spilanthes americana* (Mutis ex L.f.) Hieron.; Jansen 1985]
Ageratina jucunda (Greene) Clewell & Wooten – CH R; *9651* (= *Eupatorium jucundum* Greene)
Ambrosia artemisiifolia L. – RU R; *9563*
Aster carolinianus Walt. – CH R; *9856*
A. dumosus L. – CH & RU R; *11133*
A. subulatus Michx. – TM & CH O; *9533, 10987*
A. tenuifolius L. – TM F; *9597, 9811*
A. tortifolius Michx. – FL R; *10992*
Baccharis angustifolia Michx. – TM F; *8166, 11123*
B. glomeruliflora Pers. – TM O; *8165*
B. halimifolia L. – TM, CH, SW, FL & FP F, often locally A; *11085, 11086*
Berlandiera subacaule (Nutt.) Nutt. – FL R; *9990, 10563*
Bidens alba (L.) DC. var. *radiata* (Sch. Bip.) R. E. Ballard ex Melchert – CH R; RU O; *9077*
B. bipinnata L. – CH & RU I; *9534, 10327*
B. mitis (Michx.) Sherff – FP R; *11093*
Boltonia diffusa Ell. – RU R; *9457*
Borrichia frutescens (L.) DC. – TM F, often locally A; *8909*
Carphephorus odoratissimus (J. F. Gmel.) Hebert – FL I; *9688, 10995*
Cirsium horridulum Michx. – RU R; *8388*
C. nuttallii DC. – CH & RU I; *8933*
Conoclinium coelestinum (L.) DC. – CH I; RU O; *9167, 9415* (= *Eupatorium coelestinum* L.)
**Conyza bonariensis* (L.) Cronq. – RU R; *10738*; new
C. canadensis (L.) Cronq. var. *pusilla* (Nutt.) Cronq. – RU O; *9244*
Coreopsis leavenworthii Torr. & A. Gray – FL O; *9019, 10567, 10996*
Eclipta prostrata (L.) L. – FP R; *9605* [= *E. alba* (L.) Hassk.]
Elephantopus carolinianus Raeusch. – CH I; *10922*
E. elatus Bertol. – CH & FL F; *9474, 11041*
E. nudatus A. Gray – CH & FL; *Hall NV*
Erechtites hieracifolia (L.) Raf. ex DC. – RU R; *9151, 9236*
Erigeron quercifolius Lam. – RU O; *8389, 9968, 10348*
E. vernus (L.) Torr. & A. Gray – RU R; *10998*
Eupatorium album L. – FL I; *9695, 11038*
E. capillifolium (Lam.) Small – TM, FP & RU R; *9639*
E. mikanioides Chapman – FL & RU I; *10402*; new
E. mohrii Greene – FL R; *11003*
E. perfoliatum L. – TM & RU R; *9590*
E. rotundifolium L. – FL & RU O; *10578*
E. serotinum Michx. – FL & RU O; *9637*
Euthamia caroliniana (L.) Greene ex Porter & Britt. – FL R; *11118* [= *E. tenuifolia* (Pursh) Nutt.]
Flaveria linearis Lag. – TM & RU F; CH I; *9634, 10188, 11101*

Fleischmannia incarnata (Walt.) R. M. King & H. Rob. – CH R; *9644, 11134* (= *Eupatorium incarnatum* Walt.)
Gamochaeta pensylvanica (Willd.) Cabrera – RU R; *9950* (= *Gnaphalium pensylvanicum* Willd.; Nesom 1990)
Helianthus angustifolius L. – FL R; *11039*
H. debilis Nutt. – TM R; *11089*
H. radula (Pursh) Torr. & Gray – FL R; *11037*
Heterotheca subaxillaris (Lam.) Britt. & Rusby – FL & RU O; *9623*
Iva frutescens L. – TM A; FP I; *9190, 10981*
I. microcephala Nutt. – RU R; *11005, 11087*
Lactuca canadensis L. – CH; *Hall NV*
L. floridana (L.) Gaertn. – CH R; *9665*; new
Liatris gracilis Pursh – FL & RU R; *9627*
L. graminifolia (Walt.) Willd. – FL & RU I; *9567, 10993*
L. tenuifolia Nutt. – FL & RU R; *9675*
Melanthera nivea (L.) Small – CH & RU O; *9548*
Mikania cordifolia (L. f.) Willd. – throughout O; *9587*
M. scandens (L.) Willd. – throughout F, locally A; *9448*
Pluchea longifolia Nash – SW & FP O; *9592, 10985*
P. odorata (L.) Cass. – SW & FP O; *9468, 10396*
P. rosea R. K. Godfrey – FP O; *9115*
Polymnia uvedalia (L.) L. – CH R; *9450*
Pterocaulon pycnostachyum (Michx.) Ell. – FL R; *8918*
Pyrrhopappus carolinianus (Walt.) DC. – RU R; *9969*
Rayjacksonia phyllocephala (DC.) R. L. Hartman & M. A. Lane – TM & CH O, island hammocks; *9566* (= *Haplopappus phyllocephalus* DC.; Lane and Hartman 1996)
Rudbeckia hirta L. – RU R; *8964, 9546*
R. laciniata L. – RU R; *9591*
R. triloba L. var. *pinnatiloba* Torr. & A. Gray – CH R, in open wet area; *8174*
Senecio glabellus Poir. – FP I; *8383*
Silphium astericus L. – FL & RU I; *8941*
Solidago fistulosa Mill. – CH I; *9678*
S. odora Ait. var. *chapmanii* (Torr. & A. Gray) Cronq. – FL & RU O; *11006*
S. rugosa Mill. var. *aspera* (Ait.) Cronq. – RU R; *9477, 11083*
S. sempervirens L. – TM & CH F; *9664*
S. stricta Ait. – TM & CH F; SW I; *9798*
S. tortifolia Ell. – RU O; *11040*
**Sonchus asper* (L.) Hill – RU R; *9951*; new
**Sphagneticola trilobata* (L.) Pruski – RU R; *9672*; new [= *Wedelia trilobata* (L.) Hitchc.; Pruski 1996]
Verbesina virginica L. – CH & RU I; *9593*
**Vernonia cinerea* (L.) Less. – RU; *Hall NV*
V. gigantea (Walt.) Trel. – CH & RU F; *9222, 9456, 9515*
Xanthium strumarium L. – RU R; *9594*; new
**Youngia japonica* (L.) DC. – RU I; *8364*

AVICENNIACEAE

Avicennia germinans (L.) L. – TM I; *9197*

BATACEAE

Batis maritima L. – TM F, locally A; *9810*

BETULACEAE

Carpinus caroliniana Walt. – CH F; *8960*
Ostrya virginiana (Mill.) K. Koch – CH R; *9423*

BIGNONIACEAE

Bignonia capreolata L. – CH O; *8478*
Campsis radicans (L.) Seem. ex Bureau – CH F; *11094*

BORAGINACEAE

Heliotropium curassavicum L. – TM R; *9205*
Lithospermum tuberosum Rugel ex DC. – CH R; *8390*; new

BRASSICACEAE (= CRUCIFERAE)

Cakile lanceolata (Willd.) O. E. Schulz – TM R; *10166, 10542*
Cardamine bulbosa (Schreb. ex Muhl.) Britt. et al. – SW R; *9967*
C. pensylvanica Muhl. ex Willd. – FP F; RU I; *9938, 9983*
**Coronopus didymus* (L.) Sm. – RU R; *9957*; new
Descurainia pinnata (Walt.) Britt. – RU R; *9948*
Lepidium virginicum L. – RU R; *9940*
**Raphanus raphanistrum* L. – RU R; *9978*

BROMELIACEAE

Tillandsia bartramii Ell. – CH O; SW F, epiphytic; *9444, 9521*
T. recurvata (L.) L. – CH, SW, & FL F, epiphytic; *9522*
T. usneoides (L.) L. – TM, CH, SW & FL F, locally abundant, epiphytic; *9061*

CACTACEAE

Opuntia stricta (Haw.) Haw. – TM & CH F; *8175*

CAMPANULACEAE

Campanula floridana S. Watson – RU R; *10157*
Lobelia cardinalis L. – SW R; *9580*
L. feayana Gray – RU R; *10023*
L. glandulosa Walt. – FP & RU R; *9790*
Triodanis perfoliata (L.) Nieuwl. – RU R; *9962* (Bradley 1975)

CANNACEAE

Canna flaccida Salisb. – SW & RU R; *8959*

CAPRIFOLIACEAE (see also ADOXACEAE)

Lonicera sempervirens L. – CH I; *8359*
Symphoricarpos orbiculatus Moench – CH R; *10200*

CARYOPHYLLACEAE

Arenaria lanuginosa (Michx.) Rohrb. – CH R, near wet depression and clearing; *10328*; new
**A. serpyllifolia* L. – RU R; *10007*
**Cerastium glomeratum* Thuill. – RU R; *9943, 9979*; new
**Stellaria media* (L.) Vill. – RU R; *9942*; new

CELASTRACEAE

Euonymus americanus L. – CH R; *9643*
Maytenus phyllanthoides Benth. – CH R, island hammocks; *8379, 9930*

CELTIDACEAE (Grudzinskaja 1967; Judd et al. 1994)

Celtis laevigata Willd. – CH O; *10482*

CERATOPHYLLACEAE

Ceratophyllum echinatum A. Gray – FP R; *11097*

CHENOPODIACEAE (see AMARANTHACEAE)

CISTACEAE

Lechea mucronata Raf. – FL R; *9138*

CLUSIACEAE (= GUTTIFERAE; incl. HYPERICACEAE)

Hypericum cistifolium Lam. – FL R; *9134*
H. hypericoides (L.) Crantz – CH, FL & RU I; *9466, 9581, 9702*
H. tetrapetalum Lam. – FL R; *9142*

COMMELINACEAE

Commelina diffusa Burm. f. – RU I; *9598*; new
C. erecta L. – FL R; *10562*
**Murdannia nudiflora* (L.) Brenan – RU I; *9253*; new

CONVOLVULACEAE

Dichondra carolinensis Michx. – CH, FL & RU, F; *8397, 9973*
Evolvulus sericeus Sw. – CH & FL; *Hall NV*
Ipomoea cordatotriloba Dennst. – RU R; *9465* (= *I. trichocarpa* Ell.)
**I. hederacea* Jacq. – RU; *Hall NV*
I. lacunosa L. – RU R; *9586*
**I. macrorhiza* Michx. – RU R; *9793*
I. pandurata (L.) G. Mey. – CH & RU I; *10340, 10920*

I. pes-caprae (L.) R. Br. – TM R; *9851*
I. sagittata Poir. – TM F; CH & RU O; *9080*

CORNACEAE (incl. NYSSACEAE; e.g., Eyde 1988)

Cornus asperifolia Michx. – CH R; SW I; *9219, 10151, 10394*
C. foemina Mill. – CH R; SW I; *10150*
Nyssa biflora Walt. – CH R; SW I; *10484* (Burkhalter 1992)

CUCURBITACEAE

Melothria pendula L. – CH, FL & RU I; *9220, 9636*

CYPERACEAE

Bulbostylis stenophylla (Ell.) C. B. Clarke – FL R; *9680*
Carex blanda Dewey – CH R; *8380*; new
C. chapmannii Steud. – CH & RU I; *10014, 10027*
C. cherokeensis Schwein. – CH & RU I; *8897, 10199*
C. fissa Mack. – FP R; *10145*
C. godfreyi Naczi – CH & RU I; *10031* (Naczi 1993)
C. hyalinolepis Steud. – FP & RU I; *9991, 10185*
C. lupuliformis Sartwell ex Dewey – SW R; *8949*
C. vexans F. J. Herm. – SW R; *10148*
Carex sp. nov. (sect. *Granulares*) – CH R; *10029, 10146* (R. Naczi, pers. comm.)
Carex sp. nov. (sect. *Griseae*) – CH R; *8382* (R. Naczi, pers. comm.)
Cladium jamaicense Crantz – TM & FP F, locally A; *9032*
Cyperus compressus L. – RU R; *9235*
C. croceus Vahl – RU R; *9542* (= *C. globulosus* Aubl.)
C. distinctus Steud. – FP & RU O; *9530*
**C. esculentus* L. – TM R; *9858*
C. flavescens L. – FP & RU R; *9172, 9239, 9956*
C. haspan L. – FP I; *9455*
C. ligularis L. – FP R, brackish water; *11125*
C. odoratus L. – SW & FP F; *9569*
C. planifolius Rich. – TM & FP; *Hall NV*
C. polystachyos Rottb. – FP & RU F; *8921, 9123, 9154, 9536, 10990*
C. retrorsus Chapman – FL & RU O; *9141, 9211*
**C. rotundus* L. – RU R; *9960*; new
C. strigosus L. – RU R; *9230*
C. surinamensis Rottb. – RU R; *9224*
C. tetragonus Ell. – CH F; *9510, 9531*
C. virens Michx. – FP R; *10491*
Eleocharis albida Torr. – TM R; FP F; *8387, 9104, 9122, 9418, 9562, 10172*
E. atropurpurea (Retz.) J. Presl & C. Presl – FP R; *9472*
E. baldwinii (Torr.) Chapm. – FP; *Hall NV*
E. cellulosa Torr. – TM R; *9596*
E. geniculata (L.) Roemer & Schultes – FP F; *9062, 9105*
E. montevidensis Kunth – FP R; *10182*
Fimbristylis autumnalis (L.) Roemer & Schultes – RU R; *9701*

F. caroliniana (Lam.) Fern. – CH R, near salt marsh; *11046*

F. dichotoma (L.) Vahl – FL & RU O; *9136, 9250*

F. spadicea (L.) Vahl – TM & CH F; *8896, 9203, 9523, 9620, 10339, 10551* [= *F. castanea* (Michx.) Vahl]

Fuirena breviseta (Coville) Coville – FP R; *9789*

**Kyllinga brevifolia* Rottb. – RU R; *9240* [= *Cyperus brevifolius* (Rottb.) Endl. ex Hassk.]

K. pumila Michx. – FP & RU I; *9261, 9479* [= *Cyperus tenuifolius* (Steud.) Dandy]

Rhynchospora caduca Ell. – FL & RU O; *9027, 10362, 10573*; new

R. colorata (L.) H. Pfeiffer – CH & FP O; RU F; *8966, 9215, 9667,10353* [= *Dichromena colorata* (L.) A. S. Hitchc.]

R. corniculata (Lam.) A. Gray – SW & FP I; *9458*

R. fascicularis (Michx.) Vahl – FL & RU F, locally A; *8945, 9101, 9126, 9693, 10740, 11014*

R. megalocarpa A. Gray – FL; *Hall NV*

R. microcarpa Baldw. ex A. Gray – FL & RU O; *9028, 10335*

R. miliacea (Lam.) A. Gray – CH & SW R; *9125, 10487*

R. mixta Britt. ex Small – SW & FP; *Hall NV*

Scirpus californicus (C. A. Mey.) Steud. – FP R; *9204*

S. lineatus Michx. – SW R; *10149*

S. robustus Pursh – TM R; *9191*; new

S. tabernaemontani C. C. Gmel. – FP I; *10338* (= *S. validus* Vahl)

Scleria oligantha Michx. – CH & RU F; *8381, 9024*

S. triglomerata Michx. – CH & RU F; *8939*

S. verticillata Muhl. ex Willd. – FL I; *9686, 9791*

DIOSCOREACEAE

Dioscorea floridana Bartlett – CH R; *9441, 9642*

EBENACEAE

Diospyros virginiana L. – CH & FL F; *9045*

ERICACEAE

Bejaria racemosa Vent. – FL R; *9117*

Gaylussacia nana (Gray) Small – FL R; *9698*

Lyonia fruticosa (Michx.) G. S. Torr. – FL R; *8935, 9112*

L. lucida (Lam.) K. Koch – FL R; *8938*

Vaccinium arboreum Marsh. – CH & FL I; *8944*

V. darrowii Camp – FL; *Hall NV*

V. myrsinites Lam. – FL R; *9139*

V. stamineum L. – FL R; *11122*

EUPHORBIACEAE

Acalypha gracilens A. Gray – CH & RU R; *10984*

Chamaesyce blodgettii (Engelm. ex Hitchc.) Small – CH, FL & RU F, often on exposed limestone; *9041, 9199*

C. hyssopifolia (L.) Small – RU R; *10543*
C. maculata (L.) Small – RU R; *10544*
C. mesembrianthemifolia (Jacq.) Dugand – TM R; *10545*; new
Euphorbia commutata Engelm. ex A. Gray – CH R; *9937*
Phyllanthus caroliniensis Walt. – CH; *Hall NV*
P. liebmannianus Muell. Arg. ssp. *platylepis* (Small) G. L. Webster – CH I; *10176*
**P. urinaria* L. – RU I; *9471*; new
Poinsettia cyathophora (Murr.) Bartl. – RU; *Hall NV*

FABACEAE (= LEGUMINOSAE)

**Albizia julibrissin* Durazz. – RU R; *9786*
Amorpha fruticosa L. – CH, FL & FP O; *8919, 9201, 10154*
Centrosema virginianum (L.) Benth. – FL R; *8922*
Cercis canadensis L. – CH R; *9992*
Chamaechrista fasciculata (Michx.) Greene – RU O; *9081, 10556*
C. nictitans (L.) Moench var. *aspera* (Muhl. ex Ell.) Irwin & Barneby – RU R; *9679*
Crotalaria rotundifolia J. F. Gmel. – RU O; *10729*
**C. spectabilis* Roth – RU R; *11056*; new
Dalea carnea (Michx.) Poir. – FL R; *9710*
Desmanthus virgatus (L.) Willd. – FL & RU R; *9089*
Desmodium glabellum (Michx.) DC. – RU R; *10994*
D. incanum DC. – RU I; *9076, 9540*
D. marilandicum (L.) DC. – RU; *Hall NV*
D. paniculatum (L.) DC. – RU I; *9511*
**D. tortuosum* (Sw.) DC. – RU R; *9611*; new
**D. triflorum* (L.) DC. – RU R; *9595*
Erythrina herbacea L. – CH O; *8902*
Galactia elliottii Nutt. – FL R; *10387*
G. volubilis (L.) Britt. – CH & FL O; *8952*
Gleditsia aquatica Marsh. – SW R; *8931*
G. triacanthos L. – CH I; SW & FP R; *8480, 9060*; new
**Kummerowia striata* (Thunb.) Schindl. – RU R; *9447*
Lespedeza angustifolia (Pursh) Ell. – FL; *Hall NV*
L. hirta (L.) Hornem. – FL; *Hall NV*
**Medicago lupulina* L. – RU R; *9140*
**Melilotus albus* Medik. – RU R; *9097, 9952*
**M. indicus* (L.) All. – RU R; *10549*
Neptunia pubescens Benth. – FL & RU I; *9086*
Phaseolus smilacifolius Pollard – CH R; *8472, 9557, 9670, 11136* [This taxon was considered to be a hybrid by Isely (1990), apparently based on one sterile specimen. Field observation by the first author and 100% germination in a greenhouse of 221 seeds from 7 individual plants, with identical progeny all like the parents, strongly support the recognition of this entity as a distinct species.]
Rhynchosia michauxii Vail – RU R, sandy roadside through salt marsh; *11051*
R. minima (L.) DC. – FL & RU I; *9541*

Senna marilandica (L.) Link – RU R; *10928*
**S. obtusifolia* (L.) H. S. Irwin & Barneby – RU R; *9214, 9427*
Sesbania herbacea (Mill.) McVaugh – RU R; *9549* (= *S. macrocarpa* Muhl. ex Raf.)
S. vesicaria (Jacq.) Ell. – FP I; RU O; *9589*
**Trifolium campestre* Schreb. – RU R; *9977*
Vicia acutifolia Ell. – CH & RU O; *8406, 8492*
V. floridana S. Wats. – CH & RU O; *8407, 8467*
**V. sativa* L. – RU R; *9975*

FAGACEAE

Quercus chapmanii Sarg. – FL; *Hall NV*
Q. geminata Small – FL R; *9147*
Q. laurifolia Michx. – CH F; SW & FL O; *9451*
Q. michauxii Nutt. – CH R; *9217*
Q. myrtifolia Willd. – FL R; *11127*
Q. nigra L. – CH R; *9218, 9431*
Q. pumila Walt. – FL; *Hall NV*
Q. shumardii Buckl. – CH I; *9051*
Q. virginiana Mill. – CH F, locally A; FL O; *9114, 9422*

FUMARIACEAE (see PAPAVERACEAE)

GENTIANACEAE

Eustoma exaltatum (L.) Salisb. ex G. Don – TM, FP & RU O; *9509*
Sabatia calycina (Lam.) A. Heller – FP F; RU O; *8913, 10030*
S. stellaris Pursh – FL & FP I; RU O; *8910, 9021*

GERANIACEAE

Geranium carolinianum L. – RU R; *9945*

HALORAGACEAE

Myriophyllum pinnatum (Walt.) Britt. et al. – FP O; *9539, 9996*; new
Proserpinaca palustris L. – FP F; *8953*
P. pectinata Lam. – FP; *Hall NV*

HAMAMELIDACEAE

Liquidambar styraciflua L. – CH O; SW F; FL I; *9152*

HIPPOCASTANACEAE (see SAPINDACEAE)

HYDRANGEACEAE (distinct from SAXIFRAGACEAE; e.g., Morgan and Soltis 1993)

Decumaria barbara L. – SW R; *11084*

HYDROCHARITACEAE

**Hydrilla verticillata* (L. f.) Royle – reportedly in Kelly Creek; *Hall NV*

HYPERICACEAE (see CLUSIACEAE)

HYPOXIDACEAE

Hypoxis curtissii Rose – CH & RU O; *8479, 9429* (= *H. leptocarpa* Engelm.; Herndon 1992a, 1992b)

IRIDACEAE

Iris hexagona Walt. – FP F; *8386*
Sisyrinchium atlanticum E. P. Bickn. – CH & RU O; *8392, 10025* (This species is not synonymous with *S. angustifolium,* which does not occur in Florida; Dan Ward, pers. comm.)
**S. rosulatum* E. P. Bickn. – RU R; *10331, 10332* (incl. *S. exile* E. P. Bickn.)

JUGLANDACEAE

Carya aquatica (F. Michx.) Nutt. – SW R; *9659*
C. glabra (Mill.) Sweet – CH O; SW & FL I; *9156*

JUNCACEAE

Juncus coriaceus Mack. – CH R; RU I; *10195*
J. dichotomus Ell. – CH R, near wet depression; *9238*
J. marginatus Rostk. – FP & RU O; *8936, 8963*
J. megacephalus M. A. Curtis – FP R; *10367*
J. polycephalus Michx. – FP R; *9171*
J. roemerianus Scheele – TM A; FP R; *10017*
J. scirpoides Lam. – FP R; *10741*
J. tenuis Willd. – RU R; *10194*

JUNCAGINACEAE

Triglochin striata Ruiz & Pavon – TM F; *9417*

LAMIACEAE (= LABIATAE; incl. part of VERBENACEAE; Cantino 1992; Thorne 1992)

Callicarpa americana L. – CH & FL F; *9048*
Hyptis alata (Raf.) Shinners – RU I; *9225*
**H. mutabilis* (Rich.) Briq. – RU R; *9207, 9583*
**Lamium amplexicaule* L. – RU R; *9941*; new
Monarda punctata L. – RU R; *9621*
Salvia coccinea Buc'hoz ex Etl. – CH; *Hall NV*
S. lyrata L. – CH & RU R; *10021*
Scutellaria arenicola Small – FL R; *9691*
Teucrium canadense L. – CH O; *9185*
Trichostema dichotomum L. – FL & RU I; *9464, 9600*

LAURACEAE

Persea borbonia (L.) Spreng. – CH R, island hammocks; *9195*
P. palustris (Raf.) Sarg. – CH, SW & FL F; *9110, 10735*

LEITNERIACEAE (see SIMAROUBACEAE)

LEMNACEAE (see ARACEAE)

LENTIBULARIACEAE

Utricularia foliosa L. – FP R; *9800*; new

LINACEAE

Linum medium (Planch.) Britt. – FL & RU R; *10138, 10352*

LOGANIACEAE

Gelsemium sempervirens (L.) W. T. Ait. – CH & FL I; *9030, 9972*
Mitreola petiolata (J. F. Gmel.) Torr. & A. Gray – FP F; *9174, 9229*
M. sessilifolia (J. F. Gmel.) G. Don – FP; *Hall NV*
Polypremum procumbens L. – RU R; *8943, 9246* (Familial placement is still in doubt; see Jensen 1992.)
Spigelia loganioides (Torr. & A. Gray ex Endl. & Fenzl) A. DC. – CH R; *Judd 2660*

LYTHRACEAE

Ammania latifolia L. – FP F; *8915*; new
**Cuphea carthagenensis* (Jacq.) J. F. Macbr. – RU R; *9245*
Decodon verticillatus (L.) Ell. – SW; *Hall NV*
Lythrum alatum Pursh var. *lanceolatum* (Ell.) Torr. & A. Gray ex Rothr. – FP & RU I; *10574*
L. lineare L. – TM I; *9421*; new

MAGNOLIACEAE

Magnolia grandiflora L. – CH O; SW F; FL R; *9145*
M. virginiana L. – SW I; *9128*

MALVACEAE (incl. BOMBACACEAE, STERCULIACEAE, TILIACEAE; Judd and Manchester 1997)

Abutilon hulseanum (Torr. & A. Gray) Torr. ex A. Gray – RU R; *10397*
Hibiscus coccineus Walt. – FP O; *9795*
H. grandiflorus Michx. – FP I; *9535*; new
Kosteletzkya virginica (L.) C. Presl ex A. Gray – FP I; *10407*
**Melochia corchorifolia* L. – RU; *Hall NV*
Modiola caroliniana (L.) G. Don – RU R; *10403*
**Pavonia hastata* Cav. – RU R; *10398*
Sida rhombifolia L. – RU O; *9192, 10986*
**S. spinosa* L. – RU R; *11057*; new
Tilia americana L. var. *caroliniana* (Mill.) Castig. – CH I; *9057, 10020*

MARANTACEAE

Thalia geniculata L. – FP R; *11088*; new

MENISPERMACEAE

Cocculus carolinus (L.) DC. – RU R, boundary trail; *9043*

MORACEAE

Morus rubra L. – CH I; *8463*

MYRICACEAE

Myrica cerifera L. var. *cerifera* – CH, SW & FL F, locally A; *10026*
M. cerifera L. var. *pumila* Michx. – FL R; *10732* (This entity is not usually given taxonomic recognition, but we point it out here because we think it may be distinct and it should be studied in more detail. This entity is a fire-adapted dwarf shrub restricted to well-drained sandy soils. The habitat may represent a natural ecological barrier leading to reproductive isolation from var. *cerifera.* The two taxa may also be isolated, in part, by different blooming periods.)

MYRSINACEAE

Rapanea punctata (Lam.) Lundell – CH I; *8366, 9506* (= *Myrsine floridana* A. DC.)

MYRTACEAE

Eugenia axillaris (Sw.) Willd. – CH R, island hammocks; *9200*

NAJADACEAE

Najas marina L. – TM R, submerged aquatic; *9803*; new

NYCTAGINACEAE

Boerhavia diffusa L. – RU R; *10541*

NYMPHAEACEAE

Nymphaea elegans Hook. – FP R; *9480*; new
N. odorata Sol. – FP R; *9454*

NYSSACEAE (see CORNACEAE)

OLACACEAE

Ximenia americana L. – CH; *Hall NV*

OLEACEAE

Forestiera ligustrina (Michx.) Poir. – CH O; *9505, 9529, 9796*
F. segregata (Jacq.) Krug & Urban – TM O; CH F; *8371, 8925, 10547*
Fraxinus caroliniana Mill. – SW I; *10489*
F. pennsylvanica Marsh. – CH & SW O; *9054, 10184*

Osmanthus americana (L.) Benth. & Hook. f. ex A. Gray – SW R; *9674*

ONAGRACEAE

Gaura angustifolia Michx. – RU I; *9096*
Ludwigia maritima R. M. Harper – FL I; *10731*
L. microcarpa Michx. – FP F; *9178, 10336*
L. repens J. R. Forst. – FP O; *8948*
Oenothera laciniata Hill – RU R; *10008*

ORCHIDACEAE

Epidendrum conopseum R. Br. – CH & SW F; *8170*
Habenaria floribunda Lindl. – SW R; *9121* (= *H. odontopetala* Reichenb. f.)
Hexalectris spicata (Walt.) Barnh. – CH R; *9095*
Malaxis spicata Sw. – SW R; *10917*

OXALIDACEAE

Oxalis corniculata L. – RU R; *9963*
O. florida Salisb. ssp. *prostrata* (Haworth) Lourt. – RU I; *9243* [Perhaps this should be treated as *Oxalis dillennii* ssp. *filipes* as suggested by Eiten (1963), but we await a modern revision.]

PAPAVERACEAE (incl. FUMARIACEAE; Judd et al. 1994; Kadereit et al. 1994, 1995; Loconte et al.1995)

Corydalis micrantha (Engelm. ex A. Gray) A. Gray – RU R; *9949*; new

PASSIFLORACEAE

Passiflora lutea L. – CH; *Hall NV*
P. suberosa L. – CH I; *8461*

PHYTOLACCACEAE

Phytolacca americana L. var. *rigida* (Small) Caulkins & Wyatt – CH & RU I; *9603* (Caulkins and Wyatt 1990)

PLANTAGINACEAE

**Plantago major* L. – RU R; *8957*; new
P. virginica L. – RU R; *10143*

PLUMBAGINACEAE

Limonium carolinianum (Walt.) Britt. – TM F; *9419*

POACEAE (= GRAMINEAE)

Andropogon glomeratus (Walt.) Britt. et al. var. *glaucopsis* (Ell.) C. Mohr – FL R; *11119* (Campbell 1983)

A. glomeratus (Walt.) Britt. et al. var. *pumilus* (Vasey) Vasey ex L. H. Dewey – FL & RU F; *9625, 9654, 9797, 11060, 11121, 11124, 11128*

A. gyrans Ashe var. *stenophyllus* (Hackel) C. S. Campb. – FL & RU I; *9704*

A. longiberbis Hackel – FL; *Hall NV*

A. virginicus L. var. *virginicus* – FL & RU O; *9692, 9708* (Both old-field and smooth variants are present.)

Aristida beyrichiana Trin. & Rupr. – FL; *Hall NV*

A. patula Chapman ex Nash – FL & RU R; *10726, 11036* (Allred 1986)

A. purpurascens Poir. – FL R; *9614*; new

A. spiciformis Ell. – FL I; *9116*

Arundinaria gigantea (Walt.) Walt. ex Muhl. – RU R; *9965*; new

Axonopus fissifolius (Raddi) Kuhlm. – RU I; *9132, 9209, 9432, 9709* (= *A. affinis* Chase)

A. furcatus (Fluegge) Hitchc. – RU R; *9210*

**Bothriochloa pertusa* (L.) A. Camus – RU R; *9082, 9616* (These specimens are atypical, with non-pitted glumes.)

Cenchrus echinatus L. – RU R; *9256*

C. incertus M. A. Curtis – CH R; RU O; *9857, 11052*

C. myosuroides Kunth – CH R, open island hammock; *9518*; new

Chasmanthium laxum (L.) Yates – CH & RU F; *9653, 9711*

C. nitidum (Baldw.) Yates – CH & RU F; *8961, 9699*

C. sessiliflorum (Poir.) Yates – CH & RU F; *9669*

**Cynodon dactylon* (L.) Pers. – RU I; *10193*

Digitaria ciliaris (Retz.) Koel. – FL & RU F; *9622, 10580*

**D. violascens* Link – RU R; *11045*

Distichlis spicata (L.) Greene – TM A; *9426, 9508*

**Echinochloa colona* (L.) Link – FP & RU R; *9435, 10173*; new

**E. crusgalli* (L.) P. Beauv. – FP O; *8916, 9568*

E. walteri (Pursh) A. Heller – FP R; *9656*; new

**Eleusine indica* (L.) Gaertn. – RU I; *9226*

Elymus virginicus L. – CH I; *8912*

Eragrostis elliottii S. Wats. – FL & RU O; *9588, 11042, 11047*

E. hirsuta (Michx.) Nees – FL & RU R; *9618*

E. virginica (Zucc.) Steud. – RU R; *9683, 11013*

**Eremochloa ophiuroides* (Munro) Hack. – RU O; *9146, 9544*

Eriochloa michauxii (Poir.) Hitchc. – CH R, near wet depression; *9794*

Eustachys glauca Chapm. – RU F; *10366* [= *Chloris glauca* (Chapm.) Wood]

E. petraea (Sw.) Desv. – RU F; *9519* (= *Chloris petraea* Sw.)

Leersia hexandra Sw. – FP; *Hall NV*

L. virginica Willd. – FP & RU R; *9663*

Leptochloa fascicularis (Lam.) A. Gray – FP & RU R; *9635*

Melica mutica Walt. – CH O, RU R; *8399*

Monanthochloe littoralis Engelm. – TM; *Hall NV*

Muhlenbergia capillaris (Lam.) Trin. – RU R; *9855, 11061*

Oplismenus hirtellus (L.) Beauv. ssp. *setarius* (Lam.) Mez ex Ekman – CH F; *9652* (Scholz 1981)

Panicum aciculare Desv. ex Poir. – FL & RU I; *10358, 10569* (*Dichanthelium* is treated as a subgenus; Webster 1988; Zuloaga 1986.)

P. anceps Michx. – CH & RU F; *9460*
P. commutatum Schultes – CH F; *8401, 9119, 9929*
P. dichotomiflorum Michx. – RU R; *11009*; new
P. dichotomum L. – FL & RU F; *10488, 10933*
P. ensifolium Baldw. ex Ell. – RU R; *10357*
P. gymnocarpon Ell. – FP R; *11090*
P. laxiflorum Lam. – CH O; *8477, 9148*
P. portoricense Desv. ex Ham. – RU R; *11002*
**P. repens* L. – FP; *Hall NV*
P. rigidulum Bosc ex Nees – CH & RU F; *9437, 9538, 10932*
P. virgatum L. – CH & RU F; *9503, 9514, 9545, 10727, 11011*
Paspalum caespitosum Fluegge – RU; *Hall NV*
**P. dilatatum* Poir. – RU R; *9175*
P. floridanum Michx. – RU F; *9049, 9804, 10399*
P. langei (E. Fourn.) Nash – RU O; *9461*; new
**P. notatum* Fluegge – RU F; *10365, 10581*
P. repens Berg. – FP I; *9556, 10479* [= *P. fluitans* (Ell.) Kunth]
P. setaceum Michx. – RU O; *9501, 9649*; new
**P. urvillei* Steud. – RU O; *9050*; new
P. vaginatum Sw. - TM R; *11032*; new
**Poa annua* L. – RU R; *9954*; new
**Polypogon monspeliensis* (L.) Desf. – FP & RU R; *9173, 10175*
Saccharum giganteum (Walt.) Pers. – RU R, near salt marsh; *9624, 11049* [= *Erianthus giganteus* (Walt.) Muhl.]
Schizachyrium scoparium (Michx.) Nash – FL R; *11048*
**Secale cereale* L. – RU R; *10174*
Setaria macrosperma (Scribn. & Merr.) K. Schum. – FL & RU I; *9513*
S. parviflora (Poir.) Kerguelen – CH I; RU F; *9084, 9560* [= *S. geniculata* (Lam.) Beauv.]
Sorghastrum elliottii (C. Mohr) Nash – FL O; RU R; *9647, 9668, 9687, 11035*; new
Spartina alterniflora Loisel – TM F, locally A; *9196, 9685, 9854, 11031*
S. cf. *bakeri* Merr. – FL I; *10989*; sterile
S. patens (Ait.) Muhl. – TM F, locally A; *9202*
S. spartinae (Trin.) Merr. ex Hitchc. – TM O; *9517*; new
Sphenopholis obtusata (Michx.) Scribn. – CH & RU R; *10028*
**Sporobolus indicus* (L.) R. Br. – RU R; *9442*
S. virginicus (L.) Kunth – TM F, locally A; *9852, 10734*
Stenotaphrum secundatum (Walt.) Kuntze – CH, FL & RU A; *8899*
Tridens flavus (L.) Hitchc. – FL & RU I; *9551, 9638, 9703, 11044*
Tripsacum dactyloides (L.) L. – RU I; *9039*

POLYGALACEAE

Polygala boykinii Nutt. – RU R, near wet depression; *10155*
P. grandiflora Walt. – FL & RU O; *9018, 10564*
P. incarnata L. – FL & RU R; *8926*
P. nana (Michx.) DC. – FL R; *8942*

POLYGONACEAE

Polygonum hydropiperoides Michx. – FP O; *9232, 9478*
P. punctatum Ell. – FP O; *10936, 11001*
Rumex verticillatus L. – FP R; *10924*; new

PORTULACACEAE

**Portulaca amilis* Speg. – RU R; *9255*; new

POTAMOGETONACEAE

Potamogeton pectinatus L. – FP; *Hall NV*

PRIMULACEAE

Anagallis minima (L.) E. H. L. Krause – RU R, near salt marsh; *8396* (= *Centunculus minimus* L.)
Samolus ebracteatus Kunth – TM, CH & FP F; *8394, 10171*
S. valerandi L. ssp. *parviflorus* (Raf.) Hulten – TM I; CH, SW & FP F; *10170*

RANUNCULACEAE

Clematis catesbyana Pursh – CH R, near boundary trail; *9641*
C. crispa L. – CH R, near wet depressions; *9040, 9859*

RHAMNACEAE

Berchemia scandens (Hill) K. Koch – CH O; *9412*
Sageretia minutiflora (Michx.) C. Mohr – CH F; *8358, 8466*

ROSACEAE

Crataegus aestivalis (Walt.) Torr. & A. Gray – CH R; *9428*; new
Photinia pyrifolia (Lam.) K. R. Robertson & J. B. Phipps – FL R, edge of wet depression; *10004* [= *Aronia arbutifolia* (L.) Pers.]
Prunus americana Marsh. – CH R; *9966, 10326*
P. serotina Ehrh. – FL R; *9118*
P. umbellata Ell. – CH; *Hall NV*
Rosa palustris Marsh. – CH R, edge of wet depression; *10158*
Rubus argutus Link – CH R; *9971, 10142*
R. cuneifolius Pursh – CH R; *9103*
R. trivialis Michx. – CH O; *10005*

RUBIACEAE

Cephalanthus occidentalis L. – FP O; *9059*
Chiococca alba (L.) Hitchc. – CH R; *8173, 9504*
Diodia virginiana L. – FP O; RU I; *9249, 9462, 10329*
Galium hispidulum Michx. – CH O; *9088, 9502*
G. pilosum Ait. – CH R; *10571*
G. tinctorium L. – RU I; *10152*

**Hedyotis corymbosa* (L.) Lam. – RU R; *9254*; new
H. procumbens (J. F. Gmel.) Fosberg – FL; *Hall NV*
Mitchella repens L. – CH; *Hall NV*
**Mitracarpus hirtus* (L.) DC. – RU R; *10345*; new [Perhaps the name should be *M. villosus* (Sw.) Cham. & Schlecht.; Ward 1976.]
Psychotria nervosa Sw. – CH; *Hall NV*
**Richardia brasiliensis* Gomez – RU R; *9242*; new
Spermacoce assurgens Ruiz & Pavon – RU; *Hall NV*
**S. prostrata* Aubl. – CH & RU R; *9689* [= *Borreria ocimoides* (Burm. f.) DC.]

RUPPIACEAE

Ruppia maritima L. – TM F; FP I; *9801, 9989*

RUTACEAE

**Citrus aurantium* L. – CH R; *9169*; new
Ptelea trifoliata L. – CH R; *8360, 10198*
Zanthoxylum clava-herculis L. – CH I; *10197*
Z. fagara (L.) Sarg. – CH; *Hall NV*

SALICACEAE

Salix caroliniana Michx. – FP O; *9994, 10016*

SAPINDACEAE (incl. ACERACEAE and HIPPOCASTANACEAE; Judd et al. 1994)

Acer rubrum L. – CH I; SW O; *9037, 9926*
A. saccharum Marsh. ssp. *floridanum* (Chapman) Desmarais – CH F; SW I; *8481, 9065*
Aesculus pavia L. – CH R; *9213*
Sapindus saponaria L. – CH I; *8409, 9516* (incl. *S. marginatus* Willd.)

SAPOTACEAE

Sideroxylon celastrinum (Kunth) T. D. Penn. – CH R, island hammock; *10548* (= *Bumelia celastrina* H.B.K.; Pennington 1991)
S. lanuginosum Michx. – CH R; *8373, 9553* [= *Bumelia lanuginosa* (Michx.) Pers.]
S. reclinatum Michx. – CH; *Hall NV* (= *Bumelia reclinata* Vent.)

SAURURACEAE

Saururus cernuus L. – FP O; *8904*

SAXIFRAGACEAE (see HYDRANGEACEAE)

SCROPHULARIACEAE

Agalinis maritima (Raf.) Raf. – TM F; *8920, 9170, 9608, 10554*
A. tenuifolia (Vahl) Raf. – FL R; *9582*

Bacopa monnieri (L.) Pennell – TM, CH, FP & RU F; SW I; *9420, 10187*
Buchnera americana L. – FL R; *10566*
Conobea multifida (Michx.) Benth. – RU R; *10192*; new [= *Leucospora multifida* (Michx.) Nutt.]
Gratiola hispida (Benth. ex Lindl.) Pollard – FL R; *8940*
Linaria canadensis (L.) Chaz. – RU R; *9953*
**Lindernia crustacea* (L.) F. Muell. – RU R; *9251, 9599*; new
Mecardonia acuminata (Walt.) Small – FP R; *9258*
Penstemon multiflorus (Benth.) Chapman ex Small – FL R; *10575*
Scoparia dulcis L. – RU R; *9257, 11008*
Scrophularia marilandica L. – RU R, boundary trail near access gate; *10982*; new
**Veronica arvensis* L. – RU R; *9946*; new
V. peregrina L. – RU R; *9947*; new

SIMAROUBACEAE (incl. LEITNERIACEAE; Fernando et al. 1995)

Leitneria floridana Chapman – FP F; *8486, 9047, 9445, 9934*

SMILACACEAE

Smilax auriculata Walt. – CH F; SW & FL O; *9058, 9109*
S. bona-nox L. – CH A; SW & FL O; *8405, 9853*
S. glauca Walt. – FL R; *9700*; new
S. laurifolia L. – CH R; *10477*
S. pumila Walt. – FL R; *11120*
S. smallii Morong – CH R; *8402*
S. tamnoides L. – CH F; *9661*

SOLANACEAE

Lycium carolinianum Walt. – TM F, locally A; *8163, 9850*
Physalis walteri Nutt. – FL & RU O; *8375, 9092, 10169*
Solanum carolinense L. – RU R; *8962, 9234*
S. chenopodioides Lam. – RU R; *10550*

STERCULIACEAE (see MALVACEAE)

STYRACACEAE

Styrax americanus Lam. – CH R, edge of wet depression; *10024*

TILIACEAE (see MALVACEAE)

TURNERACEAE

Piriqueta caroliniana (Walt.) Urban – RU R, boundary trail; *9017*

TYPHACEAE

Typha domingensis Pers. – FP R; *9131*; new

ULMACEAE (excl. CELTIDACEAE)

Ulmus alata Michx. – CH F; *8496, 9414*
U. americana L. – CH F; SW I; *8376*
U. crassifolia Nutt. – CH F; *8484, 9413, 11132*

URTICACEAE

Boehmeria cylindrica (L.) Sw. – SW & FP R; *10937*
Urtica chamaedryoides Pursh – RU R; *9980*; new

VERBENACEAE (see also LAMIACEAE)

**Lantana camara* L. – RU R; *9079, 10164*
Lippia nodiflora (L.) Michx. – TM I; CH, SW, FL, FP & RU F; *8911* [= *Phyla nodiflora* (L.) Greene]
**Verbena brasiliensis* Vell. – RU R; *10201, 10552*; new
V. scabra Vahl – RU F; *9260, 9467, 10183, 10346*

VIOLACEAE

Viola affinis Le Conte – CH & SW O; *10022*
V. triloba Schwein. – CH & SW I; *9970*

VISCACEAE

Phoradendron leucarpum (Raf.) Reveal & M. C. Johnston – CH O; *9925*

VITACEAE

Ampelopsis arborea (L.) Koehne – CH & FL O; *10739*
Parthenocissus quinquefolia (L.) Planch. – CH & FL O; *10168*
Vitis aestivalis Michx. var. *aestivalis* – CH R; *10139*
V. cinerea (Engelm.) Engelm. ex Millardet var. *floridana* Munson – CH I; *9182, 9189*
V. rotundifolia Michx. var. *rotundifolia* – CH & FL R; *9183*
V. vulpina L. – CH R, forest gaps; *10135*; new

XYRIDACEAE

Xyris brevifolia Michx. – FL R; *9676*
X. caroliniana Walt. – FL R; *11000*

APPENDIX 2

LIST OF CHAROPHYTES, LIVERWORTS, MOSSES, AND MACROLICHENS OF WACASASSA BAY STATE PRESERVE

Each name is followed by a brief comment on habitat or substrate, an abundance value abbreviation, and collection number(s) of J. R. Abbott. Voucher specimens are housed in FLAS. Abundance categories are: Rare (R), Infrequent (I), Occasional (O), Frequent (F), and Abundant (A). See text for detailed information on these collections.

CHAROPHYTES

CHARACEAE

Chara zeylanica Kl. ex Willd. – two freshwater pools, R; *9443, 9792*
Nitella capillata A. Br. – one freshwater pool, attached to floating mats of *Bacopa monnieri,* R; *9999*

LIVERWORTS (HEPATICAE)

ADELANTHACEAE

Odontoschisma prostratum (Sw.) Trev. – cabbage palm trunks and wet soil in swamp, R; *B-559, B-584*

ANEURACEAE

Aneura pinguis (L.) Dum. – wet soil in swamp, R; *B-568a, B-582*
Riccardia latifrons Lindb. – wet fallen branches in swamp, R; *B-568*
R. multifida (L.) S. Gray – wet fallen branches in swamp, R; *B-530, B-566*

DILAENACEAE

Pallavicinia lyellii (Hook.) S. Gray – wet soil in swamp, R; *B-573*

FRULLANIACEAE

Frullania cobrensis Gott. ex Steph. – on *Taxodium* branchlets, R; *B-463*
F. eboracensis Lehm. – corticolous, R; *B-601*
F. kunzei (Lehm. & Lindb.) Lehm. & Lindb. – corticolous and on branches, A; *B-334, B-486*
F. obcordata (Lehm. & Lindb.) Lehm. & Lindb. – corticolous, I; *B-621*
F. squarrosa (Reinw., Blume & Nees) Nees – corticolous, I; *B-593*

LEJEUNEACEAE

Ceratolejeunea laetefusca (Aust.) Schust. – corticolous, R; *B-351*
Cheilolejeunea clausa (Nees & Mont.) Steph. – corticolous, F; *B-487*
C. rigidula (Nees & Mont.) Schust. – corticolous, A; *B-447, B-596*
Cololejeunea cardiocarpa (Mont.) Steph. – on corky *Liquidambar* saplings, R; *B-626*
Lejeunea cladogyna Evans – corticolous, I; *B-570*
L. flava (Sw.) Nees – corticolous and on logs, O; *B-436*
L. laetivirens Nees & Mont. – corticolous, O; *B-550, B-595*
Leucolejeunea unciloba (Lindenb.) Evans – corticolous, I; *B-620*
Mastigolejeunea auriculata (Wils. & Hook.) Schiffn. – corticolous, O; *B-433, B-440, B-591, B-615*
Microlejeunea ulicina (Tayl.) Evans ssp. *bullata* (Tayl.) Schust. – corticolous, on branches, and on logs, A; *B-607*

MARCHANTIACEAE

Marchantia domingensis Lehm. & Lindenb. – on moist limestone, R; *B-504, B-565*

PLAGIOCHILACEAE

Plagiochila dubia Lindenb. & Gott. – base of trees near water, O; *B-553, B-557, B-569*

RADULACEAE

Radula australis Aust. – corticolous, O; *B-432, B-480, B-556, B-590*

RICCIACEAE

Riccia fluitans L. – one freshwater pool, floating aquatic, R; *B-611*

MOSSES (MUSCI)

AMBLYSTEGIACEAE

Amblystegium varium (Hedw.) Lindb. – moist base of tree, R; *B-493a*

BRACHYTHECIACEAE

Homalotheciella subcapillata (Hedw.) Card. – corticolous, F; *B-460*
Rhynchostegium serrulatum (Hedw.) Jaeg. & Sauerb. – moist soil at base of tree, I; *B-491*

BRYACEAE

Bryum pseudocapillare Besch. – moist sandy soil, R; *B-461*

CALYMPERACEAE

Syrrhopodon incompletus Schwaegr. – primarily on cabbage palm trunks, A; *B-477, B-546, B-552*
S. texanus Sull. – on log near water, R; *B-572*

CRYPHAEACEAE

Cryphaea glomerata BSG. ex Sull – corticolous, O; *B-588, B-619*
Forsstroemia trichomitria (Hedw.) Lindb. – corticolous, O; *B-399*

DITRICHACEAE

Ditrichum pallidum (Hedw.) Hampe – sandy soil, R; *B-617*

ENTODONTACEAE

Entodon macropodus (Hedw.) C. M. – corticolous and on logs, I; *B-445*
E. seductrix (Hedw.) C. M. – corticolous and on logs, I; *B-349, B-427*

FABRONIACEAE

Schwetschkeopsis fabronia (Schwaegr.) Broth. – on logs, I; *B-560*

FISSIDENTACEAE

Fissidens cristatus Wils. ex Mitt. – moist base of trees and on logs near water, F; *B-435, B-478, B-575, B-579*
F. taxifolius Hedw. – moist log near water, R; *B-527*

HYPNACEAE

Isopterygium tenerum (Sw.) Mitt. – corticolous, on logs, and on moist soil, F; *B-350, B-414, B-549*

LESKEACEAE

Anomodon attenuatus (Hedw.) Hueb. – corticolous, I; *B-422, B-571*
A. rostratus (Hedw.) Schimp. – corticolous, R; *B-492*
Thelia hirtella (Hedw.) Sull. – corticolous, O; *B-400, B-489, B-567*

LEUCOBRYACEAE

Leucobryum albidum (Brid.) Lindb. – primarily near base of cabbage palm trunks, F; *B-434*
Octoblepharum albidum Hedw. – on cabbage palm trunks, R; *B-597, B-600*

LEUCODONTACEAE

Leucodon julaceus (Hedw.) Sull. – corticolous, O; *B-312, B-441*

METEORIACEAE

Papillaria nigrescens (Hedw.) Jaeg. & Sauerb. – corticolous, R; *B-624*

ORTHOTRICACEAE

Schlothemia rugifolia (Hook.) Schwaegr. – corticolous, R; *B-438*

POTTIACEAE

Barbula agraria Hedw. – moist limestone rocks, I; *B-622*
B. cancellata C. M. – moist sandy soil and limestone rocks, O; *B-420, B-574*

SEMATOPHYLLACEAE

Sematophyllum adnatum (Mx.) E. G. Britt. – corticolous, on logs, moist soil, and moist rocks, O; *B-598, B-606*

THUIDACEAE

Bryohaplocladium microphyllum (Hedw.) Wat. & Iwats. – moist soil, logs, and tree bases, I; *B-493* [= *Haplocladium microphyllum* (Hedw.) Broth.]
Cyrto-hypnum minutulum (Hedw.) Buck & Crum – moist soil, logs, and tree bases, I; *B-546* [= *Thuidium minutulum* (Hedw.) BSG.; Buck and Crum 1990]
Thuidium delicatulum (Hedw.) BSG. – moist soil, logs, and tree bases, I; *B-544, B-563*

MACROLICHENS

CLADONIACEAE

Cladina subtenuis (Abbayes) Hale & Culb. – on wooden bridge; *B-423*
Cladonia grayi G. Merr. ex Sandst. – on soil; *B-633*
C. leporina Fr. – on wooden bridge; *B-424*
C. peziziformis (With.) J. R. Laundon – on soil; *B-632*
C. ramulosa (With.) J. R. Laundon – on soil; *B-613*
C. ravenelii Tuck. – on soil and on bark; *B-422*

COLLEMATACEAE

Collema furfuraceum (Arnold) Du Rietz var. *luzone* (Rasanen) Degel.; *B-328a*
C. pulchellum Ach. var. *leucopeplum* (Tuck.) Degel.; *B-328*
Leptogium austroamericanum (Malme) C. W. Dodge; *B-329, B-456, B-562, B-578*
L. azureum (Sw.) Mont.; *B-583*
L. chloromelum (Sw. ex Ach.) Nyl.; *B-448, B-455*
L. cyanescens (Rabenh.) Koerber; *B-437*
L. marginellum (Sw.) Gray; *B-395*
L. phyllocarpum (Pers.) Mont.; *B-398*
L. stipitatum Vainio; *B-353*

PARMELIACEAE

Bulbothrix isidiza (Nyl.) Hale; *B-469*
Canoparmelia cryptochlorophaea (Hale) Elix & Hale; *B-466*
Parmotrema hypoleucinum (Steiner) Hale; *B-320*
P. perforatum (Jacq.) A. Massal.; *B-418*
P. rigidum (Lynge) Hale; *B-450*
P. tinctorum (Delise ex Nyl.) Hale; *B-327, B-415*
P. ultralucens (Krog) Hale; *B-325*
Pseudoparmelia sphaerospora (Nyl.) Hale; *B-326, B-333, B-457*
Punctelia rudecta (Ach.) Krog; *B-321*
Ramalina complanata (Sw.) Ach.; *B-585*
R. fastigiata (Pers.) Ach.; *B-331, B-335, B-338*
R. usnea (L.) R. Howe; *B-453*
R. willeyi R. Howe; *B-412, B-413, B-488*
Rimelia reticulata (Taylor) Hale & Fletcher; *B-462*
R. subisidiosa (Muell. Arg.) Hale & Fletcher; *B-464*
Usnea baileyi (Stirton) Zahlbr.; *B-339*
U. mutabilis Stirton; *B-602*
U. perplectata Mot.; *B-346*
U. rubicunda Stirton; *B-407*
U. strigosa (Ach.) Eaton; *B-482*
U. trichodea Ach.; *B-481*

PHYSCIACEAE

Dirinaria applanata (Fee) D. D. Awasthi; *B-470*
Heterodermia speciosa (Wulfen) Trevisan; *B-330*

Hyperphyscia syncolla (Tuck. ex Nyl.) Kalb; *B-324*
Physcia atrostriata Moberg; *B-323, B-401, B-612*
P. neogaea R. C. Harris; *B-630*
Pyxine caesiopruinosa (Tuck.) Imshaug; *B-543*

STICTACEAE

Lobaria ravenelii (Tuck.) Yoshim.; *B-525, B-592*

ADDENDUM A final site visit on February 13, 2000 yielded the following additions:

BRASSICACEAE

Rorippa teres (Michx.) Stucky – FP R; *13325*

RICCIACEAE

Ricciocarpus natans (L.) Corda – on exposed mud, R; *B–859*

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NEW ENGLAND NOTE

FIRST RECORDS OF A EUROPEAN MOSS, *PSEUDOSCLEROPODIUM PURUM,* NATURALIZED IN NEW ENGLAND

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Pseudoscleropodium purum (Hedw.) Fleisch. *in* Broth. MASSACHUSETTS. Middlesex Co., Mount Auburn Cemetery, Cambridge, ca. 1 km south of Fresh Pond: soil, mowed lawn, north-facing slope under deciduous tree canopy, between Trefoil and Bellwort paths, 1 Apr 2000, *Miller 12911* (NYS); on soil in rough lawn in shade of deciduous trees, above Rose Path, northeast of Tower, 1 Apr 2000, *Miller 12912* (NYS); soil, sparse lawn near grove of *Picea abies* trees, east and southeast and above Dell Pond, 1 Apr 2000, *Miller 12910* (NYS); shaded lawn among grass, inside Scots' Charitable Society Plot enclosure, tree canopy largely deciduous, 13 May 2000, *Miller 12985* (NYS, FH). Newton Cemetery, ca. 1.5 km west of Newton Center: damp soil, south side of central pond, mowed lawn behind Richards crypt under and near large *P. abies* trees, 13 May 2000, *Miller 12986* (NYS, FH).

Elsewhere is detailed the recent discovery of *Pseudoscleropodium purum* in New York, where this moss has been found to be widespread in the southern part of the state, from near Buffalo eastward to the Albany area (Miller and Trigoboff, in press). A large (to 8 cm long), pinnately branched feather-moss, native to Europe, *P. purum* had been observed in other parts of North America prior to its being recognized in New York. These include Washington State and adjacent British Columbia (especially in and near Seattle and Vancouver; Lawton 1960; Schofield 1965), eastern Michigan (near Ann Arbor; Rohrer and Kirkpatrick 1985), and St. John's, Newfoundland (Brassard 1983). Lawns, gardens, and fields are where this moss has been found most frequently in North America so far, suggesting that its establishment and dispersal are closely linked to horticultural practices and lawn care. The year and method of its introduction into northeastern North America are unknown.

My field studies in New York State revealed that *Pseudoscleropodium purum* occurred commonly in regularly mowed cemetery lawns on moist, clayey soil shaded by conifers (particularly *Picea abies* and *Thuja occidentalis*). While I have searched for this moss at other sites that seemed promising, for example, village commons and parks with lawns shaded by *P. abies,* I have found it only twice in places other than cemeteries. Both of these are in Cortland, New York (lawns of the Municipal Water Works and the City water tower). Thus, in New York at least, *P. purum* appears to occur in managed plant communities.

Nowhere in North America, so far, has *Pseudoscleropodium purum* been found to produce spores, so it seems likely that its dispersal takes place when plant fragments are transported by unknown vectors, ones perhaps associated with lawn care or the nursery and horticultural trades. Populations of male and female plants (this moss is dioicous) have been found in New York in different cemeteries in Rensselaer County, which was intensively surveyed for *P. purum* (Miller and Trigoboff, in press), indicating that a potential exists for its reproduction by spores in the northeastern United States. Female plants have been found in Massachusetts in the Newton Cemetery population, but those in Mount Auburn Cemetery were sexually undifferentiated at the time of collection.

I evaluated how widespread *Pseudoscleropodium purum* was in eastern Massachusetts by surveying the bryoflora of 18 cemeteries in Norfolk, Middlesex, and Suffolk counties, in an area of about 800 km^2 bounded by the towns of Framingham, Maynard, Acton, Bedford, Malden, Milton, and Natick. In addition, I examined parts of the Arnold Arboretum, Jamaica Plain (Boston), where conifers and mowed lawn occurred together. The inventory target areas were chosen utilizing the Boston North, Boston South, Framingham, and Maynard 1:25,000 metric U.S. Geological Survey topographic maps. Criteria used to select the sites included large size and prominence within the community (in eastern Massachusetts, these two factors often indicate that a cemetery was founded in the 1800s), tree cover (green overprint on the maps), and location (sites more or less evenly scattered throughout the study area). While turf mosses varied from abundant to sparse in all cemetery lawns I examined, *P. purum* occurred in only two of them, as indicated above. Moreover, my search at the Arnold Arboretum was unsuccessful.

Because *Pseudoscleropodium purum* may eventually spread to cemeteries and other places in eastern Massachusetts where it does not now occur, I list here those I searched without success in May 2000: Norfolk Co.—Milton (Town of Milton), Woodlawn (Wellesley); Middlesex Co.—Edgell Grove (Framingham), Forest Dale (Malden), Glenwood (Maynard), Glenwood (Natick), Lakeview (Wayland), Oak Grove (Medford), Ridgelawn (Watertown), St. Patricks (Watertown), Shawsheen (Bedford), Sleepy Hollow (Concord), Westview (Lexington), Wildwood (Winchester), Woodlawn (Acton); and Suffolk Co.—Forest Hills (Boston). The success rate, 11% (2 occurrences, 18 searched areas), was about the same as that obtained in the survey of Rensselaer County, New York. There, *P. purum* was found at 14 of 70 sites (20%), but about twice as much area was surveyed (1800 km^2).

In contrast to cemeteries in Rensselaer County, those in eastern Massachusetts contained fewer small groves of *Picea abies,* and therefore were locally less shaded. However, soil differences between the two regions are perhaps more important. Soil in the eastern Massachusetts cemeteries I visited was generally well drained and sandy or loamy, and wind exposure was greater owing to hilltop, ridge, or slope locations. More acid soils also characterize cemeteries in eastern Massachusetts on the basis of the absence of bryophytes associated with basic or circumneutral, calcareous soil. While a search for more stations of *Pseudoscleropodium purum* in eastern Massachusetts could be productive and should be pursued, the edaphic differences between eastern Massachusetts and New York habitats may prove to be significant determinants of different patterns of lawn moss occurrence in these two regions.

Pseudoscleropodium purum is more widely naturalized in North America than reported in the most recent regional floras (e.g., Crum and Anderson 1981). It is uncertain whether this moss will become invasive in the New York–New England region. It is so in New Zealand where male and female plants grow together and spores are produced (Lewinsky and Bartlett 1982). Additional systematic observation and field surveys are needed in northeastern North America to track the status and abundance of *P. purum.*

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NOTE

LOW CATCHMENT AREA LAKES: NEW RECORDS FOR RARE COASTAL PLAIN SHRUBS AND *UTRICULARIA* SPECIES IN NOVA SCOTIA

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Nova Scotian wetlands have long been known for their diversity of Atlantic Coastal Plain plants (Fernald 1921). They are prized for their local abundances of rare Atlantic Coastal Plain species, whose diversity is greatest in large catchment area lakes (Hill et al. 1998). The large annual water level fluctuations (1–2 m) in lakes of large catchment area (> 50,000 ha) create a wide, ephemeral lakeshore habitat where biomass is kept low by prolonged flood stress in spring, intermittent flooding in summer, and ice disturbance during winter (Hill et al. 1998). Six of ten species of plants currently listed as Endangered, Threatened, or Vulnerable in Canada by COSEWIC (Committee on the Status of Endangered Wildlife in Canada) occur on the shores of these large catchment area lakes. These species and sites are the primary focus of conservation efforts by the Atlantic Coastal Plain Recovery Team.

The temptation to concentrate conservation efforts on large CA (catchment area) lakes is undeniable given the clear monotonic increase in rare species diversity in lakes with increasing CA, but such large CA chauvinism may not be completely justifiable. This is because a few notable, rare coastal plain species occur in low CA (< 2000 ha) lakes. Taschereau (1984) made the first find of *Clethra alnifolia* L. in Canada on the shores of a low CA, Nova Scotian lake and subsequently, naturalist Charlie Allen discovered a second site at Louis Lake, another headwater lake (Newell 1997). Clearly, the shrub, *C. alnifolia,* did not obey the same CA rules that applied to the rare coastal plain herbs and the shrub discrepancy was also upheld when *Toxicodendron vernix* (L.) Kuntze, new to maritime Canada (Hill 1989), was found along peaty shorelines of two headwater lakes. With the exception of a single *C. alnifolia* individual found at Canoe Lake (10,000 ha CA) by MacKinnon and Maas (Newell 1997), all recent findings of *C. alnifolia* continue to be made at low CA lakes. In this note, we report finding two additional low CA lake sites for the taxon. We also report new discoveries of rare floating, coastal plain plants (at the opposite end of the growth-form spectrum) in the same low CA sites.

Our field work in 1998 revealed large populations of *Clethra alnifolia* in the low CA lakes, Pretty Mary and Mudflat, which are immediately upstream from populations discovered at Mill Lake by Leslie Rogers (det. Marian Zinck). Stands were healthy and cottagers, unaware of the rarity of the shrub, remarked that they had difficulty eradicating it from cleared areas on their properties. Growth in these cases appeared to be vegetative only, as was found by Taschereau for the stands of *C. alnifolia* on Belliveau Lake (Taschereau 1984). However, we collected representative seedlings from under *C. alnifolia* stands on Belliveau, Louis, and Pretty Mary Lakes on August 25, 1998, and grew them in pots for a year, both outside in a cold frame and inside the greenhouse. Seedlings were identified as *Ilex verticillata* (L.) A. Gray, *Rhododendron canadense* (L.) Torr., and *Chamaedaphne calyculata* (L.) Moench at Pretty Mary Lake; *Nemopanthus mucronatus* (L.) Loes, and *Ilex verticillata* at Belliveau Lake; and *Clethra alnifolia* at Louis Lake. This is the first evidence that any population of *C. alnifolia* in Nova Scotia can reproduce sexually. Despite the discovery of seedling recruits at Louis Lake, all young shoots under parent stems appeared to be vegetative suckers, and even in the main range of *C. alnifolia,* in New Jersey, seedling survival in intact woodland appears to be tenuous (Jordan and Hartman 1995).

While lakeshore emergent herb diversity increases with increasing disturbance along a lake CA gradient, shrub diversity is negatively correlated with fetch, a variable linked to disturbance through wind energy (Hill and Keddy 1992). The rare shrubs discussed above occur on the shores of relatively small surface area, low CA lakes and they grow in a zone essentially free of ice scour disturbance. In similar fashion, large CA lakes may not be priority habitats for rare floating plants. In Canada, *Utricularia* *radiata* Small occurs only in lakes in southwestern Nova Scotia, where it typically grows in 1–3 m deep water in association with *Brasenia schreberi* J. F. Gmelin. There have been few known reports of this species in Nova Scotia (Brown 1940; Roland 1976; Zinck and Roland 1998); the taxon has a global ranking of G4 and in Canada is considered imperilled because of rarity of occurrence (6–20 occurrences; Zinck et al. 1994). While investigating new sites for *Clethra alnifolia,* we found large populations of *U. radiata* in sheltered parts of the two low CA lakes. This reinforced our realization that while rare coastal plain herb species richness is tied to large CA lakes, coastal plain plants of quite different functional groups (viz., shrubs and floating plants) may be best represented at the opposite end of the disturbance gradient, in low CA lakes. *Utricularia radiata* records include old herbarium data (ACAD), findings made at Kejimkujic Park (Roland 1976; updates by Peter Hope) and new findings of our own over the past two summers (see Appendix). When these records are put into catchment area classes, it is evident that the species is more likely to occur in low CA lakes; out of a total of twenty lake records, eleven were from low CA, two from large CA, and six from intermediate CA lakes between these extremes. At the large CA lake sites, the taxon was found in the most sheltered locations.

Our last low CA lake addition to Nova Scotia's rare Atlantic Coastal Plain plants is a white-flowered form of *Utricularia purpurea* Walter, discovered in 1998 at Pretty Mary Lake. There were extensive mats of this form and none of the typical, lilac-flowered form, which suggests that regeneration at this site may be strictly clonal. *Utricularia purpurea* forma *alba* has been reported from a pond in New Hampshire where, as in the present case, only mats of white-flowered plants were present (Hellquist 1974). Vouchers of our specimens are housed at the E. C. Smith Herbarium at Acadia University (ACAD).

Conservation planning for Atlantic Coastal Plain plants has benefitted from our knowledge of the relationship between hydrology and diversity of rare coastal plain communities in Nova Scotia (Hill et al. 1998). This model allows us to concentrate field efforts on lakes of large CA and to make recovery plans for a suite of rare herbs occurring on these naturally disturbed lakeshores. Despite the value of this approach in time saving and habitat acquisition, our new records clearly indicate a need to gather more information on low CA lakes. Further, there is a need to assess and accomodate the conservation needs in Nova Scotia for these species in addition to those of the disturbance-linked, rare coastal plain herbs.

ACKNOWLEDGMENTS. We greatly appreciate the help given by A. A. Reznicek, P. Hope, and S. P. VanderKloet.

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APPENDIX

RECORDS FOR *UTRICULARIA RADIATA*

The records have been annotated for lakes of three catchment area classes: low CA (< 2000 ha), intermediate CA (2000–50,000 ha), and large CA (> 50,000 ha). Records were taken from three sources: E. C. Smith Herbarium

(ACAD) sheets for the taxon, Kejimkujic National Park records (Roland 1976, with map updates provided by Peter Hope), and the authors' findings for 1998–1999. Sites listed on ACAD herbarium sheets were revisited to re-locate the taxon in the field.

ACAD Herbarium Records

1. Halifax Co., Sawlor's L. (low CA), 1940, S. Mason, A. Gorham, and H. P. Bell; re-located 1998.
2. Lunenburg Co., Ashland L. (low CA), 1957, E. C. Smith, A. C. MacDonald, and W. J. Curry; re-located 1998.
3. Lunenburg Co., Huey L. (low CA), 1957, E. C. Smith, A. C. MacDonald, and W. J. Curry; unable to re-locate in 1998.
4. Lunenburg Co., Lawson L., syn. "Larsen L." (intermediate CA), 1953, E. C. Smith, J. Taylor, D. H. Webster, and L. B. Slipp; re-located 1998.
5. Yarmouth Co., Carleton—lake not recorded on sheet, may refer to Mill L. (intermediate CA), 1952, E. C. Smith, J. C. Taylor, D. H. Webster, and L. B. Slipp; re-located at Mill L. in 1999, see New Findings below, # 6.

Kejimkujic National Park Records (P. Hope, Chief Interpreter, pers. comm.)

1. Annapolis Co., Kejimkujic L. (large CA).
2. Annapolis Co., Grafton L. (intermediate CA), A. E. Roland.
3. Annapolis Co., Puzzle L. (low CA), A. E. Roland.
4. Annapolis Co., North Cranberry L. (low CA).
5. Annapolis Co., Little Peskowesk L. (low CA).
6. Annapolis Co., Loon L. (large CA), R. Belliveau.
7. Annapolis Co., Big Dam L. (intermediate CA), 1976, A. E. Roland.
8. Annapolis Co., Turtle L. (low CA), 1976, T. Bowers.

New Findings

1. Lunenburg Co., Pretty Mary L. (low CA), 1998, J. S. Boates, M. F. Elderkin, and N. M. Hill.
2. Lunenburg Co., Mudflat L. (low CA), 1998, J. S. Boates, M. F. Elderkin, and N. M. Hill.
3. Lunenburg Co., Horseshoe L. (low CA), 1998, P. Mills and J. S. Boates.
4. Lunenburg Co., Darling L. (low CA), 1998, P. Mills and J. S. Boates.
5. Shelburne Co., Gold L. (low CA), 1998, J. S. Boates.
6. Yarmouth Co., Mill L. (intermediate CA), 1999, N. M. Hill, M. Myra, and J. W. Hill.
7. Annapolis Co., Eleven Mile L. (intermediate CA), 1999, N. M. Hill and J. W. Hill.

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BOOK REVIEW

Aquatic and Wetland Plants of Northeastern North America by G. E. Crow and C. B. Hellquist. 2000. *Volume 1. Pteridophytes, Gymnosperms, and Angiosperms: Dicotyledons,* lv + 480 pp. illus. ISBN 0-299-16330-X; *Volume 2. Angiosperms: Monocotyledons,* lv + 400 pp. illus. ISBN 0-299-16280-X $90.00 per volume (hardcover). The University of Wisconsin Press, Madison, WI.

Fassett's classic *Manual of Aquatic Plants* has been the mainstay of aquatic and wetland plant taxonomy in northeastern North America for over 60 years. Never revised by the author, the treatment was resuscitated in1957 by E. C. Ogden who added a "Revision Appendix" in an attempt to "bring the nomenclature into agreement with present-day usage." Happily, Crow and Hellquist have accomplished a complete rewrite of the manual from cover to cover. This thoroughly revised and comprehensive work finally brings coverage of northeastern aquatics up to speed with other regions such as the southeast (e.g., Godfrey and Wooten, *Aquatic and Wetland Plants of Southeastern United States*) and the southwest (e.g., Correll and Correll, *Aquatic and Wetland Plants of Southwestern United States*).

Like Fassett's original manual, the geographical coverage of the new edition extends outside of the United States to include portions of southeastern Canada, but does not cover extreme northeastern portions of North America as might be misconstrued from the title.

Although Crow and Hellquist are accomplished water-plant taxonomists, they have consulted more than 30 other experts to achieve current and dependable treatments of all taxonomic groups. The end result represents more than 20 years of painstaking and meticulous taxonomic work by the authors.

The new revision bears the familiar UW trademark on the spine. The enhanced coverage required publication in two volumes (see above titles), in an 8¾″ × 11¼″ format that is considerably larger than its predecessor. Blue laminated boards replace the textured cloth cover of the earlier edition's most recent printings. All taxon listings are presented in a new two-column format. These large tomes are not meant to be field guides, and are best left back at base camp for later referral. The complete set is also pricey at $180. The original manual is still available at $30, but will probably soon be out-of-print permanently. (If you don't already own one, you'd be advised to grab one of these to use as a field book before they disappear.) Understandably, the size and price of the new manual will deter its use as a textbook or a field course manual.

Debuting in this edition are a section on "Nuisance Aquatic Plants of the Northeast" and a useful glossary of 64 habitat terms. The glossary is expanded to 582 terms and a full list of abbreviations is provided. The sections on "Use of aquatic plants by birds and mammals" and "The relation of plants to fish" of the earlier edition are omitted.

The new manual increases coverage from 752 to 1186 taxa. Many new illustrations have been added, while keeping most of the incredibly useful line drawings of the previous edition. Other enhancements include expanded coverage of salt marsh and bog species, pteridophytes, and gymnosperms (algae and bryophytes have been excluded entirely). Treatments have been vastly improved for many difficult genera. For example, for *Carex,* 76 species are treated as compared to fewer than 30 species in the previous edition.

A key to "General Keys" is retained, but unlike the cumbersome 17-choice menu of the previous edition, it is strictly dichotomous. Readers are lead efficiently to eight specialized keys that more or less reflect the major morphological categories emphasized by the original book. These keys ultimately lead to families whose locations in the book are identified by volume and page numbers. All keys have been reworked to avoid confusing "jumping around" to odd couplets in other keys (a problem with the original edition).

Keys are indented throughout as compared to the bracketed format used in the old manual. The indented format is helpful by enabling the visualization of similar taxa as they are grouped together. Taxon names appear at the right margin of keys and include sequential reference numbers for easy location in the accompanying text. This feature vastly simplifies the location of species names and allows one to easily count numbers of taxa in each family or genus. Species names are now separated from descriptions and distribution data, which makes it much easier to locate them in the text.

The keys I tried out were excellent and user-friendly. The parallel leads and non-overlapping character states in couplets are a hallmark of excellence in key construction. So far, I have not run into any major problems, although certain keys might still be improved. For example, the key to *Polygonum* species still relies on the traditional distinction between annual versus perennial growth habit, which is often difficult to determine from specimens collected without roots. Following the precedent of the original manual, vegetative features are emphasized in keys whenever possible, even in problematic groups like *Salix* and the Lemnaceae.

There is a good selection of references and the inclusion of separate "References" sections at the back of each volume is a welcome improvement over citations embedded within the text as in the old manual. References are not duplicated in the two volumes. This modification simplifies the location of citations because one does not have to wade through a single, longer list as in many two-volume books.

Of course, there are a few typos (e.g., drupelet misspelled as "druplet" in the glossary) and minor errors [e.g., the authorship of *Neobeckia aquatica* (Eat.) Greene listed as *Neobeckia aquatica* (Eat.) Britt.], but overall this is a well-edited text, especially for its size and complexity.

I should also mention a few dislikes. Like the earlier edition, many keys are interrupted by intervening plates of illustrations, making it necessary to page back and forth when using the key. The worst instance occurs in the key to Hydrocharitaceae where the very first couplet is separated by 16 pages of plates (all *Sagittaria* species, no less). However, most keys were uninterrupted.

I also disliked the redundancy of the general keys, section on nuisance aquatic plants, list of abbreviations, glossary of plant terms, glossary of habitat terms, and index in each volume. The 97 pages of identical information (along with 17 entirely blank pages) comprises roughly 10% of the book. I would have preferred a shorter, possibly less expensive book. Although this feature was intended to make each volume "stand alone" if purchased separately, it does not fully achieve this objective given that the general keys refer to 53 illustrations from *Volume 1* and to 33 illustrations from *Volume 2* that are not included among the 18 figures reproduced along with the general keys. Consequently, not all figures in the general keys will be available to owners of only a single volume.

The single most useful feature of the original Fassett manual was its detailed line drawings. These are supplemented by many illustrations carefully selected from appropriate sources. The result is a thoroughly illustrated work that greatly lessens the burden of water plant identification. However, the quality of printing used in reproducing the illustrations is mediocre. Many illustrations are printed poorly, with broken lines and/or overly light or dark print. The quality of several identical illustrations is superior in the original manual. Although most of the figures are presentable, the poor clarity of others lessens their utility as an aid to identification. Furthermore, none of the figures include a scale, making them less useful for size comparisons than those in the original manual.

Despite the few printing and format problems, *Aquatic and Wetland Plants of Northeastern North America* is more than just a worthy successor of the old Fassett's manual. Even though some parts of the original manual live on in the new one, the many improvements and innovations have resulted in a unique treatment of North American aquatic plants that is a credit to the authors. The taxonomic quality of this fine work earns a top ranking among the aquatic floras written for North America. This book is an essential resource and will surely become the new standard for aquatic plant taxonomy in the region. Hats off to Crow and Hellquist for providing us with a new classic that Fassett himself would envy.

—DONALD H. LES, Department of Ecology and Evolutionary Biology, University of Connecticut, U-43, Storrs, CT 06269-3043.

RHODORA, Vol. 102, No. 912, pp. 527–528, 2000

NEW BOOKS

Annotated Checklist of the Vascular Plants of the Washington—Baltimore Area. Part I. Ferns, Fern Allies, Gymnosperms, and Dicotyledons by S. G. Shetler and S. S. Orli. 2000. xv +189 pp. + 2 pp. corrections. map of checklist area. (softcover, spiral bound). [available from the authors, Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0166]

Contemporary Plant Systematics, 3rd Edition by D. W. Woodland. 2000. xiv + 569 pp. black and white photos, line drawings, and the latest CD version of the University of Wisconsin's *Photo Atlas of Vascular Plants.* ISBN 1-883925-25-8 $64.99 (hardcover). Andrews University Press, Berrien Springs, MI. [FAX 616-471-6224; aupress@andrews.edu]

The Flora of Manitoulin Island, 3rd Edition by J. K. Morton and J. M. Venn. 2000. 376 pp. 124 color photographs and 996 dot distribution maps. ISSN 0317–3348 $37.50 (softcover, spiral bound, outside Canada). University of Waterloo Biology Series No. 40. Department of Biology, University of Waterloo, Waterloo, Ont. N2L 3G1, Canada.

Flora of the Northeast: A Manual of the Vascular Flora of New England and Adjacent New York by D. W. Magee and H. E. Ahles. 1999. xxxi + 1213 pp. 2433 dot distribution maps and 995 line drawings. ISBN 1-55849-189-9 $69.95 (hardcover). University of Massachusetts Press, Amherst, MA. [available from the publisher, Box 429, Amherst, MA 01004]

The Vascular Plants of Massachusetts: A County Checklist by Bruce A. Sorrie and Paul Somers. 1999. xvii + 186 pp. + map of Massachusetts towns and counties. $10.00 (softcover). Massachusetts Division of Fisheries and Wildlife, Natural Heritage & Endangered Species Program, Westborough, MA. [available from the publisher, Route 135, Westborough, MA 01581; for orders of 30 or more, cost is $8.00 each]

Wildflowers of the Western Great Lakes Region by J. R. Wells, F. W. Case, Jr., and T. L. Mellichamp. 1999. xvi + 284 pp. color photographs and line drawings. ISBN 0-87737-042-7 $39.00 (hardcover). Cranbrook Institute of Science Bulletin 63. Cranbrook Institute of Science, Bloomfield Hills, MI. [available from the publisher, P. O. Box 801, Bloomfield Hills, MI 48303]

RHODORA, Vol. 102, No. 912, pp. 529–531, 2000

NEBC MEETING NEWS

June 2000 Field Trip. On Friday afternoon, Mt. Tekoa in Westfield, Massachusetts, was climbed by 14 members and guests to examine the effects of repeated fires on a rocky outcrop community. The mountain is a prominent rocky ridge behind the former Stratford Paper Company mills, and is a prominent landmark viewed from the eastbound Massachusetts Turnpike. The ridge has burned twice in the last six years. The group hiked up through densely re-sprouting oak, hickory, red maple, chestnut, mountain laurel, and witch hazel to the summit, where the oak-pitch pine community was starting to regenerate. Several species of *Vaccinium* were dominant, and promised good berry picking later in the season. Highlights of the walk included the ant-dispersed sedge *Carex umbellata, Asclepias purpurascens,* and *Geranium bicknellii* (or *caroliniana*). Thirteen species of *Carex* were observed. Blackflies, thunder, lightning, and a brief downpour added excitement to the experience, and presaged the early evening storm that toppled sugar maples on the Mount Holyoke campus.

June 2000. On Friday evening, Dr. Elizabeth Farnsworth of Smith College spoke on "Present and future impacts of invasive plant species on wetland systems." She discussed the impacts that invasive species currently have on wetland systems, and what impacts they may have in a future of climatic change.

Based on county-level floras and checklists, Massachusetts and Connecticut currently have the largest number of invasive plant species (approximately 60 and 50) and observed invasions, with a positive correlation between the number of invasive species and the size of the human population.

Dr. Farnsworth described her research on *Lythrum salicaria* in Connecticut, comparing species diversity and biomass in wetlands dominated by *Lythrum* to wetlands that were composed of native species. Studies showed *Lythrum* did not suppress diversity of other plant species, but did reduce biomass, and that *Lythrum* may capture resources more efficiently than other species, changing the wetland's nutrient and detrital dynamics. *Phragmites australis* was studied at two sites where it had been removed by spraying gylphosate herbicide. Removal was associated with a dramatic increase in the abundance and diversity of other wetland species, resulting in a wetland species composition similar to undisturbed freshwater tidal marshes.

Dr. Farnsworth looked at the future of invasive species dynamics, in the probable scenario of continued increases in atmospheric CO_2 and other greenhouse gas emissions, particularly since marshes are currently effective as carbon sinks. She examined the ways that photosynthesis and water use differ among invasive (*Phragmites* and *Typha angustifolia*) and non-invasive (*Leersia oryzoides* and *Spartina alterniflora*) species of freshwater and salt marshes, with respect to the seasonal length of effective photosynthesis, photosynthetic rates, and nutrient balance. Changing species composition in wetlands toward dominance of one or two invasive species will likely alter carbon cycling in wetlands, which in turn may have a climatic feedback effect.

June 2000 Workshop and Field Trip. On Saturday, five members participated in a workshop, offered by Lisa Standley, on the identification of *Carex.* Following a lecture and slide presentation, which included discussion of the best keys and references as well as important diagnostic features, the group hiked up Bare Mountain in the Holyoke range. Twelve early-flowering woodland species of *Carex* were found, including *C. platyphylla, C. albursina, C. laxiflora, C. digitalis, C. communis, C. albicans,* and *C. hirsutella.* The woodland bulrush, *Scirpus verecundus* was abundant.

A small group journeyed to nearby Lawrence Swamp and Elf Creek Conservation area to hunt for ferns. Led by the intrepid Don Lubin, the group searched successfully for a nice population of *Lygodium palmatum* at Elf Creek, but failed to find the reported *Ophioglossum pusillum* at Lawrence Swamp. Among highlights of the natural areas and Caroline Arnold's garden in North Amherst were *Dryopteris clintoniana, Botrychium,* and *Selaginella apoda.*

July 2000 Field Trip: In the Footsteps of Fernald. George Newman led a party of 21 Club members and family around the Gaspé Peninsula of Quebec, from Mont Albert in the central mountains to Grand Rivière on the southeast coast. Merritt Lyndon Fernald botanized the Gaspé from 1902 to 1934. During this period, 143 of the 200 new taxa that he named were based on populations on the Gaspé. Many of the taxa Fernald named are no longer recognized as distinct species or varieties, but are thought to be disjunct populations of variable western or circumboreal taxa. The area also provided much of the support of his "nunatak" theory to explain the presence of western and arctic disjuncts. Fernald was followed on the Gaspé by a series of remarkable Canadian botanists, including Fr. Marie-Victorin, Jacques Rousseau, Ernest Lepage, and A. E. Porsild, among others.

The group sampled most of the range of habitats of the Gaspé: serpentine barrens, *Thuja* bogs and valleys, beaches, sea cliffs, scree summits, talus slopes, limestone cliffs, coastal spruce-fir forests, and wide gravel rivers. Unusual ferns were abundant: *Polystichum scopulinum* (a western serpentine endemic), *Aspidotis densa, Cystopteris montana, Dryopteris fragrans,* and *Adiantum aleuticum* at Mont Albert; *Polystichum lonchitis* at Cap Bon Ami in Forillon National Park; *Dryopteris filix-mas* at many locations; *Cryptogramma stelleri* on limestone; and tiny *Botrychium lunaria.* Orchids were also frequently observed. We saw abundantly blooming *Orchis rotundifolia* in a *Thuja* bog in the Parc Gaspésie. At other locations, particularly on Bonaventure Island, we saw *Platanthera dilatata, P. hyperborea, P. obtusata, P. orbiculata, Listera cordata, L. convallarioides, Coralorhiza maculata, C. striata, Goodyera repens,* and amazingly, *Cypripedium parviflorum* var. *parviflorum* growing on the dry limestone cliffs and talus at Cap Bon Ami.

The dry scree summits and ledges of Devonian sandstone and conglomerates yielded a western montane/alpine flora that included *Arnica chionopappa, Saxifraga cernua, S. caespitosa, S. aizoon, Anemone multifida, Erigeron compositus, Hedysarum alpinum, Shepherdia canadensis, Elaeagnus commutata, Senecio multiradiata, Oxytropis,* and *Astragalus scrupulicola.* The wet, mossy sea cliffs along the north coast harbored *Pinguicula vulgaris, Saxifraga aizoides, Parnassia parviflora, Malaxis brachypoda, Polygonum viviparum,* and *Primula laurentiana.* Shale and cobble sea beaches contained *Mertensia maritima, Senecio pseudo-arnica, Iris hookeri, Anemone canadensis,* and *Zygadenus glauca.* The serpentine barrens of Mont Albert were one of the highlights of the trip, both visually and botanically, with *Lychnis alpina, Armeria labradorica, Artemesia borealis,* various *Salix* species, *Eriophorum russeolum (E. chamissonis),* and woodland caribou. In total, the group recorded 415 species of vascular plants in 65 families (including 34 species of *Carex*), and 47 species of ferns and fern allies.

—LISA STANDLEY, Recording Secretary *pro tempore.*

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1999–2000

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