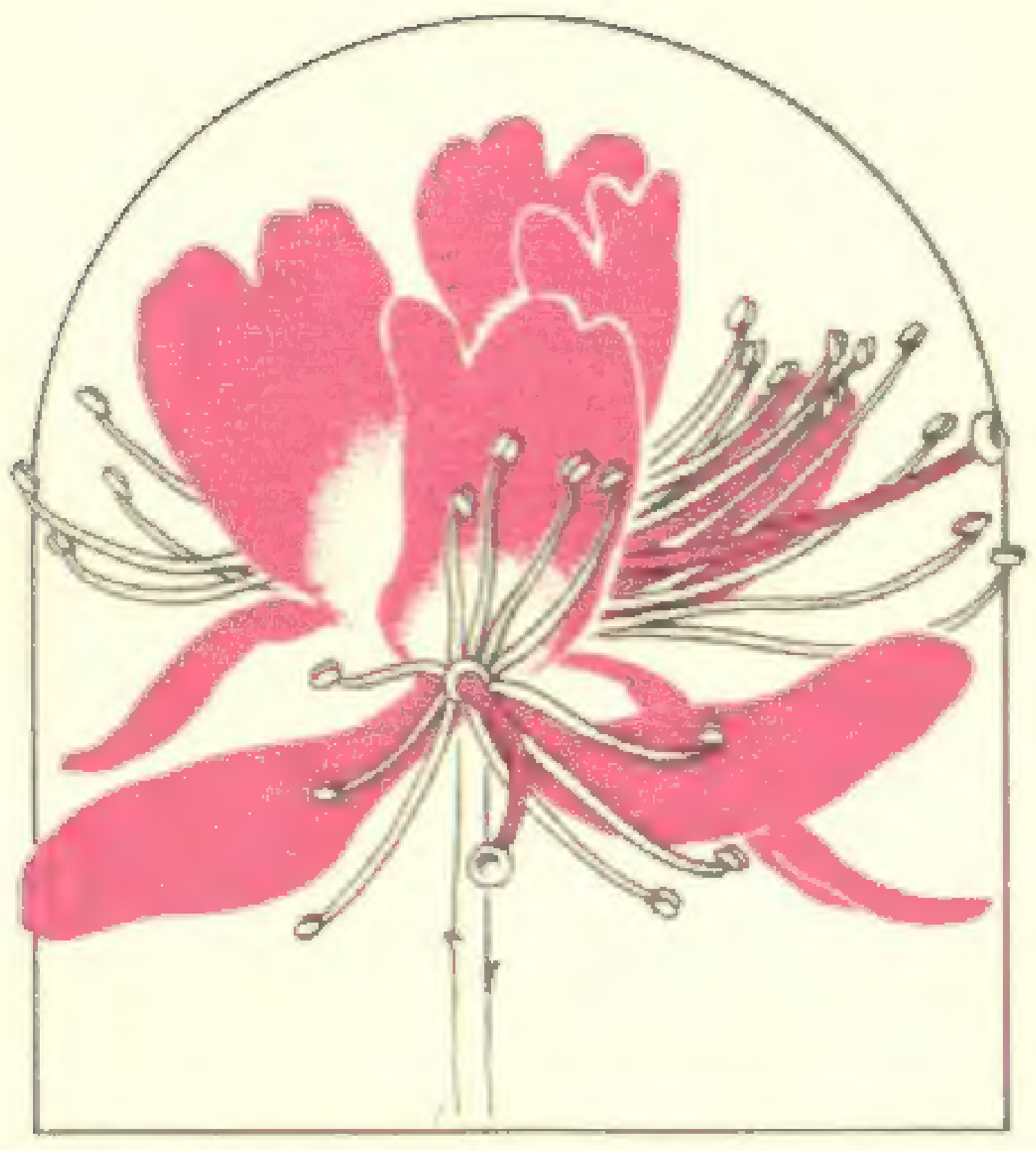

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EXPANSION OF THE ASIATIC GREEN ALGA *CODIUM FRAGILE* SUBSP. *TOMENTOSOIDES* IN THE GULF OF MAINE

Arthur C. Mathieson

Department of Plant Biology and Jackson Estuarine Laboratory,
University of New Hampshire, Durham, NH 03824
e-mail: arthur@hopper.unh.edu

Clinton J. Dawes

Department of Biology, University of South Florida, Tampa, FL 33620

Larry G. Harris

Department of Zoology, University of New Hampshire, Durham, NH 03824

Edward J. Hehre

Department of Plant Biology and Jackson Estuarine Laboratory,
University of New Hampshire, Durham, NH 03824

ABSTRACT. The invasive Asiatic green alga *Codium fragile* subsp. *tomentosoides,* which was introduced to the northwestern Atlantic in eastern Long Island Sound, New York during 1957, has recently colonized several parts of the Gulf of Maine via two invasion sites: (1) mid-coastal Maine at Boothbay Harbor after transplantation of Long Island oysters (1964); and (2) southern Massachusetts as a result of the expansion of attached plants from the Cape Cod Canal (1969) into nearby Cape Cod Bay (1972). Because of its warm-water affinities, southern New England populations initially expanded more rapidly than northern ones, becoming particularly invasive in shallow subtidal habitats. By contrast, the Boothbay Harbor populations were rather "quiescent," long-lived, and circumscribed until the early 1970s. After a buildup of significant biomass, extensive fragmentation and drifting occurred via strong south-flowing currents; thereafter, *Codium* colonized mid-coastal Maine, New Hampshire, and northern Massachusetts. Currently, the Casco Bay area just south of Boothbay Harbor has the highest number of invasion sites, particularly at offshore islands. Attached populations are limited to a few contiguous sites just north of Boothbay Harbor, with only drift specimens occurring in "Downeast" Maine. Recent introductions have also been recorded in the Canadian Maritime Provinces, both within the Atlantic (1989) and the Gulf of St. Lawrence (1996) shorelines. Thus, the species' expansion in the northwestern Atlantic has involved multiple introductions, different vectors (shellfish and vessels), dispersal by major south-flowing currents, and differential viability/abundance of *in situ* populations due to varying hydrographic and exposure conditions. In comparing a series of permanent study sites in southern Maine and New Hampshire during 1982 to 2001, *Codium* increased from one to 26 sites during 19 years, with the most evident expansion between 1996–1998. A comparison of several demographic features (length, weight, density, biomass, and percent occurrence) for six *Codium* populations ranging from mid-coastal Maine to New Hampshire showed that outer estuarine and nearshore open coastal plants were smaller and had more limited densities and biomass than those found at warmer offshore insular sites like Star Island, New Hampshire. *Codium* is now the dominant canopy species in some southern Maine and New Hampshire locations, extending to ~8 m below mean low water; it occurs in both disturbed sites (e.g., former urchin barrens) and established kelp beds at sheltered and exposed locations. The Asiatic red alga *Neosiphonia* (= *Polysiphonia*) *harveyi,* which is the dominant epiphyte on *Codium,* is also exhibiting a rapid expansion in this same geography. Drifting populations of *Codium* may be a good vector for its introduction, as well as for several other epiphytes. Another aspect of the invasion of *Codium* into the Gulf of Maine is the spread of the introduced bryozoan *Membranipora membranacea,* which is common on kelps but appears to be exhibiting enhanced survival on *Codium* because of its perennial growth pattern and lack of epibiontic sloughing.

Key Words: green alga, Chlorophyta, *Codium fragile* subsp. *tomentosoides,* Asiatic, introduced, nonindigenous, invasive, Gulf of Maine, dispersal, distribution, ecology, epiphytes

Introduced species are a major problem throughout the world's oceans, causing altered natural communities and significant economic losses (Boudouresque et al. 1994; Carlton 1979, 1996, 2000; De Clerk et al. 2002; Chapman et al. in press; Jousson et al. 2000; Karlsson and Loo 1999; Lein 1999; Maggs and Stegena 1999; Meinesz 1999; Meinesz et al. 1993; Pederson 2000; Piazzi and Cinelli 2000; Ramus 1971; Reise 1999; Rueness and Rueness 2000; Stiger and Payri 1999; Thresher 2000). In the northwestern Atlantic ten nonindigenous seaweeds are known (cf. Broom et al. 2002; Coll and Cox 1977; Humm 1979; Kjellman 1897; McIvor et al. 2000, 2001; Sears 2002; Taylor 1962; Villalard-Bohnsack 2002; Vitousek et al. 1996): the invasive green alga *Codium fragile* (Suringar) Har. subsp. *tomentosoides* (Goor) P. C. Silva (hereafter *Codium*); the brown algae *Colpomenia peregrina* Sauv. and *Fucus serratus* L.; and the red algae *Antithamnion pectinatum* (Mont.) Brauner, *Bonnemaisonia hamifera* Har. [including the "*Trailliella intricata*" (J. Agardh) Batters stage], *Furcellaria lumbricalis* (Huds.) J. V. Lamour., *Grateloupia turuturu* Yamada [= *G. doryphora* (Mont.) M. Howe; cf. Gavio and Fredericq 2002], *Lomentaria clavellosa* (Turner) Gaillon, *Neosiphonia* (= *Polysiphonia*) *harveyi* (Bailey) Kim, Choi, Guiry & G. W. Saunders, and *Porphyra suborbiculata* Kjellm. (= *P. carolinensis* Coll & J. Cox; cf. Broom et al. 2002). *Bonnemaisonia hamifera, Codium, N. harveyi,* and *P. suborbiculata* are Asiatic, while the rest are from Europe, the Pacific, or unknown locations (Blackler 1964; Coleman 1996; Dale 1982; Foertch et al. 1991; Goff et al. 1992; Harvey 1853; Kjellman 1897; Lewis and Taylor 1928, 1933; Marston and Villalard-Bohnsack 2000; McIvor et al. 2000, 2001; Silva 1955, 1957; Villalard-Bohnsack 2002; Wilce and Lee 1964). The earliest documented introductions within this geography date back to the early to late 1800s and include *F. serratus* from the Canadian Maritime Provinces (Dale 1982; Hay and Mackay 1887; Novaczek 2001; Robinson 1903), *F. lumbricalis* from Newfoundland (Harvey 1853; Novaczek 2001), and *N. harveyi* from Connecticut (Harvey 1853; McIvor et al. 2000, 2001); most recently, the foliose red alga *G. turuturu* was recorded from Rhode Island (Marston and Villalard-Bohnsack 2000; Villalard-Bohnsack and Harlin 1997). Of these ten seaweeds, *Bonnemaisonia* is persistent and broadly distributed; *Codium, Grateloupia,* and *N. harveyi* are rapidly expanding; *C. peregrina* is restricted to a few locations; and the others exhibit limited expansions (Bird and Edelstein 1978; Blackler 1964; Broom et al. 2002; Carlton and Scanlon 1985; Marston and Villalard-Bohnsack 2000; McIvor et al. 2000, 2001; Sears 2002; South and Tittley 1986; Villalard-Bohnsack 2002). The Asiatic red alga *Porphyra yezoensis* Ueda (i.e., nori) has recently been cultivated within "Downeast" Maine and New Brunswick, Canada but has shown no signs of escaping or becoming invasive (Watson et al. 1998, 2000).

Trowbridge (1995, 1996, 1998) has described the introduction and spread of several seaweeds throughout the world that show varying patterns. After escaping from a coastal aquarium, the tropical/subtropical green alga *Caulerpa taxifolia* (Vahl) C. Agardh has become a major pest within the Mediterranean (Boudouresque et al. 1994; Meinesz 1999; Meinesz et al. 1993; Raloff 1998; Wiedenmann et al. 2001), as well as being recently found in California (Jousson et al. 2000). Vectors for other seaweed introductions include: Lessepsian migrations into the Mediterranean via the Suez Canal, shellfish/algal transplants, mariculture introductions, and accidental transfers via ballast water, anchors, fishing nets, ships' hulls, oil platforms, and shellfish packaging (Aleem 1948, 1992; Carlton 1987; De Clerk et al. 2002; Hay

1990; Loosanoff 1975; Maggs and Hommersand 1993; Modena et al. 2000; Moss et al. 1981; Piazzi et al. 1997; Russell 1982, 1983; Scagel 1956; Verlaque 1994). The temperate brown algae *Laminaria japonica* Kjellm., *Sargassum muticum* (Yendo) Fensholt, and *Undaria pinnatifida* (Harv.) Suringar have spread dramatically during the last century, extending between different ocean basins and hemispheres (Cecere et al. 2000; Critchley et al. 1983, 1990; Floc'h et al. 1991; Hay 1990; Hay and Villouta 1993; Karlsson and Loo 1999; Rueness 1989; Sanderson 1990; Scagel 1956; Staehr et al. 2000; Trowbridge 1995, 1996). Their dispersal is attributable in large part to shipping and oyster importation activities. *Sargassum,* like *Codium* (see below), has become an ecological and economic pest, disrupting oyster beds, boat harbors, etc. (Rueness 1989). By contrast at least 95 introduced seaweeds are more localized (Farnham 1980; Verlaque 1994), with some producing naturalized and viable populations (Russell 1983, 1992; Russell and Balazs 1994).

The invasive Asiatic green alga *Codium fragile* subsp. *tomentosoides* is commonly called "sputnik weed" or "oyster thief" because of its rapid growth, as well as its ability to attach, uplift, and transport shellfish (Hanisak 1980; Novaczek 2001). The first record of foreign travel by *Codium* dates back to ~1900 in Holland, where it was presumably introduced with shellfish (Silva 1955, 1957; van Goor 1923). Thereafter it expanded rapidly in Europe, extending from Norway to Spain into the western edge of the Mediterranean (Jones 1974; Lüning 1990; Meslin 1964; Parriaud 1957; Silva 1955; Trowbridge and Todd 1999, 2001). *Codium* was first recorded in 1957 from the northwestern Atlantic in eastern Long Island Sound (Bouck and Morgan 1957). Other recent introductions have occurred in Australia, New Zealand, the central Pacific Islands, Japan, Alaska to Pacific Mexico, and western South America (Lüning 1990; Nelson 1999; Trowbridge 1995, 1996, 1998). Carlton and Scanlon (1985) considered three possible vectors for the transoceanic dispersal of *Codium* to the northwestern Atlantic: (1) fouling of the flat oyster *Ostrea edulis* L. from Europe; (2) fouling of the Pacific or Japanese oyster *Crassostrea gigas* (Thunb.) from Washington and British Columbia; and (3) fouling of ships' hulls from Europe. They concluded that it was most likely transported as a fouling organism on ships' hulls (cf. Loosanoff 1975; Malinowski 1974), as there was daily shipping between Europe and New York during the mid-1950s just prior to the discovery of *Codium* (Bouck and Morgan 1957). Dromgoole (1975, 1979) stated that *Codium* has several features that would preadapt it for ship-borne dispersal: (1) settlement on floating structures imperfectly coated with antifouling paint; (2) attachment to diverse substrata with minimal relief; and (3) regeneration from residual holdfasts subjected to reduced shear stress during ship-borne dispersal (Hanisak 1980). Carlton and Scanlon (1985) suggested a fourth factor that would be critically important, namely the species' physiological plasticity, which would permit it to exist through broad and changing temperature and salinity regimes. They suggested that the species' localized dispersal was largely caused by currents, transport of fishery products, and other natural mechanisms. For example, the initial establishment of *Codium* on the south shore of Massachusetts (MA) during 1961 and at Boothbay Harbor, Maine (ME) in 1964 probably occurred after transfer of juvenile/microscopic plants (i.e., "green bumps") on oysters (Coffin and Stickney 1966; Galstoff 1962a,b; Malinowski 1974; Wood 1962). Other possibilities include transport of plants on boat propellers, the cutting off of *Codium* thalli from shellfish (oysters) and tossing them back into the water, entrainment on commercial drag nets, and dispersal via packing material for lobsters, bait worms, etc. (Carlton 1979; Dawson and Foster 1982; Garbary et al. 1997; Hillson 1976; Novaczek 2001; Orris 1980). Aside from human causes, natural dispersal mechanisms may include motile reproductive cells, vegetative fragments, and floatation of whole plants via currents.

Codium populations within the northwestern Atlantic, like those in Europe, have expanded rapidly and now extend from the Canadian Maritime Provinces (i.e., Nova Scotia, New Brunswick, and Prince Edward Island) to North Carolina (Bird et al. 1993; Bleakney 1996; Chapman 1999; Chapman et al. in press; Coleman and Mathieson 1974; Davis 1971; Garbary and Jess 2000; Garbary et al. 1997; Hubbard and Garbary 2001, 2002; Meimer 1972; Scheibling 2001; Schneider and Searles 1991; Schumacher and Fiore 1963; Searles et al. 1984; Sisson 1968; Taylor 1967; Wassman and Ramus 1973a,b). Currently it dominates many subtidal habitats in the Canadian Maritime Provinces and New England, replacing *Laminaria* as the major taxon, and often impacting shellfish communities (Berman et al. 1992; Carlton and Scanlon 1985; Hanisak 1980; Harris and Mathieson 2000; Harris and Tyrrell 2001; Hulbert 1980; Lüning 1990; Martin et al. 1988; Ramus

1971; Scheibling 2001; Tacy et al. 1977; Van Patten 1992). In contrast to New England and the Canadian Maritime Provinces where *Codium* is often a subtidal pest (Coleman 1996; Garbary et al. 1997; Hubbard and Garbary 2001, 2002; Prince 1987), it is less abundant in Europe and New Zealand, often producing small distinct intertidal populations (Bartsch and Kuhlenkamp 2000; Chapman 1999; Chapman et al. 2001; Freeman and Smith 2000). In New England, *Codium* is more abundant south than north of Cape Cod, MA, presumably because of its warm-temperate affinities and the occurrence of a major phytogeographic boundary at Cape Cod (Carlton and Scanlon 1985; Fralick and Mathieson 1973; Hanisak 1980; Hutchins 1947; Lüning 1990; Mathieson et al. 1991; Ramus 1971). The goal of this paper is to review the recent rapid spread of *Codium* within the Gulf of Maine (Figure 1), which extends from the mouth of the Bay of Fundy southward to Cape Cod, MA. We will use a combination of historical and recent studies, including extensive collections and quantitative sampling, to describe the plant's current status. Among others, Davis et al. (2001) have emphasized the importance of comparing historical and present-day collections in understanding the temporal occurrences of marine biota.

MATERIALS AND METHODS

The distribution of *Codium* throughout the Gulf of Maine is summarized based upon ten previous floristic studies conducted between 1965 and 2001 (Mathieson 1979; Mathieson et al. 1993, 1996, 1998, 2001; Mathieson and Fralick 1972; Mathieson and Hehre 1986; Mathieson and Penniman 1986a,b, 1991), including several unpublished studies (Mathieson and Hehre). That is, seasonal collections of all conspicuous seaweeds were taken within the intertidal (on foot) and subtidal zones (by SCUBA) at 922 sites within Maine, New Hampshire (NH) and Massachusetts. A variety of taxonomic references were employed for the identification of various epiphyte populations (cf. Mathieson et al. 1998, 2001). Nomenclature primarily follows South and Tittley (1986) and Sears (2002), except for some recent changes noted by Broom et al. (2002), Choi et al. (2001), Gavio and Fredericq (2002), and Maggs et al. (2002). Voucher specimens of all *Codium* populations were prepared and deposited in the Albion R.

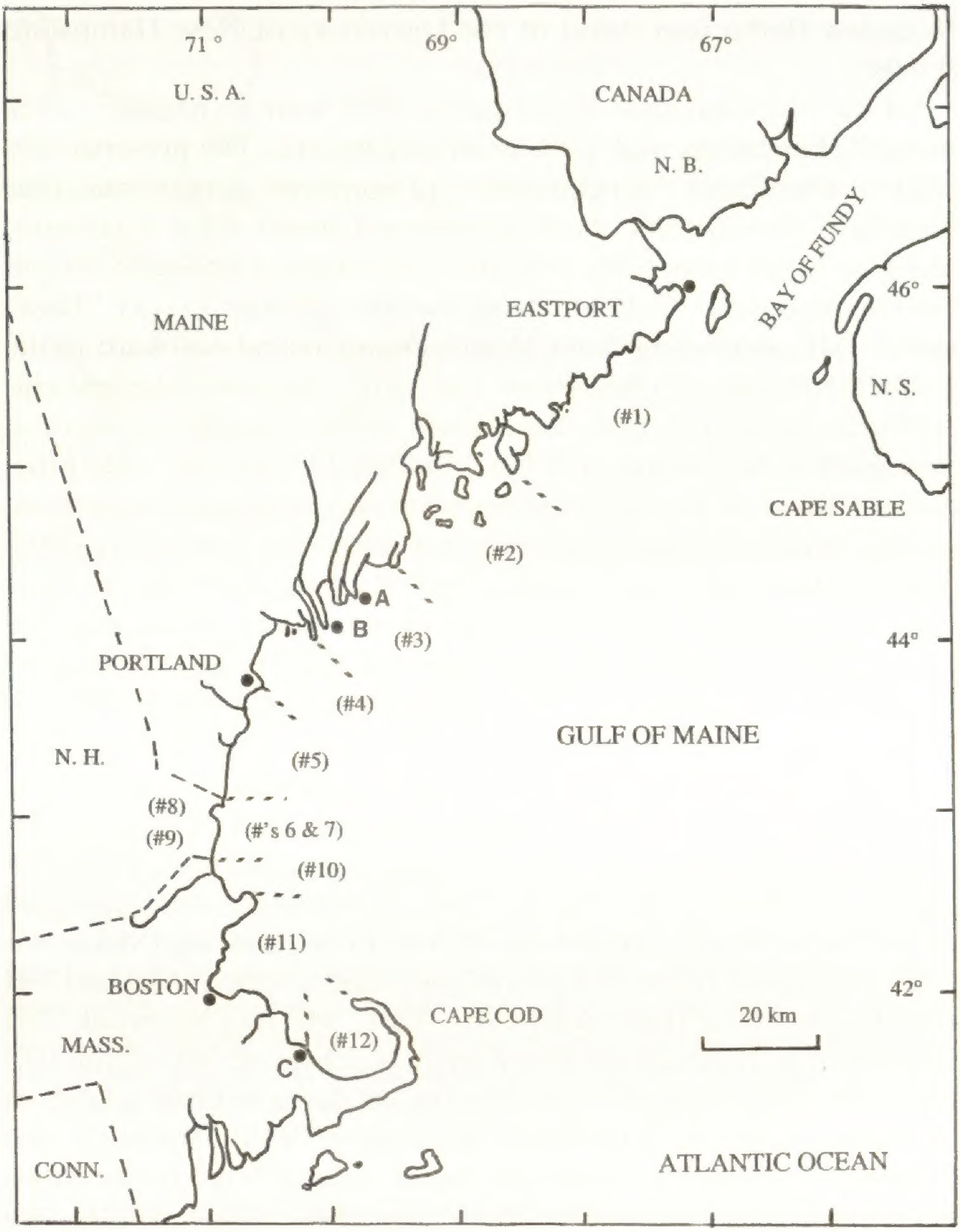

Figure 1. The northwestern Atlantic coastline from Nova Scotia, Canada to Cape Cod, including the northern invasion site for *Codium* at Boothbay Harbor, ME ("A"), a study site at Jaquish Island, ME ("B"), it's southern invasion site near the mouth of the Cape Cod Canal and Cape Cod Bay ("C"), plus twelve major habitats within the Gulf of Maine: #1 "Down East" ME; #2 Penobscot Bay, ME; #3 the "Indented Coastline" of ME; #4 Casco Bay, ME; #5 the southern ME coastline; #6 the NH/ME Isles of Shoals; #7 the NH nearshore open coast; #8 the NH/ME Great Bay Estuarine System; #9 the NH Hampton-Seabrook Estuarine System; #10 the "North Shore" of MA, or Salisbury to Gloucester, MA; #11 Salem to Sagamore, MA; #12 the Cape Cod peninsula, or Sandwich to Provincetown, MA. Abbreviations: MASS. = Massachusetts; N.B. = New Brunswick, Canada; N.H. = New Hampshire; N.S. = Nova Scotia, Canada.

Hodgdon Herbarium (NHA) of the University of New Hampshire (UNH).

Of the 922 total sites investigated, 68% were in Maine, ~25% in New Hampshire, and ~7% in Massachusetts. The presence and relative abundance (% occurrence) of epiphytic populations, plus their host populations, were enumerated based upon a subsampling of 150 herbarium voucher specimens (Appendix) from twelve contiguous Gulf of Maine habitats (Figure 1): (1) "Downeast" ME, extending from Mount Desert Island eastward to the Canadian border; (2) Penobscot Bay (ME), the state's largest embayment, extending from the mouth of the Penobscot River at Searsport to St. George; (3) the "Indented Coastline" (ME) that extends from St. George to Brunswick and consists of a series of eroded peninsulas and river drainage areas; (4) Casco Bay (ME) near Portland, the state's second largest embayment that extends from Phippsburg to Cape Elizabeth; (5) the southern ME coastline from Cape Elizabeth to Kittery near the NH border; (6) Isles of Shoals, an archipelago of nine offshore islands within ME and NH; (7) the NH nearshore open coast; (8) the NH/ME Great Bay Estuarine System; (9) the NH Hampton Seabrook Estuarine System; (10) the North Shore of Massachusetts, extending from Salisbury to Gloucester; (11) the MA shoreline extending from Salem to Sagamore; (12) the northern shoreline of the Cape Cod peninsula extending from Sandwich to Provincetown (MA).

The temporal invasion by *Codium* of the southern ME and NH coastline between Bald Head Cliff, York, ME and Seabrook, NH (Figure 2) is summarized based upon a subset of 276 of the 922 total sites. The locations include nine offshore NH/ME islands at the Isles of Shoals (Mathieson and Hehre 1986; Mathieson and Penniman 1986a), 17 nearshore open coastal NH/ME locations (Mathieson and Hehre 1986; Mathieson et al. 2001), 20 ME sites within the York River Estuary (Mathieson et al. 1993), 44 ME sites within Brave Boat Harbor (Mathieson et al. 2001), 137 NH/ME sites within the Great Bay Estuarine System (Mathieson and Hehre 1986; Mathieson and Penniman 1986b), and 49 NH locations within the Hampton-Seabrook Estuarine System (Mathieson and Fralick 1972).

Detailed ecological studies have been conducted by L. Harris and students at Star Island, NH Isles of Shoals (Figure 2) since 1974 and at five other Shoals sites since 1992 (Berman et al. 1992; Harris et al. 1994, 1996; Harris and Chester 1996; Harris

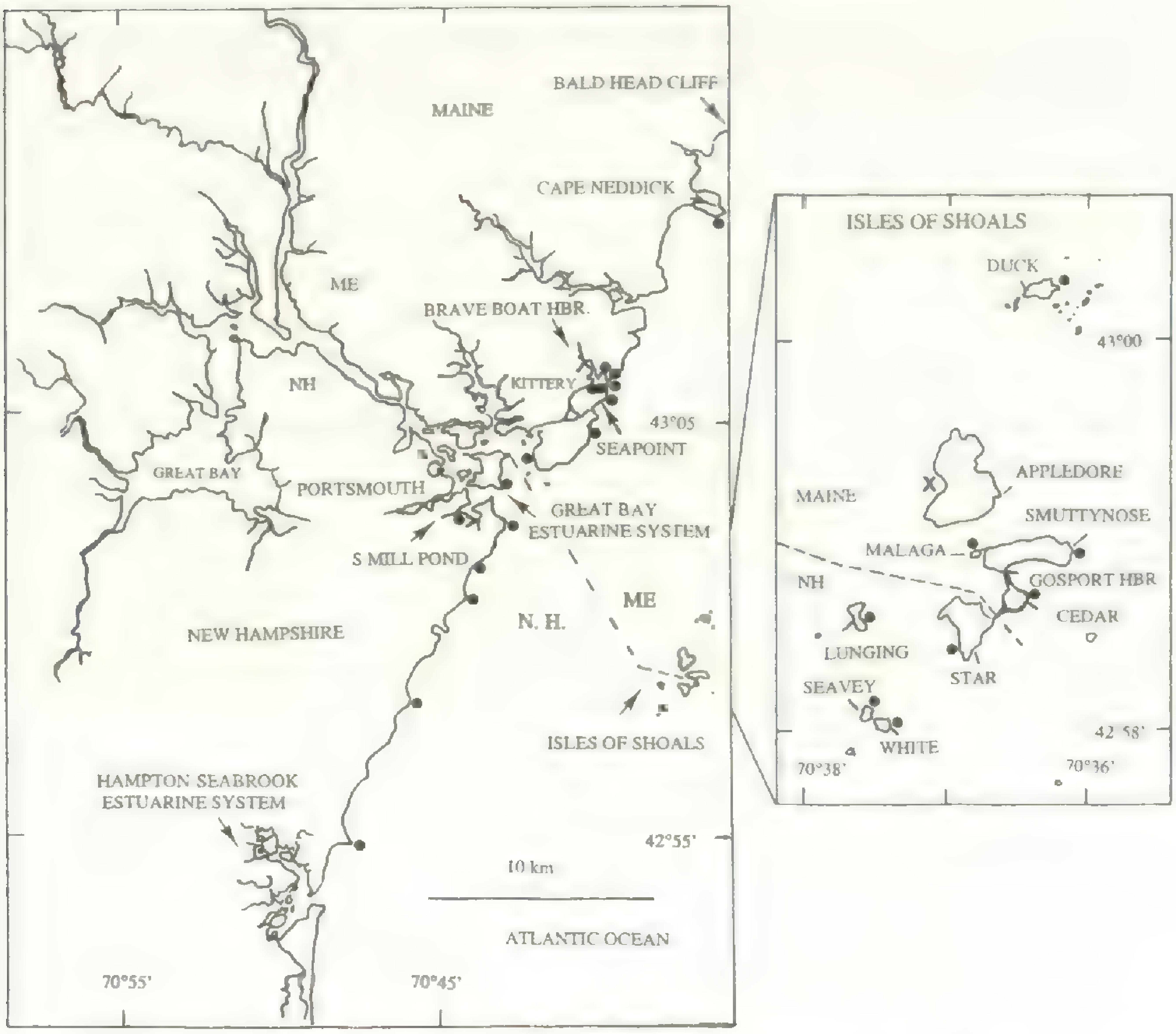

Figure 2. Locations of attached *Codium* populations on the southern Maine and New Hampshire coastlines during 1983 and 2001; the enlarged area on the right shows the Isles of Shoals, an archipelago of nine interstate islands. Symbols: X = initial occurrence in 1983, as well as during 2001; black circles = occurrences in 2001. Five of the six study sites for *Codium* populations are also shown with arrows (lines): Cape Neddick, Brave Boat Harbor, and Seapoint, ME, plus South Mill Pond and Star Island, NH. The location of the Jaquish Island study site is shown in Figure 1.

and Tyrrell 2001; Hulbert 1980; Martin et al. 1988; Tacy et al. 1977; Witman 1984, 1985, 1987; Witman et al. 1982). These studies have provided a general understanding of the changing patterns of diverse benthic organisms, including several native seaweeds (*Agarum clathratum* Dumort., *Chondrus crispus* Stackh., *Laminaria* spp., and *Ptilora serrata* Kütz.) and the green sea urchin *Strongylocentrotus droebachiensis* (Müller), plus the invasive, introduced green alga *Codium* and the non-native bryozoan *Membranipora membranacea* (L.). Upper horizontal rocky substrata were studied at all six Shoals sites, which have historically either been dominated by large algal canopies (e.g., *Lam-*

inaria spp.) or, if destructively grazed by sea urchins, they have consisted of barrens dominated by crustose coralline algae (Hulbert 1980; Martin et al. 1988; Ojeda and Dearborn 1989; Sebens 1985; Witman 1984, 1985, 1987; Witman et al. 1982). Patterns of canopy, algal distribution, and relative abundance of different taxa at five of these six NH Shoals sites (i.e., White Island #1 & 2, Lunging Island #3, Star Island #4 & 5; cf. Harris et al. 1994, 1998) are compared. A Nikonos V underwater camera, outfitted with a flash, 15 mm lens, and 35 mm Ektachrome slide film, was used to document changes in relative abundance and community structure from ~+3.0 to −12 m relative to mean low water (MLW). Counts of canopy species were made by projecting these pictures on a screen and documenting relative abundance based upon 30 photographs per site (cf. Harris and Mathieson 2000). Data for *Codium* and the brown alga *Desmarestia aculeata* (L.) J. V. Lamour. are probably an underestimate since neither small nor individual plants could be distinguished. By contrast, the single blades of the brown algae *A. clathratum* and *Laminaria* spp. are more accurately represented. Subtidal canopy populations of *C. fragile* subsp. *tomentosoides*, *A. clathratum*, and *L. saccharina* at Star Island were sampled (−4 to −15 m) just prior to the spring recruitment of the bryozoan *M. membranacea* (June 2000) in order to assess patterns of host specificity.

A series of permanent transect studies have been conducted annually by students at the Shoals Marine Laboratory, with these documenting percent coverage of the dominant intertidal organisms on Star Island, NH from 1965–1972 (cf. Kingsbury 1976) and on Appledore Island, ME from 1973 to the present. Ten years of intertidal transect data on Appledore (Figure 2) were evaluated to confirm the initial establishment of *Codium* during 1986–1995, with the data being supplied by present (Dr. Jim Morin, Director) and former Shoals Marine Laboratory personnel (Drs. Sarah Cohen and Michael Lesser). Twenty-eight transects are located around the perimeter of Appledore Island, with these ranging from fully exposed to very sheltered locations. Four sheltered transects with *Codium* populations were compared, with their locations (directions) relative to magnetic north being as follows: T2 (W shore at 250° and in Babb's Cove), T5 (W shore at 242°), T24 (SE shore at 159°), and T28 (SW shore at 230°). Data from earlier floristic surveys of the Shoals (Mathieson and Hehre 1986; Mathieson and Penniman 1986a) also served as a baseline to compare the initial occurrence of *Codium*; these were supplemented in 1994 by Ms. Amy Cook (a former UNH undergraduate) who documented the species' potential occurrence on all nine islands (Figure 2). Voucher specimens of her collections are deposited in NHA.

Several demographic features of *Codium* populations at six sites from mid-coastal ME to NH (Figures 1 and 2) were studied in order to compare geographical patterns of colonization, abundance, and physiological optima under variable hydrographic conditions. The six sites included: an insular NH site at Star Island, Isles of Shoals; a Maine nearshore open coastal location at Jaquish Island near the Boothbay Harbor invasion site at the Commercial Fisheries Biological Laboratory, plus Cape Neddick, York and Seapoint, Kittery; and two outer estuarine sites, one in Brave Boat Harbor, York/Kittery, ME, and the other in South Mill Pond, Portsmouth, NH. Mean frond length (cm), damp-dried weight (g), density (no./m^2), biomass (g/m^2), and percent occurrence were enumerated for each location, except Cape Neddick where no destructive sampling for weight and biomass was taken due to the plant's low density in a permanent study site (cf. Chavanich and Harris 2000). The above measurements were based upon a sampling of 25–30 randomly tossed quadrats (0.1 m^2). As plants at Brave Boat Harbor, ME are restricted to the perimeter of relatively deep salt marsh pannes, area-based density and biomass estimates at this site are not directly comparable to the other five sites. Therefore, linear- (i.e., perimeter) and area-based assessments of density and biomass at Brave Boat Harbor are given.

A comparison of surface water temperatures at an insular (Isles of Shoals, NH/ME) and a contiguous nearshore open coastal site (Cape Neddick, ME) within the Gulf of Maine (Figure 2) was made during the summers of 2000 and 2001 (i.e., June–September). The data, which were collected from the web site http://marine/rutgers.edu/mrs after imputing corresponding latitude and longitude values, showed variable color codings and surface water temperatures (°C). Usable images (i.e., data) were available only if both sites were simultaneously visible and if measurements were made between a 6:00–10:00 am period.

RESULTS

Insular and nearshore surface water temperatures. Figure 3 shows a comparison of mean weekly surface water temperatures

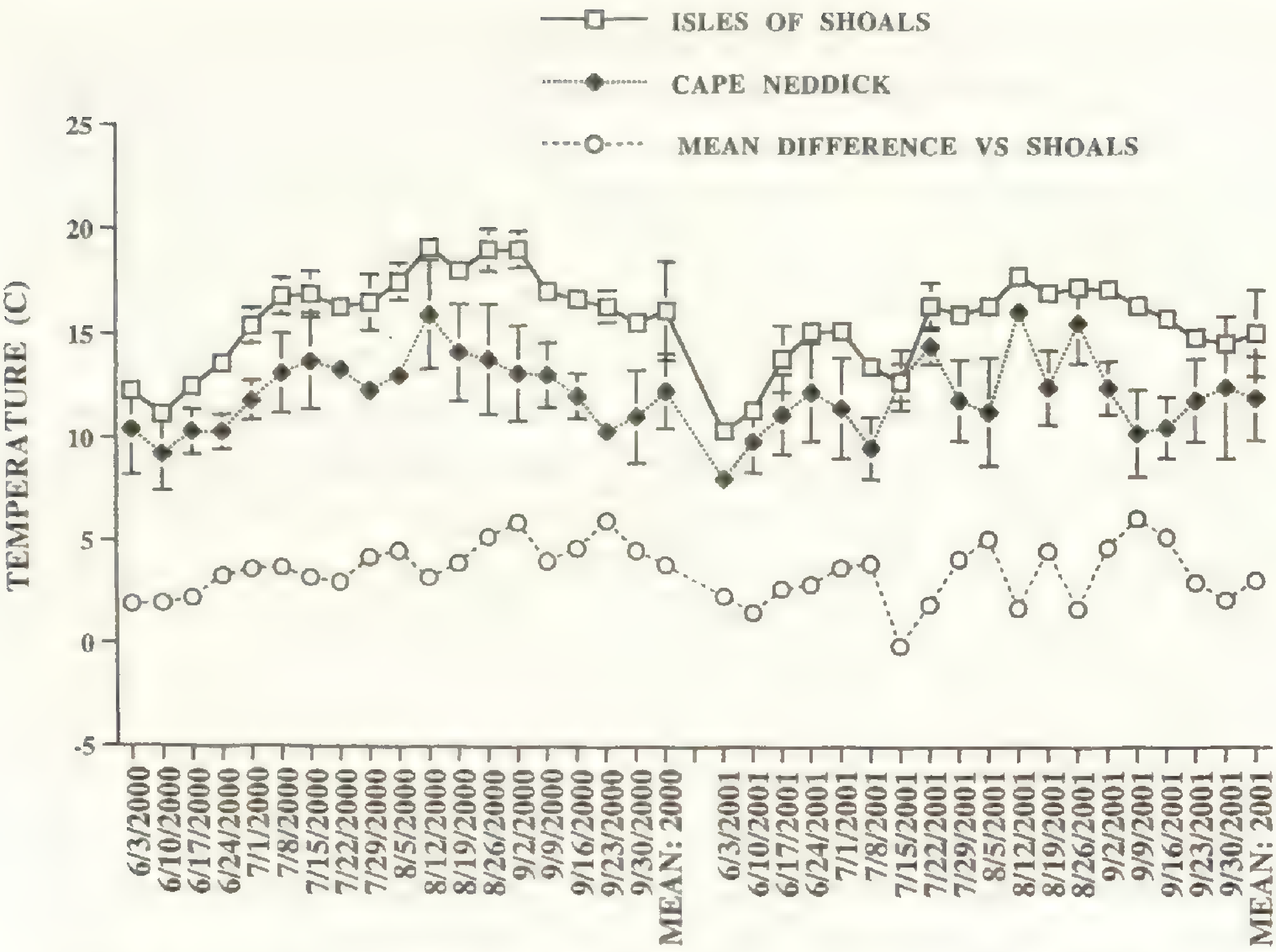

Figure 3. A comparison of surface water temperatures at the Isles of Shoals, NH/ME and Cape Neddick, ME during the summers of 2000 and 2001 (i.e., June–September), with the data being based upon satellite imagery and expressed as mean weekly temperatures (± SD). A synopsis of mean weekly differences between sites is also shown.

(± SD) at the Isles of Shoals, NH/ME (insular) and Cape Neddick, ME (nearshore) during two consecutive summers, plus mean differences versus the Shoals (i.e., + or −). The insular (i.e., Shoals) site was consistently warmer than Cape Neddick (i.e., +1.7 to 6.1°C), except during one week in early July, 2001 (i.e., −0.1°C). Mean values for both sites also showed a conspicuous difference, with those at the Shoals during 2000 being 16.1 ± 2.3°C versus 12.1 ± 1.8°C at Cape Neddick; the corresponding values for 2001 were 15.0 ± 2.1°C and 11.9 ± 2.0°C, respectively.

Present distribution of *Codium* within the Gulf of Maine. Figure 4A illustrates the occurrence of attached (Figure 5A–5D) and drift plants of *Codium* (Figure 5E–5H) within the Gulf of Maine, expressed as the number of collection sites within twelve contiguous habitats ranging from "Downeast" ME to Provincetown, MA. The numbers of identifiable epiphyte taxa are also shown in Figure 4B. Only drift specimens of *Codium*, composed of small fragments or larger proliferous fronds (Figure 5E–5H), are known from "Downeast" ME, plus the Great Bay (ME/NH) and Hampton-Seabrook (NH) Estuarine Systems. No populations (drift or attached) are known from Penobscot Bay (ME); further south, attached populations are recorded at 12 sites within Maine's "Indented Coastline," at 21 Casco Bay, ME sites, 15 southern ME nearshore sites (including outermost Brave Boat Harbor), nine islands within the NH/ME Isles of Shoals, seven NH nearshore open coastal sites (including outermost Portsmouth Harbor), one "North Shore" MA site, and at four sites each between Salem and Sagamore, MA, and Sandwich and Provincetown, MA. Two major patterns are evident: (1) a prevalence of sites downstream from the initial 1964 introduction at Boothbay Harbor, ME; and (2) a reduced and clinal decrease from Provincetown to the "North Shore" of MA, which is northward of a second invasion site via the Cape Cod Canal (1969–1972). As shown in the Appendix, *Codium* has a restricted contiguous distribution north of Boothbay Harbor, only occurring at Bristol and South Bristol, ME.

Chronological occurrence and invasion of *Codium* within southern Maine and New Hampshire. The invasion of southern ME and NH by *Codium* between 1982 and 2001 is summarized in Figure 6 and Table 1. Drift specimens (Figure 5E–5H) were often found prior to attached populations (Table 1). For example, at the Isles of Shoals (Figure 2) drift samples were initially observed at Appledore Island, ME during 1982, followed by attached populations one year later within Babb's Cove and contiguous sheltered sites on the same island. By 1986, *Codium* had formed dense subtidal beds in many sheltered Appledore sites, as well as expanded into the sheltered Gosport Harbor side of Smuttynose Island, ME. Two years later, student transect studies on Appledore (Table 2) documented an initial 6–12% coverage in the low intertidal at three sheltered sites (T2, T5, and T24), increasing to 15 and 12% on two transects (T2 and T24) during 1995. *Codium* was well established on the exposed side of Appledore during 1993 (Table 1). A floristic survey in 1994 showed its presence on Appledore, Duck, Malaga, and Smuttynose Islands, ME, plus Lunging, Seavey, and White Islands, NH. In 1995

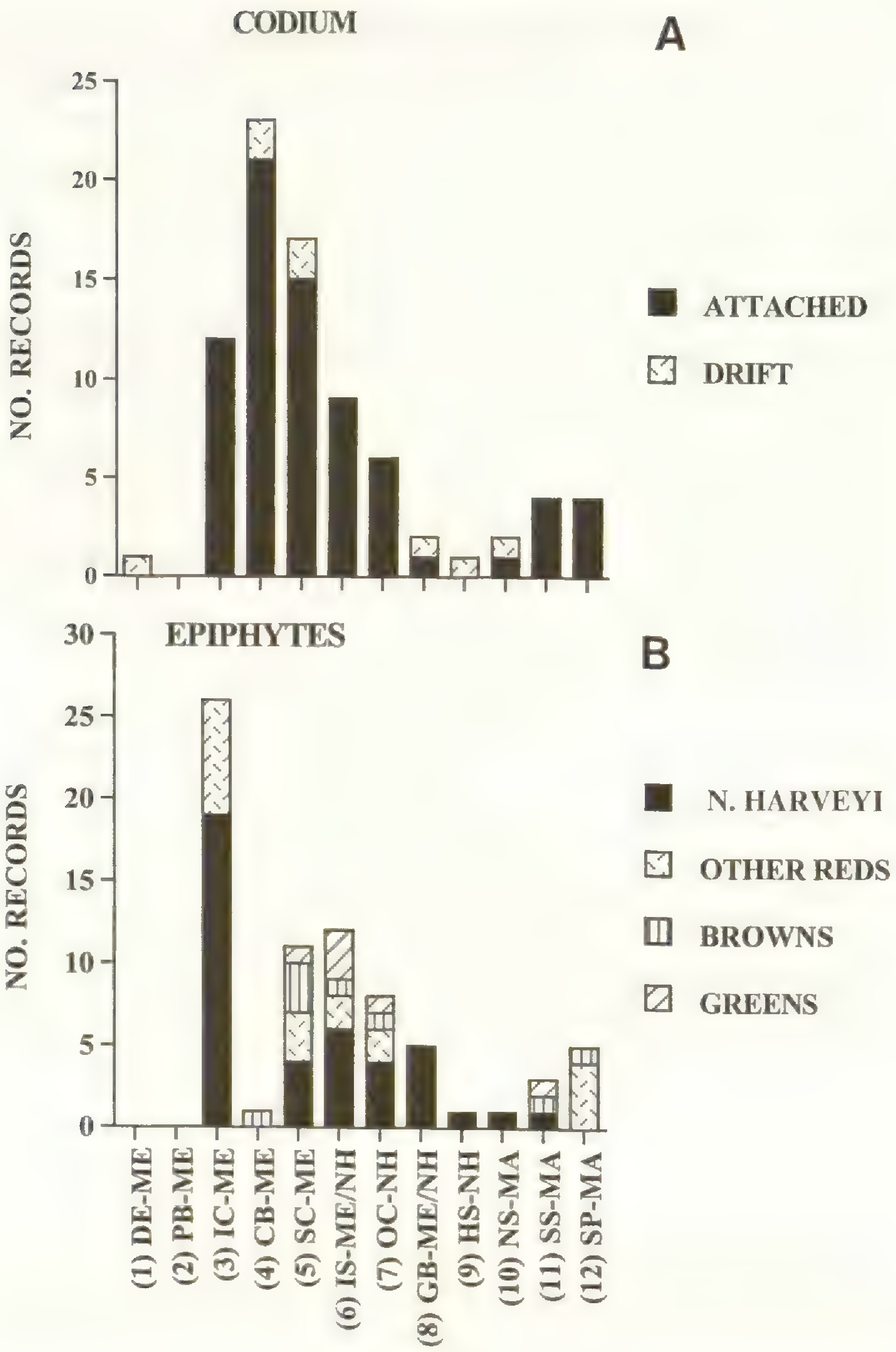

Figure 4. The distribution of attached and drift populations of *Codium* within twelve contiguous Gulf of Maine habitats (A). The presence of the Asiatic red alga *Neosiphonia harveyi*, plus various red, brown, and green algal epiphytes, are also shown within the same habitats (B). See Figure 1 for location of the twelve sites, with these being abbreviated as follows: (1) DE-ME = "Down East" ME; (2) PB-ME = Penobscot Bay, ME; (3) IC-ME = the "Indented Coastline" of ME; (4) CB-ME = Casco Bay, ME; (5) SC-ME = the southern ME coastline; (6) IS-ME/NH = the ME/NH Isles of Shoals;

it had extended to Star Island, NH, while in 1998 it was present on Cedar Island Ledge, ME.

The temporal occurrence of *Codium* on the nearshore open coast of southern ME and NH is also summarized in Figure 6 and Table 1. Drift populations were initially recorded in 1985 at Rye Ledge, Rye, NH (42°58′20″N, 70°45′33″W). During the same year, drift populations were also found at Weeks Point, Greenland, NH (43°03′32″N, 70°51′42″W) within the inner reaches of the Great Bay Estuarine System (Table 1). Four years later (1989) attached plants were first recorded from southern ME at Cape Neddick, York (43°09′56″N, 70°35′25″W). In NH, *Codium* was first found on the nearshore open coast at Fort Stark, Newcastle (43°03′22″N, 70°42′49″W) during 1992. By 1994, it was recorded at a third nearshore site, followed by four in 1995, nine in 1997, 15 in 1998, and 16 in 2001. *Codium* was just recently found (2001) at a eutrophied outer estuarine site near Portsmouth, NH. In summary, the nearshore open coast of southern ME and NH was colonized five years later than the Shoals, with a rapid increase in number of sites between 1997 and 1998. A comparison of the situation at Rye Ledge and Weeks Point, where drift populations were found in 1985, shows that it took approximately nine years for a permanent population to become established at Rye Ledge (1994); the inner estuarine Weeks Point site was never colonized.

After its initial recording within Babb's Cove on Appledore Island, ME, *Codium* spread to 25 other sites during the next 17 years (Figure 6; Table 1). Presently, it is known from each of the nine islands at the Isles of Shoals, from 12 nearshore open coastal sites, plus four outer estuarine sites in Brave Boat Harbor, ME, and one outer estuarine site in Portsmouth Harbor, NH. Three additional drift records include Long Sands, York, ME (43°09′57″N, 70°35′26″W); Weeks Point, Greenland, NH within the inner reaches of the Great Bay Estuarine System; and Knowles Island, Hampton, NH (42°53′20″N, 70°49′24″W) within the

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←

(7) OC-NH = the NH nearshore open coast; (8) GB-ME/NH = the ME/NH Great Bay Estuarine System; (9) HS-NH = the NH Hampton-Seabrook Estuarine System; (10) NS-MA = the "North Shore" of MA, or Salisbury to Gloucester, MA; (11) SS-MA = Salem to Sagamore, MA; (12) SP-MA = the Cape Cod peninsula, or Sandwich to Provincetown, MA.

Figure 5. Morphology of attached fronds and detached fragments of *Codium*: note variability of frond stature for attached plants (A–D), including the abundance of the epiphytic red alga *Neosiphonia harveyi* (D); drift fragments (E–H) also exhibit pronounced variability of stature, segmentation, and proliferation, with some being small, thick fragments (E and F), others being constricted and having incipient "winter fragmentation" (G), or relatively large and proliferous (H).

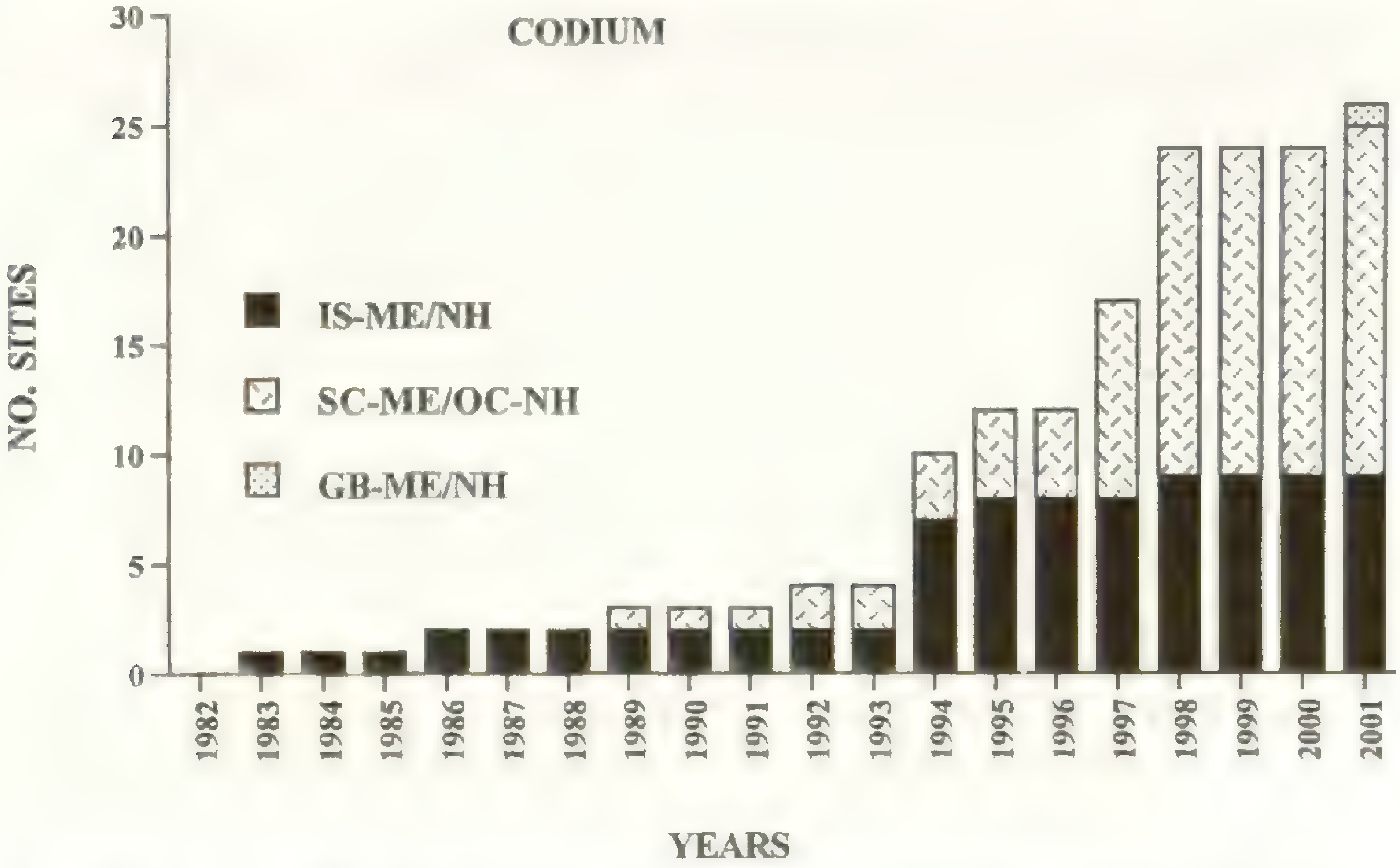

Figure 6. Annual variation of attached *Codium* populations (i.e., number of sites) within southern Maine and New Hampshire between 1982 and 2001, with the data being based upon seasonal collections at 276 open coastal and estuarine locations. Abbreviations: Isles of Shoals = IS-ME/NH; southern ME coast and nearshore NH open coast = SC-ME/OC-NH; Great Bay Estuarine System = GB-ME/NH.

Hampton-Seabrook Estuarine System. The 1985 drift sample from Weeks Point is well beyond its current distribution (Figure 2; Appendix), which is decidedly coastal (82%).

Variability of subtidal communities at the Isles of Shoals. Figure 7 shows the relative abundance of four subtidal canopy species at the Isles of Shoals based upon two depth groupings (0 to −7 m and −8 to −12 m) and a composite of five contiguous locations. *Codium* dominates the shallow subtidal zone (~77% cover), while the three native taxa are rare at these depths (~0.7–1.1% cover). By contrast, the mid-subtidal zone has a mixture of the four species: *Agarum clathratum* (~21% cover), *Codium* (~29% cover), *Desmarestia aculeata* (~16% cover), and *Laminaria* spp. (~15% cover). An assessment of percent coverage variability for the different shallow-water populations indicates that they are relatively uniform, with standard deviations only ranging from ± 0.7% (*Desmarestia*) to ± 2.3% (*Codium*). Variability of the four taxa is much greater within the mid-subtidal, ranging from ± 9.7% (*Laminaria* spp.) to ± 28%. Some of

Table 1. Local chronology and dispersal of *Codium* in southern Maine and New Hampshire following its colonization in 1964 at Boothbay Harbor, ME (cf. Figure 1 and 2).

Year	Localities
1982	Drift populations initially found on Appledore Island, Kittery, ME, Isles of Shoals (Dr. A. Borror, emeritus Professor, Dept. Zoology, Univ. New Hampshire, pers. comm.; Prince 1988)
1983	First attached populations found at the Isles of Shoals within Babb's Cove on the western (i.e., sheltered) side of Appledore Island, Kittery, ME near the Shoals Marine Laboratory (cf. Carlton and Scanlon 1985 for P. Sze's initial record)
1984	Attached populations found at Babb's Cove and contiguous sheltered sites on Appledore Island, Kittery, ME
1985	Detached populations recorded from Rye Ledge, Rye, NH (nearshore open coast) and at Weeks Point, NH (inner reaches of the Great Bay Estuary System)
1986	Dense subtidal beds (1–13 m below MLW) found at many sheltered Appledore Island, ME sites, particularly where kelps had been stripped by urchin grazing (Prince 1987); attached populations recorded from the Gosport Harbor (i.e., sheltered) side of Smuttynose Island, Kittery, ME
1988	Student transect studies documented the presence of *Codium* (6–12% coverage) in the low intertidal zone at three sheltered transect sites (i.e., T2, T5, and T24) on Appledore Island, Kittery, ME (cf. Table 2)
1989	Student transect studies on Appledore Island, Kittery, ME documented the presence of *Codium* (7% coverage) at a fourth sheltered transect site (i.e., T28; cf. Table 2); first attached populations recorded from the nearshore open coast of southern Maine at Cape Neddick, York
1992	Abundant at several sheltered locations on Appledore and Smuttynose Islands, Kittery, ME (i.e., within Gosport Harbor); first record of attached populations from the nearshore open coast of New Hampshire at Fort Stark (Jaffrey Point), Newcastle
1993	Well established on the exposed side of Appledore Island, Kittery, ME (L. G. Harris, unpubl. obs.)
1994	First attached populations found at Duck and Malaga Islands, Kittery, ME, plus Lunging, Seavey, and White Islands, Rye, NH at the Isles of Shoals; attached populations found at Rye Ledge, Rye, NH on the nearshore open coast, plus drift populations at Long Sands, York, ME and Odiorne Point State Park, Rye, NH
1995	Initial attached populations found on Star Island, Rye, NH; abundant populations also found on the exposed side of Smuttynose Island, Kittery, ME; student transect studies on Appledore Island, ME documented increased coverage (12–15%) on transects T2 and T4 (Table 2); initial attached populations found at Odiorne Point, Rye, NH

Table 1. Continued.

Year	Localities
1997	Attached populations found at Seapoint, Kittery, ME on the nearshore open coast, at three nearby sites within the outermost part of Brave Boat Harbor Marsh, York-Kittery, ME, and at Great Boar's Head, Rye, NH
1998	Attached populations initially found at Cedar Island Ledge, ME, Isles of Shoals, plus at two other outer Brave Boat Harbor, York-Kittery, ME sites, and nearby Sisters Point and Fort Foster on Gerrish Island, Kittery, ME; initial collections also found at North Wallis Sands and Concord Point, Rye, NH
1999	Detached populations recorded from the Knowles Island area, Hampton-Seabrook Estuary System, NH
2001	Attached population found within South Mill Pond (i.e., backwater of Piscataqua River), Portsmouth, NH and at a site just south of Odiorne Point State Park, Rye, NH

this variability is no doubt associated with the historical presence or absence of urchin "barrens," with White Island, NH always having kelp beds and the others urchin barrens. The consistent shallow-water dominance of *Codium* at the Shoals suggests that it has become "adapted" to diverse exposure conditions. The presence of young plants among established adults also indicates that it will persist for some time.

Demographic patterns of *Codium* populations at six Gulf of Maine sites. Figure 8 illustrates the size frequency and mean (± SD) stature (frond length) of *Codium* populations at Jaquish Island, Cape Neddick, Seapoint, and Brave Boat Harbor, ME, plus South Mill Pond and Star Island, NH. The highest frequency (35.4%) of large fronds (41–80 cm long) was recorded at Star Island, while 100% of the plants were small (0–20 cm long) in the relatively deep salt marsh pannes at Brave Boat Harbor (~0.6 ± 0.7 m, n = 21). Mean frond length and frequency patterns corresponded, being highest at Star Island (28.5 ± 17.0 cm) and lowest at Brave Boat Harbor (10.9 ± 3.2 cm). Table 3 summarizes the values for mean frond weight, length, density, and biomass, plus the percent occurrence values per site; no weight and biomass values are shown for Cape Neddick (cf. Materials and Methods section). Mean frond weights were smallest at Brave Boat Harbor (11.2 ± 16.6 g) and largest at Star Island (177.4 ± 198.9 g). Tide pool populations at Jaquish Island had the highest

Table 2. Percent coverage of *Codium fragile* subsp. *tomentosoides* within the low intertidal zone on four sheltered permanent transects (T2, T5, T24, and T28) at Appledore Island, Maine, Isles of Shoals during 1986–1995. — = no sample taken.

	% Coverage										
Transect	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	Mean ± SD (SE)
T2	0	0	6.0	2.0	4.0	0	2.0	0	4.0	15.0	3.3% ± 4.6% (1.4%)
T5	0	0	8.0	3.0	16.0	0	0	1.0	0	0	2.8% ± 5.3% (1.7%)
T24	—	0	12	0	4	0	5	0	1	12	3.8% ± 5.0% (1.7%)
T28	0	0	0	7	0	1.0	0	0	0	1.0	0.9% ± 2.2% (0.7%)

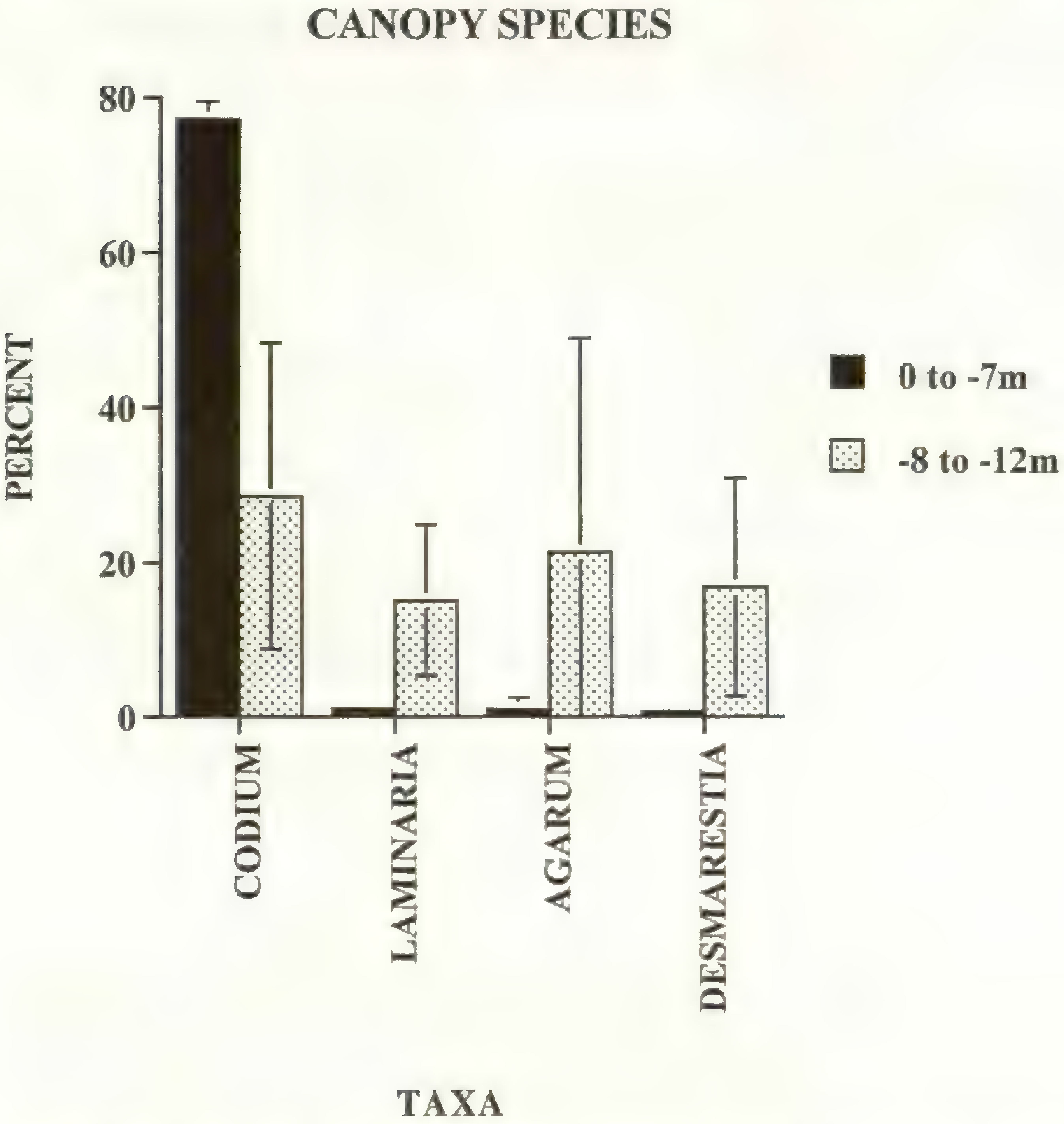

Figure 7. Relative abundance of four subtidal canopy species at the Isles of Shoals, based upon two depth intervals (0 to −7 m and −8 to −12 m) and a composite of five contiguous locations measured in 2000.

density (49.0 ± 79.4 plants/m^2) and Cape Neddick the lowest (0.1 ± 0.4 plants/m^2). Biomass was greatest at Star Island (6103.0 ± 4137.0 g/m^2) and lowest at Brave Boat Harbor (4.0 ± 1.0 g/m^2). Linear- and area-based comparisons of density and biomass at Brave Boat Harbor showed dramatic differences, with densities of 107 ± 93 plants/m versus 0.4 ± 0.06 plants/m^2 and biomass values of 1198.4 ± 1543.8 g/m and 4.0 ± 1.0 g/m^2. Percent occurrence was highest at Star Island (100%) and lowest at Cape Neddick (7.5%).

Occurrence of encrusting invertebrates and algal epiphytes on *Codium*. Older, perennial fronds of *Codium* are often heavily

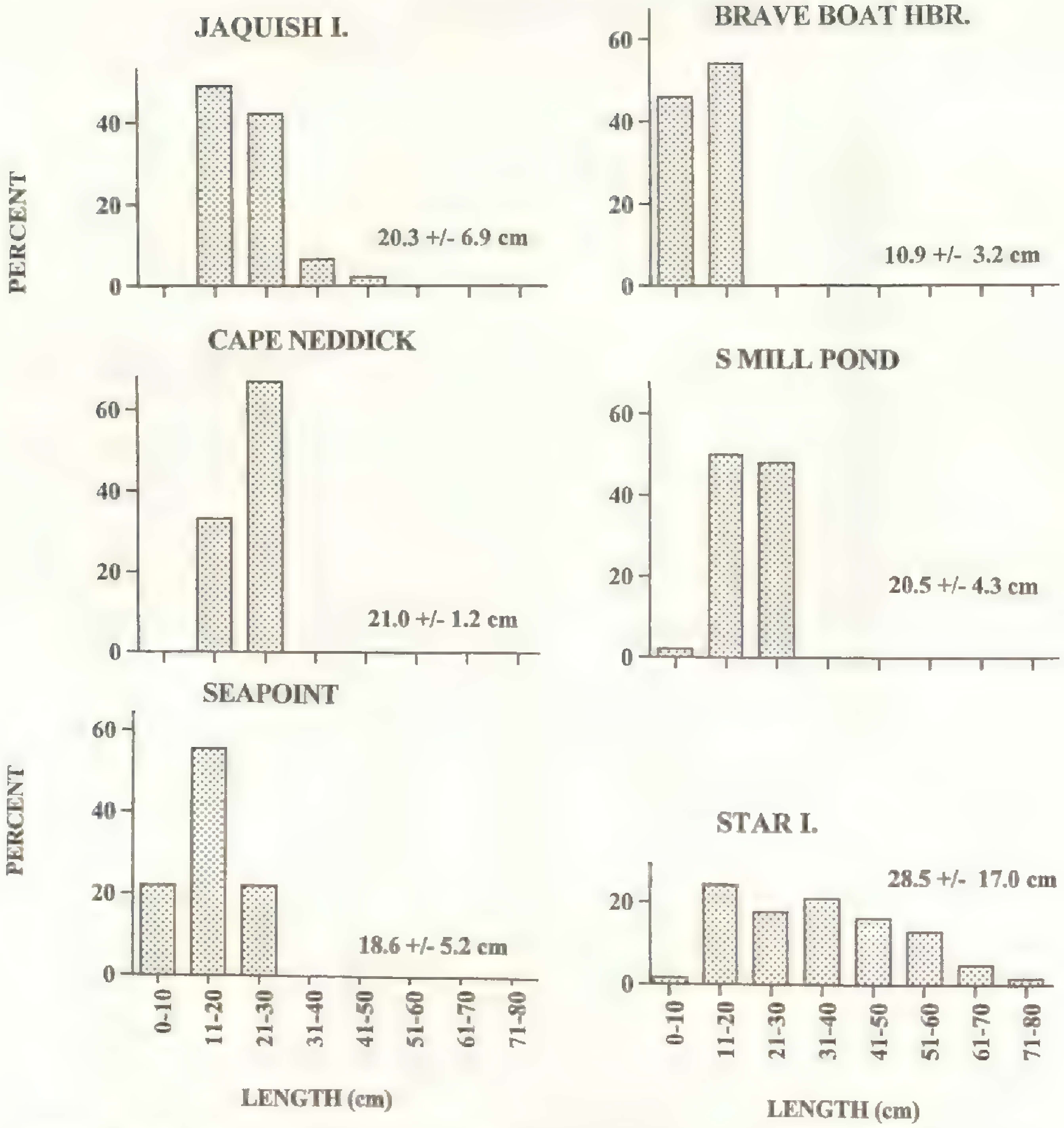

Figure 8. Size frequency distribution patterns for *Codium* frond lengths (cm) at six Gulf of Maine sites, plus mean frond lengths ± SD.

overgrown by encrusting, colonial invertebrates and epiphytes, including the introduced bryozoan *Membranipora membranacea* and the non-native tunicates *Botrylloides violaceus* Oka and *Diplosoma listerianum* (Milne-Edwards). Based upon recent sampling (June 21, 2000) of three major subtidal canopy species at Star Island, NH (i.e., *Codium, Agarum clathratum,* and *Laminaria saccharina*) it appears that winter survival of *M. membranacea* is higher on *Codium* than kelps, presumably because the blades of *Codium* stay intact while kelps slough off their terminal fronds and associated epibionts (cf. Lambert et al. 1992). Thus, approximately 76% of the *Codium* thalli sampled had abundant *M. mem-*

Table 3. Mean (± SD) frond weight, length, density, biomass, and percent occurrence of *Codium* populations at six sites ranging from mid-coastal Maine to New Hampshire. [a] Units for area-based assessment. [b] Units for linear-based assessment.

Sites	Frond Weight (g)	Frond Length (cm)	Density (no./m^2)[a] or (no./m)[b]	Biomass, Fresh Wt. (g/m^2)[a] or (g/m)[b]	% Occurrence
Area-based Assessment					
Jaquish Island, Harpswell, ME (nearshore open coast)	49.5 ± 58.4	20.3 ± 6.9	49.0 ± 79.4	2423.0 ± 4637.0	50.0
Cape Neddick, York, ME (nearshore open coast)	—	21.0 ± 1.2	0.1 ± 0.38	—	7.5
Brave Boat Harbor, Kittery, ME (outer estuarine)	11.2 ± 16.6	10.9 ± 3.2	0.4 ± 0.6	4.0 ± 1.0	26.3
Seapoint, Kittery, ME (nearshore open coast)	18.8 ± 5.03	18.6 ± 5.2	1.4 ± 1.9	26.6 ± 9.6	5.0
South Mill Pond, Portsmouth, NH (outer estuarine)	—	20.5 ± 4.3	24.0 ± 33.0	3049.6 ± 4047.2	55.5
Star Island, NH, Isles of Shoals (offshore island)	177.4 ± 198.9	28.5 ± 17.0	34.4 ± 20.8	6103.0 ± 4137.0	100
Linear-based Assessment					
Brave Boat Harbor, Kittery, ME (outer estuarine)	—	—	107.0 ± 93.0	1198.4 ± 1543.8	—

Table 4. Percent occurrence of different epiphytes on *Codium* samples collected throughout the Gulf of Maine (cf. Appendix).

Chlorophyceae

Chaetomorpha linum (O. F. Müll.) Kütz. (entangled, 0.7%)
Chaetomorpha picquotiana Mont. *ex* Kütz. (entangled, 0.7%)
Cladophora sericea (Huds.) Kütz. (0.7%)
Spongomorpha spinescens Kütz. (0.7%)
Ulva lactuca L. (1.3%)

Phaeophyceae

Ectocarpus fasciculatus Harv. (0.7%)
Melanosiphon intestinalis (D. A. Saunders) M. J. Wynne (0.7%)
Petalonia fascia (O. F. Müll.) Kuntze (0.7%)
Pilayella littoralis (L.) Kjellm. (0.7%)
Sphacelaria cirrosa (Roth) C. Agardh (3.3%)

Rhodophyceae

Callithamnion tetragonum (With.) S. F. Gray (0.7%)
Ceramium virgatum Roth (5.3%)
Ceramium strictum Harv. (0.7%)
Cystoclonium purpureum (Huds.) Batters (0.7%)
Erythrotrichia carnea (Dillwyn) J. Agardh (0.7%)
Neosiphonia harveyi (Bailey) Kim, Choi, Guiry & G. W. Saunders (23.3%)
Palmaria palmata (L.) Kuntze (0.7%)
Polysiphonia fucoides (Huds.) Grev. (0.7%)
Spermothamnion repens (Dillwyn) Rosenv. (2.0%)
Titanoderma pustulatum (J. V. Lamour.) Nägeli (0.7%)
"*Trailliella intricata*" stage of *Bonnemaisonia hamifera* Har. (0.7%)

Cyanophyceae

Microcoleus lyngbyaceus (Kütz.) P. Crouan & H. Crouan (0.7%)

Bacillariophyceae

Berkeleya rutilans (Trentophohl) Grünow (3.3%)

branacea on their midportions and often on multiple blades, while most kelps only had small residual colonies near their tips. Of the two kelps, *L. saccharina* exhibited a lower frequency of *M. membranacea* (~7.0%) than *A. clathratum* (~69%). In assessing 150 samples of *Codium* throughout the Gulf of Maine (Appendix), 21 algal epiphytes were recorded, including one macroscopic benthic colonial diatom, 3 green, 5 brown, 11 red algae, and 1 cyanobacteria (Table 4). Two filamentous green algae, *Chaetomorpha linum* (O. F. Müll.) Kuntze and *C. picquotiana* Mont. *ex* Kütz., were occasionally found entangled amongst

Codium. The relative abundances of the different epiphyte taxa are also summarized in Table 4, with the Asiatic red alga *Neosiphonia harveyi* being most conspicuous (23.3% occurrence), followed by five native species: *Ceramium virgatum* Roth [= *C. rubrum* (Huds.) Batters: cf. Maggs et al. 2002 (5.3%)]; *Sphacelaria cirrosa* (Roth) C. Agardh (3.3%), *Berkeleya rutilans* (Trentopohl) Grünow (3.3%), *Spermothamnion repens* (Dillwyn) Rosenv. (2.0%), and *Ulva lactuca* L. (1.3%). The other 15 epiphytic taxa were restricted to a single site (0.07%), while the two entangled *Chaetomorpha* species exhibited a similar pattern. Although *Codium* typically grows on hard substrata (i.e., rocks and/or shellfish), one epiphytic population was found on *Ascophyllum nodosum* (L.) Le Jol. and another on *Fucus vesiculosus* L. var. *sphaerocarpus* J. Agardh. The spatial distribution of diverse epiphyte populations within the Gulf of Maine is shown in Figure 4B, expressed as the number of site records (cf. Appendix) within each of the 12 contiguous habitats described above. The dominance of red algae, particularly *N. harveyi,* is readily apparent, plus a major peak within Maine's "Indented Coastline."

DISCUSSION

It should be emphasized that the invasion of the Gulf of Maine by *Codium* occurred at two locations and times: (1) mid-coastal ME near Boothbay Harbor in 1964, probably via transplantation of oysters from Long Island (i.e., *Crassostrea virginica* Gmel. and/or *Ostrea edulis*) with small microscopic plants (Boerner 1972; Coffin and Stickney 1966; Davis 1971; Malinowski 1974); and (2) southern MA due to the expansion of attached plants from the Cape Cod Canal (1969) into nearby Cape Cod Bay during 1972 (Carlton and Scanlon 1985; Coleman and Mathieson 1974; Fairbanks et al. 1971). The prevalence of populations downstream from the initial Boothbay Harbor site (Figure 4A) suggests that the first attached plants (Figure 5A–5D) grew, fragmented (Figure 5E–5H), and were then carried southward by strong currents (A. Borror, pers. comm.; Brooks 1985; Harris and Mathieson 2000; Prince 1988). The limited occurrence of contiguous populations just north of Boothbay at Bristol and South Bristol, ME suggests that dispersal of its single-celled reproductive cells ("gametes") is restricted by south-flowing currents (Apollonio 1979; Bigelow 1927; Mathieson et al. 1991). The second more southerly pattern suggests an expansion of attached plants after their passage through the Cape Cod Canal (1969–1972), which connects Buzzards and Cape Cod Bays (Carlton and Scanlon 1985; Coleman and Mathieson 1974).

Because of the warm-water affinities of *Codium* (Fralick and Mathieson 1973; Lüning 1990), it initially expanded more rapidly south than north of Cape Cod, dominating shallow subtidal habitats. By contrast, populations in Boothay Harbor were initially (1964 to the early 1970s) "quiescent," long-lived, and rather circumscribed (Coffin and Stickney 1966; Fralick 1970; Fralick and Mathieson 1973); ultimately, their biomass and stature increased, allowing a drifting of detached fragments like those first observed at the Shoals in 1982 (Table 1; i.e., ~125 km SW of Boothbay Harbor, ME). According to Searles et al. (1984) it took nine years for the first significant southward expansion of *Codium* from eastern Long Island (1957) to Barnegat Bay, New Jersey (Taylor 1967); 10 years later Hillson (1976) discovered a population in Virginia, 250 km south of New Jersey; in 1979 it was collected near Cape Hatteras, North Carolina, with this representing another 450 km southern extension (Searles et al. 1984). Once established in North Carolina it has spread rapidly throughout several inlets and sounds between Cape Fear and Cape Lookout, south of Cape Hatteras. Thus, it took variable and often extensive time periods (i.e., decades) for such expansions (Burrows 1991; Carlton and Scanlon 1985). The rate of spread described above is comparable to that noted from Boothbay Harbor, ME (1964) to the NH/ME Isles of Shoals (1983), and the nearshore open coast of southern ME (1989) and NH (1992). According to Hubbard and Garbary (2001, 2002) the distribution and spread of *Codium* within eastern Canada has also been very rapid; that is, within 10 years of its discovery on the south shore of Nova Scotia (Bird et al. 1993) it has dispersed over 1200 km to sites in northern Nova Scotia, New Brunswick, and Prince Edward Island. Hubbard and Garbary (2001, 2002) also note that two groups of plants seem to occur, with one being smaller, regularly dichotomously branched, and having flat-topped utricles with small mucrons [i.e., like *C. fragile* subsp. *atlanticum* (Cotton) P. C. Silva] and the other larger, more irregularly branched and having utricles with lanceolate tips and larger mucrons (i.e., *C. fragile* subsp. *tomentosoides*). Whether these different morphologies represent independent introductions, adaptations to local environments, or patterns of phenotypic plasticity needs to be established (cf. Garbary and Jess 2000; Hubbard and Garbary 2002).

The growth of *Codium* in the Gulf of Maine varies seasonally and spatially, being greatest during peak summer temperatures and insolation. Elongation rates of ~5.5 and ~10 cm/month have been recorded at Boothbay Harbor, ME and southern MA, respectively (Fralick and Mathieson 1973) versus 2.7–8.4 cm/month in Rhode Island (Hanisak 1979a). Like many other warm-temperate organisms found north of Cape Cod, MA (Hooper et al. 2002; Mathieson and Hehre 1986), *Codium* is most abundant at scattered warm water sites like Boothbay and Brave Boat Harbors, ME, the Isles of Shoals, NH/ME (Figure 3), and inner South Mill Pond, NH (Carlton and Scanlon 1985; Harris and Mathieson 2000; Loder et al. 1983; Mathieson et al. 2001; C. C. Taylor et al. 1957), with its growth (and reproduction) probably restricted by winter cold-water temperatures (Hutchins 1947). After its initial expansion into Cape Cod Bay, MA (1969), *Codium* demonstrated its warm-water affinities as it was reported (1974) at the nuclear power station at Plymouth, MA within Cape Cod Bay shortly after it commenced operation and warm-water discharge (Carlton and Scanlon 1985). In discussing the introduction of *Codium* into the southern Gulf of St. Lawrence, Garbary et. al. (1997) speculated that many of the negative features associated with its presence on Cape Cod, namely its adverse effects on shellfish and the fouling of tourist beaches (Hanisak 1980; Sheran and Prince 1973), may ultimately occur within the southern Gulf of St. Lawrence because of similarities of subtidal habitats.

The growth of *Codium* is initiated at 10–12°C; it is optimal at ~21–24°C, and it can survive −2.0°C (Fralick and Mathieson 1973; Hanisak 1979a, 1980; Malinowski and Ramus 1973; Moeller 1969). At some shallow-water locations, *Codium* becomes fragmented during winter, leaving only a residual basal holdfast from which it may regenerate (Fralick and Mathieson 1972; Hanisak 1980). At other (i.e., deeper) subtidal locations, such as Cape Neddick, York, ME and the NH/ME Isles of Shoals, plants may be "quiescent" or cease growth during winter, but they continue to increase in stature for two or more years (Harris and Mathieson 2000; Harris and Tyrrell 2001). Malinowski and Ramus (1973) studied the growth of *Codium* in the Niantic River Estuary of Connecticut, finding that it was initiated when temperatures and salinities exceeded 10°C and 22‰, respectively and was greatest at > 16°C and > 27‰. According to Hanisak (1979a, 1980), the light-physiology of *Codium* is of critical importance in determining its seasonal growth and competition with other seaweeds. It exhibits a low light saturation requirement, yet is efficient under higher light levels. He stated that limited nitrogen availability during summer limits its growth (cf. Hanisak 1979b, 2001). Even so, *Codium* is quite competitive in obtaining nitrogen during periods of low nutrient availability, and it can grow equally well on nitrate, nitrite, ammonium, and urea. It can take up different forms of inorganic nitrogen simultaneously and at relatively high rates, providing a major competitive advantage. Although *Codium* does not grow appreciably during winter, it is capable of taking up nitrogen and storing it until spring growth.

Reproduction in *Codium fragile* subsp. *tomentosoides* occurs either by motile unicells or vegetative fragments (Boerner 1972; Churchill and Moeller 1972; Fralick and Mathieson 1972; Garbary et al. 1997; Malinowski 1974; Malinowski and Ramus 1973; Moeller 1969; Ramus 1971, 1972; Rosenvinge 1920). Initiation of motile unicells, which have been variously designated as gametes or zoospores, occurs between 12–15°C (Churchill and Moeller 1972), and it is maximal at ~24°C (Hanisak 1979a). In the North Pacific, biflagellate anisogamous gametes have been reported, resulting in zygotes, initial dissociated filaments, and ultimately erect thalli (Arasaki et al. 1955; Borden and Stein 1969; Williams 1925). By contrast, most accounts of North Atlantic populations have reported either no male gametangia (Garbary et al. 1997; Ramus 1972) or parthenogenetic female gametes (Churchill and Moeller 1972; Fralick and Mathieson 1973; Hanisak 1979a; Lüning 1990; Moeller 1969); again the latter cells initially produce a juvenile tuft of dissociated filaments from which erect thalli grow under favorable conditions (Fletcher et al. 1989; Ramus 1972; Yang et al. 1997). Similar patterns of parthenogenetic female gametes have been reported from the Atlantic and Mediterranean coasts of France (Dangeard 1958; Dangeard and Parriaud 1956; Delépine 1959; Feldmann 1956; Parriaud 1957). Prince (1988) and Prince and LeBlanc (1997) found both large and small cells within the same gametangia for Appledore, ME populations of *Codium*, with the larger ones (female) being approximately six times more numerous than the smaller ones (male). Fusion appears to require gametes from different gametangia if not from different plants. They stated that this was the first report of *Codium* producing male and female gametes within the same gametangium (Arasaki et al. 1955; Borden and Stein 1969; Williams 1925), which is unique for algae in general (Burr and West 1970; Feldmann 1956). Churchill and Moeller (1972) found variable-sized swarmers in the same gametangia of Long Island populations; however, there was no sign of fusion nor did they differentiate male and female gametes. Several other investigators have reported variable-sized swarmers in *C. fragile* subsp. *tomentosoides* (Dangeard 1958; Delépine 1959; Moeller 1969; Weber 1969). In studying five populations of *Codium* ranging from Boothbay Harbor, ME to Long Island Sound, Prince (1990) found male and female gametes in each, the latter always occurring in greater numbers than the former. Surprisingly, two samples from Boothbay Harbor had small cells similar to those described by Coffin and Stickney (1966) and Malinowski (1974).

Several investigators have shown that *Codium* can exhibit extensive vegetative reproduction (Boerner 1972; Chapman 1999; Churchill and Moeller 1972; Fletcher et al. 1989; Fralick and Mathieson 1972; Hanisak 1980; Malinowski 1974; Malinowski and Ramus 1973; Moeller 1969; Ramus 1972; Rosenvinge 1920; Yang et al. 1997). Fletcher et al. (1989) stated that dissociated, siphonaceous filaments (see above) could occur as an independent, widely distributed, and more tolerant stage than the mature, macroscopic growth form; these filaments can propagate themselves vegetatively after detachment, dispersal, and entrapment (cf. Ramus 1972; Yang et al. 1997). Fralick (1970) found that macroscopic fragments were capable of reattachment to any solid substrata after initiating colorless filaments from their terminus (Dromgoole 1975, 1979; Garbary et al. 1997; Hanisak 1979a; Moeller 1969). Chapman (1999) stated that budding of adult thalli may occur during summer, allowing a subsequent release of vegetative juveniles (i.e., fragments) several cm in length. Extensive fragmentation of some shallow-water populations may occur during winter (Fralick and Mathieson 1972; Hanisak 1980; Malinowski and Ramus 1973) because of low temperatures (< 9°C) causing thallar constriction, segmentation (Figure 5G), and the production of a pseudoperennial residual base that can produce new fronds the following spring (Dromgoole 1975, 1979; Knight and Parke 1931; Mathieson and Hehre 1986; Sears and Wilce 1975; Trowbridge 1996). Other (i.e., deeper) populations tend to act as true perennials, with their thalli staying intact and often surviving for several years. Harris and Mathieson (2000) noted that the saccoglossan *Placida dendritica* (Alder & Hancock) had become an important specialized herbivore on *Codium* (cf. Trowbridge and Todd 1999, 2001), causing a reduction of this alga in protected areas (e.g., Gosport Harbor, Isles of Shoals) and facilitating its dispersal by enhanced fragmentation. *Placida* is common in salt marsh environments where it primarily feeds on the siphonaceous green alga *Bryopsis plumosa* (Huds.) C. Agardh, a close relative of *Codium* (Bleakney 1996). The slug aggregates at the junction of shaded, inner branches of *Codium,* puncturing cell walls and pumping out its cytoplasm (cf. Trowbridge 1992). The resulting plants become chlorotic, ragged, and break easily, detaching fragments that may either accumulate within localized (i.e., sheltered) depressions or float away. As outlined above, macroscopic fragments can be produced in many ways; whatever their source they are often quite buoyant (i.e., due to their internal gas entrapment) and very proliferous (Figure 5H), like many detached marsh fucoids (Mathieson and Dawes 2001). These fragments, as well as rafted *Codium* plants on shells, pebbles, and stones, are capable of floating long distances via surficial wind and currents; they may also move on the bottom as deep-drift specimens transported by bottom currents (Anonymous 1967; Bouck and Morgan 1957; Carlton and Scanlon 1985; Churchill and Moeller 1972; Dromgoole 1982; Dromgoole and Foster 1983; Fralick 1970; Galstoff 1962a,b; Garbary et al. 1997; Hanisak 1980; Malinowski 1974; Moeller 1969; Norton and Mathieson 1983; Parkes 1975; Ramus 1971; Rosenvinge 1920; Taylor 1967). The magnitude of this drifting process is suggested by the extensive accumulation of rafted *Codium* populations on Cape Cod and other Atlantic beaches (Ben-Avraham 1971; Carlton and Scanlon 1985; Grieve 1929).

Fralick (1970) suggested that *Codium* could be dispersed on migrating molluscs, as mature plants have been collected on oyster shells off the Delaware coast at depths of 200 feet (Anonymous 1967). He further speculated that it may be dispersed by herbivorous invertebrates, such as the green urchin *Strongylocentrotus droebachiensis,* which can contain healthy-looking reproductive structures (gametangia) in its fecal material. Although it is not a preferred food source, some shallow-water molluscs may graze upon *Codium* (Prince and LeBlanc 1992; Trowbridge 1995). Carlton and Scanlon (1985) stated that it has probably been spread most extensively by humans via ships' hulls, ballast water, fishing nets, aquaculture projects, etc. Loosanoff's (1955) early transplant experiments with the European oyster *Ostrea edulis* should be noted, as he transferred ~3000 oysters from Holland to Boothbay Harbor, ME during late 1949 or early 1950. His experiments were successful but he warned against the impending danger of such transplants!

Many of the invasive traits of *Codium* parallel those of the introduced tropical/subtropical green alga *Caulerpa taxifolia* within the Mediterranean (Boudouresque et al. 1994; Meinesz 1999; Meinesz et al. 1993; Raloff 1998; Trowbridge 1998; Wiedenmann et al. 2001) and recently reported from California (Jousson et al. 2000). It is taller than native populations, grows more vigorously, is more tolerant to cold temperatures, and capable of reproducing itself asexually via fragmentation (cf. Aleem 1992; Modena et al. 2000). Raloff (1998) suggested that the Mediterranean plant may be a hybrid or a new species that evolved through selective pressure in the aquarium industry. Prince (1988) stated that Appledore, ME populations of *Codium* may represent a new ecotype because of its unusual mode of reproduction (i.e., anisogametes in the same gametangia) and the fact that it has spread rapidly at water temperatures between 0–18°C (Loder et al. 1983), previously thought to be unsuitable for this species (Fralick and Mathieson 1973). Malinowski (1974) suggested that Boothbay Harbor populations may have diverged through natural selection from southern ones, as their germlings are able to grow at 4°C, while those from "parental" Long Island Sound cannot. He noted that Boothbay Harbor plants grew significantly less at higher temperatures (18–24°C) than did other populations. Kapraun and Martin's (1987) cytological studies of North Carolina *C. fragile* subsp. *tomentosoides* suggest that nuclear variability might have occurred, as the plant's haploid chromosomes were enlarged and exhibited increased DNA content versus autochthonous species. Such cytological patterns parallel the well-known polypoid features of other weedy species (Lüning 1990). Using DNA restriction studies, Goff et al. (1992) found that North Atlantic populations of the adventive subsp. *tomentosoides* differed from the closely related Northeast Pacific subsp. *fragile*. The subsp. *novae-zealandia* on New Zealand shores also differed physiologically from subsp. *tomentosoides* (Dromgoole 1980, 1982; Dromgoole et al. 1979).

As noted by Trowbridge (1995), the density of *Codium* varies geographically, with 10,170 thalli/m^2 being recorded near Cape Cod, MA (Fralick and Mathieson 1973), ~20 adult thalli/m^2 in Connecticut (Malinowski 1974), and 12–84 thalli/m^2 in Rhode Island (Hanisak 1979a). Typically, densities of *Codium* in New Zealand (Dromgoole 1979) were lower than those reported for southern New England, while they were more comparable to Gulf of Maine populations (Table 3). Trowbridge (1995) suggested several potential reasons for this differential: (1) the population size of New Zealand plants is still increasing, while reports from the North Atlantic indicate that it takes several decades to reach high densities (Burrows 1991; Carlton and Scanlon 1985; Table 3); (2) the New Zealand species-rich communities may be more resistant to invasion than species-poor communities like the northwestern Atlantic (Chapman 1999; Chapman et al. 2001, in press; Diamond and Case 1986; Elton 1958); (3) the presence of indigenous species that are ecologically and/or taxonomically similar may contribute to biotic or community resistance (Baltz and Moyle 1993; Diamond and Case 1986; Moulton and Pimm 1984); (4) the New Zealand populations studied by Dromgoole (1979) were mostly intertidal while those in southern New England were primarily subtidal; (5) salinity patterns in the two areas differed, the Hauraki Gulf of New Zealand being fully marine (~35‰) and the northwestern Atlantic less saline (32‰); and (6) the annual variability of surface water temperatures in the Hauraki Gulf is more limited (~12–21°C) than the northwestern Atlantic where winter conditions are much cooler (0°C). Harris and Mathieson (2000) documented differential density patterns for *Codium* at the Shoals, with the species initially being most abundant and dense in sheltered areas (1984–1990) and subsequently (1991) expanding to more exposed sites (cf. Table 1). Although the mechanism by which this shift in habitat breadth occurred is unknown, it may have been associated with extensive overgrowth of *Laminaria* spp. by the introduced bryozoan *Membranipora membranacea*, facilitating expansion of *Codium*. Harris and Tyrrell (2001) emphasized that *Codium* was not the only species undergoing a rapid expansion at this time.

Most *Codium* populations from nearshore open coastal sites in southern Maine and New Hampshire are smaller and have more limited densities and biomass than at warmer offshore insular sites like Star Island, NH (cf. Figures 3, 8; Table 3). For example, only small aggregations were present at Seapoint, ME; further they were smaller in stature (mean = 18.6 cm, 18.8 g), slightly branched, and had limited densities (1.4 plants/m^2) and biomass (mean = 27.0 g/m^2). By contrast, at protected Star Island sites the stature of *Codium* was larger (mean = 28.5 cm, 177.4 g), it was extensively branched, and it had high densities (mean = 34.4 plants/m^2) and biomass values (mean = 6103.0 g/m^2). Early studies (1964–1965) by Coffin and Stickney (1966) at Boothbay Harbor, ME showed a dominance of relatively small plants throughout the year (mean = 10.5–23.0 cm) and modest winter growth rates of ~5 cm/month. Fralick (1970) compared the stature and biomass of *Codium* populations at a southern New England site near Wings Neck, Bourne, MA (41°31′N, 70°40′W), finding the plants to be relatively small (rarely exceeding 30 cm) and exhibiting a seasonal biomass variation of ~350 g/m^2 (February) to ~2900 g/m^2 (August). Thus, its stature was similar to nearshore populations in mid-coastal Maine and New Hampshire, while its peak summer biomass was approximately half (48%) that recorded at Star Island and much higher (197–725×) than those at other nearshore sites. The stature and biomass of Star Island populations suggest a more optimal temperature regime (Figure 3) and a relatively mature community versus nearshore populations in mid-coastal Maine and New Hampshire (Table 3). In characterizing Nova Scotian populations of *Codium,* Bird et al. (1993) noted that they were relatively large (50–60 cm maximum) and abundant subtidally (i.e., like those at Star Island).

The contrasting patterns of insular versus nearshore populations described above may be associated with enhanced temperature stratification at the former (Figure 3) versus the latter habitats (cf. Lambert and Harris 2000; Loder et al. 1983). That is, offshore winds appear to cause nearshore upwelling and lower temperatures that reduce the growth and reproductive potential of these populations (see above). Harris et al. (1996) also described a pattern of increasing summer temperatures within the southern Gulf of Maine, which enhanced the growth of *Codium* and altered its community interactions at the Isles of Shoals (Figure 7). For example, it now dominates a variety of shallow (i.e., warmer) subtidal habitats above the thermocline (~−10 m), with *Agarum clathratum* and *Laminaria* spp. occurring below (Harris and Mathieson 2000). During the 1970s and 1980s both kelps were spatially separated, with *Laminaria* occurring above and *Agarum* below the ~−10 m thermocline (Hulbert 1980; Martin et al. 1988; Tacy et al. 1977; Witman 1984, 1985, 1987; Witman et al. 1982). Thus, changing environmental conditions and community instability due to overfishing of urchins and multiple introductions may have provided an ecological vacuum that *Codium* could fill, expanding its abundance and distribution (Chapman et al. 2001; Harris and Tyrrell 2001; Hay 1990; Malinowski and Ramus 1973; Prince 1989; Prince and LeBlanc 1992; Sanderson 1990; Scheibling 2001; Trowbridge 1995). Garbary et al. (1997) described an analogous pattern within the Gulf of St. Lawrence (Nova Scotia) where *Codium* grows in scours of eelgrass beds (i.e., *Zostera marina* L.) caused by storms or ice damage.

The rapid spread of the red alga *Neosiphonia harveyi* throughout the northwestern Atlantic suggests a variety of interesting parallels with *Codium,* as both species are invasive warm-temperate Asiatic species. The status of *N. harveyi* as a non-indigenous taxon has just recently been clarified (McIvor et al. 2000, 2001) based upon detailed molecular studies (cf. Rueness and Rueness 2000). Its abundance, along with several other epiphytes (Table 4), suggests that *Codium* beds may enhance their development and potential transport via drifting fragments (cf. Bartsch and Kuhlenkamp 2000). The enhancement of epiphyte populations on older perennial plants of *Codium* contrasts with the intercalary growth and sloughing of epiphytes in kelps (Lambert et al. 1992). Epibiontic drag and dislodgement may also be significant factors affecting the dispersal of *Codium* and its associated biota (cf. Witman 1987; Witman and Suchanek 1984). Chapman (1999) stated that the recent establishment and enhancement of the non-native broyozoan *Membranipora membranacea* on kelps within the northwestern Atlantic (cf. Scheibling 2001) may have been facilitated by previous species invasions, allowing an expansion of *Codium* as in the shallow subtidal zone at the Isles of Shoals (Figure 7). That is, *Membranipora* infests and rapidly overgrows large portions of kelp blades, increasing fragility and blade loss, and causing plant loss (Chapman et al. 2001; Chavanich and Harris 2000; Harris and Mathieson 2000; Harris and Tyrrell 2001; Lambert et al. 1992). Until recently *Codium* seems to have been less fouled by *Membranipora* than kelps, allowing a competitive advantage. The bryozoan's potential switching from kelps to *Desmarestia aculeata,* and various red and green algae, including *Codium* (see above), could provide other competitive interactions.

In summary, the rapid expansion of *Codium* north of Cape Cod, MA shows no sign of decline. Gulf of Maine populations may soon be augmented by Canadian Maritime specimens, which are now abundant and rapidly expanding (Hubbard and Garbary 2001, 2002; Scheibling 2001). Hence, the absence of attached populations within the "Downeast" and Penobscot Bay areas of ME (Figure 4A) may be short-lived, with a future expansion of drifting, south-flowing populations occurring like those described above for mid-coastal ME and other areas of the Atlantic seaboard (i.e., New York to North Carolina). The invasive pattern of *C. fragile* subsp. *tomentosoides* is no doubt based upon its genetic makeup, which is expressed as broad physiological tolerances, extensive vegetative reproduction, morphological plasticity, etc. (Chapman 1999; Dromgoole 1975, 1979; Hanisak 1980). Several weedy life history characteristics are also important, including rapid growth, parthenogenetic development in many populations, dispersal by drifting, etc. (Carlton and Scanlon 1985; Fralick and Mathieson 1972, 1973; Garbary et al. 1997; Hanisak 1979a, 1980; Prince 1988; Trowbridge 1995, 1996). With the exception of a few ascoglossan sea slugs that can cause thallus fragmentation after grazing (Clark 1975; Clark and Franz 1969; Harris and Mathieson 2000; Trowbridge 1993, 1995), *Codium* has largely escaped herbivory within the northwestern Atlantic (Hanisak 1980; Malinowski and Ramus 1973; Ramus 1971; Scheibling 2001, pers. comm.; Trowbridge 1995). The green urchin *Strongylocentrotus droebachiensis* has a low attraction to *Codium,* even though it is capable of consuming it (Freeman and Smith 2000; Prince and LeBlanc 1992). Thus, the lack of a major subtidal herbivore, coupled with the species high potential for dispersal, regeneration, and rapid growth may have allowed it to dominate native species within the Gulf of Maine (Prince 1988; Staehr et al. 2000) and the Canadian Maritime Provinces (Bird et al. 1993; Garbary et al. 1997; Scheibling 2001). In comparing *Codium* abundance in Japan (i.e., original source area), New Zealand, and the northwestern Atlantic, Trowbridge (1995) speculated that it was most abundant in the northwestern Atlantic possibly because low herbivory had allowed its successful invasion (cf. Chapman 1999; Chapman et al. 2001). By contrast, in areas with large endemic grazers, such as the North Pacific where the red sea urchin *S. franciscana* (A. Agassiz) occurs, *C. fragile* (non-invasive subspecies) is more circumscribed and largely confined to the intertidal (Freeman and Smith 2000). The same authors also noted that the future success of *C. fragile* subsp. *tomentosoides* in areas of differing endemic urchin grazers (e.g., Atlantic, eastern Pacific, New Zealand, Australia) may be influenced by a general decrease in urchin sizes due to local urchin fisheries.

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APPENDIX

HERBARIUM VOUCHER RECORDS FOR GULF OF MAINE *CODIUM* POPULATIONS

MAINE

WASHINGTON CO: Pembroke, Wilbur's Neck, 8 Oct 1995, *True & Carpenter* (NHA # 63966), = small detached fragments.

LINCOLN CO: Bristol, Rachel Carson Salt Pond Preserve, 20 Oct 1995, *Mathieson* (NHA # 59553), with epiphytic *Neosiphonia harveyi*; South Bristol, tip of peninsula opposite Crow Island and at the end of Rt. 219, 15 Jun 1994, *Hehre, Mathieson & Gerweck* (NHA # 50692, 50771), = drift specimens; 3 Aug 1997, *Mathieson & Dawes* (NHA # 65814, 65815), = attached material with epiphytic *N. harveyi*; South Bristol, Foster's Point, 12 Jul 1995, *Mathieson & Gerweck* (NHA # 58001), with epiphytic *N. harveyi & Palmaria palmata*; Southport, Capitol Island, bridge from Cross Road and West Southport, 20 Nov 1995, *Mathieson* (NHA # 60301); Boothbay Harbor, Jul 1964, *Coffin* (MICH # 33991); 26 Sep 1967, *Coffin* (MICH # 33990); Boothbay Harbor, Townsend Gut, 18 Aug 1983, *Morse* (NHA # 48275), collected while harvesting fucoid algae; Boothbay Harbor, Spruce Point, Linekin Neck, 20 Nov 1995, *Mathieson* (NHA # 60371), with epiphytic *N. harveyi*; (NHA # 60372); Boothbay, Ocean Harbor, 14 Mar 2000, *Mathieson* (NHA # 71719), epiphytic on *Ascophyllum nodosum*; Boothbay, East Boothbay Pond, 9 May 1995, *Gerweck* (NHA # 56189), with epiphytic *N. harveyi*; (NHA # 56190); Boothbay, Ocean Point, Linekin Neck, 7 Sep 1994, *Mathieson & Hehre* (NHA # 52461–52462), with epiphytic *Ceramium virgatum*; (NHA # 52463), attached in low tide pool; 29 Sep 1995, *Mathieson* (NHA # 59612), with epiphytic *N. harveyi.*

SAGADAHOC CO: Georgetown, Reid State Park, 30 Jun 1994, *Mathieson & Hehre* (NHA # 50653, 52141); 27 Oct 1995, *Mathieson* (NHA # 60209–60210), with epiphytic *Neosiphonia harveyi*; Phippsburg, Head Beach (Casco Bay), 10 Jun 1995, *Mathieson* (NHA # 57830); Phippsburg, Bald Head (Casco Bay), 10 Jun 1995, *Mathieson* (NHA # 58289); 28 Aug 1995, *Mathieson & Hehre* (NHA # 59241–59242), with epiphytic *N. harveyi*; Phippsburg, Sebasco Harbor boat ramp off Rt. 127 (Casco Bay), 9 Sep 1995, *Mathieson* (NHA # 59347), with epiphytic *N. harveyi.*

CUMBERLAND CO: Brunswick, Bunganuc Rock, off Bunganuc Point, Maquoit Bay (Casco Bay), 6 Jun 2001, *Short* (NHA # 74344–74345), growing on rope for a marker buoy; Wharton Point, Maquoit Bay (Casco Bay), 13 Jun 1995, *Mathieson & Hehre* (NHA # 56984); 4 Dec 1995, *Mathieson* (NHA # 59907); Brunswick, Middle Bay Cove, opposite Pennellville, 20 Nov 1999, *Mathieson* (NHA # 70141); Brunswick, Middle Bay, off Pennellville Rd., 20 Nov 1999, *Mathieson* (NHA # 70038, 70209); Brunswick, Mere Point, end of Mere Point Rd., Mere Point Neck, 20 Nov 1999, *Mathieson* (NHA # 70058); 11 Nov 2000, *Mathieson* (NHA # 72964), with epiphytic *Ceramium virgatum & Neosiphonia harveyi*; (NHA # 72978), with *Callithamnion tetragonum & N. harveyi*; Harpswell, Bailey's Island, end of Rt. 24 near Land's End Store and opposite Jaquish Island (Casco Bay), 6 Sep 1994, *Mathieson & Hehre* (NHA # 53943); Harpswell, Bailey's Island, "the Steps" (Casco Bay), 7 Sep 1999, *Mathieson & Dawes* (NHA # 70191); Harpswell, Jaquish Island (Casco Bay), 6 Jul 2000, *Dawes & Lamson* (NHA # 71749–71753), with epiphytic *N. harveyi*; Harpswell, Lookout Point boat ramp, Middle Bay (Casco Bay), 30 Jul 1995, *Mathieson* (NHA # 57690), = drift specimens; Harpswell, Mark Island (Casco Bay), 6 Jul 2000, *Neefus & Shay* (NHA # 71756); Harpswell, Pond Island (Casco Bay), 6 Jul 2000, *Neefus & Shay* (NHA # 71754), with epiphytic *C. virgatum*; (NHA # 71755), with epiphytic *Cystoclonium purpureum*; Harpswell, Ragged Island (Casco Bay), 6 Jul 2000, *Mathieson & Teasdale* (NHA # 71727–71729); Harpswell, Potts Point Cove, near old Harpswell Laboratory of Tufts University, 16 Sep 1999, *Mathieson* (NHA # 70016), with epiphytic *Ceramium virgatum* & *N. harveyi*; Harpswell, Potts Point, shoreline above old Harpswell Laboratory of Tufts University, 16 Sep 1999, *Hehre* (NHA # 69937, 69945), with epiphytic *N. harveyi*; (NHA # 69946), on *Fucus vesiculosus* var. *sphaerocarpus* with epiphytic *N. harveyi*; Harpswell, Basin Cove Falls, Potts Harbor (Casco Bay), 20 Feb 1995, *Mathieson & Hehre* (NHA # 54225); Harpswell, Basin Cove, opposite Peters Cove, 18 Sep 1999, *Mathieson* (NHA # 70231), = drift; Harpswell, Basin Point, near Dolphin Restaurant/Marina, Potts Harbor, 18 Sep 1999, *Mathieson* (NHA # 69923); Harpswell, tip of Ash Point Cove, lobster pound, Potts Harbor, 18 Sep 1999, *Mathieson* (NHA # 70646); Yarmouth, Doyle Point, Cousins Island (Casco Bay), 22 May 1995, *Mathieson* (NHA # 65149), = detached fragments with epiphytic *Ectocarpus fasciculatus*; Yarmouth, Little John Island, near Cousins Island, Talbot Rd. (Casco Bay), 31 Aug 1998, *Mathieson* (NHA # 67182); Long Island, South Beach, 13 May 2000, *Mathieson & Hehre* (NHA # 71718), = drift specimens; Portland, "The Bluffs", Cliff Island (Casco Bay), 6 Oct 1998, *Hehre & Mathieson* (NHA # 67269); Portland, Stinky Beach, Cliff Island (Casco Bay), 15 Apr 2000, *Mathieson & Hehre* (NHA # 71726); Scarborough, Spurwink River Marsh near Higgins Beach, 6 Aug 1999, *Mathieson, Dawes & Hehre* (NHA # 70907); Scarborough, Pine Point Breakwater, mouth of Scarborough River, Saco Bay, 5 May 1995, *Mathieson* (NHA # 56201); Scarborough, Pine Point Breakwater, 28 Oct 1995, *True* (NHA # 59817), = drift specimen; Scarborough, Jones Creek, mouth of Scarborough Marsh (S side), 22 Jul 1998, *Mathieson & Dawes* (NHA # 69287), with epiphytic *N. harveyi*.

YORK CO: Old Orchard Beach, Stratton Island (NW side), Saco Bay, 9 Jun 1995, *Cook* (NHA # 59968); 15 Jun 1995, *Cook* (NHA # 59969); Old Orchard Beach, Little Stratton Island, 19 Jun 1995, *Cook* (NHA # 60048); Saco, Ferry Beach State Park, 3 May 1995, *Mathieson, Hehre & Cook* (NHA # 55249), = drift specimens; Biddeford, Biddeford Pool, 31 Mar 1996, *Mathieson* (NHA # 63022), with epiphytic *Neosiphonia harveyi*; 5 Jul 1997, *Mathieson* (NHA # 65345), with epiphytic *N. harveyi*; York, Nubble Light (Cape Neddick), 16 Nov 1989, *Mathieson* (NHA # 50042), growing in low tide pool with epiphytic *Sphacelaria cirrosa* and entangled *Chaetomorpha linum*, = first nearshore coastal record from southern Maine and New Hampshire; York, Long Sands Beach, 9 Jul 1994, *Hehre* (NHA # 51069), = drift specimens; York, Brave Boat Harbor Marsh, ~0.42 km inland from the Harbor's mouth near old bridge pilings (in deep pannes), 16 Nov 1998, *Mathieson* (NHA # 68526–68527); Kittery, south bank of Brave Boat Harbor mouth, 23 Sep 1998, *Mathieson* (NHA # 68232), low tide pool; 24 Oct 1998, *Mathieson* (NHA # 68555), low tide pool; Kittery, Brave Boat Harbor Marsh, ~0.38 km inland from the Harbor's mouth, just upstream from the outermost bridge pilings and near the mouth (W side) of a tributary delineating Cutts Island (in deep pannes), 19 Nov 1997, *Anderson* (NHA # 68302), with epiphytic *Ceramium virgatum, Berkeleya rutilans, Microco-*

leus lyngbyaceus & Erythrotrichia carnea; (NHA # 68582), with epiphytic *S. cirrosa & C. virgatum*; Kittery, Brave Boat Harbor Marsh, ~0.39 km inland from the Harbor's mouth on Cutts Island, near bridge pilings and the mouth of a major tidal tributary (in deep pannes), 21 Dec 1997, *Mathieson* (NHA # 67808); 11 Jan 1998, *Mathieson* (NHA # 66460); (NHA # 66467), with epiphytic *B. rutilans*; Kittery, Brave Boat Harbor Marsh, ~0.48 km inland from the Harbor's mouth on Cutts Island and behind a coastal berm (in deep pannes), 3 Dec 1997, *Mathieson* (NHA # 68028–68029), with epiphytic *S. cirrosa*; (NHA # 68031); Kittery, Seapoint, 19 Dec 1997, *Mathieson & Anderson* (NHA # 65973), with epiphytic *B. rutilans & N. harveyi*; Kittery, Sisters Point, Gerrish Island, 14 Mar 1998, *Mathieson* (NHA # 66782); Kittery, Fort Foster, Gerrish Island, 31 Jan 1998, *Smith, Harris & Wingate* (NHA # 66997).

ISLES OF SHOALS (ME): Kittery, Appledore Island, Babb's Cove near the Shoals Marine Laboratory, 7 Aug 1984, *Brady-Campbell* (NHA # 25897–25898), growing attached in shallow subtidal zone, with epiphytic *Neosiphonia harveyi*; exposed eastern side of island, 14 Oct 1993, *Stepenuck* (NHA # 50574), with epiphytic *N. harveyi*; exposed NE side, 17 Jun 2000, *Mathieson & Zechman* (NHA # 71720–71721, 71723–71724), with epiphytic *N. harveyi, Spongomorpha spinescens & Pilayella littoralis*; Kittery, Duck Island, Isles of Shoals, 2 Aug 1994, *Cook* (NHA # 52130); Kittery, Malaga Island, Isles of Shoals, 16 Aug 1994, *Pellitier & Cook* (NHA # 52133), with epiphytic *Ceramium virgatum*; Kittery, Smuttynose Island, Gosport Harbor side of Isles of Shoals, 29 Apr 1986, *Penniman* (NHA # 49343), with epiphytic *N. harveyi & Ulva lactuca*; = first occurrence beyond Babb's Cove (Appledore Island); 12 Aug 1994, *Totman* (NHA # 52132), with epiphytic *Trailliella intricata*; eastern (exposed) side of island, 3 Nov 1995, *Mathieson* (NHA # 60296).

NEW HAMPSHIRE

ISLES OF SHOALS (NH): Rye/Kittery, Gosport Harbor, 15 Jan 1997, *Harris* (NHA # 12519), SCUBA –20 ft., with epiphytic *Neosiphonia harveyi*; Rye, Lunging Island, Isles of Shoals, 14 Aug 1994, *Cook* (NHA # 52131); Rye, Seavey Island, Isles of Shoals, 16 Aug 1994, *Pellitier & Cook* (NHA # 52129); Rye, Star Island, Isles of Shoals, 15 Jan 1997, *Harris* (NHA # 12517), SCUBA –30 to –40 ft.; Rye, White Island, Isles of Shoals, 16 Aug 1994, *Pellitier & Cook* (NHA # 52128); 15 Jan 1997, *Harris* (NHA # 12508), SCUBA –20 to –30 ft., with epiphytic *N. harveyi*; 23 Aug 1997, *Harris* (NHA # 62092–62093), SCUBA –20 ft., drift and proliferous material, with entangled *Chaetomorpha picquotiana.*

NEARSHORE OPEN COAST, ROCKINGHAM CO: Newcastle, Jaffrey Point (Fort Stark), low tide pool, 14 Sep 1992, *Mathieson* (NHA # 50039), = first nearshore open coastal record from New Hampshire; 17 Feb 2000, low tide pool, *Kozuck & Beck* (NHA # 71418), with epiphytic *Polysiphonia fucoides, Titanoderma pustulatum, Ulva lactuca & Berkeleya rutilans*; Rye, Odiorne's Point, 5 Jun 1994, *Hehre* (NHA # 50779), = drift specimen; 18 Mar 1995, mid-tidal tide pool, *van Fleet* (NHA # 54355), = first attached material at the site; May 1995, *Cook* (NHA # 60115); 5 Dec 1999, low tide pool, *Plummer* (NHA # 71552), with epiphytic *Neosiphonia harveyi*; Rye, North Wallis Sands, 3 Mar 1998, *Weymouth & Turnbull* (no specimen in NHA); Rye, Concord Point, 6 Feb 1998, *Wanat & Mayer* (NHA # 66792), in deep tide pool with epiphytic *N. harveyi*; Rye, Rye Ledge, 16 Oct 1985, *Zamojski* (NHA # 49072), = drift specimen; 30 Nov 1994, *Gerweck* (NHA # 52559), low tide pool, with epiphytic *N. harveyi*, = first attached material at the site; 5 Feb 2000, *Gunther, Hahn & Irwin* (NHA # 71108), with epiphytic *N. harveyi & Petalonia fascia*; North Hampton, Great Boar's Head, 1 Feb 1997, *Dick, Glaub & Jalbert* (no specimen in NHA).

GREAT BAY ESTUARY SYSTEM, ROCKINGHAM CO: Portsmouth, Inner South Mill Pond, 8 Jun 2001, *Mathieson & Grizzle* (NHA # 74346); ibid. (NHA # 74347–74349), with epiphytic *Neosiphonia harveyi*; Greenland, Week's Point, Great Bay, 6 Sep 1985, *Nelson* (NHA # 48860), = drift fragment entangled amongst *Zostera marina*.

HAMPTON-SEABROOK ESTUARY SYSTEM, ROCKINGHAM CO: Seabrook, mouth of creek between Knowles Island and mainland, 29 Jul 1998, *Mathieson & Dawes* (NHA # 69217–69218), with epiphytic *Neosiphonia harveyi*.

MASSACHUSETTS

ESSEX CO: Gloucester, Jones River town landing, Long Wharf, opposite Ram Island, 8 Aug 1998, *Mathieson* (NHA # 68490), with epiphytic *Neosiphonia harveyi*; Salem Harbor, Hawthorne Cove Marina, Salem, 8 Aug 2000, *Mathieson* (NHA # 72336); 14 Sep 2000, *Mathieson* (NHA # 72322).

NORFOLK CO: Cohasset, Cohasset Harbor Marsh, off Heatherly Rd., 21 Feb 1999, *Mathieson* (NHA # 69357), with epiphytic *Neosiphonia harveyi, Cladophora sericea, Melanosiphon intestinalis & Berkeleya rutilans*; (NHA # 69358).

PLYMOUTH CO: Scituate, off Driftway Rd. near mouth of North River, 21 Feb 1999, *Mathieson* (NHA # 69586); Plymouth, Gurnet Point, 23 Nov 1995, *North* (NHA # 59825).

BARNSTABLE CO: CAPE COD BAY, GULF OF MAINE: Barnstable, Barnstable Harbor, end of Bone Hill Rd., opposite Bone Point Light, 27 Mar 1999, *Mathieson* (NHA # 69518); Brewster, Quivett Creek Marsh, 1 Apr 2000, *Mathieson* (NHA # 71738), with epiphytic *Spermothamnion repens*; (NHA # 71739); Eastham, First Encounter Beach, end of Samoset Rd., 27 Mar 1999, *Mathieson* (NHA # 69537–69538), with epiphytic *S. repens*; (NHA # 69539), with epiphytic *Sphacelaria cirrosa*; Eastham, Coast Guard Beach, 1 Apr 2000, *Mathieson* (NHA # 71736–71737); Witchmere Harbor, 7 May 1966, *O'Brien* (NHA # 3106); South Wellfleet, Indian Neck, Wellfleet Harbor, 1 Apr 2000, *Mathieson* (NHA # 71733), with epiphytic *Sphacelaria cirrosa & S. repens*; South Wellfleet, Wellfleet Harbor, Old Wharf Rd., 27 Mar 1999, *Mathieson* (NHA # 69614); Provincetown, Provincetown Harbor, 4 Nov 2000, *Mathieson* (NHA #73061–73062), with epiphytic *Ceramium virgatum*.

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PRELIMINARY CHECKLIST OF MARINE ALGAE FROM MARTHA'S VINEYARD, MASSACHUSETTS

ROSE TREAT

RR#1, Box 475A, Edgartown, MA 02539

ALLAN R. KEITH

Turtle Brook Farm, P.O. Box 247, Chilmark, MA 02535
Author for correspondence; e-mail: keiths@vineyard.net

ROBERT T. WILCE

Biology Department, University of Massachusetts, Amherst, MA 01002

ABSTRACT. The island of Martha's Vineyard lies in the western Atlantic Ocean off the southwest corner of Cape Cod, Massachusetts. The island's marine algal populations have been the subject of intermittent study for approximately 130 years, most intensively in the last 40 years. Four herbaria known to contain specimens collected at the island were examined, and a bibliographical search for additional collections was made. The 155 documented species found by this process are listed with notes on habitat, abundance, and seasonality. Thus, 39% of the 396 species known between the Strait of Belle Isle and northern New Jersey have been found at Martha's Vineyard. A second list is included of 24 additional species that are known to occur within ten miles of the Martha's Vineyard shoreline and that can be expected to be found there with additional field work. Brief comparisons are made between the Vineyard marine flora and those of the more boreal floras of New Hampshire, coastal Maine, and New Brunswick, Canada.

Key Words: marine algae, seaweeds, Martha's Vineyard

This study originated with the Martha's Vineyard algal collections of Rose Treat that have their start about 1959. Treat, as many previous algal collectors, developed an interest in benthic algae because of their intrinsic beauty. In the following 43 years, she assembled a large collection of seaweeds preserved as dry mounts. The value of this collection as a local reference and educational resource, as well as being of general scientific interest, motivated one of the authors (A.R.K.) to begin a search for other algal specimens collected at Martha's Vineyard. The combination of the Treat collections and the surveys of literature and additional herbaria for taxa from this island forms the basis of this Martha's Vineyard algal flora. The checklist provides an historical meter that can be used to evaluate changes in the island's habitats and a record for comparison with other insular floras.

MATERIALS AND METHODS

To assemble a list of the known marine algae flora of Martha's Vineyard, we began with the collections of Rose Treat made over a period of more than four decades. Her mounted specimens and collages are in the permanent collections of the Marine Biological Laboratory at Woods Hole, the State University College of Arts and Sciences in Potsdam, New York, and at Harvard University. All the specimens in the Treat collection were sent for identification to professional phycologists, primarily W. R. Taylor, R. T. Wilce, and J. R. Sears.

Several additional herbaria in the region were examined for collections from Martha's Vineyard. Keith searched the algae catalog and collection at the Marine Biological Laboratory (SPWH) at Woods Hole, Massachusetts (originally the algal collection of the George Gray Museum of Woods Hole). Only those species not already known from Martha's Vineyard were recorded during the catalog search. Robert T. Wilce reviewed the marine algae collection in the herbarium at the University of Massachusetts at Amherst. Keith visited the Farlow Herbarium (FH) at Harvard University and examined that algal collection for holdings of 32 species that could reasonably be expected to occur at Martha's Vineyard based on earlier research, but which had not yet been located in other collections. Because of its size, the FH collection was not surveyed in its entirety. In August 2002, a scrapbook found on Martha's Vineyard containing 75 mounted specimens made by Mary A. Robinson about 1885 was donated to the Farlow Herbarium (Warnement 2002). While the specimens were almost certainly taken on Martha's Vineyard, this cannot be proven unequivocally. Most of the specimens appear to be of common species already known from the island, though definitive identifications have not yet been made. Through the courtesy of J. R. Sears, the herbarium at the University of Massachusetts at North Dartmouth was also checked for Martha's Vineyard specimens.

Keith also examined the marine algae collections at the Martha's Vineyard Historical Society at Edgartown. The collections originated from several sources during the era when collecting and mounting seaweed specimens was a modestly popular pastime (ca. 1870–1930). There is a notebook by Ruth Dunham (1873–74) of mounted specimens collected at Edgartown, Gay Head, and Chappaquiddick. There is also a collection made by Irvin E. Strickland at Vineyard Haven in 1934, and a series of excellent mounted specimens received in 1957 by the Society from the Sarah Joy Mayhew Estate that appear to be of 1900–1930 vintage. None of these collections has been examined or the species identified by a professional phycologist.

Keith also performed a bibliographical search of published references to marine algae collections made at Martha's Vineyard. Several species in the following checklist were found as a result of this search. Appropriate citations concerning these taxa have been included in the species list though, in some cases, no specimens have been found to verify their occurrence on the island.

This paper does not presume to provide an exhaustive report on the marine algal species of Martha's Vineyard. Many species listed in Appendix I have been recorded only once or twice in the last century. This does not mean that they are especially rare, merely that few people with knowledge to identify the species have actively searched in the correct habitat, or at the right time of year. The records of Mathieson et al. (1993, 2001) from numerous estuarine habitats include a number of species and forms of species not included in the Vineyard flora. Many other habitats and parts of the island are not yet fully explored, a process that would require diving (SCUBA) in many cases. We recognize that there are a number of marine algal species that probably occur around the island that have yet to be found. A second list of such species appears in Appendix II. Based on these data and the suggested range of occurrence of many species listed in Sears (2002), a motivated field worker might find half as many more as those already cited in Appendix I. This second list provides interested biologists knowledge of some algal species likely present, but as yet unreported on Martha's Vineyard.

Taxonomic sequence of species and nomenclature used here follow Sears (2002), the most recent and comprehensive publication of algal nomenclature available. As the life histories and structures of some species have become better known, specific, even generic, names have changed, especially from those in use several decades past. Sears (2002) provides synonymy for many, but not all, of the names in general use for the last 50 years and found in Taylor (1962), Kingsbury (1969), and Villalard-Bohnsack (1995).

RESULTS

The Treat algal collection currently consists of approximately 330 mounted specimens of 67 species. Additional algal mounts are added regularly. The collection is being transferred to the Polly Hill Arboretum in North Tisbury on Martha's Vineyard to assure its proper curatorial care and long-term availability to researchers. The Polly Hill Arboretum has also agreed that if the Treat collection can no longer be housed for any reason, it will be given to the Farlow Herbarium. All the Treat specimens were collected around the shore of Martha's Vineyard, and each has information that identifies locality and collection date on each mount. In the following list of known algae taxa from Martha's Vineyard (Appendix I), those in the Treat collection are indicated by "RT/PHA." Collection or specimen numbers have not yet been assigned to mounted specimens in the Treat collection.

At least 100 specimens of marine algal species at the SPWH have been collected at Martha's Vineyard. The earliest such collections were made by W. R. Dudley in 1879, followed by R. A. Esten in 1895, and B. M. Davis in 1903–04. The first half of the last century saw the arrival of three other active collectors, T. M. Douthart in 1912, Hannah T. Croasdale in 1931–32, and Edward T. Moul in 1947. They were followed by A. J. Bernatowicz in 1951; a collector with the initials "G. B. B." in 1958; and J. R. Sears, R. T. Wilce, and J. R. Conway in the 1967–69 period. Davis and Croasdale both published scholarly papers on marine algae of the region in their time, though none specifically on species from Martha's Vineyard that we have located. In the following list of taxa from the island, 23 species documented by specimens in the SPWH collection are indicated by "SPWH," the name of the collector, the date, and the locality, when that information was available.

The collection at the University of Massachusetts at Amherst contains specimens of at least 98 species taken at Martha's Vineyard, many of which were collected from sublittoral sites. Specimens were collected with the aid of SCUBA from four sites around the island's shore: West Chop, Menemsha jetty, Devil's Bridge off the Gay Head cliffs, and the Southwest Shoal, just southwest of Noman's Land Island, which lies just offshore of the west end of Martha's Vineyard. As more fully described in Sears and Wilce (1975), the purpose of these surveys, done at these sites at different times of year, was to better understand "algal seasonal periodicity, associations, diversity and floristic composition." Full data on collection date and locality are available for all specimens in this collection but are not included here. Species in the following list of known Martha's Vineyard taxa from the collection at the University of Massachusetts at Amherst are indicated by "MASS."

The seven species documented by specimens in the Farlow Herbarium collection are indicated by "FH," together with the available collection data. Specimens of 87 species collected at Martha's Vineyard sites are in the herbarium of the University of Massachusetts at North Dartmouth in the care of J. R. Sears. These species are marked by "HDSM" in the following list. The names of the collectors and dates of collection accompany the specimens, but are not provided here.

In the process of examining the SPWH collection and the literature, documentation was obtained for 24 marine algae species from sites within 10 miles of the Martha's Vineyard shoreline. A list of these species appears in Appendix II.

DISCUSSION

The 155 species documented in the Martha's Vineyard flora likely represent more than half of the yet unknown total Vineyard marine flora, estimated between 300–350 species. Even a cursory survey of the species list (Appendix I) reveals a lack of most of the cryptic species one expects in this flora. Species cited are those collected in the drift and from shore substrata, with the exception of species from the Sears and Wilce collections, all made with the aid of SCUBA, and followed by intensive laboratory study. This species list likely represents the greater number of the macroalgae in the total Vineyard flora. Even so, these 155 species are appreciable when compared to the better known floras of New Hampshire (216 species; Mathieson and Hehre 1986) and New Brunswick (171 species; South et al. 1988). Species numbers of these marine floras are based on long-term investigations, especially the New Hampshire study, and prepared by teams of professional phycologists. The greater length of both lists is largely due to recognition of species of small or minute stature, not the macroscopic forms. Differences in the various lists are also apparent by the lack of boreal species not expected, or at least considered unusual in the Vineyard flora (e.g., *Agarum clathratum, Alaria esculenta, Coilodesme bulligera, Delamarea attenuata, Laminaria longicruris, Ralfsia fungiformis, Saccorhiza dermatodea, Stictyosiphon tortilis, Devaleraea ramentacea, Pantoneura fabriciana, Peyssonnelia rosenvingii, Phycodrys rubens, Plumaria plumosa,* and *Polysiphonia arctica*). Other species present in the northern Gulf of Maine, and further north, could certainly support floral discontinuities, or at least floral differences between the Vineyard and the Gulf of Maine floras. Floristic differences, even when the cryptic species are omitted, are those largely represented by the brown algae, followed by red algal species. The Vineyard green algal flora can be assumed to be more similar to that of New Hampshire than that of New Brunswick, but the green algal floral composition along the entire Gulf of Maine is strikingly uniform. With the possible exception of *Arthrocladia villosa,* the composition of the Vineyard flora does not reflect a more southerly flora. Floristically, the Vineyard flora lies at what might be considered the southern fringe of the Boreal Province.

Haemescharia hennedyi (Wilce and Maggs 1989) is considered new to the Vineyard, and to the entire Northwest North Atlantic. Only tetrasporic crusts of this species are known from the Vineyard collections, but they agree in all respects with the description and illustrations of the better-known British populations of this species (Fletcher and Irvine 1982). The fleshy crustose red algal species, *Plagiospora gracilis* (Kuckuck 1897) is another addition to the Vineyard flora, but it is known elsewhere in the Gulf of Maine and Newfoundland.

The algal flora of Cape Cod and its adjacent islands, including Martha's Vineyard, is only partially known (Collins 1899; Doty 1948; Farlow 1881; Taylor 1962). Sufficient information about the character of that algal flora exists to recognize it is a combination of floras found both to the north and south of Cape Cod. Consequently, it is likely a larger flora than that of the Gulf of Maine, or of the hard-substratum impoverished regions immediately to the south of Cape Cod. Our best guide to that flora remains that of Taylor (1962). Fortunately, we also have the numerous studies of Mathieson with his colleagues and students that reveal the floristic character of coastal New Hampshire (Mathieson and Hehre 1986) and coasts of the Gulf of Maine (Mathieson et al. 1993, 1996, 1998, 2001). This flora is recognizably smaller than that of the immediate Cape Cod area; it includes few of the truly northern (arctic) algal species, and few that have their greater occurrence south of Cape Cod. A single endemic species (*Laminaria longicruris*; De la Pylaie 1829) occurs in the Gulf of Maine, otherwise that flora is somewhat impoverished with approximately 350 species.

Reportedly, the algal flora at the West Chop site at Martha's Vineyard changed dramatically between 1969 and 1984 (J. R. Sears, pers. comm.). The muddy bottom with a covering of *Crepidula fornicata* shells and cobble at approximately 10–12 m depth was the habitat of several small, fragile species of marine algae in 1969. Fifteen years later, despite the swift currents in the area, the site had been heavily invaded by *Codium fragile* subsp. *tomentosoides*. It is unknown if the previously dominant *Crepidula fornicata* and the smaller, crustose and fragile species that formed an understory in the West Chop habitat remain. A similar and more northern invasion of *Codium* is reported by Mathieson and Hehre (1986) and Mathieson et al. (2001, 2003) in the offshore Isles of Shoals, New Hampshire and several other sites in the Gulf of Maine. Clearly, with the advent of a dominant sublittoral population of *C. fragile*, associated biological change can be expected.

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APPENDIX I

LIST OF KNOWN MARINE ALGAE FROM MARTHA'S VINEYARD

Species documented by specimens in the Treat collection, to be housed at Polly Hill Arboretum, Martha's Vineyard, are indicated by "RT/PHA"; collection or specimen numbers have not yet been assigned to the specimens in the Treat collection. For other collections herbarium acronyms follow Index Herbariorum. Explanations for inclusion of collection data and/or references are given in the Materials and Methods or Results sections. MLW denotes Mean Low Water.

CHLOROPHYTA

CHLOROPHYCEAE

PRASIOLACEAE

Prasiola stipitata Suhr *ex* Jess. – on rocks in upper intertidal zone favored by roosting birds; near its southern limit. (Kingsbury 1969).

ULVOPHYCEAE

MONOSTROMATACEAE

Blidingia minima (Nägeli *ex* Kütz.) Kylin – common year-round on open coast and in estuaries throughout the littoral and, more rarely, in the upper sublittoral. Gay Head, 19 Jul 1932, *H. T. Croasdale*, SPWH.

ULVACEAE

Enteromorpha clathrata (Roth) Grev. – aseasonal annual found from early spring to late fall; attached to hard substrata, free-floating, or epiphytic. 1880 specimen, no other data available, FH.

Enteromorpha intestinalis (L.) Nees – common seasonal annual throughout the littoral zone; attached, or loose-lying in both sand and mud areas. RT/PHA.

Enteromorpha linza (L.) J. Agardh – common annual year-round on open coasts and in estuaries in the lower littoral and shallow sublittoral. (Sears 1971) HDSM.

Ulva lactuca L. – common in quiet warm bays, especially those with high nitrogen concentrations, from MLW to 24 m. RT/PHA, HDSM.

ULVELLACEAE

Bolbocoleon piliferum Pringsh. – annual; found as an epiphyte or endophyte in the littoral and sublittoral. (Sears 1971).

CODIOLACEAE

Urospora wormskjoldii (Mert. *in* Hornem.) Rosenv. – uncommon winter-spring annual; on upper littoral rocks in exposed areas on open coasts. Noman's Land, Jan 1969, *J. R. Conway*, SPWH.

CHAETOSIPHONACEAE

Blastophysa rhizopus Reinke – perennial; endophytic, or on or under crusts on stones or shells from low littoral to 15 m. (Sears 1971).

CLADOPHORACEAE

Chaetomorpha aerea (Dillwyn) Kütz. – year-round on open coasts in tide pools; on hard substrata in the upper sublittoral. West Chop, Jul, no collector or year given, HDSM.

Chaetomorpha linum (O. F. Müll.) Kütz. – aseasonal annual in shallow to upper sublittoral. Gay Head, 26 Jul 1944, *W. R. Taylor*, FH.

Chaetomorpha melagonium (F. Weber & D. Mohr) Kütz. – low littoral tide pools and below low tide line on rocks. (Kingsbury 1969) HDSM.

Cladophora albida (Nees) Kütz. – year-round in estuaries and bays, in tide pools throughout the intertidal zone to depths of 3 m; attached to rocks and epiphytic on other algae. Noman's Land, 16 Aug, 1932, *H. T. Croasdale*, SPWH.

Cladophora flexuosa (O. F. Müll.) Kütz. – uncommon. Early Gay Head specimen identified by H. K. Phiney in June 1946, FH.

Cladophora rupestris (L.) Kütz. – uncommon; probably perennial; in low shore and upper sublittoral. (Sears 1971).

Cladophora sericea (Huds.) Kütz. – annual in late fall and winter; attached to shell and rocks at 3–5 m. (Sears 1971) HDSM.

BRYOPSIDACEAE

Bryopsis plumosa (Huds.) C. Agardh – year-round but mostly evident in spring and early summer; occurs in upper sublittoral in shade. RT/PHA, HDSM.

Derbesia marina (Lyngb.) Solier – year-round in tide pools or more often growing on shells or stones in shallow sublittoral to 33 m. (Collins 1899; Sears and Wilce 1970) HDSM.

CODIACEAE

Codium fragile (Suringar) Harv. subsp. *tomentosoides* (Goor) P. C. Silva – common; on rocks, pilings, etc. from MLW to 10 m. RT/PHA, HDSM.

PHAEOPHYTA

PHAEOPHYCEAE

ECTOCARPACEAE

Botrytella micromora Bory – short-lived, uncommon summer annual. Reported in Edgartown before 1900 (Collins 1899).

Ectocarpus fasciculatus Harv. – aseasonal annual most common in winter and spring; open coasts to estuaries in the lower littoral and sublittoral. Gay Head, 16 Jul 1941, *W. R. Taylor,* HDSM.

Ectocarpus siliculosus (Dillwyn) Lyngb. – annual in quiet waters; reproduces in winter, most abundant in spring and summer. RT/PHA, HDSM.

Hincksia granulosa (J. E. Smith) P. C. Silva – aseasonal annual; year-round on shells and small stones from shallow sublittoral to 15 m. (Sears 1971) HDSM.

Hincksia ovata (Kjellm.) P. C. Silva – present in the shallow sublittoral attached to shells and small stones. Reported in Edgartown before 1900 (Collins 1899). HDSM.

Hincksia sandriana (Zanardini) P. C. Silva – seasonal annual in autumn and winter; present on shells and stones in shallow sublittoral from 2–8 m. Reported in Edgartown before 1900 (Collins 1899).

Hincksia secunda (Kütz.) Batters – annual in shallow sublittoral on shells or stones. (Sears 1971).

Pilayella littoralis (L.) Kjellm. – common in spring and early summer; attached to stones, pilings, other algae. RT/PHA.

Spongonema tomentosum (Huds.) Kütz. – epiphyte on diverse algae, stones, and shells; present in late winter to late fall on open coasts; occurs in the intertidal and uppermost sublittoral zones. Noman's Land, 16 Aug 1932, *H. T. Croasdale,* SPWH.

LITHODERMATACEAE

Petroderma maculiforme (Wollny) Kuck. – common crustose species of shallow sublittoral to 20 m, on shells and stones. (Sears 1971) HDSM.

Pseudolithoderma paradoxum Sears & R. T. Wilce – perennial crustose species present on stones and shells in sublittoral zone to 15 m. (Sears and Wilce 1973) MASS, HDSM.

Pseudolithoderma subextensum (Waern) S. Lund – perennial crustose species in sublittoral. (Sears and Wilce 1975) MASS, HDSM.

Sorapion kjellmanii (Wille) Rosenv. – perennial crustose species on sublittoral hard substrates. MASS, HDSM.

Sorapion simulans Kuck. – perennial crustose species on stones in sublittoral zone. Possibly synonymous with *S. kjellmanii* (Sears 2002). MASS, HDSM.

Symphyocarpus strangulans Rosenv. – perennial crustose species on stones and shells in shallow bays. West Chop, 1968, *J. R. Sears,* MASS.

MYRIONEMATACEAE

Myrionema balticum (Reinke) Foslie – probable annual; attached to old blades of *Laminaria saccharina* in Sep–Dec at West Chop at 5–15 m; first record south of Cape Cod. (Sears 1971) HDSM.

Myrionema strangulans Grev. – annual from midwinter to autumn; found in low intertidal tide pools and shallow sublittoral zone. Gay Head, Aug 1895, *R. A. Esten,* SPWH; Gay Head, 25 Jul 1947, *E. T. Moul,* SPWH; MASS.

RALFSIACEAE

Ralfsia fungiformis (Gunnerus) Setch. & N. L. Gardner – perennial in tide pools and low littoral. Likely the southernmost record of this species in the western North Atlantic Ocean. MASS.

ACROTHRICACEAE

Acrothrix gracilis Kylin – present in quiet warm bays on solid substrates; summer annual. RT/PHA, MASS, HDSM.

CHORDARIACEAE

Chordaria flagelliformis (O. F. Müll.) C. Agardh – attached to solid substrates in lower intertidal zone and below; year-round but more conspicuous in spring and summer. RT/PHA, MASS.

Eudesme virescens (Carmich. *ex* Berk.) J. Agardh – annual in spring and summer; found at or just below MLW to 10 m. RT/PHA, HDSM.

Sphaerotrichia divaricata (C. Agardh) Kylin – summer annual; usually attached to various coarse seaweeds near or below MLW, especially in quiet coves and bays. RT/PHA.

CORYNOPHLAEACEAE

Leathesia difformis (L.) Aresch. – common epiphyte on coarse algae in late spring to summer in the littoral to shallow sublittoral. Noman's Land, 16 Aug 1932, *H. T. Croasdale,* SPWH.

ELACHISTACEAE

Elachista fucicola (Velley) Aresch. – common year-round on open coasts and in estuaries within the intertidal zone and below; often attached to *Fucus* spp. or *Ascophylum nodosum.* Noman's Land, 7 Aug 1931, *H. T. Croasdale,* SPWH; MASS.

Leptonematella fasciculata (Reinke) P. C. Silva – common epiphyte of *Laminaria* spp., *Saccorhiza dermatodea,* and *Polysiphonia* spp. in sublittoral to 20 m. MASS, HDSM.

SPERMATOCHNACEAE

Stilophora tenella (Esper) P. C. Silva – common in quiet bays with muddy bottoms; epiphytic on eelgrass and sometimes free floating. MASS.

TILOPTERIDACEAE

Haplospora globosa Kjellm. – winter-spring annual; common on shells and small stones in protected areas, to 15 m. This cold boreal/arctic species occurs further south along the western shore of Long Island Sound, likely the southernmost extent of its western North Atlantic occurrence. (Collins 1899) MASS, HDSM.

Tilopteris mertensii (Turner *in* Sm.) Kütz. – winter-spring annual usually on shells and small stones in semiprotected bays. West Chop, 8 Jun 1967, *J. R. Sears,* SPWH; MASS, HDSM.

CLADOSTEPHACEAE

Cladostephus spongiosus (Huds.) C. Agardh – perennial; present in sandy areas attached to rocks, jetties; from MLW to 10 m. RT/PHA, HDSM.

SPHACELARIACEAE

Sphacelaria cirrosa (Roth) C. Agardh – common perennial alga on any solid substrate; also a common epiphyte on fucoid algae. RT/PHA, MASS, HDSM.

Sphacelaria fusca (Huds.) Gray – perennial; found on stones on the open coast. MASS.

Sphacelaria plumigera Holmes *ex* Hauck – perennial; found on small stones or shells from sublittoral to 15 m. MASS, HDSM.

Sphacelaria racemosa Grev. – perennial; found in tide pools and shallow sublittoral. MASS, HDSM.

Sphacelaria radicans (Dillwyn) Harv. – perennial; common in tide pools on sand-covered rocks to 10–12 m. MASS, HDSM.

DICTYOSIPHONACEAE

Dictyosiphon foeniculaceus (Huds.) Grev. – summer annual; found in shallow sublittoral pools; often epiphytic on *Chordaria.* RT/PHA.

GIRAUDIACEAE

Giraudia sphacelaroides Derbés & Solier *in* Castagne – rare; most often found in autumn. Reported in Vineyard Haven in 1892 (Schuh 1900); record needs confirmation.

MYRIOTRICHIACEAE

Myriotrichia clavaeformis Harv. – uncommon; epiphytic on other algae. Gay Head specimen in Jul, no other data available, SPWH.

POGOTRICHACEAE

Pogotrichum filiforme Reinke – rare annual; grows on solid substrate or as an epiphyte in shallow sublittoral in late winter and spring. Reported at Oak Bluffs in Jan 1895 (Schuh 1900). MASS, HDSM.

PUNCTARIACEAE

Asperococcus fistulosus (Huds.) Hook. – late winter to summer annual on solid substrates in wave protected low littoral to shallow sublittoral areas. MASS, HDSM.

Punctaria latifolia Grev. – seasonal annual present in the shallow sublittoral. MASS, HDSM.

Punctaria plantaginea (Roth) Grev. – annual; common in spring and early summer; present in tide pools and upper sublittoral. This species may be a cold season form of *P. latifolia* (Pedersen 1984). HDSM, MASS.

Punctaria tenuissima (C. Agardh) Grev. – seasonal annual; most common in spring and summer; usually in estuaries. RT/PHA, MASS, HDSM.

Rhadinocladia farlowii Schuh – uncommon epiphyte of *Zostera marina* and *Chorda filum* that reproduces in late summer. Vineyard Haven, 26 Aug 1904, *B. M. Davis,* SPWH.

STRIARIACEAE

Stictyosiphon tortilis (Rupr.) Reinke – uncommon annual at Martha's Vineyard, but along with *Pilayella litoralis,* the most common of brown algae in northern waters; occurs in winter and spring. *Stictyosiphon tortilis* is at the southern limit of its occurrence in the western North Atlantic. MASS.

Striaria attenuata (Grev.) Grev. – uncommon annual in spring; on shells and stones. MASS, HDSM.

SCYTOSIPHONACEAE

Petalonia fascia (O. F. Müll.) Kuntze – annual in winter and spring; occurs in tide pools attached to rocks and most solid substrates. RT/PHA.

Petalonia zosterifolia (Reinke) Kuntze – uncommon epiphyte, especially on *Zostera marina* blades in estuaries and shallow bays, but also on rocks of the open coast; from spring to early winter. Noman's Land, 30 Jan 1967, *J. R. Conway,* SPWH; HDSM.

Scytosiphon dotyi M. J. Wynne – aseasonal annual found most often from winter to early summer in tide pools to shallow sublittoral. RT/PHA.

Scytosiphon lomentaria (Lyngb.) Link – annual in winter and spring; present in tide pools throughout the mid- and low shore. RT/PHA.

Petalonia/Scytosiphon – Note: both "*Ralfsia borneti*" and "*Ralfsia clavata*" have been recorded from Martha's Vineyard; both are now considered reproductive stages of either or both of the indicated two genera. MASS, HDSM.

ARTHROCLADIACEAE

Arthrocladia villosa (Huds.) Duby – summer annual; attached to small pebbles in muddy or sandy bottoms areas in protected bays. (Collins 1899; Sears 1971).

DESMARESTIACEAE

Desmarestia aculeata (L.) J. V. Lamour. – perennial; present in spring and summer; occurs from 5–20+ m. RT/PHA, MASS, HDSM.

Desmarestia viridis (O. F. Müll.) J. V. Lamour. – annual in winter and spring; attached to rocks from MLW to 20+ m. RT/PHA, MASS, HDSM.

HALOSYPHONACEAE

Halosiphon tomentosus (Lyngb.) Jaasund – common on rocks from spring to autumn; on open coasts and in estuaries from the lower littoral to 12 m. See Peters (1998) for taxonomic change from *Chorda tomentosa* and the suggested family relationships of this taxon. Gay Head, 18 Jun 1963, no collector given, SPWH; MASS, HDSM.

CHORDACEAE

Chorda filum (L.) Stackh. – common annual in summer and autumn; present in sheltered pools from MLW to 10 m. RT/PHA, MASS, HDSM.

LAMINARIACEAE

Laminaria digitata (Huds.) J. V. Lamour. – attached to rocks from below MLW to 10 m. RT/PHA, MASS, HDSM.

Laminaria saccharina (L.) J. V. Lamour. – perennial; common in deep tide pools and sublittoral to 30 m. RT/PHA, MASS, HDSM.

FUCACEAE

Ascophyllum nodosum (L.) Le Jol. – perennial in wave-protected areas; often abundant in mid- to low intertidal zone; may live 20 years or more. RT/PHA.

Fucus evanescens C. Agardh – present year-round on rocks in both sheltered areas and open coasts, in the intertidal zone and just below MLW. Gay Head, 17 Jul 1958, *G. B. B.*, SPWH; MASS.

Fucus spiralis L. – moderately common in upper intertidal zone; perennial; present in salt marshes, tidal creeks, ditch banks, etc. RT/PHA.

Fucus vesiculosus L. – perennial; common; tolerant of wave exposure; present in mid- to low intertidal zone in bays, estuaries, and salt marshes. RT/PHA.

SARGASSACEAE

Sargassum filipendula C. Agardh – common; perennial in shallow, warm, sheltered areas from just below MLW to at least 5 m. RT/PHA, MASS, HDSM.

Sargassum fluitans (Børgesen) Børgesen – pelagic species of the Gulf Stream, not native to the Massachusetts coast or to Martha's Vineyard, but sometimes in drift after storms. Gay Head, 29 Jul 1951, *A. J. Bernatowicz*, SPWH.

RHODOPHYTA

BANGIOPHYCEAE

PORPHYRIDIACEAE

Stylonema alsidii (Zanardini) K. M. Drew – uncommon; on shells or stones, or epiphytic on other algae. MASS, HDSM.

ERYTHROTRICHIACEAE

Erythrotrichia carnea (Dillwyn) J. Agardh – aseasonal annual present on shells or stones, or epiphytic on other algae in quiet waters from mid-littoral to 15 m. MASS.

Porphyropsis coccinea (J. Agardh *ex* Aresch.) Rosenv. – annual in spring and summer; epiphytic on other algal species from sublittoral to 15 m. MASS, HDSM.

BANGIACEAE

Porphyra leucosticta Thur. *in* Le Jol. – annual epiphyte in winter and spring in low littoral to about 10 m. MASS, HDSM.

Porphyra umbilicalis (L.) Kütz. – aseasonal annual in the low littoral; reproductive year-round; present on rocks or an epiphyte; sometimes abundant. MASS.

FLORIDEOPHYCEAE

ACROCHAETIACEAE

Audouinella dasyae (Collins) Woelk. – uncommon annual in shallow sublittoral; reproductive in Feb. (Sears 1971).

Audouinella efflorescens (J. Agardh) Papenf. – uncommon annual present in autumn and early winter. (Sears 1971).

Audouinella endozoica (Darbishire) P. S. Dixon – uncommon sublittoral species at 18–20 m, perhaps also throughout the upper sublittoral. (Sears 1971).

PALMARIACEAE

Palmaria palmata (L.) Kuntze – perennial; present in tide pools to 20+ m; on rocks, or as an epiphyte. RT/PHA, MASS, HDSM.

RHODOPHYSEMATACEAE

Rhodophysema elegans (P. Crouan & H. Crouan *ex* J. Agardh) P. S. Dixon – perennial crust on stones, shells, glass, etc. from sublittoral to ca. 20 m. MASS, HDSM.

Rhodophysema georgii Batters – annual crust on eelgrass within shallow sublittoral during summer. MASS, HDSM.

LIAGORACEAE

Nemalion helminthoides (Velley *in* With.) Batters – sporadic annual; present from summer to autumn on rocks in exposed locations within the lower intertidal. RT/PHA.

GALAXAURACEAE

Scinaia furcellata (Turner) J. Agardh – uncommon summer annual from MLW to 10 m on rocks in non-wave-exposed waters. RT/PHA.

BONNEMAISONIACEAE

Bonnemaisonia hamifera (Hariot) Okamura – most common as a summer annual from below MLW to at least 15 m on rocks or epiphytic. The putative diploid phase of this species known as *Trailliella intricata* (J. Agardh) Batters is also present in our area. RT/PHA, MASS, HDSM.

GELIDIACEAE

Gelidium pusillum (Stackh.) Le Jol. – perennial; mid- to low intertidal zone on rocks and on mud at the edges of salt marshes. Gay Head, 1912, *T. M. Douthart,* SPWH.

AHNFELTIACEAE

Ahnfeltia plicata (Huds.) Fr. – perennial, moderately common; present well below MLW. Gay Head, 17 Aug 1903, *B. M. Davis,* SPWH; Noman's Land, 16 Aug 1932, *H. T. Croasdale,* SPWH; RT/PHA, MASS, HDSM.

GRACILARIACEAE

Gracilaria tikvahiae McLachlan – perennial in sheltered areas with warm quiet water from MLW to 5 m; very common; includes *G. foliifera* (Forsskål) Børgesen and *G. verrucosa* (Huds.) Papenfuss (Taylor 1962). RT/PHA, MASS.

HILDENBRANDIACEAE

Hildenbrandia rubra (Sommerf.) Menegh. – perennial crust species; from low littoral to 20 m. Includes *H. prototypes* Nardo (Taylor 1962). MASS, HDSM.

CORALLINACEAE

Corallina officinalis L. – perennial; on open coasts and estuaries on rocks and other solid substrates, from low intertidal tidepools to 20 m. Gay Head, 17 Aug 1903, *B. M. Davis,* SPWH; Noman's Land, 7 Aug 1931, *H. T. Croasdale,* SPWH; MASS, HDSM.

Melobesia membranacea (Esper.) J. V. Lamour. – annual, especially midwinter to autumn; on open coasts and estuaries; usually an epiphyte on red algae and eelgrass. Gay Head, 17 Aug 1903, *B. M. Davis,* SPWH.

Phymatolithon laevigatum (Foslie) Foslie – perennial coralline crust species; found on rocks and shells in tide pools and the upper sublittoral. MASS.

CYSTOCLONIACEAE

Cystoclonium purpureum (Huds.) Batters – perennial in quiet water areas near MLW to 10–15 m; on rocks or an epiphyte; common in summer. RT/PHA, HDSM.

DUMONTIACEAE

Dumontia contorta (S. G. Gmel.) Rupr. – annual in late winter and spring, especially in tide pools and below MLW to 7 m; often abundant in spring. RT/PHA.

GIGARTINACEAE

Chondrus crispus Stackh. – perennial in low littoral and sublittoral to 20 m; abundant; often present as large continuous populations on shelf rocks in exposed coastal areas. RT/PHA, MASS, HDSM.

GLOIOSIPHONIACEAE

Gloiosiphonia capillaris (Huds.) Berk. – sporadically present in tide pools, low littoral and sublittoral to 4 m on rocks and shells; in spring to summer. *Cruoriopsis* sp., possibly *C. ensis* Jao, believed to be the tetrasporic crust phase of this species, is also present at Martha's Vineyard. West Chop, 24 May 1969, *J. R. Sears*, SPWH; RT/PHA, MASS, HDSM.

Plagiospora gracilis Kuck. – possibly perennial crustose species of the mid- to deep sublittoral to 20 m; only the tetrasporophyte phase is known. MASS.

HAEMESCHARIACEAE

Haemescharia hennedyi (Harv.) R. T. Wilce & Maggs – this well-known European species was found year-round at the West Chop, Devil's Bridge and Southwest Shoal sites by J. R. Sears in 1967–68. "*Petrocelis* sp. a" in Sears 1971; current determination by R. T. Wilce.

HYPNEACEAE

Hypnea musciformis (Wulfen *in* Jacq.) J. V. Lamour. – usually an epiphyte on coarse algae to 5 m. Gay Head, 1884, *J. E. Humphrey*, FH; Edgartown, Sep 1883, *F. S. Collins*, FH.

KALLYMENIACEAE

Callophyllis cristata (C. Agardh) Kütz. – perennial in sublittoral zone to ca. 30 m on open coasts or estuaries; on rocks, invertebrates or epiphytic on coarser algae. Gay Head, 16 Aug 1932, *H. T. Croasdale*, SPWH. (Sears 1971).

NEMASTOMATACEAE

Tsengia bairdii (Farl.) K. C. Fan & Y. P. Fan – rarely collected; only on sublittoral hard substrates; at Gay Head once before 1880 and twice in 1940 (Kingsbury 1969), and also in 1960 and 1961 (SPWH catalog). MASS, HDSM.

PEYSSONNELIACEAE

Peyssonnelia dubyi P. Crouan & H. Crouan – perennial crust species on shells and stones from 3–20 m. MASS, HDSM.

PHYLLOPHORACEAE

Coccotylus truncatus (Pallas) M. J. Wynne & J. M. Heine – perennial on rocks, shells, or other hard substrates to 40 m. MASS, HDSM.

Phyllophora pseudoceranoides (S. G. Gmel.) Newroth & A. R. A. Taylor – perennial in shallow sublittoral to 20 m; common; includes *P. membranifolia* (Taylor 1962). RT/PHA, MASS, HDSM.

POLYIDACEAE

Polyides rotundus (Huds.) Greville – perennial; common in low tide pools with sandy bottoms, and in the upper sublittoral; most commonly attached to hard substrates submerged in the sand. RT/PHA, MASS, HDSM.

SOLIERACEAE

Agardhiella subulata (C. Agardh) Kraft & M. J. Wynne – perennial in quiet water just below MLW to 10 m; common but observed mostly in summer; near the northern limit of the species' range at Martha's Vineyard. RT/PHA, MASS, HDSM.

CHAMPIACEAE

Champia parvula (C. Agardh) Harv. – annual; abundant in summer in protected pools and bays from the shallow sublittoral to 12 m; near the northern limit of the species' range at Martha's Vineyard. RT/PHA, MASS, HDSM.

LOMENTARIACEAE

Lomentaria baileyana (Harv.) Farl. – abundant summer annual in tide pools at and below MLW to 8 m. RT/PHA, MASS, HDSM.

Lomentaria clavellosa (Turner) Gaillon – European species first reported in Massachusetts in 1963 (Wilce and Lee 1964); present on rocks below MLW to 12 m. RT/PHA, MASS, HDSM.

Lomentaria orcadensis (Harv.) Collins *ex* W. R. Taylor – perennial; abundant in summer in pools and shallow sublittoral to 30 m. RT/PHA, MASS, HDSM.

CERAMIACEAE

Aglaothamnion roseum (Roth) Maggs & L'Hardy-Halos – summer annual, usually an epiphyte in the low littoral and in tide pools to the upper sublittoral. MASS, HDSM.

Anotrichium tenue (C. Agardh) Nägeli – summer annual in the shallow sublittoral, primarily south of Cape Cod; likely near the northern limit of its distribution in the western North Atlantic Ocean. MASS.

Antithamnion cruciatum (C. Agardh) Nägeli – aseasonal annual or pseudoperennial epiphyte or on stones in the sublittoral to 20 m. MASS, HDSM.

Callithamnion corymbosum (Sm.) Lyngb. – summer annual; common; virtually always growing on the surface of another alga or on eelgrass from MLW to 10 m. RT/PHA, MASS.

Callithamnion tetragonum (With.) S. F. Gray – summer annual from MLW to 10 m; common; on rocks and sometimes epiphytic on other algal species. RT/PHA, MASS, HDSM.

Ceramium cimbricum H. E. Petersen *in* Rosenv. – present in the sublittoral zone of sheltered bays and estuaries, usually epiphytic on eelgrass or other algae; includes *C. fastigiatum* (Roth) Harv. (Taylor 1962). Vineyard Haven, Aug and Sep 1879, *W. R. Dudley,* SPWH.

Ceramium deslongchampii Chauv. *ex* Duby – annual from late spring to autumn in the lower intertidal zone. RT/PHA.

Ceramium diaphanum (Lightf.) Roth – annual from late spring to autumn. RT/PHA.

Ceramium strictum Harv. – perennial, but common only from spring to autumn in sheltered bays and estuaries; in the shallow sublittoral, on rocks or shells, or epiphytic on eelgrass or other algae. South Beach, 21 Aug 1879, *W. R. Dudley,* SPWH. RT/PHA.

Ceramium virgatum Roth – Annual from late spring to autumn; attached to solid substrates or an epiphyte; includes *C. nodulosum* (Lightf.) Ducluze (Sears 2002), *C. rubrum* (Huds.) C. Agardh, and *C. rubriforme* Kylin; see Maggs et al. 2002. RT/PHA, MASS, HDSM.

Griffithsia globulifera Harv. *ex* Kütz. – common in summer; present on rocks, shells below MLW. RT/PHA.

Pleonosporium borreri (Sm.) Nägeli *ex* Hauck – summer annual on shells, stones, or an epiphyte in sublittoral to 5 m. Gay Head, undated, collector unknown, FH; Cape Poge, Sep 1881, collector unknown, FH.

Plumeria plumosa (Huds.) Kuntze – perennial; present in warmer waters in sublittoral on stones or an epiphyte, to 8 m. RT/PHA, MASS, HDSM.

Pterothamnion plumula (J. Ellis) Nägeli – perennial in warmer bays and estuaries in shallow sublittoral to 12 m on rocks, wood, even attached to detrital fragments in the bottom mud. West Chop, 29 May 1969, *J. R. Sears,* SPWH; MASS, HDSM.

Ptilota serrata Kütz. – perennial; occurs in sublittoral to 40 m; uncommon in our area, probably at or near the southern extent of its range along the western North Atlantic coast. RT/PHA.

Scagelia pylaisaei (Mont.) M. J. Wynne – perennial epiphyte or on rocks or shells in sublittoral to 40 m. MASS, HDSM.

Seirospora interrupta (Sm.) F. Schmitz – perennial; present in sublittoral on eelgrass, stones, shells, to 8 m. RT/PHA, MASS, HDSM.

Spermothamnion repens (Dillwyn) Rosenv. – annual; abundant in summer; from MLW to at least 10 m. RT/PHA, MASS, HDSM.

Spyridia filamentosa (Wulfen) Harv. *in* Hook. – annual; present mostly in spring and summer in warmer waters; near its northern limit of occurrence along the western North Atlantic coast at Martha's Vineyard. RT/PHA, MASS, HDSM.

DASYACEAE

Dasya baillouviana (S. G. Gmel.) Mont. – late summer annual in quiet waters to 15 m; the holdfast and portions of the main axes of this species perennate. RT/PHA, MASS, HDSM.

DELESSERIACEAE

Grinnellia americana (C. Agardh) Harv. – mostly present in late summer in shallow warm water to 10 m; basal portions of the thallus perennate. One of the relatively few endemic species that occur in the western North Atlantic. RT/PHA, MASS, HDSM.

Phycodrys rubens Batters – perennial; found in deep cool water to 40 m; common here but more so north of Cape Cod. RT/PHA, MASS, HDSM.

RHODOMELACEAE

Chondria baileyana (Mont.) Harv. – summer annual; common; present on stones and other solid substrates just below MLW in quiet water. RT/PHA.

Chondria dasyphylla (Woodw.) C. Agardh – summer annual, but holdfast perennates; present from MLW to 5 m; includes *C. sedifolia* Harv. (Sears 2002). RT/PHA, MASS, HDSM.

Polysiphonia denudata (Dillwyn) Grev. *ex* Harv. *in* Hook. – perennial; common in littoral and sublittoral in sandy areas of warm bays on solid substrates; present in winter and early spring. RT/PHA, MASS, HDSM.

Polysiphonia elongata (Huds.) Spreng. – present from MLW to at least 10 m along semisheltered coasts, on a solid substratum. RT/PHA, MASS, HDSM.

Polysiphonia fibrillosa (Dillwyn) Spreng. – primarily present in summer. RT/PHA, MASS, HDSM.

Polysiphonia flexicaulis (Harv.) Collins – summer annual. RT/PHA.

Polysiphonia fucoides (Huds.) Grev. – common pseudoperennial in sublittoral from 5–15 m on shells and stones. Gay Head, 26 Jul 1944, *W. R. Taylor*, FH; Gay Head, Sep 1881 and in 1884, *J. E. Humphrey*, FH; RT/PHA, HDSM.

Polysiphonia harveyi Bailey – summer annual on rocks. RT/PHA, MASS.

Polysiphonia nigra (Huds.) Batters – summer annual attached to solid substrates. RT/PHA, MASS, HDSM.

Polysiphonia stricta (Dillwyn) Grev. – winter annual. RT/PHA, MASS, HDSM.

Polysiphonia subtilissima Mont. – annual; present in estuaries and salt marshes, brackish to a nearly fresh water environment. RT/PHA.

Rhodomela confervoides (Huds.) P. C. Silva – common; perennial; present on stones in low littoral tide pool to 15 m; in estuaries and along open coasts; includes *Rhodomela virgata* Kjellm. (Sears 2002). RT/PHA, MASS, HDSM.

Rhodomela lycopodioides (L.) C. Agardh – uncommon perennial of the sublittoral; likely a seasonal growth form of *R. confervoides*. RT/PHA, MASS.

APPENDIX II

MARINE ALGAE BELIEVED TO OCCUR AT MARTHA'S VINEYARD

CHLOROPHYTA

Ulothrix flacca (Dillwyn) Thur. *in* Le Jol. – SPWH specimens from Woods Hole.

Monostroma grevillei (Thur.) Wittr. – SPWH specimen from Cuttyhunk Island.

Monostroma oxyspermum (Kütz.) Doty – found in Falmouth.

Percursaria percursa (C. Agardh) Rosenv. – SPWH specimen from West Falmouth, Jul.

Capsosiphon fulvescens (C. Agardh) W. A. Setch. & N. L. Gardner – SPWH specimen from Woods Hole, 31 Jul.

Enteromorpha flexuosa (Wulfen *ex* Roth) J. Agardh – SPWH specimens from Woods Hole, Jul–Sep.

Enteromorpha prolifera (O. F. Müll.) J. Agardh – SPWH specimens from Woods Hole.

Acrochaete repens N. Pringsh. – common at Woods Hole (Collins 1906).

Codiolum gregarium – SPWH specimens from Woods Hole, 22 Jul; this "species" is recognized as the putative sporophyte phase of one or more filamentous green algae.

Cladophora sericea (Huds.) Kütz. – SPWH specimens from Woods Hole.

Rhizoclonium riparium (Roth) Harv. – SPWH specimens from Woods Hole.

Rhizoclonium tortuosum (Dillwyn) Kütz. – SPWH specimens from Penikese Island.

PHAEOPHYTA

Streblonema parasiticum (Sauv.) Levring – known only as an endophyte of *Cystoclonium purpureum*; common in Woods Hole (Collins 1906).

Cladosiphon zosterae (J. Agardh) Kylin – SPWH specimens from Woods Hole.

Alaria esculenta (L.) Grev. – SPWH specimens from Woods Hole.

RHODOPHYTA

Bangia atropurpurea (Roth) C. Agardh – intertidal zone near Woods Hole.

Audouinella secundata (Lyngb.) P. S. Dixon – SPWH specimens from Woods Hole.

Audouinella virgatula (Harv.) P. S. Dixon – SPWH specimens from Woods Hole.

Lithophyllum orbiculatum (Foslie) Foslie – SPWH specimens from Woods Hole and Tarpaulin Cove, Naushon Island.

Phymatolithon lenormandii (Aresch. *in* J. Agardh) W. H. Adey – intertidal zone near Woods Hole.

Pneophyllum fragile Kütz. – SPWH specimens from Woods Hole.

Rhodymenia delicatula P. J. L. Dang – present at Woods Hole (Sears 2002).

Ceramium elegans (Roth) Ducluzea – SPWH specimens from Waquoit Bay.

Polysiphonia lanosa (L.) Tandy – occurs as an epiphyte on *Ascophyllum nodosum*; moderately common; SPWH specimens from Woods Hole.

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MOLECULAR SYSTEMATICS OF THE EASTERN NORTH AMERICAN *SILENE* (CARYOPHYLLACEAE): EVIDENCE FROM NUCLEAR ITS AND CHLOROPLAST *trn*L INTRON SEQUENCES

J. GORDON BURLEIGH[1] AND TIMOTHY P. HOLTSFORD

Division of Biological Sciences, University of Missouri,
105 Tucker Hall, Columbia, MO 65211
[1]Current Address: Department of Botany, Iowa State University,
353 Bessey Hall, Ames, IA 50011
e-mail: gburleig@iastate.edu; holtsfordt@missouri.edu

ABSTRACT. This study examines the phylogenetic relationships of the nine *Silene* species endemic to eastern North America using nuclear ITS and chloroplast *trn*L intron sequence data. The ITS region is highly variable among taxa and is more phylogenetically informative than the less variable *trn*L intron DNA data. The ITS sequences indicate that the eastern North American taxa are not monophyletic, but instead occur in two clades that are nested within a clade including western species. *Silene* section *Occidentales* is also not monophyletic. The diverse floral morphologies of the eastern North American *Silene* appear to be evolutionarily labile. Neither floral morphology nor pollinator syndromes are conserved within clades. Both ITS and *trn*L intron data indicate that the hummingbird-pollinated taxa are not monophyletic. There is weak evidence for differences in the nuclear and chloroplast phylogenies that may be a result of reticulate evolution.

Key Words: Caryophyllaceae, ITS, *trn*L intron, *Silene*

With over 700 taxa, *Silene* is the largest genus within the Caryophyllaceae (Bittrich 1993; Greuter 1995). Though diversity is greatest in the Mediterranean region (Greuter 1995), approximately 50 taxa are endemic to North America, and nine taxa are found exclusively east of the Rocky Mountains (Hitchcock and Maguire 1947). The nine taxa endemic to eastern North America are presumably closely related, yet they are morphologically diverse (Hitchcock and Maguire 1947). The flowers of the nine taxa exhibit a large range of shapes, sizes, and colors (Table 1). Four of these taxa are among the few hummingbird-pollinated species endemic to eastern North America (Austin 1975). Though the characteristics of the eastern North American *Silene* are well described, their evolutionary relationships are unclear. This study uses DNA sequence analysis to examine the relationships within

Table 1. *Silene* taxa used in this study using the sectional classification of Chowdhuri (1957).

Species	Section	Floral Color
Eastern North American taxa		
S. caroliniana Walter		
subsp. *caroliniana* Walter	*Occidentales*	pink
subsp. *pensylvanica* R. T. Clausen	*Occidentales*	pink
subsp. *wherryi* (Small) R. T. Clausen	*Occidentales*	pink
S. nivea (Nutt.) Muhl. *ex* DC.	*Siphonomorpha*	white
S. ovata Pursh	*Paniculatae*	white
S. polypetala (Walter) Fernald & B. G. Schub.	*Occidentales*	pink
S. regia Sims	*Occidentales*	red
S. rotundifolia Nutt.	*Occidentales*	red
S. stellata Aiton	*Siphonomorpha*	white
S. subciliata B. L. Rob.	*Occidentales*	red
S. virginica L.	*Occidentales*	red
Western North American taxa		
S. californica Durand	*Occidentales*	red
S. lemmonii S. Watson	*Siphonomorpha*	white
S. petersonii Maguire	*Occidentales*	pink
Other taxa		
S. acaulis (L.) Jacq.		
subsp. *subacaulescens* (F. N. Williams) Hulten	*Nanosilene*	pink
S. furcata Raf.	*Physolychnis*	white
S. viscosa Pers.	*Chloranthae*	white

eastern North American *Silene* and surveys the evolution of floral diversity in these taxa.

Studies of *Silene* taxonomy and systematics are complicated by polyploidy and interspecific hybridization. The initial classifications of *Silene* focused on European and Asian taxa. Hitchcock and Maguire's (1947) study was the first thorough description and classification of the North American *Silene*. They applied Williams' (1896) subgeneric classification to the North American species, grouping the eastern North American *S. stellata* and *S. ovata* in subgenus *Eusilene* and the other seven taxa in subgenus *Melandryum*. Chowdhuri's (1957) taxonomic description of the entire genus divided *Silene* into 44 sections. He placed the white-flowered eastern North American taxon *S. ovata* alone among

North American taxa in section *Paniculatae,* subsection *Laciniatae.* The red-flowered, hummingbird-pollinated *S. regia, S. rotundifolia, S. subciliata,* and *S. virginica* were grouped in section *Occidentales,* and the white-flowered *S. nivea* and *S. stellata* were grouped in section *Siphonomorpha* (Table 1). Though not classified by Chowdhuri (1957), the pink-flowered *S. caroliniana* and *S. polypetala* fit in section *Occidentales* based on their ciliate claws and pilose filaments (pers. obs.).

Cytological studies and crossing experiments indicate substantial genetic separation between North American and European *Silene.* Kruckeberg (1960) observed that most North American taxa, including all seven eastern North American species he examined, have $2n = 48$ chromosomes, while many Eurasian species have $2n = 24$ chromosomes. Heaslip's (1950, 1951) crossing experiments found that crosses between the four North American and the European *S. latifolia* (Mill.) Britton & Rendle (*S. alba* Mill.) taxa produced no seed, but crosses between four North American taxa produced seed and sterile offspring. Kruckeberg's crosses between North American and European taxa also produced no progeny, and his extensive crosses among western (1961) and eastern (1963) North American *Silene* yielded mostly sterile hybrids. In one exception, crosses between the eastern North American taxa *S. virginica* and *S. caroliniana* produced fertile hybrids (Kruckeberg 1963). These hybrids are also noted to occur naturally (Mitchell and Uttal 1969; Steyermark 1963).

Recent molecular studies have examined *Silene* systematics at the generic (Desfeux and Lejeune 1996; Oxelman et al. 1997; Oxelman and Lidén 1995), sectional (Oxelman 1996), and species (Vellekoop et al. 1996) levels. However, these studies include few, if any, North American taxa. Oxelman and Lidén (1995) found that, based on nrDNA sequences, the eastern North American *S. rotundifolia* and the western North American *S. petersonii* from section *Occidentales* form a well supported clade among the sections *Physolychnis* and *Odontopetalae.*

This study focuses on the relationships within the eastern North American *Silene* using both nuclear and chloroplast DNA sequence data. Since previously described chromosome number, crossing, and molecular data suggest that many endemic North American *Silene* may be monophyletic, and the nine eastern North American taxa are geographically separated from the majority of North American taxa, the study examines if the eastern

North American taxa are monophyletic. Next, it addresses the monophyly of the sectional classifications, hummingbird pollination, and floral color of the eastern North American taxa. Finally, it will compare chloroplast and nuclear phylogenies for evidence of hybridization among taxa.

MATERIALS AND METHODS

Plant tissue was obtained from all nine of the *Silene* taxa endemic to eastern North America (east of the Rocky Mountains) including all three subspecies of *S. caroliniana* (Clausen 1939; Wilbur 1970; Table 2). Tissue from western North American taxa *S. californica,* section *Occidentales,* and *S. lemmonii,* section *Siphonomorpha,* was sampled from herbarium specimens. The trees were rooted with *S. acaulis,* a circumpolar taxon in section *Nanosilene* (Chowdhuri 1957). There are no endemic North American taxa in *Nanosilene* (Chowdhuri 1957), and previous molecular studies indicate that *S. acaulis* is a distant sister to the endemic North American taxa (Oxelman and Lidén 1995). Furthermore, ITS and *trn*L intron alignments are uncertain when including outgroups outside *Silene* (pers. obs.). For the ITS tree, we also included sequences from *S. viscosa* and *S. furcata,* European taxa that appear to be sister to the North American taxa (Oxelman and Lidén 1995), as outgroups. Six ITS sequences from GenBank, including all previously sequenced North American taxa and the two European sister taxa (Oxelman and Lidén 1995), were included in the phylogenetic analysis (Table 2).

DNA was extracted using the DNeasy plant mini kit (Qiagen Inc., La Jolla, CA). The *trn*L intron was amplified with universal primers c and d (Taberlet et al. 1991). The DNA was amplified for 35 cycles of the polymerase chain reaction (1 min. at 94°C, 30 sec. at 58°C, and 1 min. at 72°C) in 50 μl reactions containing 5 μl 10× *Taq* polymerase reaction buffer (Promega, Madison, WI), 0.2 mM dNTPs, 0.6 μM each primer, and 0.5 units *Taq* polymerase. ITS was amplified with primers Fred and Barney (Buckler and Holtsford 1996), located in the 18S and 26S nrDNA genes respectively. Various PCR protocols were followed running from 35 to 40 cycles (1 min. at 94°C, 30 sec. at 54–58°C, and 1 min. at 72°C) containing 5 μl Promega 10× *Taq* polymerase reaction buffer, 6.0 mM $MgCl_2$ total, 0.2 mM dNTPs, 10% DMSO, 0.4 μM each primer, and 0.5 units *Taq* polymerase.

Table 2. Accession table of *Silene* taxa used in this study. Key to sources: GB = Göteborg University herbarium, MO = Missouri Botanic Garden herabarium, NLU = Northeast Louisiana University herbarium, UMO = University of Missouri herbarium, GP = Green Plant Market Nursery, JA = Antonovics, JB = Burleigh, LG = Galloway, MP = Puterbaugh. The "-" in the GenBank numbers signifies that the accession number beings with "AY1164-".

Species	Source; Origin (GenBank #)	ITS/*trn*L Clone #
S. acaulis subacaulescens	MP; no voucher; Park Co., Colo. (AY116473 / -82)	1 / 1
S. acaulis	GB; *Ox. 2243*; garden (X86860)	12 / –
S. californica	UMO; *Morris 336*; Jackson Co., Ore. (AY116483)	– / 2
S. caroliniana caroliniana	JA; no voucher; Aiken Co., S. C. (AY116474 / -86)	2 / 3
S. caroliniana pensylvanica	JA; no voucher; Franklin Co., N. C. (AY116484)	– / 4
S. caroliniana wherryi	JA; no voucher; Jessamine Co., Ky. (AY116481 / -85)	3 / 5
S. furcata	GB; *Ox. 1887*; Sweden (X86859)	13 / –
S. lemmonii	UMO; *Kenney 391*; Siskiyou Co., Calif. (AY116487)	– / 6
S. nivea	UMO; *Rickett*; Tippecanoe Co., Ind. (AY116488)	– / 7
S. ovata	MO; *Kral 59396*; Marengo Co., Ala. (AY116475 / -89)	4 / 8
S. petersonii	GB; *Ox. 2239*; garden (X86886)	14 / –
S. polypetala	GP; no voucher; garden (AY116480)	5 / –
S. polypetala	MO; *Mohr 4000*; Ala. (AY116490)	– / 9
S. regia	JB; no voucher; Dade Co., Mo. (AY116476)	6 / –
S. regia	JB; no voucher; Dade Co., Mo. (AY116495)	– / 10
S. regia	GB; no voucher, Benton Co., Ark. (X86885)	16 / –
S. rotundifolia	JA; no voucher; Dickenson Co., Va. (AY116477 / -91)	7 / 11
S. rotundifolia	GB; *Ox. 2231*; garden (X86887)	15 / –
S. stellata	LG; no voucher; Giles Co., Va. (AY116477)	– / 12
S. stellata	JB; no voucher; Boone Co., Mo. (AY116472)	8 / –
S. subciliata	NLU; *79543*; Allen Par., La. (AY116471, -78 / -93)	9, 10 / 13
S. virginica	JB; no voucher; Wake Co., N. C. (AY116479 / -94)	11 / 14
S. viscosa	GB; *Ox. 2288*; Greece (X86831)	17 / –

All ITS and approximately half of the *trn*L intron PCR products were cut from a 1.5% low melt agarose gel and cleaned using a Geneclean III kit (Bio 101, La Jolla, CA). The remaining *trn*L intron PCR products were cleaned directly using the same kit. All clean PCR products were then ligated into a pGEM-T vector system (Promega, Madison, WI) and were cloned into DH5α competent cells using the protocol from the Promega pGEM-T vector system technical manual. Transformed cells were grown in LB medium for 18 to 24 hours at 37°C while shaking. The plasmid vectors were extracted from the cell culture using the Promega Wizard Plus miniprep kit (Promega, Madison, WI). Miniprep products were sequenced in both the forward and reverse direction at the University of Missouri DNA core facility using an ABI 377 automated sequencer.

Forward and reverse traces for each sequence were compared and edited in Seqman (DNASTAR, Madison, WI) to construct a consensus sequence. Both *trn*L intron and ITS sequences were aligned in Megalign (DNASTAR, Madison, WI), and the alignments were manually adjusted. The alignments are available on TreeBASE. A parsimony analysis of each dataset was performed using a branch and bound search retaining 100 parsimonious trees on PAUP* version 4.0b2 (Swofford 1999). Gaps were treated as a fifth base, and preliminary analysis determined that gap handling had no major effect on the overall topology of either ITS or the *trn*L intron trees. One hundred nonparametric bootstrap replicates of each dataset were generated using the same search options to test the support of the branches on each phylogeny. A Bayesian analysis was conducted on the ITS dataset using MrBayes version 2.01 (Huelsenbeck 2000). The Bayesian analysis used a general reversible model (REV; e.g., Yang 1994a) with rate variation among nucleotides following a discrete gamma distribution with four rate categories (Yang 1994b). Gaps were treated as missing data in the Bayesian analysis. The MCMC search consisted of four chains, three of which were heated to a temperature of 0.2 (Huelsenbeck 2000). The Markov chain was sampled once every 100 generations for 1,000,000 generations. The posterior probability was then calculated from a consensus tree of all trees sampled after the Markov chain reached stationarity (after 30,000 generations). The somewhat limited taxon overlap between the two datasets made a combined analysis problematic.

RESULTS

The ITS alignment contained 662 characters, 420 of which were constant and 119 of which were parsimony informative. The parsimony search found a single most parsimonious tree. The most parsimonious tree had a length of 354 steps, a consistency index of 0.825, and a retention index of 0.786 (Figure 1). There was little variation within taxa and no evidence of divergent ITS paralogs. The two sequences from *Silene acaulis, S. regia, S. rotundifolia,* and *S. subciliata* each formed clades with bootstrap support values of 99% or 100%. The two subspecies of *S. caroliniana* were in a strongly supported clade with *S. virginica* and *S. stellata* (Figure 1). *Silene caroliniana* subspecies are geographically separated, morphologically distinct (Clausen 1939), and naturally hybridize with *S. virginica* (Mitchell and Uttal 1969; Steyermark 1963) and *S. polypetala* (Georgia Department of Natural Resources, pers. comm). Therefore, the distance between the two *S. caroliniana* sequences may be the result of genetic divergence between the subspecies or hybridization.

The eastern North American *Silene* formed two distinct clades in the ITS phylogeny (Figure 1). The white-flowered *S. ovata* and the red-flowered, hummingbird-pollinated *S. regia* and *S. subciliata* formed one clade with bootstrap support of 79%. *Silene rotundifolia, S. polypetala, S. caroliniana, S. virginica,* and *S. stellata* composed the second clade with bootstrap support of 64%. Within this second clade there was a very strongly supported clade containing the white-flowered *S. stellata,* the pink-flowered *S. caroliniana,* and the red-flowered *S. virginica.* The western North American *S. petersonii* was basal to this second clade, though bootstrap support was lacking. The European *S. furcata* and *S. viscosa* and circumpolar *S. acaulis* were basal to all North American taxa (Figure 1).

The basal position of the western North American *S. petersonii* relative to one clade of eastern North American taxa indicates that the eastern North American taxa may not be monophyletic. A parsimony search using a constraint tree that enforces the monophyly of the eastern North American taxa found a most parsimonious tree with 357 steps. A nonparametric Templeton test (Templeton 1983) could not reject the null hypothesis that support for the most parsimonious tree is significantly better than the constraint tree (p-value = 0.083).

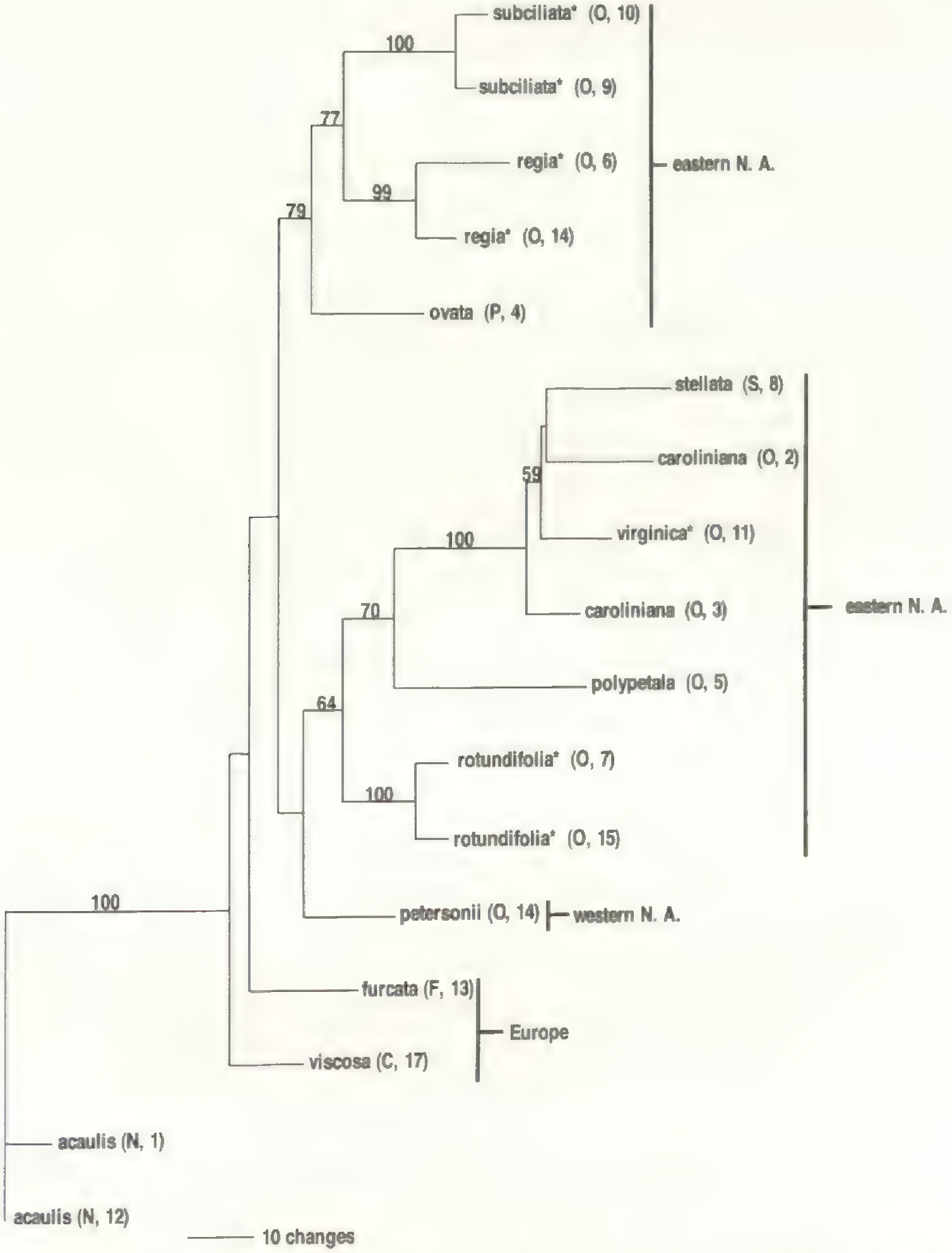

Figure 1. Phylogram of *Silene* taxa from a parsimony analysis of ITS sequences treating gaps as a fifth base. All bootstrap values above 50 are on the branches. The letters in parentheses represent the sectional classification of the taxa: C = *Chloranthae*, N = *Nanosilene*, O = *Occidentales*, P = *Paniculatae*, F = *Physolychnis*, S = *Siphonomorpha*. The numbers in parentheses are the sequence numbers from the accession table (Table 2). A star (*) by a taxon indicates hummingbird pollination.

The Bayesian and parsimony analysis of the ITS data support the same topology (Figures 1 and 2). In most cases, the posterior probabilities from the Bayesian analysis exceeded the nonparametric bootstrap values from the parsimony tree (Figures 1 and 2). The Bayesian analysis strongly supports the back branches of the phylogeny that are unsupported in the parsimony analysis. The Bayesian analysis supports the monophyly of the North American *Silene* with a posterior probability of 100%. It also supports the position of *S. petersonii* as sister to the clade of the eastern North American *S. stellata, S. virginica, S. caroliniana, S. polypetala,* and *S. rotundifolia* with a posterior probability of 95%. This further supports the hypothesis that the eastern North American *Silene* are not monophyletic.

There was little variation among *Silene* taxa in the *trn*L intron. Of the 676 characters in the alignment, 506 were constant and only 34 were parsimony informative. Therefore, the *trn*L intron did not resolve the relationships within the eastern North American *Silene* as well as ITS did (Figure 3). The branch and bound search retained two nearly identical most parsimonious trees, each with 191 total steps. The consistency index was 0.932 and the retention index was 0.787. The consensus tree supports the basal position of the western North American *S. californica* to the eastern North American taxa with a bootstrap value of 73%. The analysis also supports a clade of *S. carolinana, S. polypetala,* and *S. virginica* with bootstrap support of 71% (Figure 3). A clade with the white-flowered *S. nivea* and *S. stellata* and the red, hummingbird-pollinated *S. regia* has 62% bootstrap support (Figure 3).

The lack of resolution of the chloroplast *trn*L intron phylogeny makes it difficult to assess potential conflict between the nuclear and chloroplast phylogenies. Both phylogenies indicate a close relationship among *Silene caroliniana, S. polypetala, S. virginica,* and *S. stellata.* The position of *S. regia* is the most different in the ITS and *trn*L intron phylogenies (Figures 1, 2, and 3).

DISCUSSION

Though not conclusive, ITS evidence indicates that the eastern North American *Silene* are not monophyletic (Figures 1 and 2). The parsimony analysis lacks bootstrap support for the placement of the western North American *S. petersonii* in a clade among

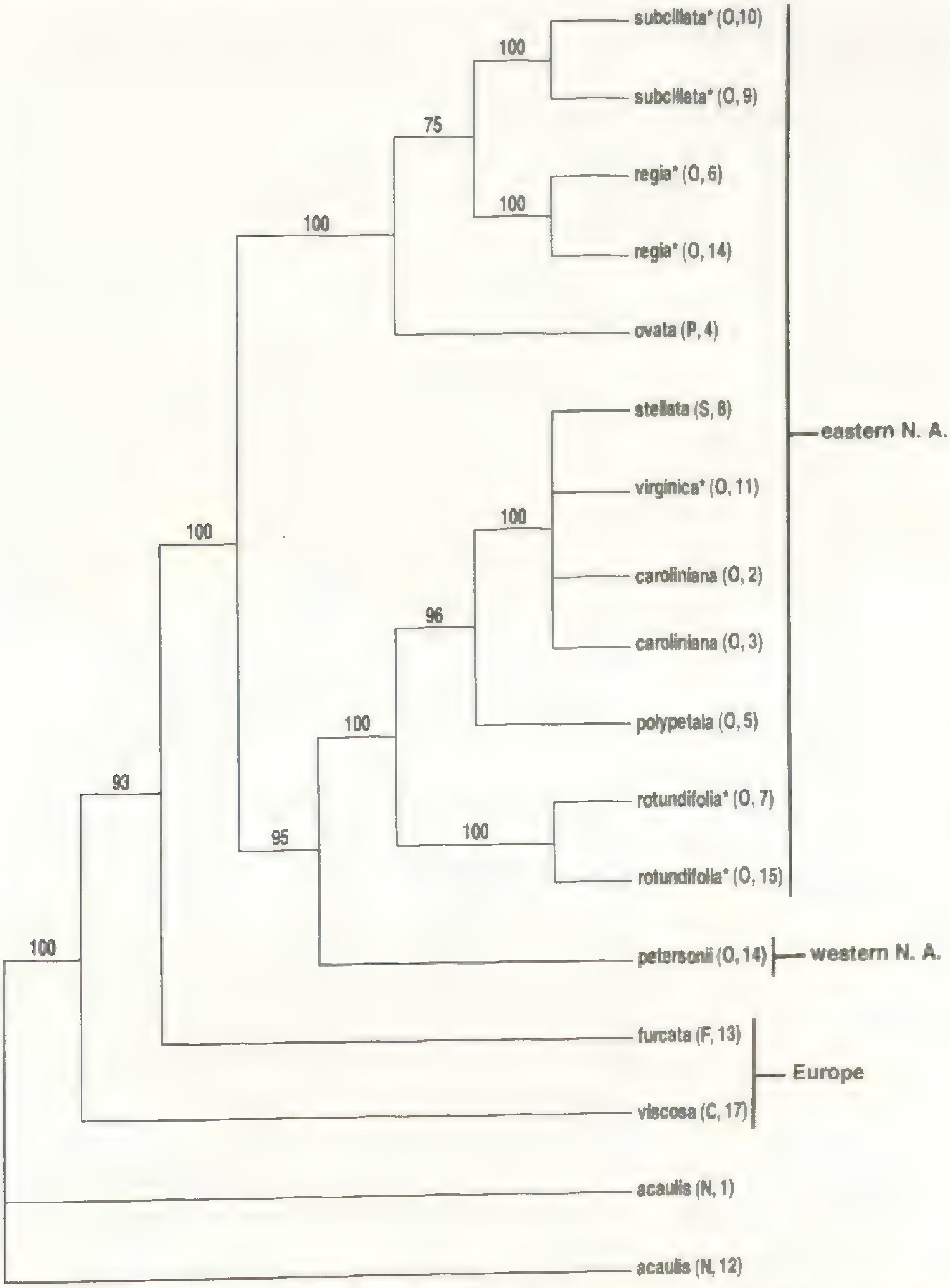

Figure 2. Cladogram from the Bayesian analysis of the ITS data. The number on each branch is the posterior probability of the branch. The letters in parentheses represent the sectional classification of the taxa: C = *Chloranthae*, N = *Nanosilene*, O = *Occidentales*, P = *Paniculatae*, F = *Physolychnis*, S = *Siphonomorpha*. The numbers in parentheses are the sequence numbers from the accession table (Table 2). A star (*) by a taxon indicates hummingbird pollination.

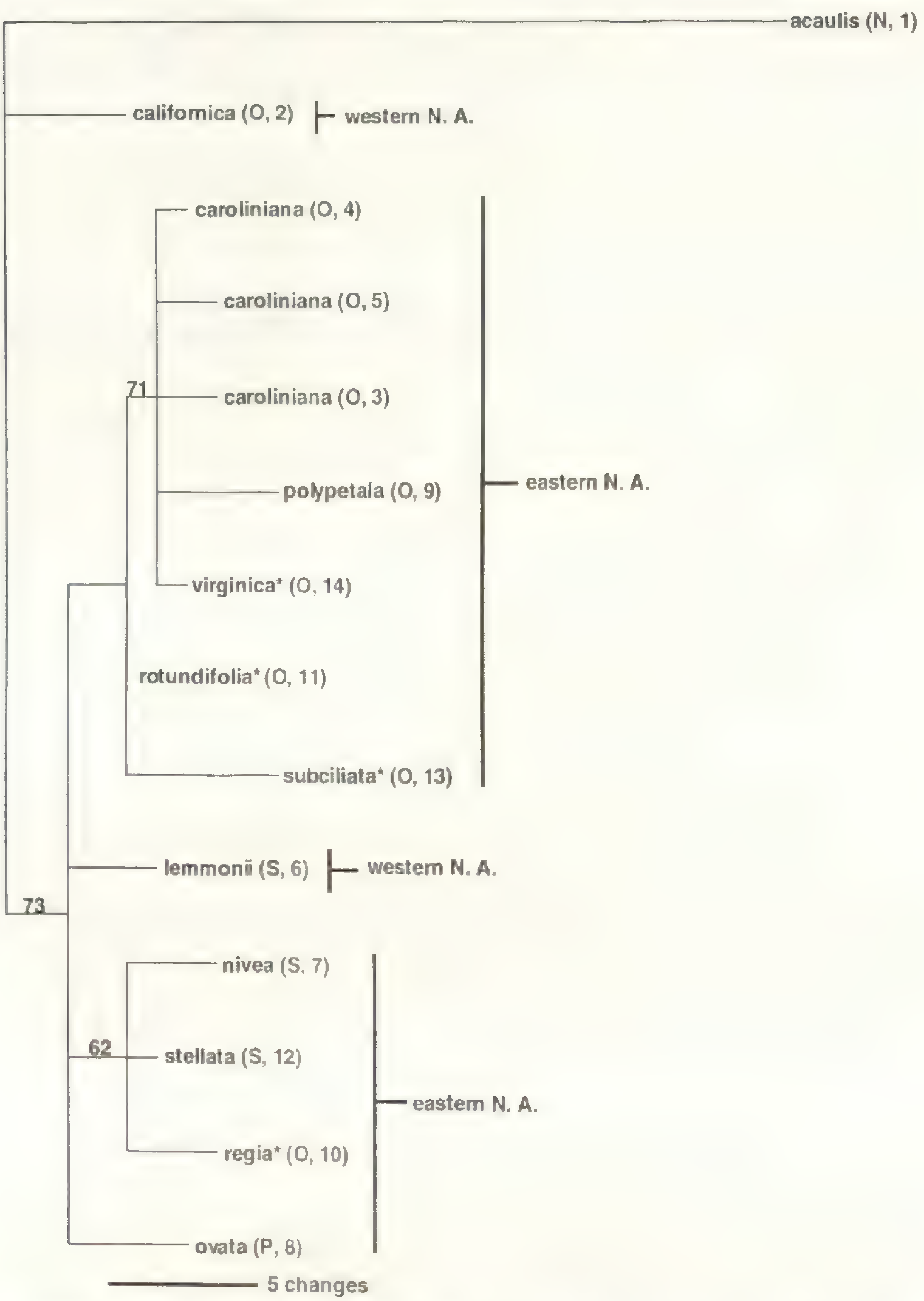

Figure 3. Phylogram of *Silene* taxa based on a consensus tree from parsimony analysis of the *trn*L intron. The letters in parentheses represent the sectional classification of the taxa: N = *Nanosilene*, O = *Occidentales*, P = *Paniculatae*, S = *Siphonomorpha*. Bootstrap values above 50 are shown. The numbers in parentheses are the sequence numbers from the accession table (Table 2). A star (*) by a taxon indicates hummingbird pollination.

eastern North American taxa (Figure 1). However, the Bayesian analysis strongly supports the position of *S. petersonii* as sister to one of two eastern North American clades (Figure 2). The Templeton test to reject the monophyly of the eastern North American taxa was nearly significant, but the short sequence length and lack of variation among North American *Silene* contributed to the failure to reject the null hypothesis. The *trn*L intron lacks the variation to test the monophyly of the eastern North American taxa (Figure 3).

The ITS phylogeny does provide evidence of the evolutionary lability of floral morphology and pollination systems within the eastern North American *Silene*. The clades are not organized with respect to floral morphology or pollinator syndrome. The red, hummingbird-pollinated *S. virginica* forms a strong clade with the pink-flowered *S. caroliniana* and the white-flowered *S. stellata* (Figures 1 and 2). The white-flowered taxon *S. ovata* forms a well-supported clade with the red, hummingbird-pollinated *S. regia* and *S. subciliata*. Neither red-, pink-, nor white-flowered taxa are monophyletic. Hitchcock and Maguire (1947) and Oxelman and Lidén (1995) previously noted the extensive homoplasy of floral traits within *Silene*. Different reproductive systems have also evolved multiple times within *Silene* (Desfeux et al. 1996). This study further emphasizes the great lability of floral traits in *Silene*, and demonstrates that homoplasies occur at a very low taxonomic level among closely related taxa in the same section. Chowdhuri's (1957) section *Occidentales* is also not monophyletic. Both *S. stellata*, section *Siphonomorpha*, and *S. ovata*, section *Paniculate*, are found within clades containing only *Occidentales* taxa (Figures 1 and 2).

The two eastern North American clades partially correspond to phenology and geography. *Silene polypetala*, *S. caroliniana*, and *S. virginica* all bloom in the spring in similar habitats in the southeastern United States. While *S. stellata* flowers later in the summer, its distribution overlaps with that of *S. caroliniana*, *S. virginica*, and *S. polypetala*. *Silene ovata*, *S. regia*, and *S. subciliata*, grouped together in this phylogeny, flower latest in the summer and fall. The closely related *S. regia* and *S. subciliata* are the only two eastern North American taxa with distributions almost totally west of the Appalachians. The geographic proximity of the genetically similar taxa may be the result of more recent speciation or gene flow among the taxa.

Though the *trn*L intron phylogeny contains few strongly supported clades, it also indicates the evolutionary lability of floral morphology. The hummingbird-pollinated *Silene regia* forms a clade with the small, white-flowered *S. nivea* and *S. stellata* (Figure 3), and *S. virginica* again groups together with *S. polypetala* and *S. caroliniana*. The basal position of *S. californica* to all other North American taxa also indicates that Chowdhuri's (1957) section *Occidentales* is polyphyletic. The placement of *S. regia* differs in the ITS and *trn*L intron phylogenies. In the ITS phylogeny *S. regia* is in a strongly supported clade with *S. subciliata*, but in the *trn*L intron phylogeny it is in a weakly supported clade with *S. nivea*, which is lacking in the ITS phylogeny, and *S. stellata* (Figures 1 and 2). Major discrepancies between nuclear and chloroplast phylogenies may be evidence of hybridization in the recent history of the taxa (Avise 1994). Though the difference in the placement of *S. regia* does not conclusively demonstrate the importance of hybridization in the species history of the eastern North American *Silene*, it does deserve more investigation. The polyphyly of *S. caroliniana* in the ITS phylogeny may also indicate gene flow with closely related taxa. A more variable chloroplast marker and greater population sampling is needed to further examine reticulate evolution and resolve the relationships within the eastern North American *Silene*.

ACKNOWLEDGMENTS. This research was supported by a grant from the University of Missouri Conservation Biology Program to J.G.B. We are grateful to Janis Antonovics, Laura Galloway, Mary Puterbaugh, Robin Kennedy, and the Green Plant Market Nursery for their assistance in the tissue collection. Herbaria at the University of Missouri, Missouri Botanic Garden, and Northeast Louisiana University loaned specimens. We also thank Dean Bergstrom for helping with the sequencing and Sarah Mathews, Kim McBreen, and two anonymous reviewers for comments on the manuscript.

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NEW BOOKS

Cultivated and Native Asters of Ontario (Compositae: Astereae) by John C. Semple, Stephen B. Heard, and Luc Brouillet. 2002. viii + 134 pp. line drawings, dot distribution maps, black & white and color photos. ISSN 0317-3348 $28.00 (soft cover). University of Waterloo Biology Series 41. Published by the Department of Botany, University of Waterloo, Waterloo, Ontario, N2L 3G1, Canada.

Flora of North America, Volume 23: Magnoliophyta: Commelinidae (in part): Cyperaceae by Flora of North America Editorial Committee, eds. 2002. xxiv + 608 pp. line drawings, distribution maps. ISBN 0-19-515207-7 $95.00 (hardcover). Oxford University Press, New York and London.

Flora of North America, Volume 26: Magnoliophyta: Liliidae: Liliales and Orchidales by Flora of North America Editorial Committee, eds. 2002. xxvi + 723 pp. line drawings, distribution maps. ISBN 0-19-515208-5 $120.00 (hardcover). Oxford University Press, New York and London.

Guide to the Trees, Shrubs, and Woody Vines of Tennessee by Eugene Wofford and Edward W. Chester. 2002. x + 190 pp. 380 color plates. ISBN 1-57233-205-0 $29.95 (soft cover). The University of Tennessee Press, Knoxville, TN.

The Illustrated Flora of Illinois. Grasses: Bromus *to* Paspalum, *Second Edition* by Robert H. Mohlenbrock. 2002. xvi + 404 pp. line drawings, dot distribution maps. ISBN 0-8093-2359-1 $60.00 (hardcover). Southern Illinois University Press, Carbondale, IL.

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Vascular Flora of Illinois by Robert H. Mohlenbrock. 2002. 490 pp. 2 maps of Illinois. ISBN 0-8093-2421-0 $50.00 (hardcover). Southern Illinois University Press, Carbondale, IL.

RHODORA, Vol. 105, No. 921, pp. 92–93, 2003

NEBC MEETING NEWS

November 2002. Vice President Art Gilman introduced Dr. Dorothy J. Allard, who spoke on "A New Epiphytic Species of *Pedicularis* from Nepal: Description and Demography." An enjoyable evening was spent in vicariously traveling to the King Mahendra Trust for Nature Conservation in Nepal where Dorothy had collected data on the influence of grazing on the vegetation of the subalpine fir forest zone as part of her doctoral research.

The Annapurna Conservation Area is in central Nepal south of the crest of the Himalayas. Fir forests occur from 2900–3500 m in elevation there, but are not continuous. The canopy trees are *Abies spectabilis* with an understory of two *Rhododendron* species, *R. campanulatum* and *R. barbatum.* The largest firs had diameters approaching 2.5 m. The fir–rhododendron forest zone where the *Pedicularis* was found has a full exposure to the summer monsoon with a high precipitation during the growing season, while being snow-covered from December through March. Orographically induced circulation patterns cause cloud forest conditions in this region, resulting in the highest recorded rainfall in Nepal (6000 mm/year). The cloud forest conditions promote a luxuriant growth of epiphytes, where vascular species grow with their roots under and inside a layer of bryophytes. It was in this situation that Dr. Allard encountered an unknown species of *Pedicularis.*

Dr. Robert Mill at the Royal Botanic Gardens in Edinburgh confirmed that the find represented a species new to science. *Pedicularis* has a center of distribution in SW China and ranges throughout the northern hemisphere, commonly in montane and alpine areas. There are about 600 species in the genus. All known species are hemiparasitic, however no epiphytic species are known to exist. Further, the typical *Pedicularis* flower has an upper lip (galea) and a lower lip (labellum) that face outward from the inflorescence axis; in this new species the entire corolla is rotated such that the galea faces inward toward the axis of the inflorescence.

In 2001, Dr. Allard returned to the study area to collect additional flowering material of the new *Pedicularis.* She was unable to find the plant in study sites to the east or west of this area, suggesting that there may be only one isolated population. She surveyed and mapped its locations and studied its flower development and pollination biology. The new species grows on living trees and on dead wood, rarely on other substrates. While it has a strong dependence on *Abies*, it also grows on *Rhododendron*. It was observed to grow as far as 35 m above the ground. As leaf length and number increased, so did the likelihood of flowering. Plants with the longest leaf length (> 20 cm) had a 40% flowering rate with 1–4 stalks per plant. The plants are probably perennial.

While Dr. Allard's 2001 field work provided additional information on the life history characteristics of the new *Pedicularis*, many questions remain unanswered. For example, no pollinators were detected during 90 hours of observation, though the flowers seemed not to self-pollinate. The dispersal mechanism is unknown, and the seeds had no structure that would provide for movement upward into the canopy, such as wings or elaiosomes. Clearly more study is needed to fit this novel *Pedicularis* into our understanding of this genus.

—NEAL W. ANDERSON, Recording Secretary.

CHECKLIST FOR CONTRIBUTORS TO *RHODORA*

Please check items and submit with manuscript.

General Instructions

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

Introductory Material

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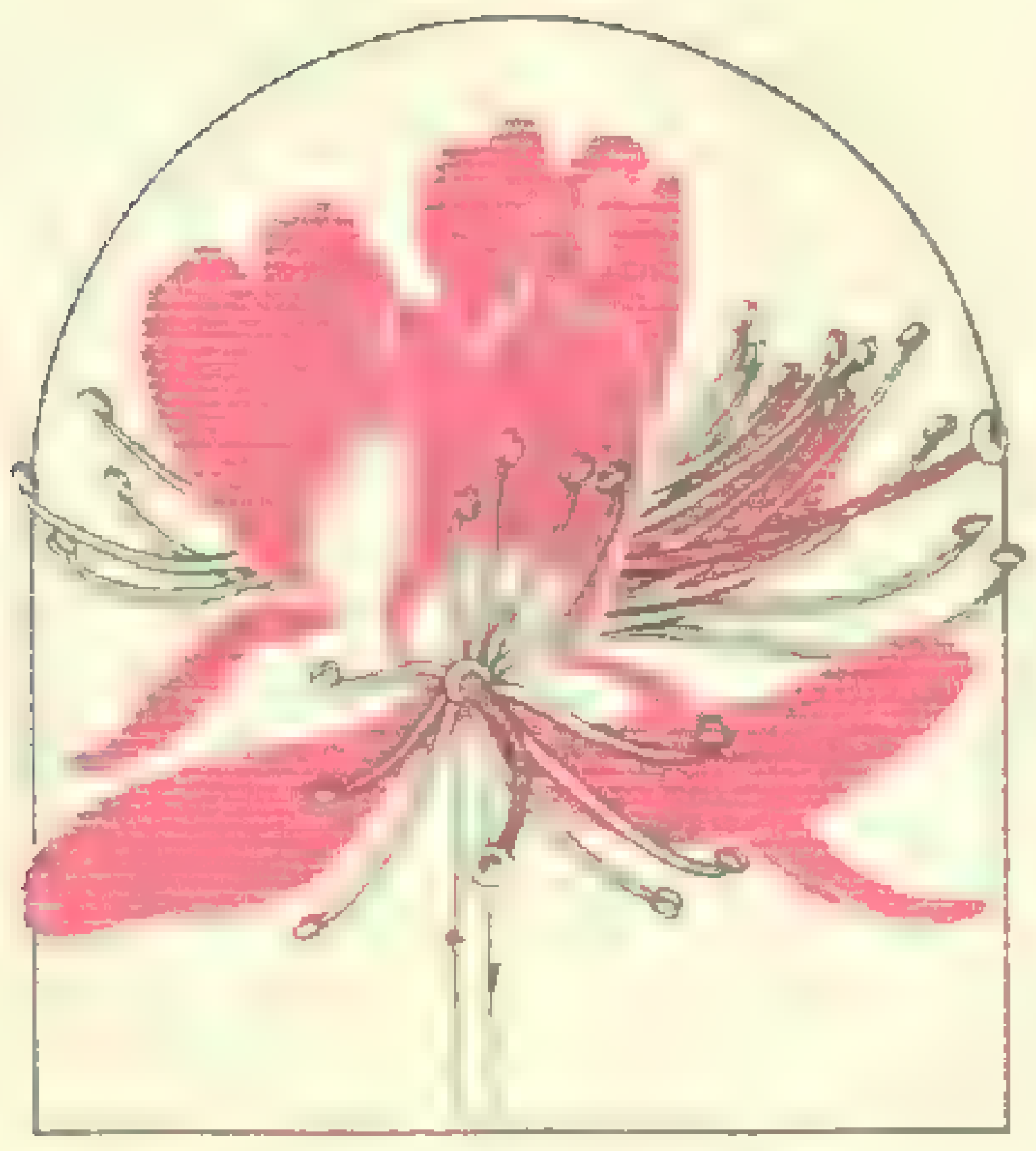

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A NEW SPECIES OF *DAHLIA* (ASTERACEAE, COREOPSIDEAE) FROM HIDALGO STATE, MÉXICO

Hans V. Hansen
University of Copenhagen Botanic Garden,
Ø. Farimagsgade 2 B, DK-1353 Copenhagen K, Denmark
e-mail: hansvh@bot.ku.dk

Paul D. Sørensen
Department of Biological Sciences,
Northern Illinois University, DeKalb, IL 60115-0461
e-mail: psorensen@niu.edu

ABSTRACT. *Dahlia hjertingii*, a new species from the State of Hidalgo, México, is described and illustrated. Although in some aspects morphologically similar to the allopatric and purple-rayed *D. tubulata*, this new dahlia is distinct biochemically and genetically. With the addition of *D. hjertingii*, there is an increased recognition that the mountainous State of Hidalgo and adjacent areas is the region of greatest diversification among the purple-rayed dahlias.

RESUMEN. Se provee una descripción e illustración de *Dahlia hjertingii*, una nueva especie del estado de Hidalgo, México. A pesar de ser similar en algunos aspectos morfológicos a la alopátrica de *D. tubulata* con lígulas moradas, esta nueva especie de dália se diferencia de por características bioquímicas y genéticas. Con la adición de *D. hjertingii*, existe un mayor reconocimiento de que la regíon del estado montañoso de Hidalgo y las áreas adyacentes es de mayor diversificación de dálias con lígulas moradas.

Key Words: *Dahlia*, Asteraceae, Coreopsideae, Hidalgo State, México

The purple-rayed dahlias of *Dahlia* sect. *Dahlia* Sherff (Asteraceae, Coreopsideae) continue to reveal themselves as the most diverse group within the genus. It is not surprising, therefore, that when Jens Peter Hjerting collected seeds (*Hjerting 7362*) of a purple-rayed dahlia in the mountains northeast of the city of México in the State of Hidalgo, México, the resulting greenhouse-grown plants did not conform to any recognized species. The plants were morphologically similar to *D. tubulata* P. D. Sørensen (Sørensen 1980). Continued evaluation, however, led to the conclusion that they were of an undescribed species. Realization of this brought about, in part, a resolve to visit the site from which the original seeds were collected and to gather the necessary voucher material from natural populations in order to prepare an authentic description. This was accomplished during a prolonged field trip through México in 1995. We are pleased to describe and name this new dahlia in honor of Jens Peter Hjerting, who was its discoverer and who has over many years aided in the advancement of our understanding of *Dahlia*. Hjerting and his colleagues have steadfastly maintained a living reference and research collection of the native Mexican taxa of *Dahlia* at the University of Copenhagen Botanic Garden.

Dahlia hjertingii H. V. Hansen & P. D. Sørensen, *sp. nov.* TYPE: MÉXICO. Hidalgo: 5.3 km S of Agua Blanca along road from San Alejo (NE of Tulancingo) to Huayacocotla, Veracruz, zone of pine and oak, clay ledges along roadside, 2220 m, 11 Sep 1995, *Hjerting, Saar & Sørensen 95-91* (HOLOTYPE: MEXU!; ISOTYPE: C!). Figure 1.

Herba perennis, 1.2 m alta. Caules glabri, pruinosa. Folia pleurumque bipinnata, foliolis primaris 5–7; laminis bicoloribus, glaberrimis, dorsaliter nitidis, marginae sparsem pubescentibus; petiolis solidis. Flores ligulati purpureis. Crescet in México. Chromosomatum numerus: $n = 16$, $2n = 32$.

Perennial herb, 1.2 m tall, from fascicled tubers. Stems 4–9 mm in diameter, glabrous, glaucous when fresh, hollow but with septa at the nodes; median internodes 8.0–13.0 cm long. Leaves (median) bipinnately compound, 19–25 cm long (including petioles), petioles 5–6.5 cm long, solid; primary leaflets 7, opposite on the rachis, the basal pair 9–12.5 cm long, petiolules 3–5.2 cm long; secondary leaflets of the basal pinnae opposite, or less often sub-opposite, on the rachilla; ultimate segments ovate or elliptic, rarely slightly obovate, the terminal segment usually larger than its companion leaflets, apices attenuate; surfaces bicolored, lighter green beneath, more or less completely glabrous, upper surface glossy; margins irregularly coarsely toothed, very sparsely pubescent; stipels, when present, attached at the basal and median rachis nodes, rarely also attached at the basal rachilla node. Capitula solitary on the central flowering axis, 1–3 (–5) on each of the lateral flowering axes, erect or obliquely erect, elevated above the leafy portion of the stem on peduncles 15–25 cm long; outer involucral bracts 5, reflexed at anthesis, slightly spatulate, acute, glabrous, 10–13 mm long, 1.8–2.5 mm wide; inner bracts 8, 5–6.5 mm wide, 10–13 mm long, pale tan with hyaline margins; ray florets 8, corollas light purple or lavender, laminae 2.5–3.2 cm long, 1.3–1.6 cm wide, broadly elliptic, apex acute; disc florets 38–57, corollas yellow; achenes slightly obovoid, 8.7–13.3 mm long, 1.7–2.4 mm wide at widest point, pappus absent. Chromosome number: $n = 16$, $2n = 32$.

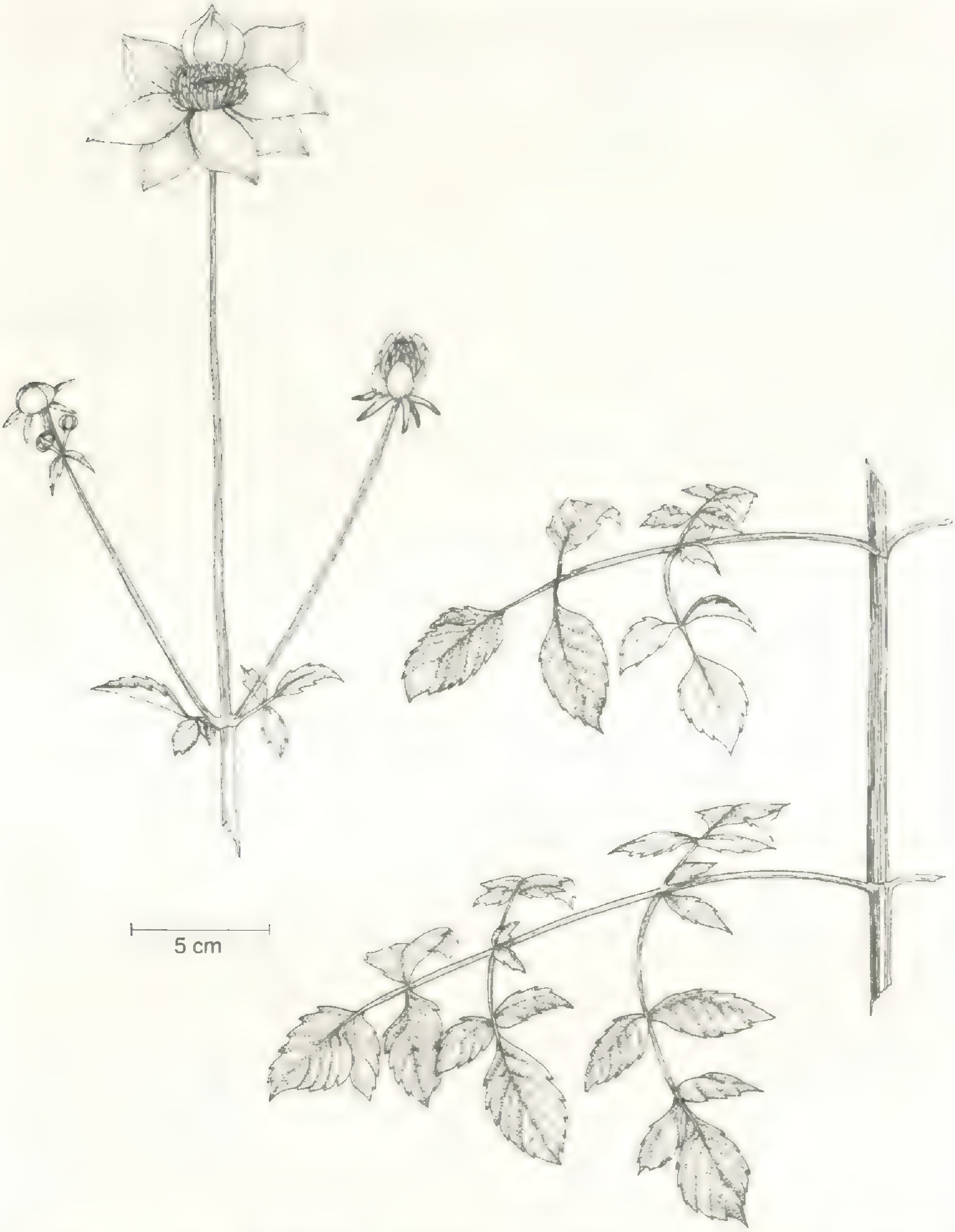

Figure 1. *Dahlia hjertingii*. Drawing by Suzanne Wegener from specimens collected at the type locality, *Hjerting, Saar & Sørensen 95-91*.

The new species is known from two locations, both in the State of Hidalgo, México: 1) the type locality as noted above; the site is essentially the same as that where seeds were gathered by Jens Peter Hjerting (his No. *7362*) in 1991; and 2) at K-84, 20.6 km N of the bridge crossing at San Pedro, along México Ruta 105, Pachuca-Huejutla, in a zone of mimosoid scrub with *Buddleia*, at an elevation of 1900 m, 11 Sep 1995, *Hjerting, Saar & Sørensen 95-92* (DEK).

There are morphological similarities between *Dahlia hjertingii* and *D. tubulata*, another of the purple-rayed dahlias from the mountains of eastern México. The similarity is most apparent in the position of the secondary leaflets (or segments of the primary leaflets) that are irregularly alternate on their rachillae. *Dahlia tubulata*, known from the States of Nuevo León and Tamaulipas, though superficially similar in appearance to *D. hjertingii*, is notably distinct in having hollow, not solid petioles. So far as is known these species are not sympatric but are separated by about 350 km. The following key may be used to distinguish them:

Petioles usually hollow at a point midway between the basal primary leaflets and the main stem; known only from the States of Nuevo León and Tamaulipas .... *Dahlia tubulata*
Petioles regularly solid; known only from the State of Hidalgo .... *Dahlia hjertingii*

Dahlia tubulata is also unique among all dahlia species so far investigated in possessing thiophenes, sulfur-containing compounds (Christensen et al. 1990). In as much as *D. hjertingii* was at first thought to be allied with *D. tubulata* it seemed worthwhile to consider whether sulfur-containing compounds might be found in this new taxon. To this end, seeds of the original gathering by Hjerting (*7362*) were forwarded to Jørgen Lam, University of Aarhus, Denmark. In a personal communication (1994), Lam informed us that plants grown in Aarhus from the seeds of *D. hjertingii* failed to produce sulfur-containing compounds. Later, Lam (1998) asserted that among the dahlias so far investigated "*Dahlia tubulata* ... is unique because of its sulfur compounds, which have not been observed in any other *Dahlia* species."

Material from the type locality of *Dahlia hjertingii* was included in a cladistic study of the genus that employed molecular sequences of the internal and external transcribed spacer regions of nuclear ribosomal DNA (Saar, Polans, and Sørensen, in press). Based on the combined ITS and ETS data sets, *D. hjertingii* is included in a clade that encompasses 12 other recognized species in sect. *Dahlia*. However, *D. hjertingii* occurs by itself on a single branch originating from the basal node within the clade; bootstrap support for this branch is 87%.

The State of Hidalgo and adjacent areas are increasingly the focus of attention as the region of the greatest diversification among dahlias. With the publication of *Dahlia hjertingii* there are now 32 species (including *D. spectabilis*; Saar, Sørensen, and Hjerting 2002) plus 6 infraspecific taxa recognized for the genus. Additionally, at least 4 more new taxa await formal description. Of the described and new taxa, 10 species are known from the State of Hidalgo, and an additional 6 or 7 taxa have ranges within the same cordillera to the north and west. Only two species are confined to western México in the Sierra Madre Occidental. Other taxa lie scattered in the central Sierra Volcánica Transversal and the southern Sierra Madre del Sur (see maps in Sørensen 1969, 1980).

ACKNOWLEDGMENTS. We thank Suzanne Wegener for her preparation of Figure 1. Lisbeth Knudsen counted the somatic chromosomes from root tips. Andrea Previtali prepared the Spanish abstract. Jørgen Lam kindly worked on an analysis of the chemical constituents of *Dahlia hjertingii* even while retired from his former duties at the University of Aarhus. Dayle Saar helped enormously with the field work during the 1995 trip through México as did Jens Peter Hjerting, whose fluency with Spanish made interactions with local people a greater pleasure.

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PHYLOGENY AND BIOGEOGRAPHY OF *CHAMAECYPARIS* (CUPRESSACEAE) INFERRED FROM DNA SEQUENCES OF THE NUCLEAR RIBOSOMAL ITS REGION

JIANHUA LI

Arnold Arboretum of Harvard University, 125 Arborway,
Jamaica Plain, MA 02130-3500
e-mail: jli@oeb.harvard.edu

DONGLIN ZHANG

Department of Plant, Soil, and Environmental Sciences,
University of Maine, 5722 Deering Hall, Orono, ME 04469-5722

MICHAEL J. DONOGHUE

Department of Ecology and Evolutionary Biology,
Yale University, New Haven, CT 06520

ABSTRACT. Phylogenetic analyses of the five extant species of *Chamaecyparis* (Cupressaceae) based on nrDNA ITS sequences yield a single most parsimonious tree in which *C. pisifera* (Japan) and *C. formosensis* (Taiwan) form a clade that is sister to a clade including *C. lawsoniana* (western North America) and *C. obtusa* (Japan and Taiwan) plus *C. thyoides* (eastern North America). Dispersal-vicariance analyses (DIVA) suggest a minimum of two dispersal events between eastern Asia and North America.

Key Words: phylogeny, biogeography, *Chamaecyparis*, eastern Asian–North American disjunct, nrDNA ITS

The floristic similarities between eastern Asia and North America (EA-NA) have attracted the attention of systematists and biogeographers since the nineteenth century (Axelrod et al. 1998; Boufford 1998; Boufford and Spongberg 1983; Graham 1999; Gray 1846, 1859; Hong 1993; Li 1952; Manos and Donoghue 2001; Tiffney 1985a, b; Wen 1999; Wu 1983). Our current understanding is that there was a more homogeneous mesophytic "boreotropical flora" in the early to middle Tertiary around the Northern Hemisphere. The modern biogeographic pattern resulted from differential loss of species in different geographic regions in response to orogenic and climatic changes in the late Tertiary (Axelrod 1960; Axelrod et al. 1998; Chaney 1947; Guo 1999; Manchester 1999; Qian and Ricklefs 1999; Stewart and Lister 2001; Tiffney 1985a, b; Wolfe 1975). However, this explanation does not provide much insight into the pathways of migration and patterns of diversification of plant lineages around the Northern Hemisphere.

Recently, molecular analyses have shed light on phylogenetic patterns in plant clades that are disjunctly distributed between eastern Asia and North America (Wen 1999). Xiang et al. (1998) summarized results from phylogenetic studies of seven plant genera with such a disjunction, and concluded that there was a congruent pattern wherein species of western and eastern North America form a clade relative to Asian species. However, when a molecular clock was used to estimate divergence times in these and other lineages, a wide range of divergence times was inferred, indicating that multiple vicariant events, at different times, might have resulted in a similar phylogenetic pattern (Xiang et al. 2000). This is known as "pseudocongruence" (Cunningham and Collins 1994). With the analysis of more clades, additional phylogenetic patterns have come to light, and the range in disjunction times has likewise expanded (e.g., Donoghue et al. 2001; also see Li et al. 2001a, b). Nonetheless, the number of clades that have been investigated is still very limited.

Chamaecyparis Spach is a disjunct genus between eastern Asia and North America (Li 1952). Plants of *Chamaecyparis* are small to large evergreen trees with branchlets in flat sprays bearing scale-like leaves in four rows. Their cone scales are peltate, subglobose, and bear two seeds. Recent phylogenetic analyses indicate that *Chamaecyparis* belongs to a well-supported clade, the Cupressoideae of the Cupressaceae (Brunsfeld et al. 1994; Gadek et al. 2000). *Chamaecyparis* contains five species (Farjon 1998), two of which are endemic to the United States: *C. thyoides* (L.) Britton, Stearns & Poggenb. in the east from Maine to Florida and westward to Mississippi, and *C. lawsoniana* (A. Murray) Parl. in the western States including southwestern Oregon and northern California (Vidakivic 1991). There are three species in eastern Asia: *C. formosensis* Matsum. endemic to Taiwan, *C. pisifera* (Siebold & Zucc.) Endl. endemic to Honshu and Kyushu of Japan, and *C. obtusa* (Siebold & Zucc.) Endl. endemic to central and northern Taiwan, and to Honsu, Kyushu, and Shikoku of Japan (Hwang et al. 2001; Iwatsuki et al. 1995). The Taiwan plants of *C. obtusa* have sometimes been segregated as a separate species, *C. taiwanensis* Masam. & Suzuki; we treat these here as *C. obtusa* var. *formosana* (Hayata) Hayata.

The objectives of the present study were (1) to reconstruct phylogenetic relationships of *Chamaecyparis*, and (2) to elucidate its historical biogeography based on the inferred phylogeny. We chose to use sequences of the nrDNA ITS region because such data have been used successfully in resolving phylogenetic relationships of other conifer lineages (Gernandt and Liston 1999; Li et al. 2001a, b; Liston et al. 1999).

Table 1. Specimens used in this study. AA = Arnold Arboretum.

Taxon & JLI DNA number	Voucher & Locale	GenBank #
Chamaecyparis formosensis 2751	*Hwang, S.-Y. s.n.*, Taiwan	AY211257
C. formosensis 2752	*Hwang, S.-Y. s.n.*, Taiwan	AY211258
C. lawsoniana 2702	AA 1164-71B, Ore., U.S.A.	AY211253
C. lawsoniana 2753	AA 1625-83B, Ore., U.S.A.	AY211254
C. obtusa 2705	AA 13038A, Japan	AY211251
C. obtusa 2706	AA 447-38A, Japan	AY211250
C. obtusa var. *formosana* 2701	AA 833-69B, Taiwan	AY211252
C. pisifera 2707	AA 22799A, Japan	AY211256
C. pisifera 2708	AA 1067-38A, Japan	AY211255
C. thyoides 2709	AA 13047A, Ala., U.S.A.	AY211248
C. thyoides 2710	AA 13047C, Ala., U.S.A.	AY211249
Fokienia hodginsii 2730	AA 1562-80A, Fujian, China	AY211260
F. hodginsii 2749	*Li, J.*, Guangdong, China	AY211259

MATERIALS AND METHODS

Thirteen samples were included in this study, representing all species of *Chamaecyparis*; *Fokienia hodginsii* (Dunn) A. Henry & H. H. Thomas was included for rooting purposes because of its well-supported sister relationship with *Chamaecyparis* (Brunsfeld et al. 1994; Gadek et al. 2000). For each species we sampled two accessions; in the case of *C. obtusa* we included two accessions from Japan and one from Taiwan to represent var. *formosana* (Table 1).

We extracted DNAs from silica-gel dried or fresh leaf material using a Qiagen DNeasy Plant Mini Kit (cat. # 69104, Germantown, MD). Polymerase Chain Reactions (PCR) were conducted to amplify the nrDNA ITS region in a Perkin-Elmer thermocycler using primers ITS4 (White et al. 1990) and ITS-LEU (Baum et al. 1998). The Qiagen PCR purification kit (Santa Clarita, CA) was used to clean PCR products for direct cycle sequencing using an ABI DigDye Terminator Cycle Sequencing Ready Reaction Kit (Foster City, CA). For each sample the ITS region was sequenced using three primers including ITS4, ITS-LEU, and 5.8Sgym (Liston et al. 1996). Sequences were read using an ABI Capillary Genetic Analyzer 3100 (Applied Biosystems, La Jolla, CA) and were then edited using Sequencher (3.0, GeneCode Inc., Ann Arbor, MI). Sequence alignment was done manually. Sequence boundaries of the ITS-1, 5.8S, and ITS-2 regions were determined by comparing published sequences of *Calocedrus* Kurz in the GenBank (AF287248).

Parsimony analyses were carried out with PAUP* (Swofford 2002, version 4.0 b10) using branch and bound tree search with default options. Characters were equally weighted and their states were unordered. Gaps were treated as missing data. Bootstrap analyses using 500 replicates were conducted to evaluate support for individual clades (Felsenstein 1985).

Three biogeographic processes—dispersal, vicariance, and extinction—are responsible for the formation of modern geographic distribution (Morrone and Crisci 1995). In dispersal-vicariance analysis, costs are assigned to particular events and areas are inferred for ancestral nodes in a phylogenetic tree so as to minimize the sum of these costs (Ronquist 1997). This method has been used successfully in elucidating biogeographic patterns of families and genera of angiosperms in the Northern Hemisphere (Manos and Donoghue 2001). To infer ancestral areas and migration pathways in *Chamaecyparis* we implemented the dispersal-vicariance analysis using the computer program DIVA 1.1 (Ronquist 1996), using the default event costs (0 for vicariance, 1 for both dispersal and extinction). Three areas of endemism were recognized in these analyses: eastern North America (ENA), western North America (WNA), and eastern Asia (EA), the latter including Mainland China, Taiwan, and Japan.

RESULTS

The alignment generated a data set of 1,134 characters, 198 of which were parsimony informative. The length of the 5.8S was 146 base pairs in all species except for *Chamaecyparis obtusa* var. *formosana*, whose 5.8S was one base pair shorter. The ITS-1 region was 3.5 times as long as the ITS-2. Sequence divergences between *Fokienia hodginsii* and species of *Chamaecyparis* ranged from 6–12.6%, while those within *Chamaecyparis* were from 4.3–12.8%.

Parsimony analyses produced a single tree of 134 steps (Figure 1; CI = 0.88, RI = 0.9). The accessions of each species clustered together. In the case of *Chamaecyparis obtusa*, the Taiwan accession was united with one of the Japanese specimens to the exclusion of the other. The basal split within *Chamaecyparis* separated a *C. pisifera*–*C. formosensis* clade (bootstrap = 91%) from a clade containing *C. lawsoniana*, *C. thyoides*, and *C. obtusa* (bootstrap = 77%). *Chamaecyparis thyoides* and *C. obtusa* appear to be more closely related to one another (bootstrap = 73%) than either is to *C. lawsoniana*.

Dispersal and vicariance analyses identified two equally parsimonious ancestral area assignments for *Chamaecyparis* (Figures 2a, b): (a) the composite of all three areas (EA, WNA, ENA), and (b) eastern Asia

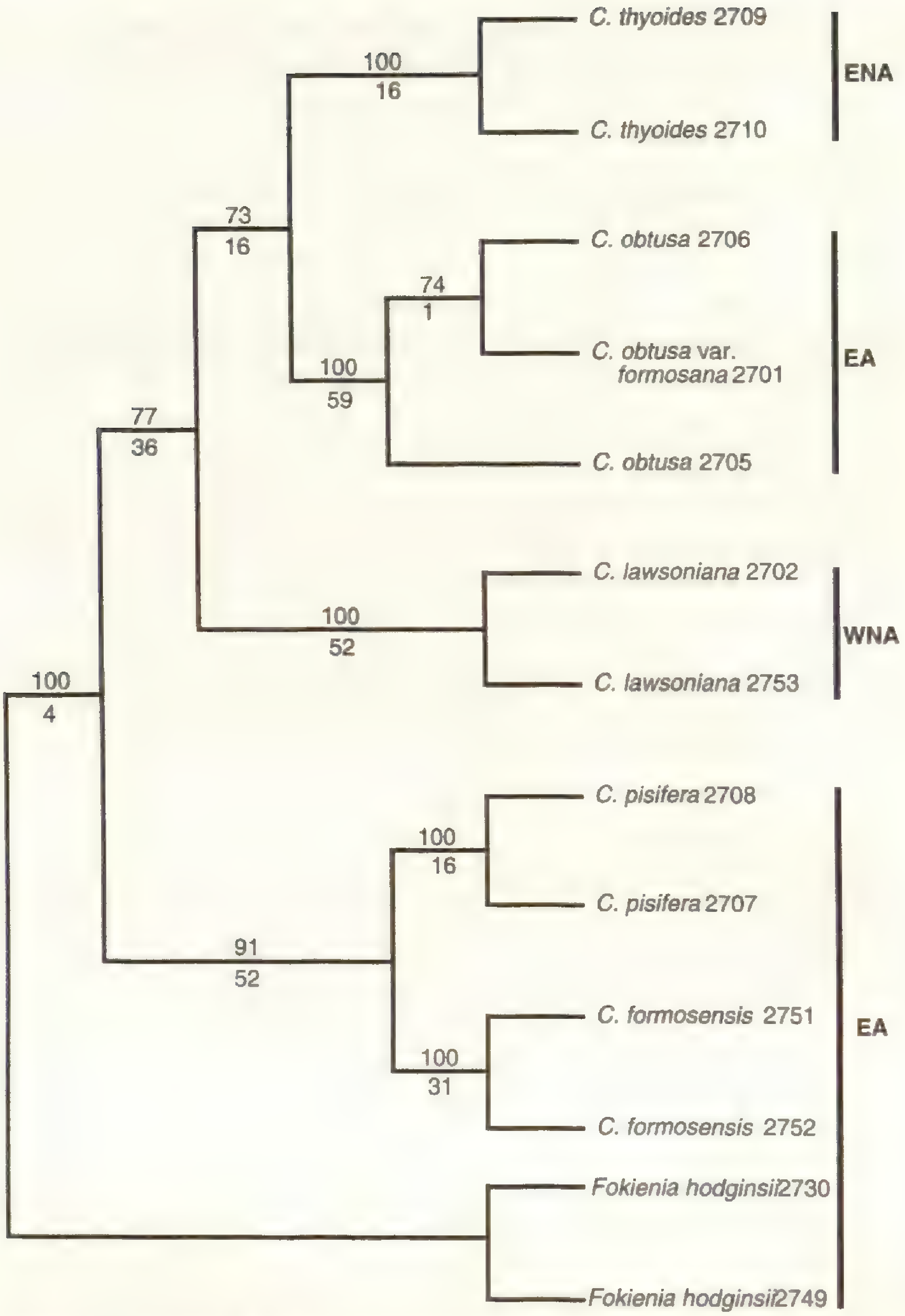

Figure 1. The single most parsimonious tree generated for *Chamaecyparis* using sequences of nuclear ribosomal DNA ITS region (134 steps; CI = 0.88, RI = 0.9). *Fokienia hodginsii* was included for rooting purposes. Numbers above and below the branches are bootstrap percentages and number of base substitutions, respectively. Acronyms denote geographic distribution. ENA = eastern North America, EA = eastern Asia, WNA = western North America.

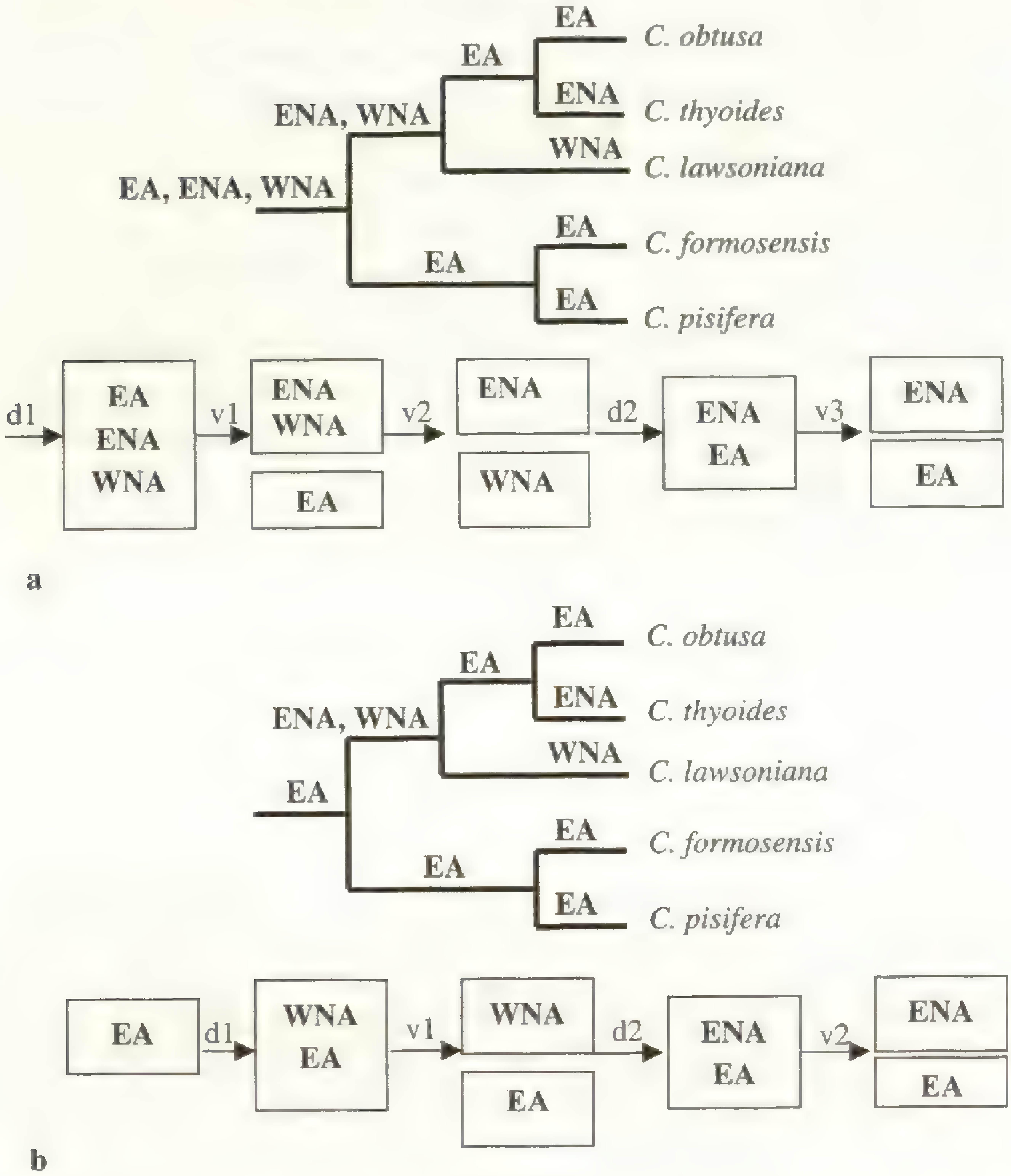

Figure 2. Alternative scenarios from DIVA analyses, showing inferred ancestral areas and vicariance and dispersal events (see text for discussion). Dispersal events are denoted by d1 and d2, and vicariance events by v1, v2, and v3. Areas of endemism are denoted by EA (eastern Asia), ENA (eastern North America), and WNA (western North America).

(EA). In both cases two dispersal events were inferred to explain the modern distribution pattern. When the maximum number of areas assigned to an ancestral node was constrained to two, EA was inferred to be the ancestral area. Again, two dispersal events were required (Figure 2b).

DISCUSSION

In *Chamaecyparis* the ITS-1 is more than three times as long as the ITS-2. This appears to be true for other conifer lineages (Li et al. 2001a, b), but is not the case in most angiosperms where ITS-1, whose length ranges from 187–298 bp, is equal to, or only slightly longer than ITS-2, which is from 187–252 bp long (Baldwin et al. 1995). The reason for this remains unclear, but the longer ITS region in conifers provides more informative sites for resolving relationships.

As noted above, *Chamaecyparis obtusa* in Taiwan has been treated as *C. obtusa* var. *formosana* (Cheng and Fu 1978), or sometimes as a separate species, *C. taiwanensis* (Liu 1966). In our ITS tree the three accessions of *C. obtusa* form a clade within which the Taiwan accession is more closely related to one of the Japanese accessions than it is to the other.

Glands are conspicuous on the upper side of the leaves in all species of *Chamaecyparis* except for *C. obtusa*. Our results imply that leaf glands are a plesiomorphy, and were probably lost in *C. obtusa*.

In a number of disjunctly distributed plant genera, the Asian species and the North American species form separate clades (e.g., Li et al. 2001b; Liston et al. 1999; Xiang et al. 2000). This has sometimes been assumed in making statistical comparisons of species richness and diversification between eastern Asia and North America (Guo and Ricklefs 2000; Qian and Ricklefs 2000). However, this pattern is not universal (Donoghue et al. 2001). For example, the Japanese species *Hamamelis japonica* (Hamamelidaceae) is more closely related to the North American species (*H. virginiana*, *H. vernalis*, and *H. mexicana*) than it is to another Asian species, the Chinese *H. mollis* (Li et al. 2000; Wen and Shi 1999). The North American species of *Taxus* (Taxaceae) form a clade with the exception of *T. canadensis*, which appears to be more closely related to the Eurasian species (Li et al. 2001a). In *Chamaecyparis*, it appears that the eastern North American species, *C. thyoides*, is more closely related to the eastern Asian *C. obtusa* than it is to the western North American *C. lawsoniana*. Therefore, no matter where the group originated, more than one biogeographic event was involved in the formation of the modern distribution pattern. Our unconstrained DIVA analyses suggest two alternatives, both entailing two dispersal events (Figure 2). In the first (Figure 2a), the ancestor of *Chameacyparis* became widespread in eastern Asia (EA), western, and eastern North America (WNA, ENA) via dispersal (d1). This was followed by a vicariance event (v1) that created an EA line containing modern *C. formosensis* and *C. pisifera*, and an NA line. Subsequently, within North America the western and eastern populations were separated (v2). Finally, the ENA species spread to Asia (d2), followed by vicariance (v3). In the second alternative, which is preferred when the number of areas occupied by ancestral species is limited to two, the first species of *Chamaecyparis* lived in EA. This species spread to WNA (d1) and a subsequent vicariance event (v1) resulted in a WNA and an EA species. This Asian species later spread to ENA (d2), and another vicariance (v2) then resulted in modern *C. thyoides* and *C. obtusa*.

At present we see no strong reason to prefer one scenario over the other. However, additional data could potentially sort this out. First, additional sampling within species could reveal a pattern that favors one scenario over the other. For example, analyses including additional samples within *Chamaecyparis thyoides* might indicate that some of its populations are more closely related to *C. obtusa*, suggesting dispersal from ENA to EA, as in Figure 2a. Alternatively, finding some *C. obtusa* populations more closely related to *C. thyoides* would suggest dispersal from EA to ENA, favoring the Figure 2b scenario. Second, evidence on the distributions and ages of fossils could help. For example, the scenario depicted in Figure 2a implies that *Chamaecyparis* was present in ENA early in the evolution of the group, whereas ENA was occupied only later in the Figure 2b scenario. There have been reports of fossil leaves and seed cones of both *Chamaecyparis* and *Fokienia* from the upper Cretaceous and early Paleocene (Bell 1957; McIver and Basinger 1989, 1990; Tao 1992). However, it is difficult to reliably relate these fossils to extant species of *Chamaecyparis*, and hence they have not been included in our DIVA analyses. Edwards (1984, 1992) examined morphological differences among the modern species of *Chamaecyparis* and used interspecific differences to assign fossils to the extant species. According to his analysis both *C. thyoides* and *C. lawsoniana* were present in western North America by the early to middle Eocene (43–58 MYA; Edwards 1984). This seems to support the first scenario. However, this explanation may be erroneous for the following two reasons. First, *Chamaecyparis* has a much more ancient history than the Eocene (Bell 1957; McIver and Basinger 1989, 1990; Tao 1992) and there exists the possibility that North American species are derivatives from EA. Second, so far we have not found fossils that are widespread and represent the common ancestor of species of *Chamaecyparis*. Nevertheless, Edwards' (1984) findings at least suggest the extinction of *C. thyoides* in western North America. Clearly, much more attention is needed for precise phylogenetic placement of fossils of *Chamaecyparis* from both NA and EA.

Our DIVA analyses, albeit inconclusive, indicate that the geographic history of *Chamaecyparis* has been complex, involving several intercontinental migration events at different times. In general, this is consistent with previous findings of movement in both directions and at several times (e.g., Donoghue et al. 2001; Xiang and Soltis 2001; Xiang et al. 2000; Schultheis and Donoghue, unpubl. data). Additional molecular data (such as chloroplast DNA sequences) would test the phylogenetic hypothesis, and, together with the placement of the fossil material, would provide the possibility of inferring divergence times.

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LATE-FLOWERING PLANTS FROM NORTHERN NOVA SCOTIA, CANADA

BARRY R. TAYLOR[1] AND DAVID J. GARBARY

Department of Biology, St. Francis Xavier University,
Antigonish, Nova Scotia, B2G 2W5, Canada
[1]e-mail: btaylor@stfx.ca

ABSTRACT. Over 90 species of herbaceous dicotyledonous plants, representing 62 genera and 19 families, were recorded in blossom from northern Nova Scotia, Canada, during November and December 2001. Most observations were made during 10–20 November, but 29 species were in flower after 10 December. The number of species flowering declined steadily with time, rather than declining precipitously after the first frost. Only 6 of these 92 species are specifically reported in the floras of Nova Scotia as flowering in November. Examination of plant collections in the primary Nova Scotia herbaria showed that our collections represent the latest flowering records for all but one of these species in Nova Scotia. Accordingly, our collection extends the known flowering times for these species by an average of 45 days. For most species the late flowering is interpreted as an extension of normal phenology in response to unusually warm autumn weather, but for some species (e.g., *Viola cucullata*, *Ranunculus acris*, *Fragaria virginiana*) it appears to represent a second flowering period. Our collections establish a base line of late flowering times that could be used as an indicator of regional climate change.

Key Words: climate change, flowering, global warming, Nova Scotia, phenology

The reproductive period of flowering plants is determined by external environmental constraints (both biotic and abiotic) and physiological adaptations to those constraints (Daubenmire 1974; Zeevaart 1962). In temperate zones, the growing and flowering season is abruptly terminated in autumn by waning sunlight intensity and falling temperatures, especially those that produce frost. Given that temperatures, and hence the length of the growing season, vary from year to year, it is natural to expect that the flowering periods of at least some plant species will be flexible enough to reflect those differences; many late-flowering species continue to grow until they are killed by frost. Hence, one effect of warmer temperatures or late frost in a given year would be an extension of the flowering season (Salisbury and Ross 1992).

Flexibility in plant flowering periods is pertinent to the question of global warming, which is anticipated to increase mean annual temperatures by 2–4°C in Atlantic Canada (Moore et al. 1999), with an attendant lengthening of the annual period of above-zero temperatures. Autumn of 2001 provided a glimpse of what the future might hold: the weather was exceptionally moderate from September through

December, with only a few (and mild) frosts late into the season, accompanied by warm temperatures and gentle rainfall. If plants can adapt to longer growing seasons associated with transient or directional changes in their environment, we predict that reproductive periods would be extended in concert with a lengthening frost-free period.

Here, we document the apparently extended periods of flowering in the flora of Antigonish County, on the northern mainland of Nova Scotia, Canada. To confirm that the season was unusually warm, we compared weather records for autumn 2001 against climate normals (long-term averages) for the area. Our data provide the latest records of flowering for most of these species in Nova Scotia, and thereby establish a base line against which extensions or contractions of the flowering season in future years can be compared.

Our observations began in October when casual observations of roadsides and meadows revealed that many late-summer and fall plants were unexpectedly still in flower. Synoptic observations of the day-to-day weather suggested that the autumn was unusually warm. We began keeping records of species in which flowering persisted as the autumn progressed. From early November onward we began a concerted effort to observe and collect any flowering plants still in blossom. These observations continued until flowering in all native and naturalized species in the local flora had ceased, in mid-December.

MATERIALS AND METHODS

Regional climate. Antigonish County occupies the northeast end of mainland Nova Scotia, on the eastern edge of Canada (Figure 1). As Nova Scotia is a peninsula protruding into the Atlantic Ocean, there is a strong maritime influence on the continental climate of the province. Annual mean temperature inland in Antigonish County is 5.6°C for 1916–1990; the mean is 18.1°C in July and −6.7°C in January, the greatest range for any part of the province. The growing season is about 200 days (Nova Scotia Museum 1996).

Because of the maritime influence there is a powerful moderation of temperatures along the coast compared with sites inland. In addition, seasonal changes are delayed and extended compared with regions at the same latitude in central Canada. A long warm autumn, interrupted by occasional storms moving up the Atlantic coast, is typical of northern Nova Scotia (Nova Scotia Museum 1996). Nighttime frosts begin inland in early October in most years but may be delayed by two to three weeks along the coast. Snow does not begin to accumulate until late December.

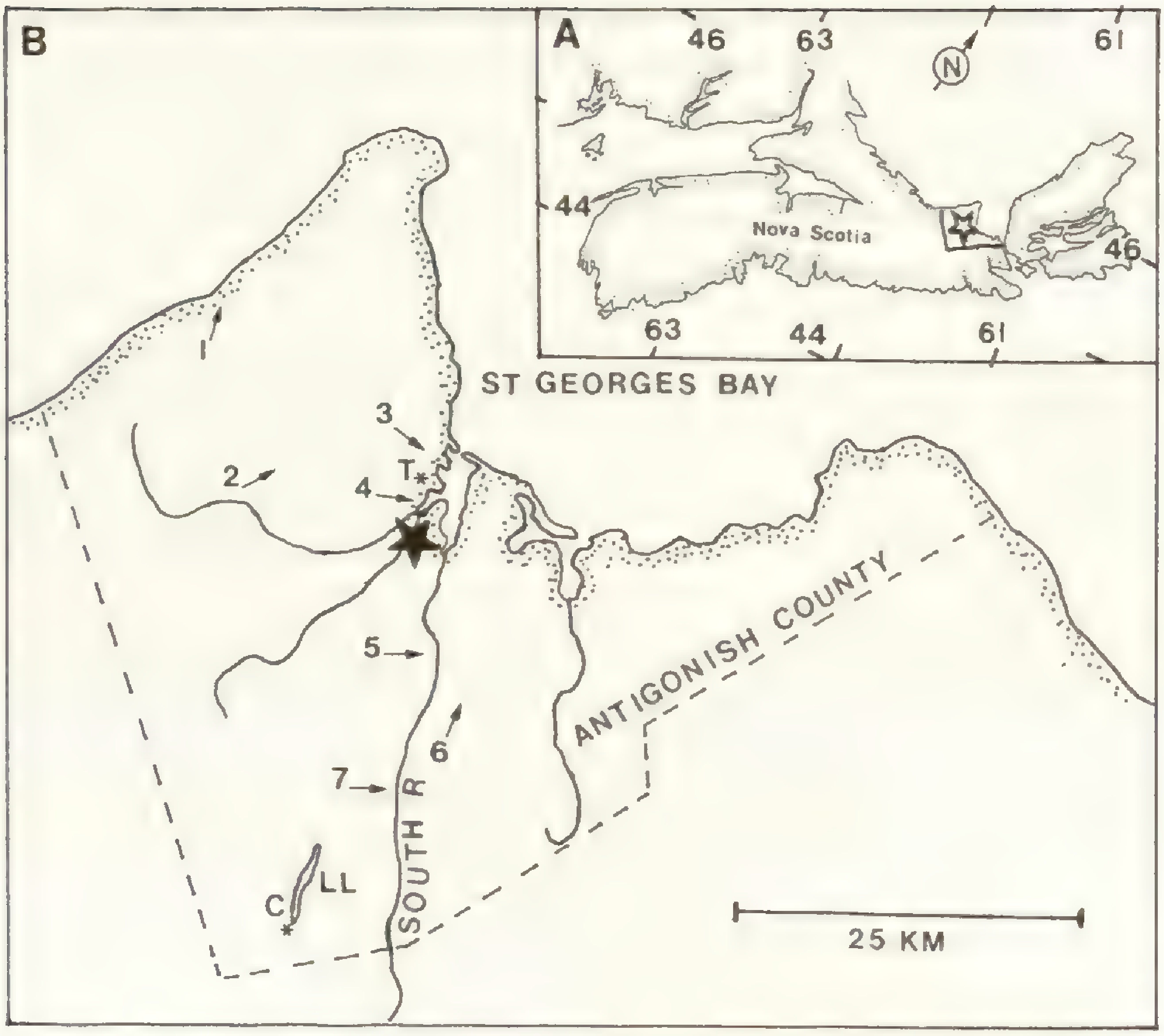

Figure 1. Map of Nova Scotia. A. Province, showing location of Antigonish County (star). B. Enlargement of Antigonish County showing sites of weather stations (*) at Collegeville (C) near Lochaber Lake (LL) and Town Point (T) and primary collecting sites: star – Antigonish Town; 1 = Malignant Cove; 2 = North Grant; 3 = roadside, Highway 337; 4 = Antigonish Landing; 5 = Dunmore Road; 6 = St. Andrews; 7 = Frasers Mills.

The Town of Antigonish lies on the coast adjacent to Northumberland Strait (Figure 1). The local climate of the town is therefore warmer in autumn and more moderate than sites even a few kilometres inland. The landscape of Antigonish County is composed of gently rolling hills defining shallow, wide river valleys. The varying elevations and aspects, coupled with a variety of land uses and vegetation types (chiefly residential, mixed forest, and farmland) creates many microclimates throughout the county. It is typical, for example, for river valleys to experience autumn frosts earlier than upland sites because of the accumulation of cooler air in depressions.

We obtained weather data from two standard Environment Canada weather stations at Antigonish and Collegeville. Daily records of minimum and maximum temperatures at the two sites for the months

Table 1. Summary of daily temperature data (°C) from a coastal station (Antigonish) and an inland station (Collegeville) in northern Nova Scotia, autumn 2001. Normals are 85-year averages (1916–1990) for Collegeville. [1]Daily temperature is average of maximum (Max.) and minimum (Min.) for each day. [2]Days with minimum temperature < 0°C. [3]Units are degree-days.

Month	Mean Temperature °C			Frost	Heat Units[3]	
Site	Max.	Min.	Daily[1]	no. of days[2]	> 5°C	< 0°C
September						
Antigonish	22.8	10.5	16.7	0	349.8	0
Collegeville	22.8	9.1	15.9	2	328.3	0
Normal	18.8	7.8	13.3	–	249.2	0
October						
Antigonish	17.2	5.0	11.1	4	192.1	0
Collegeville	16.1	3.9	10.0	5	163.8	0
Normal	13.0	3.3	8.2	–	111.9	0.3
November						
Antigonish	8.7	0.4	4.6	17	51.2	5.5
Collegeville	8.8	0.3	4.5	14	51.6	13.5
Normal	6.9	−0.9	3.0	–	30.8	19.8
December						
Antigonish	3.6	−2.6	0.5	25	12.5	31.7
Collegeville	2.6	−3.5	−0.5	27	8.5	58.5
Normal	1.0	−7.5	−3.2	–	5.1	130.5

of September through December 2001, along with precipitation and qualitative observations of sky conditions, were provided by the Atlantic Climate Centre of Environment Canada (Fredericton, New Brunswick). The Antigonish station is located in South Side Harbour, just outside the Town of Antigonish (45°37′N, 61°54′W; 30 m) and measures the coastal microclimate. The station at Collegeville (45°29′N, 62°01′W; 76 m) is located approximately 25 km inland (Figure 1).

We used climate normals from the Collegeville station, based on weather records from 1916–1990, as a base line against which to compare the weather in autumn 2001 (Table 1). Climate normals for Collegeville were downloaded from the webpage of the Meteorological Service of Canada, Environment Canada (www.msc-smc.ec.gc.ca/climate/index_e.cfm). The weather station at Antigonish is too recent (1990 onward) for climate normals to be established.

Plant collecting. We collected flowering plants in and about the Town of Antigonish. These collections were supplemented by additional collections in rural areas of Antigonish County, in particular along the valley of South River and along the roadside to Malignant Cove on the Northumberland Strait (Figure 1). Most species were found in waste ground in mixed herbaceous vegetation; however, collections were made from roadsides, agricultural land, regenerating woodlots, pasture land, and mixed forest. While we did not undertake a systematic survey of every habitat in the county we did make a concerted effort to seek out a variety of habitats and to thoroughly explore places where flowering plants were most persistent.

We collected only non-graminoid, herbaceous plants with conspicuous flowers. Grasses and some herbaceous species with cryptic flowers were excluded because it proved difficult to confirm whether they were fully in flower at the time of collection. No woody plants flower into fall in this region.

Collecting was initially terminated after 11 November because of a snowfall late in the day, followed by several days of heavy frost and subzero temperatures. Minimum temperatures for 12–15 November ranged from −2 to −6°C at Antigonish and from −3 to −6.5°C at Collegeville. Despite this apparently "killing" frost, many plants (17 species) were found in flower at a diversity of sites after 15 November, after the snow melted. Therefore we resumed collecting, and continued for as long as flowering plants could be found. The last collecting day was 15 December, when permanent snow cover began to accumulate.

All species in flower were noted during each sampling expedition, along with their habitat and general condition. At least one specimen of each species in flower was collected, pressed, and mounted. For some species, later or more conspicuously flowering specimens were also mounted. In the species list (Appendix), we have noted dates when plants were observed in flower after the date when a specimen was collected. Vouchers are deposited in the herbarium of St. Francis Xavier University, Antigonish, Nova Scotia (STFX). Phenology of species we collected was evaluated based on published accounts in Roland and Smith (1969) and Zinck (1998) and collections in the following herbaria: E. C. Smith Herbarium (ACAD), Nova Scotia Museum of Natural History (NSPM), and the A. E. Roland Herbarium (NSAC).

RESULTS

Weather. Temperature data from Environment Canada confirm that the autumn of 2001 was unusually warm in northern Nova Scotia (Table 1). Based on monthly averages for September through December, mean maximum, minimum, and daily temperatures at Collegeville for those months in 2001 were significantly warmer than the long-term average (t-tests, $P < 0.05$, $n = 4$), although the difference for daily minimum was barely significant. The daily maximum temperature averaged 4°C warmer in September, declining to 1.6°C warmer in December. Conversely, the difference in mean minimum temperature increased from 0.6°C to 4°C over the same period (October to December; Table 1). Mean daily temperature at Collegeville (the average of the daily maximum and minimum) was 1.5°C to 2.7°C warmer in 2001 than the long-term average. This is a substantial difference, equivalent in the short term to the degree of warming expected under projected increases in global CO_2 concentrations (Moore et al. 1999).

Calculation of heat units above 5°C, taken as the threshold temperature for plant growth, illustrates the extent of warmer weather in 2001. Heat units declined steeply from October to November as the days shortened; nevertheless, mean heat units in 2001 were 30–70% greater than the long-term average (Table 1). Similarly, negative heat units, calculated as the sum of degrees below zero for each daily minimum, summarize the frequency and severity of frost. Negative heat units were substantially less in November and December 2001 than the long-term average, indicating less severe frost (Table 1).

Average temperatures at the inland station, Collegeville, were about 1°C cooler than near the coast, except in November (Table 1). The first frosts occurred on 20 September (−2°C) and 30 September (−1°C) at Collegeville, but were delayed for a month at Antigonish (24 and 28 October). After September there was no marked difference in the frequency of frosts between the two sites, but because of the lower minima inland, frost there was generally more severe. There was a substantial difference in heat units between the two sites as well (Table 1).

Plant collections. A total of 92 species of herbaceous plants, representing 19 families, were found in flower in Antigonish County during November–December 2001 (Appendix; Table 2). All were dicots. One-third of the total (30 species) were native, with the remainder (62 species) being introduced from elsewhere, chiefly Europe (Zinck 1998). Although the greatest number of species was collected in early November, almost a third of the total (29 species) were still blooming after 10 December. All plants in our collection were terrestrial; despite regular inspections of aquatic habitats, we found no aquatic plants blooming in November. One specimen of *Polygonum*

Table 2. Distribution among families of late-flowering plants from Antigonish, Nova Scotia, in autumn 2001 in order of species richness. [1]Ratio of number of species collected to number of species listed in Zinck (1998).

Family	Number of Species Collected	Number of Species in Nova Scotia	Proportion of Known Species Collected[1]
Asteraceae	30	166	0.18
Brassicaceae	12	51	0.24
Fabaceae	7	41	0.17
Caryophyllaceae	7	35	0.20
Polygonaceae	7	41	0.17
Scrophulariaceae	5	38	0.13
Rosaceae	5	97	0.05
Lamiaceae	3	28	0.11
Apiaceae	3	30	0.10
Onagraceae	2	16	0.13
Malvaceae	2	7	0.29
Violaceae	2	15	0.13
Campanulaceae	1	8	0.13
Chenopodiaceae	1	23	0.04
Clusiaceae	1	9	0.11
Euphorbiaceae	1	9	0.11
Plantaginaceae	1	7	0.14
Ranunculaceae	1	24	0.04
Solanaceae	1	9	0.11
TOTAL	92	654	

sagittatum, a plant of damp ground, was collected from a sandbar bordering South River.

Several species were recorded based on single collections of one or very few individual plants. This group includes *Campanula rapunculoides*, *Hesperis matronalis*, *Viola cucullata*, *Polygonum persicaria*, and *P. sagittatum*. In several cases only a small population of individuals was present, growing in highly protected environments (e.g., *Cardamine pensylvanica*, *Centaurea nigra*, *Malva neglecta*, *Chaenorrhinum minus*, and *Dianthus armeria*). These species cannot confidently be said to be members of the late-flowering flora: the occurrence of a single plant blooming out of season could be a sport or a unique event caused by unusual habitat conditions, such as a heat-reflecting wall.

Our collections included members of 19 plant families of which 12 were represented by more than one species (Table 2). Greatest diversity occurred in Asteraceae (30 species) and Brassicaceae (12 species). These two families, along with the Caryophyllaceae, Fabaceae, and

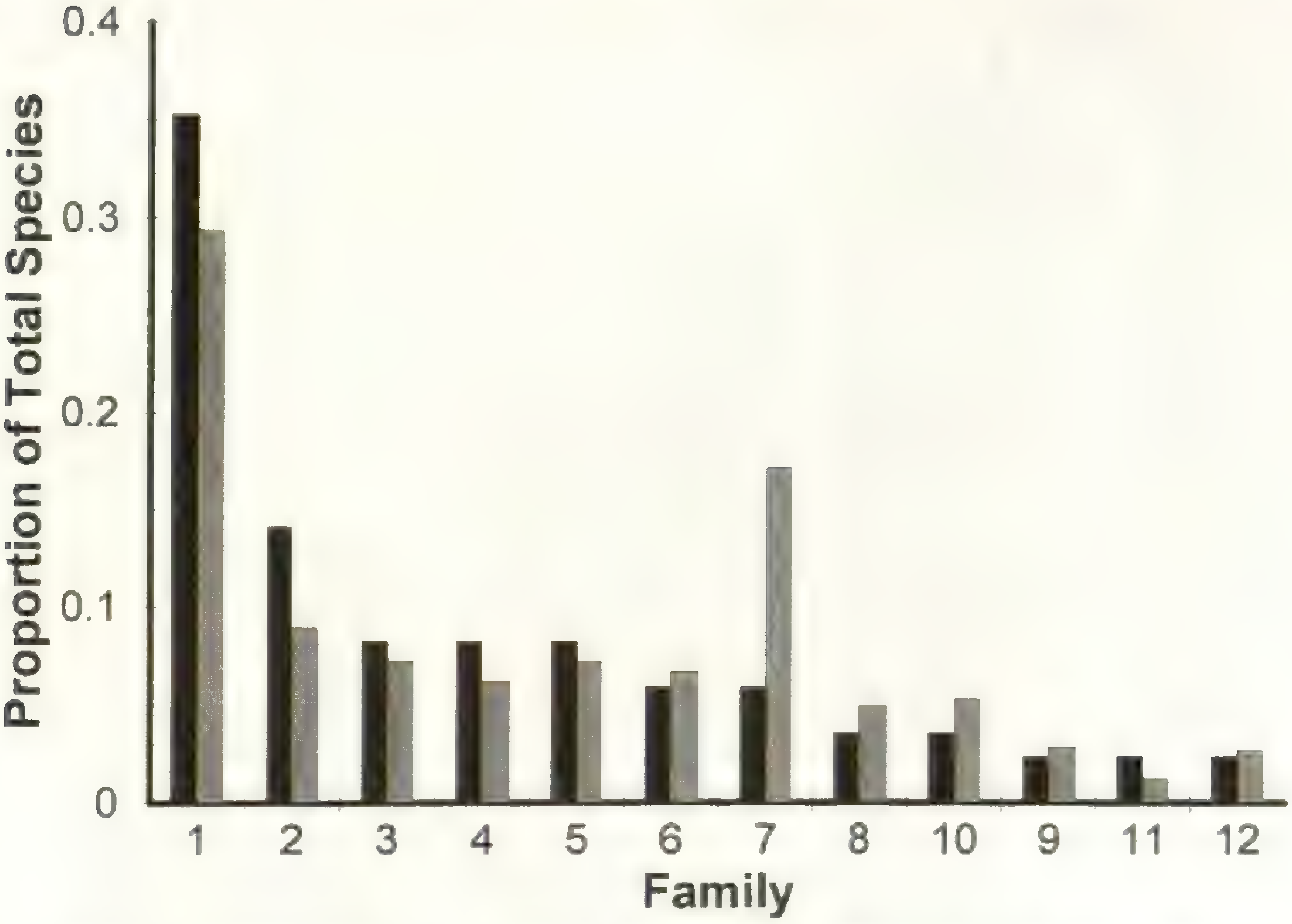

Figure 2. Proportions of species in the twelve families with more than one species in our collections. Dark bars indicate proportions in our collections; light bars indicate proportions in Zinck (1998). 1 = Asteraceae; 2 = Brassicaceae; 3 = Fabaceae; 4 = Caryophyllaceae; 5 = Polygonaceae; 6 = Scrophulariaceae; 7 = Rosaceae; 8 = Lamiaceae; 9 = Apiaceae; 10 = Onagraceae; 11 = Malvaceae; 12 = Violaceae.

Polygonaceae (7 species each) constituted almost 70% of all the late-flowering species. Asteraceae alone contributed almost a third of the total. The dominance of these families could be a consequence of a high proportion of late-flowering members, or merely the size of the family. In Figure 2, the number of species in each family is expressed as a proportion of the total number of species collected. Only the 12 most abundant families, those represented by more than one species in our collection, were included in the calculation. For comparison, the total number of species in each family as a proportion of the number of all species known from Nova Scotia (Zinck 1998) is also shown.

With the exception of the Rosaceae (7), the proportions of families in our collection are not very different from the proportions in the whole flora of Nova Scotia (Figure 2). There are proportionately more Asteraceae, Brassicaceae, Caryophyllaceae, and Polygonaceae among the late-flowering plants than in the whole flora, but the differences are not great. Hence, the dominance of Asteraceae among the late-flowering plants appears to be a result of the great number of species in this family, not a propensity toward extended flowering; the Asteraceae would be

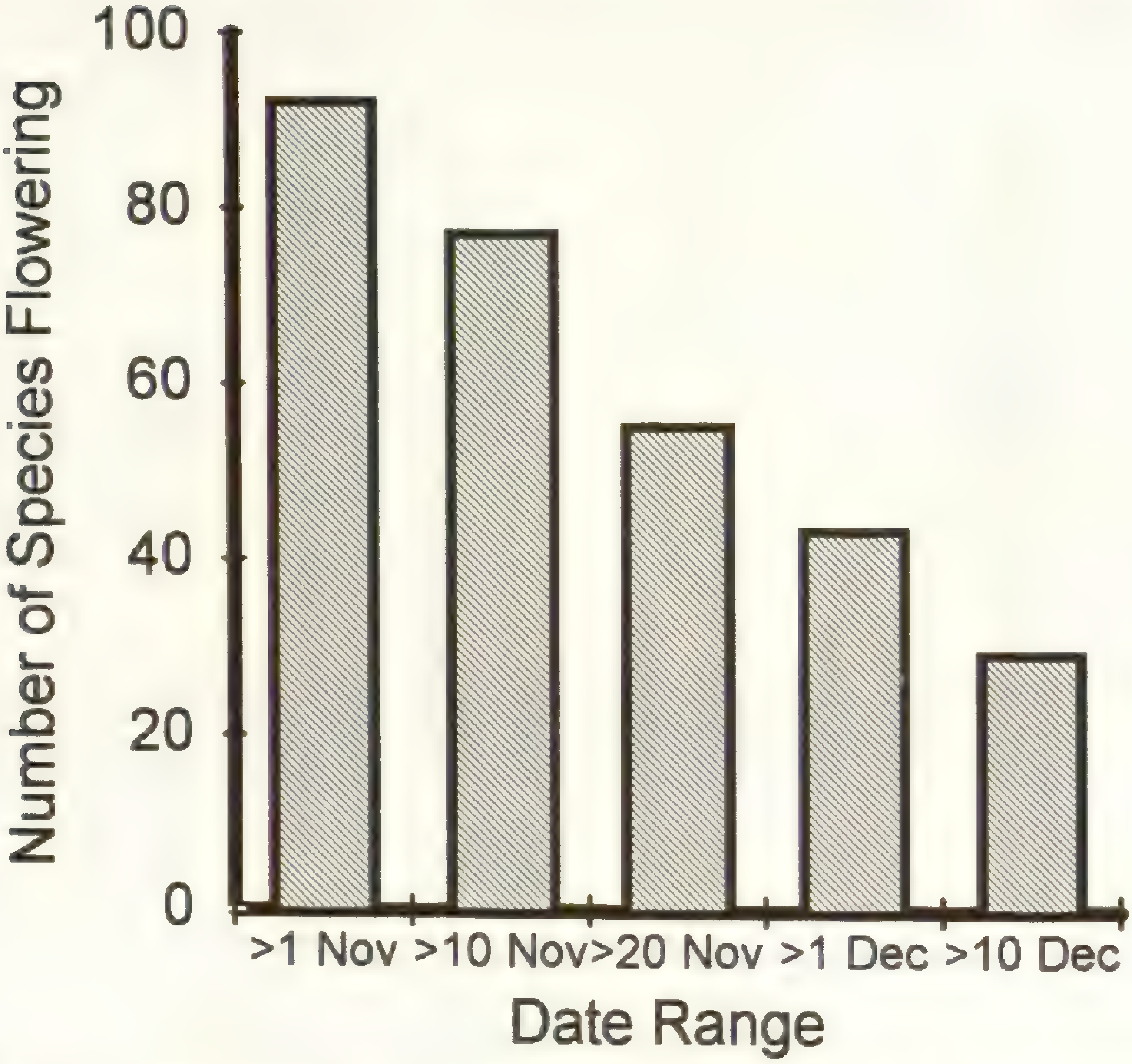

Figure 3. Number of species in flower in Antigonish County in 10-day intervals beginning 1 November 2001.

expected to dominate collections in any season. In fact, the only family that deviates conspicuously from the expected proportion is the Rosaceae, which is under-represented in the late-flowering plants. Most members of the Rosaceae in Nova Scotia bloom in spring (Zinck 1998).

To examine the temporal distribution of late-flowering plants, we divided the November–December season into five periods of 10 days each (Figure 3). Flowering ended in the middle of the fifth period, on 15 December. We assumed that each species was in bloom until the last day that flowers were observed, regardless of when the first flowering specimens were discovered. Hence, a species collected in flower for the first time on 18 November was assumed to have been blooming, undiscovered, before that date.

The growing season in 2001 did not end abruptly, as we had expected. Rather, the number of species in flower declined steadily from one period to the next (Figure 3), until the remaining plants died or were covered in snow on 15 December. The pattern in Figure 3 can be described with a simple linear function:

$$N = 107.2 - 16.0\ T$$

Where N = number of species in flower and T = sequential time period. The coefficient of determination (r^2) for this regression is 0.99 (n = 5).

Thus, it appears that, rather than truncating the growing season for all plants, bouts of cold weather during each period eliminated groups of species that had reached the limits of their cold tolerance. By the last period, after 10 December, only the hardiest species, or those populations growing in protected coastal sites, persisted. Nevertheless, these 29 species, nearly one-third of the total, were still blooming within the next five days. There was a major decline in flowering of native species relative to introduced species as the season proceeded. In early November 33% (30 of 92) of the species in flower were native; by mid-December only 15% (4 of 29) of the species were native (Figure 4).

DISCUSSION

Autumn of 2001 was remarkably mild throughout northern Nova Scotia. Comparison of Environment Canada weather records against long-term normals confirms that temperatures remained warm far longer in the fall than usual in 2001. While intermittent frosts began at about the same time in 2001 as in other years (usually the first week of October inland, unpub. data), below-zero temperatures were neither as frequent nor as severe (fewer negative heat units) as in a normal year. It is nevertheless surprising how many plant species continued to flower in the face of declining temperatures and intermittent freezing. Night temperatures regularly intercepted zero in late October, both at Antigonish and inland. After a brief warm spell in early November, night frosts became an irregular but frequent event for the rest of the month. Another brief warm spell began in December, before the final descent into winter temperatures. Despite the obvious cold, most of the plants we collected were robust and evidently healthy, and some had substantial local populations.

Our observations are consistent with long-standing conclusions of plant ecologists that sensitivity to frost, and hence the length of the growing season, varies widely among species (Daubenmire 1974). In Antigonish County, many species continued to grow and bloom despite being (apparently) repeatedly frozen several times each week, and sometimes covered with snow as well. Each period of cool weather, especially with nights of deep frost, led to the loss of progressively more

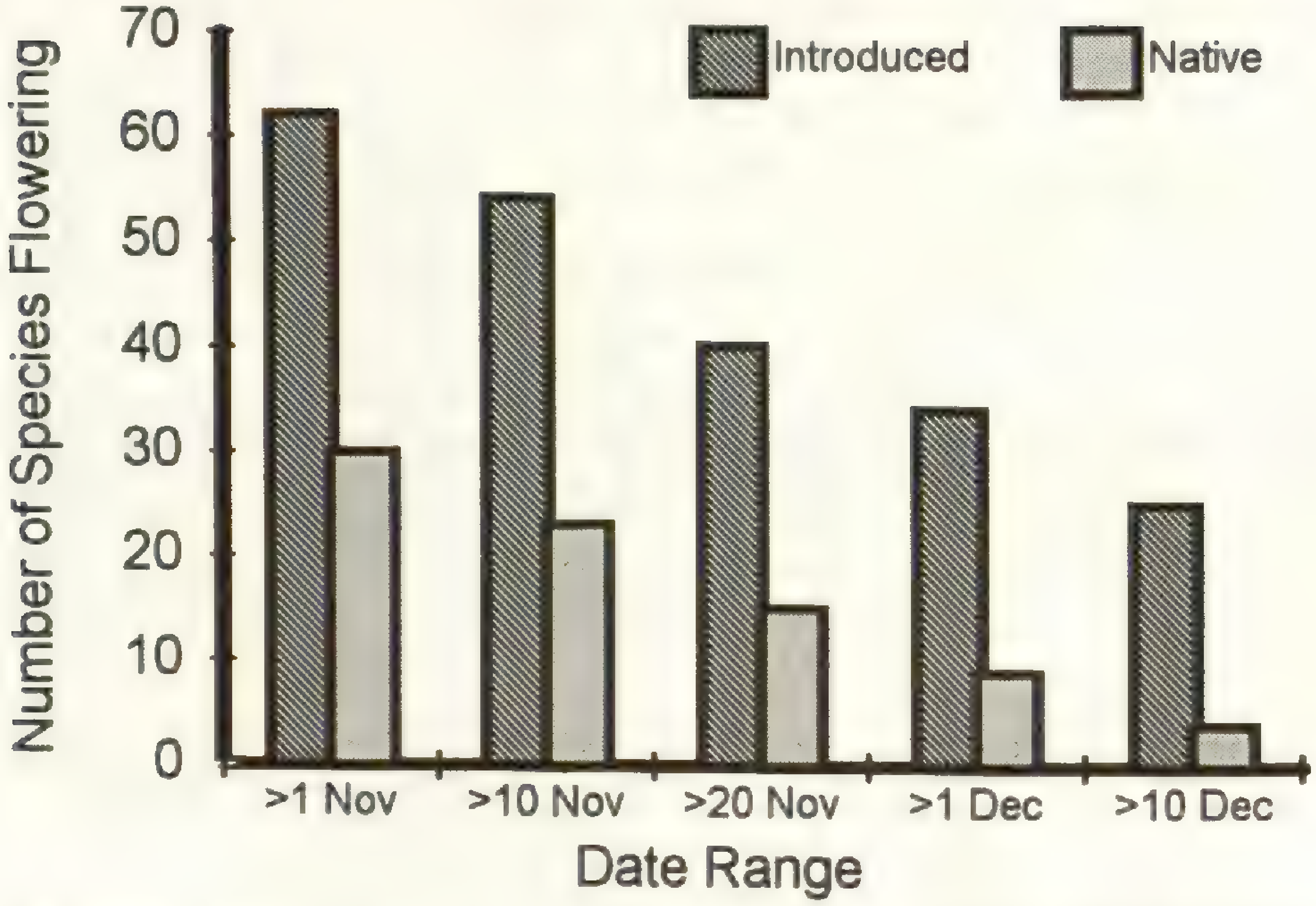

Figure 4. Numbers of introduced and native species flowering during successive 10-day intervals from early November 2001. Note the changing proportion of native species from 33% in early November to 14% in mid-December.

species from the flowering flora. Consequently, the number of species in bloom declined very steadily throughout the late autumn.

Accompanying the loss of flowering species was a steady shrinkage in the range of habitats in which flowering plants could be found. By mid-December, two groups included most surviving plants. The first group (e.g., *Cardamine pensylvanica*, *Leontodon autumnalis*, *Senecio vulgaris*) was found only in Antigonish, and many of the flowering individuals were in very protected habitats, sheltered from wind and perhaps receiving heat subsidies from nearby buildings. A second group (e.g., *Euphorbia helioscopia*, *Thlaspi arvensis*, *Trifolium pratense*) was found in agricultural fields or waste ground.

Most of the late-flowering plants we collected were growing in habitats that had been disturbed to some degree: roadsides, riverbanks, waste ground, gardens, and fields. We did not find any plants in bloom in November in forested land or in aquatic habitats. In fact, flowering in forest understoreys appeared to be over in October. Most of the plants in our collection are ruderals, growing as weeds and wildflowers in open ground where sunlight intensity is high and competition is low. It would be consistent with this *r*-selected life-cycle strategy that flowering time would be flexible, to take full advantage of extended growing seasons when they occur. In the more predictable, competitive environment of the forest, this kind of flexibility would confer less advantage. It is perhaps surprising though, that no emergent wetland plants were found blooming late.

The preponderance of weedy species in the late-flowering flora also accounts for the high proportion of introduced species. Roughly 25–30% of the flora of Nova Scotia is introduced (Nova Scotia Museum 1996), yet introduced species constitute fully two-thirds of our species list. The dominance of introduced species increased as autumn advanced. The majority of non-native species are weeds that were introduced with seeds and grain, and which have persisted in disturbed ground created by farming. These species typically have a very ruderal habit, growing quickly, seeding heavily, and showing great flexibility in phenology (Barbour et al. 1987). Native species dominate in more mature ecosystems such as forests, where we found no late-flowering plants.

We saw little evidence of selection in the taxonomic composition of the late-flowering flora. The species in our collection appear to be drawn from the flora of the region more or less in proportion with their species richness in each family. The conspicuous exception is the Rosaceae, whose members dominate the spring-blooming flora as the Asteraceae do the autumn. The only species in this family found flowering in late autumn were *Fragaria virginiana* and four species of *Potentilla*. The former species may be of special significance, however, because *F. virginiana*, along with a few other spring-flowering species (*Viola cucullata*, *Ranunculus repens*) was apparently entering a second round of flowering, as opposed to extending the flowering season. Futile autumn flowering in spring-flowering perennials has been known for a long time (Grainger 1939), and is prevalent whenever the onset of cold autumn weather is delayed (Daubenmire 1974).

We saw other evidence of "spring-like" behavior in fall 2001: flowers were expanding or breaking bud in *Sambucus* sp. and *Cornus stolonifera*, both of which normally bloom in spring or summer. Regardless of the mildness of the season, most flowering plants respond to day length as well as temperature in regulating their flowering periods (e.g., Fitter and Hay 1983; Zeevaart 1962). These observations therefore suggest metabolic confusion created by the combination of declining day length and mild temperatures.

The comparison of flowering times of the species in our collections with records in the three largest herbaria in Nova Scotia showed that for all but one species (*Centaurea nigra*), our collections represent the latest recorded flowering time for these plants in Nova Scotia. In fact, only six of the 92 species we collected are reported in Roland and Smith (1969) or Zinck (1998) as having flowering times that extend into November: *Capsella bursa-pastoris*, *Lamium amplexicaule*, *Matricaria matricarioides*, *Polygonum convovulus*, *Senecio vulgaris*, and *Stellaria media*. These authors have listed 106 species as flowering in October, 27 species as flowering in November, and 2 species as flowering in December. Of these 106 species, only 22 occurred in our collections. Thus an additional 84 species are potentially part of the November blossoming flora. These 106 species represent approximately 20% of the herbaceous dicot flora for the province. Hence, our list of 92 species is likely incomplete. Many new species were added to our collection in the final three weeks of the season. We attribute these late additions primarily to visiting new sites, as opposed to additional species coming into flower. Thus our list is probably highly constrained by collecting effort. Moreover, we cannot claim that our collections definitely establish the last date of flowering because we sampled destructively and non-systematically.

Compared with herbarium specimens and reported flowering seasons summarized in Roland and Smith (1969) or Zinck (1998), our collection extends the reported flowering season by an average of 45 days (range: 0 to 120 days; Figure 5). Notwithstanding the warm weather in 2001, a large part of this difference may be attributed to a lack of collection intensity during the late fall by previous workers in Nova Scotia. Herbarium records and phenological accounts in floras (e.g., Zinck 1998) generally reflect prime plants at the height of their development and not the extremes.

Based on a single year of collecting, it is not possible to attribute our records of late flowering in northern Nova Scotia to global warming. Nevertheless, our data suggest that the flowering phenology of many herbaceous species is very flexible. Therefore, if regional climate does change, it will be immediately reflected in the flowering periods of many herbaceous plants. In particular, we may expect more instances of autumn flowering among normally spring-blooming species if the regional climate grows warmer. It might prove advantageous to use species such as violets and wild strawberries as markers of climate change, because annual differences could be tracked by changes in the number of flowers produced by a small group of widespread species.

The bulk of the observations on flowering phenology that are associated with global warming refer to the earlier blooming of plants (e.g., Abu-Asab et al. 2001; Menzel et al. 2001; Post et al. 2001; Thorhallsdottir 1998). Phenological changes at the end of the growing

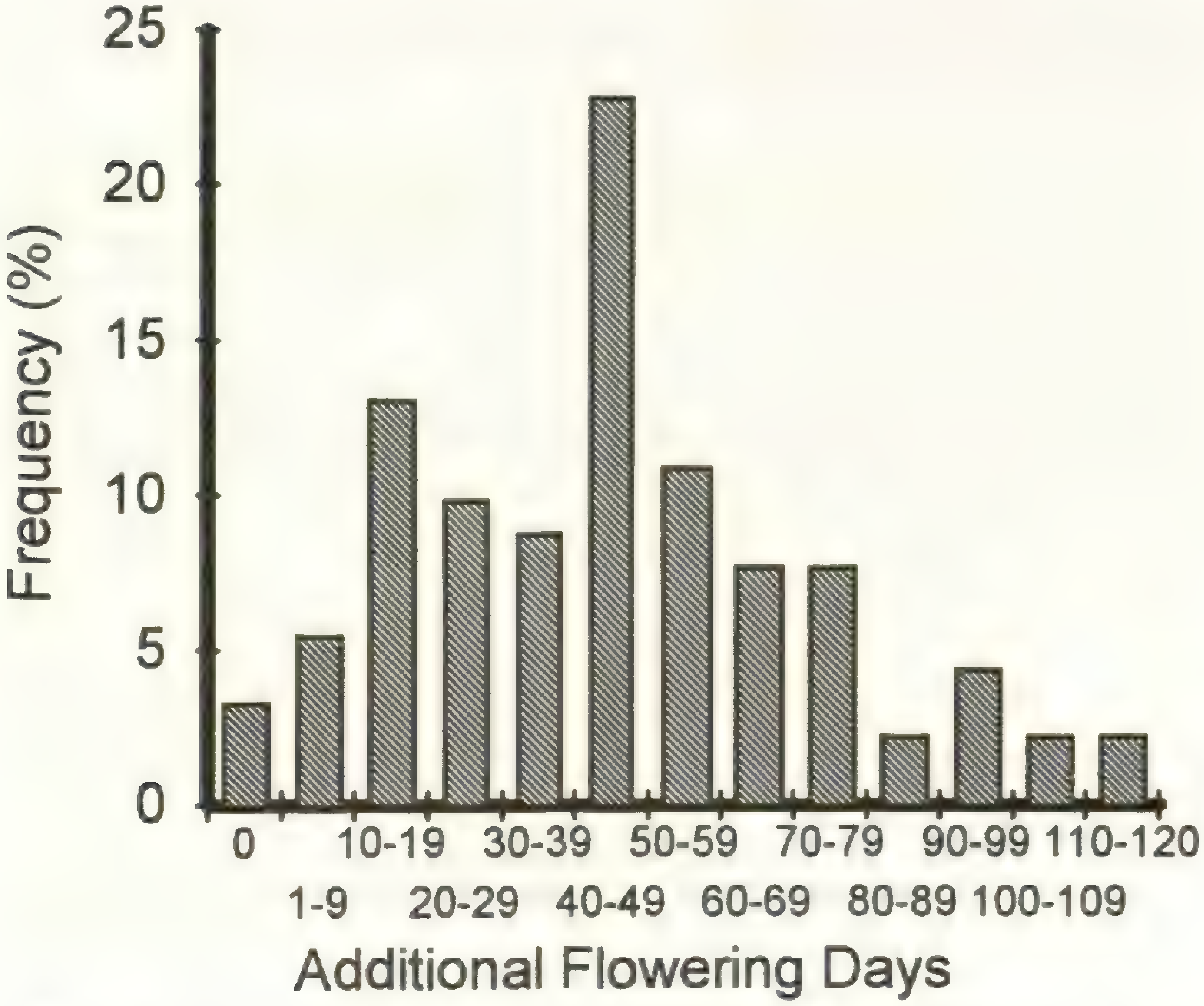

Figure 5. Extension of the flowering period in fall 2001, Antigonish County, Nova Scotia, relative to the latest herbarium specimens or flowering periods given in provincial flora. Data are frequencies among the 92 collected species falling into 10-day increments of additional flowering time.

season have been typically associated with lengthening of the period of vegetative growth rather than the period of reproduction (e.g., Menzel and Fabian 1999). Our observations suggest that flowering periods at the end of the growing season may show dramatic changes that reflect decreases in the frequency and intensity of frosts and slight increases in average daily temperature. Regardless of whether our flowering records reflect global warming, they do provide a base line against which future changes can be evaluated.

Although almost all of our collection or observation dates are the latest records of flowering for Nova Scotia, based on herbarium collections, our results cannot apply to the whole province. Antigonish County faces the Gulf of St. Lawrence in the northern mainland. Southern Nova Scotia, which has a decidedly milder climate and a longer growing season (Nova Scotia Museum 1996), may have many more late-flowering species than northern Nova Scotia. Indeed, we collected a specimen of *Raphanus raphanistrum* (wild radish) from disturbed ground near Yarmouth, at the southern tip of Nova Scotia, blooming through the snow on 25 December 2001.

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APPENDIX

List of species observed flowering in Antigonish County after 1 November 2001. The month given for Flora indicates the latest flowering time listed for the species in Zinck (1998); it is assumed that this indicates the last day of the month. The date given under Herbaria indicates the latest flowering specimen found in any of the three major herbaria for mainland Nova Scotia (NSPM, ACAD, NSAC). Additional days indicates the number of additional flowering days in Antigonish County compared with the latest time given in Zinck (1998) or a herbarium collection. Question marks indicate missing data. Nomenclature follows Zinck (1998).

	Latest Flowering Time			
Species	Flora (Zinck 1998)	Herbaria (Nova Scotia)	Antigonish Collection	Additional Days
Achillea millefolium L.	Sep	1 Nov 1987	14 Dec	34
Anaphalis margaritacea (L.) Benth. & Hook.	Sep	18 Oct 1981	5 Dec	48
Aster ciliolatus Lindl.	Sep	?	12 Dec	73
A. cordifolius L.	Oct	18 Oct 1979	12 Dec	42
A. lateriflorus (L.) Britton	Sep	28 Oct 1987	10 Dec	43
A. novi-belgii L.	Sep	20 Oct 1973	10 Dec	51
A. puniceus L.	Sep	4 Oct 1930	11 Nov	37
Bellis perennis L.	Sep	6 Jul 1950	16 Nov	47
Bidens frondosa L.	Sep	29 Sep 1941	7 Nov	37
Brassica nigra (L.) W. J. D. Koch	Oct	8 Sep 1949	10 Nov	10
B. rapa L.	Oct	27 Sep 1991	12 Dec	43
Campanula rapunculoides L.	Aug	20 Sep ?	7 Nov	48
Capsella bursa-pastoris (L.) Medik.	Nov	2 Nov 1979	14 Dec	14
Cardamine pensylvanica Muhl. *ex* Willd.	Aug	11 Sep 1949	15 Dec	96
Centaurea nigra L.	Sep	20 Nov 1994	17 Nov	0
Cerastium vulgatum L.	?	27 Oct 1915	15 Dec	49
Chaenorrhinum minus (L.) Lange	Aug	4 Sep 1948	15 Nov	73
Chenopodium album L.	?	11 Oct 1930	17 Nov	36
Chrysanthemum leucanthemum L.	Jul	10 Oct 1996	26 Nov	46
Conioselinum chinense (L.) Britton, Sterns & Poggenb.	Sep	15 Sep 1955	11 Nov	41
Daucus carota L.	Sep	19 Nov 1994	20 Nov	1
Dianthus armeria L.	Jul	1 Oct 1967	19 Nov	48
Erigeron annuus (L.) Pers.	Sep	1 Oct 1945	16 Nov	45
E. strigosus Muhl. *ex* Willd.	Sep	12 Oct 1912	8 Dec	57

Appendix Continued.

	Latest Flowering Time			
Species	Flora (Zinck 1998)	Herbaria (Nova Scotia)	Antigonish Collection	Additional Days
Erucastrum gallicum (Willd.) O. E. Schulz	Oct	18 Sep 1954	12 Dec	43
Erysimum cheiranthoides L.	Sep	23 Oct 1978	15 Dec	53
Euphorbia helioscopia L.	Sep	21 Oct 1912	14 Dec	54
Euphrasia officinalis L.	Sep	10 Oct 1930	10 Nov	30
Euthamia graminifolia (L.) Nutt.	Sep	6 Nov 1994	10 Nov	4
Fragaria virginiana Duchesne	May	5 Sep 1986	27 Nov	83
Galeopsis tetrahit L.	Sep	10 Oct 1969	14 Dec	65
Hesperis matronalis L.	Jul	5 Sep 1994	17 Nov	73
Hieracium floribundum Wimm. & Grab.	Jul	16 Sep 1979	24 Nov	69
Hypericum perforatum L.	Aug	21 Sep 1979	5 Nov	45
Lamium amplexicaule L.	Nov	18 Sep 1979	8 Dec	8
Leontodon autumnalis L.	Oct	20 Nov 1994	16 Dec	27
Lepidium campestre (L.) R. Br.	Sep	3 Sep 1969	6 Dec	95
L. virginicum L.	Sep	17 Oct 1917	5 Dec	49
Linaria vulgaris Mill.	Aug	18 Nov 1869	5 Dec	18
Malva neglecta Wallr.	Oct	1 Nov 1912	14 Dec	44
M. rotundifolia L.	?	18 Oct 1992	10 Nov	22
Matricaria maritima L.	Aug	11 Oct 1981	15 Dec	65
M. matricarioides (Less.) Porter	Nov	13 Oct 1944	14 Dec	14
Medicago lupulina L.	Sep	7 Oct 1987	12 Dec	66
Melilotus alba Desr.	Aug	9 Nov 1979	20 Nov	11
M. officinalis (L.) Lam.	Aug	19 Sep 1971	11 Nov	53
Oenothera biennis L.	Oct	16 Oct 1915	24 Nov	24
O. perennis L.	Sep	6 Sep 1938	10 Nov	40
Pastinaca sativa L.	Jul	5 Sep 1962	5 Dec	92
Plantago lanceolata L.	Oct	11 Nov 1979	11 Nov	0
Polygonum arenastrum Jord. *ex* Boreau	?	24 Oct 1923	12 Dec	49
P. convolvulus L.	Nov	11 Oct 1972	24 Nov	0
P. pensylvanicum L.	?	18 Oct 1912	11 Nov	23
P. persicaria L.	Oct	19 Oct 1915	25 Nov	25
P. sagittatum L.	Oct	10 Oct 1917	10 Nov	10
Potentilla argentea L.	Aug	24 Sep 1917	5 Dec	73
P. canadensis L.	Jun	27 Jul 1955	24 Nov	120
P. intermedia L.	Jul	21 Jul 1962	18 Nov	110
P. recta L.	Jul	28 Oct 1951	16 Nov	18
Ranunculus repens L.	Sep	21 Aug 1996	25 Nov	55
Raphanus raphanistrum L.	Oct	2 Nov 1987	20 Nov	18

Appendix Continued.

Species	Latest Flowering Time			
	Flora (Zinck 1998)	Herbaria (Nova Scotia)	Antigonish Collection	Additional Days
Rumex longifolius Alph. de Candolle	Oct	20 Oct 1930	16 Nov	16
R. obtusifolius L.	Sep	20 Oct 1930	10 Nov	20
Senecio jacobaea L.	Sep	7 Oct 1973	9 Dec	63
S. vulgaris L.	Nov	24 Oct 1923	15 Dec	62
Silene latifolia Poir.	Sep	10 Oct 1919	7 Nov	27
S. vulgaris (Moench) Garcke	Aug	24 Aug 1967	8 Dec	100
Sinapis alba L.	Aug	30 Jul 1971	14 Dec	106
Solanum dulcamara L.	Sep	23 Sep 1990	17 Nov	47
Solidago canadensis L.	Aug	11 Oct 1930	5 Dec	55
S. puberula Nutt.	Sep	30 Oct 1991	10 Nov	10
S. rugosa P. Mill.	Sep	3 Oct 1995	29 Nov	56
S. sempervirens L.	Sep	18 Oct 1979	18 Nov	30
Sonchus arvensis L.	Sep	22 Oct 1970	22 Nov	30
S. asper (L.) Hill	Oct	18 Oct 1979	9 Nov	9
S. oleraceus L.	Oct	20 Sep 1992	15 Nov	15
Spergula arvensis L.	Oct	28 Oct 1987	12 Dec	43
Spergularia rubra (L.) J. & C. Presl.	Sep	5 Oct 1928	12 Dec	68
Stellaria media (L.) Cirillo	Nov	11 Sep 1952	12 Dec	12
Tanacetum vulgare L.	Aug	15 Oct 1969	12 Dec	58
Taraxacum officinale (L.) Weber	Jun	23 Sep 1995	15 Dec	84
Thlaspi arvense L.	Sep	?	12 Dec	73
Thymus serpyllum L.	Aug	4 Sep 1964	15 Nov	72
Tragopogon pratensis L.	Aug	24 Oct 1930	7 Dec	42
Trifolium hybridum L.	?	4 Aug 1953	5 Nov	93
T. pratense L.	Sep	2 Nov 1912	12 Dec	30
T. repens L.	?	20 Oct 1930	18 Nov	29
Veronica persica Poir.	Sep	7 Sep 1951	28 Nov	59
V. serpyllifolia L.	Oct	21 Sep 1987	27 Nov	27
Vicia cracca L.	Aug	16 Oct 1997	27 Nov	42
Viola cucullata Aiton	Jul	22 Aug 1975	10 Nov	73
V. tricolor L.	Nov	13 Oct 1944	5 Dec	5

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DIPHASIASTRUM ×VERECUNDUM (LYCOPODIACEAE), *NOTHOSP. NOV.*

ARTHUR V. GILMAN

William D. Countryman Environmental Assessment & Planning,
868 Winch Hill Road, Northfield, VT 05658
e-mail: avgilman@together.net

ABSTRACT. Four live clones of the rare hybrid lycopod, *Diphasiastrum complanatum × digitatum*, have been located and studied in northern New England. This plant is described and a binomial provided.

Key Words: Lycopodiaceae, *Diphasiastrum*, hybrid

Four orthospecies and up to six hybrids of *Diphasiastrum* Holub, the flat-branched lycopods, occur in the hilly to mountainous highlands of Vermont, New Hampshire, and Maine. It is not unusual to find several species and hybrids growing together within small (< 1 ha) habitat patches. Such mixed "genus communities" (*sensu* Wagner and Wagner 1983) in northern New England present an excellent opportunity to study hybridism in the genus.

Diphasiastrum digitatum (Dill. *ex* A. Braun) Holub and *D. tristachyum* (Pursh) Holub are the most commonly encountered species in New England and, although locally rarer, *D. complanatum* (L.) Holub also regularly occurs, especially near and north of 45° north latitude. The fourth local orthospecies, *D. sitchense* (Rupr.) Holub, is primarily alpine in New England and consequently seldom occurs in mixed genus communities. Three hybrids are occasionally encountered in such communities: *D. ×sabinifolium* (Willd.) Holub (= *D. sitchense × tristachyum*), *D. ×habereri* (House) Holub (= *D. digitatum × tristachyum*), and *D. ×zeilleri* (Rouy) Holub (= *D. complanatum × tristachyum*). Two other hybrids are known from only a single collection each: *D. ×issleri* (Rouy) Holub [= *D. alpinum* (L.) Holub × *complanatum*; Wilce 1965] and *D. digitatum ×sabinifolium* (Gilman 1994).

The sixth hybrid known from the region is *Diphasiastrum complanatum × digitatum*. According to Wilce (1965, p. 160), it is the "rarest of the group of hybrids involving [*D. complanatum*, *D. digitatum*, and *D. tristachyum*]." In a thorough study of herbarium specimens from Quebec, Wilce (1965) scored 95 specimens of the putative parents for morphological characters and found only three fully intermediate hybrids, although 11 others shared some characteristics of both parents. Altogether, she was able to cite only 19 specimens of this hybrid, ranging from Quebec and Maine to Ontario, Wisconsin, and Minnesota, south to New Hampshire, Vermont, and Connecticut. However, she observed no living populations. Wagner and Beitel (1993) stated that the hybrid is "seemingly uncommon" but "probably far more common than collections indicate." My observations indicate that in northern New England, it is rare but not significantly more so than *D.* ×*habereri* or *D.* ×*zeilleri*. I have located and studied four extant populations, each of which may consist of a single clone.

Although Wilce (1965) reported partial spore abortion in several *Diphasiastrum* hybrids, mostly well-formed, presumably viable spores were observed in the *D. complanatum* × *digitatum* hybrids reported here. Spore viability and the nearly identical morphologies of the four clones studied both suggest not just isolated individuals, but a real group of lineages able to persist over time. Therefore, recognition of the taxon as a nothospecies (a reproductively competent species of hybrid origin) is merited. Both *D. digitatum* var. *ambiguum* Vict. (Victorin 1925) and *D. complanatum* var. *gartonis* B. Boivin (Boivin 1960) were suggested by their authors to apply to plants of this hybrid origin, but have been referred to *D.* ×*habereri* and *D.* ×*zeilleri*, respectively (Wilce 1965).

Diphasiastrum ×**verecundum** A. V. Gilman, *nothosp. nov.* TYPE: U.S.A. Maine: Aroostook Co., Macwahoc, large clone, uplands under powerlines, S of access road, just W of U.S. Rt. 2A, near N. Yarmouth Academy Grant town line, 31 Oct 1997, *Gilman 97395* (HOLOTYPE: NEBC; ISOTYPES: MAINE, MICH, VT). Figure 1.

Planta clavigerens, hybrida inter *Diphasiastrum complanatum* et *D. digitatum* orta; multum utrumque similata, sed pedunculo longiore, non flexile, robustiore, strobilis saepius quattuor a primo, ab altero pedunculo graciliore, ramibus secundo anno innovatis, et habitu haud flabelliforme differt.

Rhizome indeterminate, long-creeping to > 1 m, freely branching and forming large clonal patches, superficial to slightly buried, terete, 1.5–2.3 mm in diameter, loosely invested with widely spaced, short, narrow microphylls (hereafter "leaves"), these 1.8–3.0 mm long, 0.5–1.0 mm wide at base. Upright branch systems determinate, 10–16 cm tall (or with peduncles and strobili to 15–25 cm); axes terete, 1.5–2 mm in diameter, with widely spaced, short, narrow leaves, these 1.0–2.0 mm

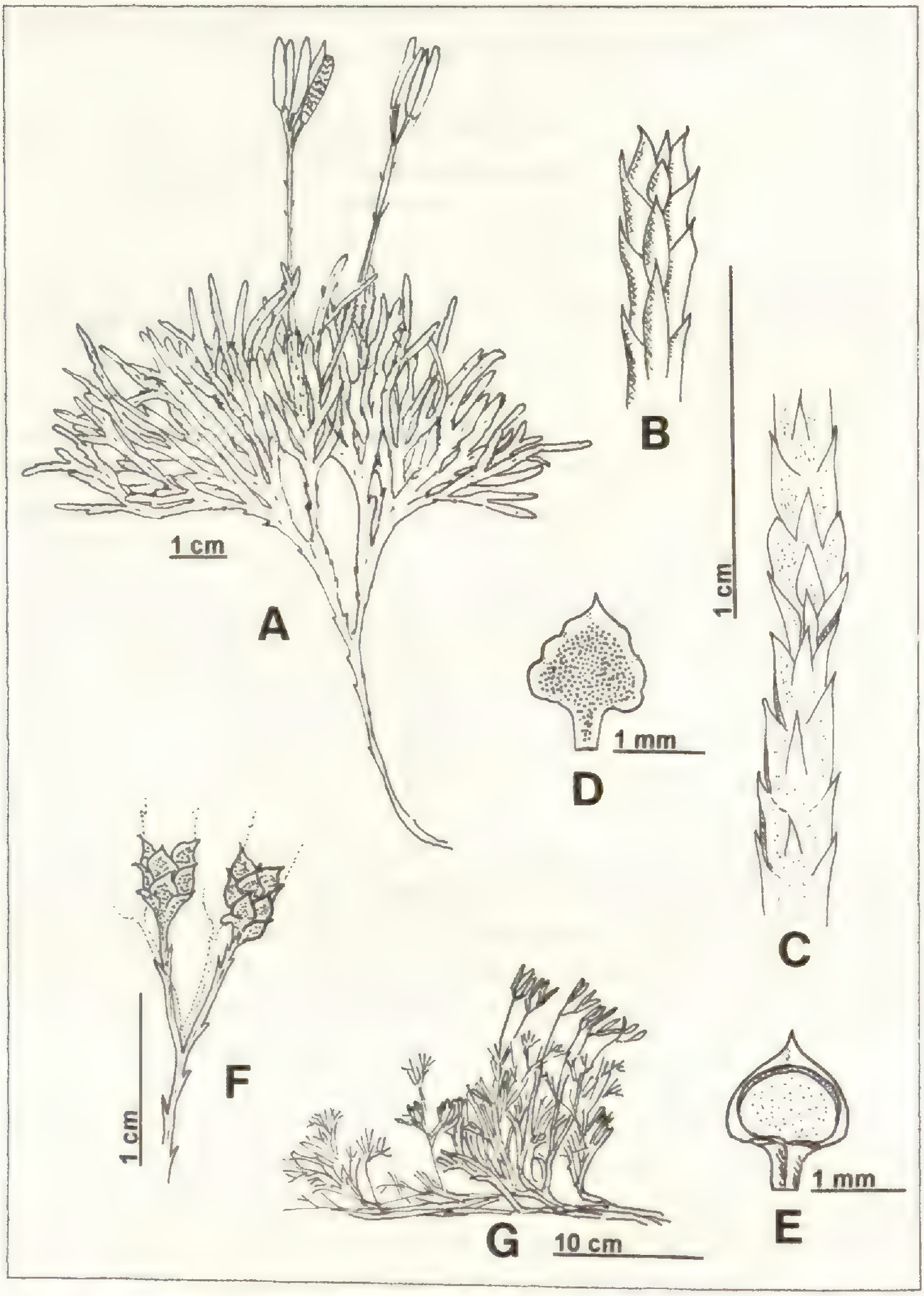

Figure 1. *Diphasiastrum* ×*verecundum*. A. Habit of one upright branch system. B. branchlet tip, dorsal view. C. Branchlet with annual constriction, ventral view showing stomata (schematic). D. Sporophyll, abaxial. E. Sporophyll, adaxial, with sporangium at dehiscence. F. Peduncle, pedicels, and base of strobili. G. Habit of entire plant. A–F drawn from *Gilman 94349* (NEBC); G drawn from *Gilman 97395* (NEBC).

long, 0.5–1.0 mm wide at base. Lateral branches spreading, dorsiventral, complanate, 1–2 mm wide, (3–) 4–7 (–8) cm long, (1–) 2 (–3) dichotomized, with 2/2 phyllotaxy; annual growth constrictions evident. Dorsal and lateral leaves prominent, each ca. 1/3 width of branch, 2.5–3 (4) mm long. Lateral leaves adnate for 0.8 their length, leaf tips hyaline, cuspidate, normally porrect, parallel to branch orientation, appressed or (in shade forms) spreading. Ventral leaves appressed, minute, < 1.0 mm wide at base, < 2.0 mm long, narrowly triangular with hyaline tip. Stomata abundant on ventral branch surface, lacking on dorsal surface. Fertile branches similar to main axis of upright branch systems, erect, terete or (if reclining) slightly complanate, 1.5–3 mm in diameter, (5–) 10–20 (–30) mm long, closely invested with numerous short, broad leaves imbricate in apparent 1/7 or 1/8 phyllotaxy; stomata abundant on abaxial leaf surfaces. Peduncles erect, slender but not flexuous, 0.8–1.2 mm in diameter, (2–) 3–6 (–7) cm long, often twice dichotomized to form 4 pedicels, angle of dichotomy narrow, 35°–40°. Peduncle leaves scattered, narrow, somewhat hyaline, usually spreading. Pedicels often four, with scattered spreading narrow leaves, slender, 0.5–0.9 mm in diameter, altogether (from base of first dichotomy) 5–15 mm long, individually (from base of second dichotomy) 2–11 mm long. Strobili 1–4 (–5), with well-defined bases, 3 mm in diameter, (1.6–) 2.0–2.5 (–3.0) cm long. Sporophylls subpeltate, spade-shaped, tips cuspidate, spreading at maturity, central portion green, margins hyaline, erose. Sporangia reniform. Spores many hundred in each sporangium, well-formed, yellow, trilete, surfaces prominently reticulate, 35–40 μm. Gametophyte unknown (in parents top- or carrot-shaped, subterranean, achlorophyllous, mycotrophic). Chromosome number undetermined ($n = 23$ in parents).

ETYMOLOGY. The specific epithet refers to the bashful nature of this taxon, which is rare, shows no outstanding features, and is consequently difficult to come to know.

HABITAT. Habitats are typically dry, with a shallow (1–2 cm) organic soil horizon overlying sandy or loamy soils.

Three of the four clones observed were growing in mixed-genus communities with at least four other *Diphasiastrum* taxa, including the putative parents; the fourth population was associated only with *D. digitatum*. One habitat was an old hayfield, mowed annually. The others, including the type locality, were electric transmission line corridors on lands that had previously been pastures or fields and were maintained in seral field and shrub associations at the time of this study.

Associated plant species, in addition to other *Diphasiastrum* taxa, included members of the regional upland flora typical of infertile soils, such as the mosses *Polytrichum juniperinum* Hedw., *P. piliferum* Hedw., and *Thuidium delicatulum* (Hedw.) BSG; clubmosses *Lycopodium clavatum* L., *L. hickeyi* W. H. Wagner, Beitel & Moran, and *L. lagopus* Zinserl. *ex* Kuzen; ferns *Pteridium aquilinum* (L.) Kuhn var. *latiusculum* (Desv.) Underw. *ex* Heller, *Dennstaedtia punctilobula* (Michx.) T. Moore, and *Thelypteris noveboracensis* (L.) Nieuwl.; grasses *Agrostis capillaris* L., *A. perennans* (Walter) Tuck., *Brachyelytrum erectum* (Schreb. *ex* Spreng.) P. Beauv. var. *glabratum* (Vasey) Koyama & Kawano, *Bromus ciliatus* L., *Danthonia spicata* (L.) F. Beauv., and *Dichanthelium boreale* (Nash) Freckmann; forbs *Anaphalis margaritacea* (L.) Benth. & Hook., *Antennaria neglecta* Greene var. *canadensis* (Greene) Cronquist, *Cornus canadensis* L., *Euthamia graminifolia* (L.) Nutt., *Hieracium pilosella* L., *Lysimachia quadrifolia* L., *Solidago nemoralis* Aiton; and low shrubs *Rubus hispidus* L., *Gaultheria procumbens* L., *Vaccinium angustifolium* Aiton, and *Spiraea alba* Duroi var. *latifolia* (Aiton) Dippel.

Diphasiastrum ×verecundum is much like *D. complanatum* and *D. digitatum*, but it differs from the first in a longer, less flexuous, more robust peduncle, and more often four strobili on each peduncle. From *D. digitatum* it differs in a more gracile peduncle and lateral branches growing through two or more successive years. The dorsal leaves are often slightly wider than in *D. digitatum*, although this character is difficult to assess due to variation. It also has somewhat the straggling or discomposed habit of *D. complanatum* and lacks the regular, fanlike branching habit that normally strongly characterizes *D. digitatum*.

Wilce (1965, p. 160) stated that this hybrid "is probably the least difficult to recognize and identify," based on intermediacy of characters. Unfortunately this intermediacy results in a merely "generic" appearance. There are no unique, idiosyncratic, or transgressive characters that allow immediate recognition. Field identification is aided in mixed communities by comparison with living material of the other taxa, especially if one is familiar with its progenitors as well as with *Diphasiastrum tristachyum* and its hybrid progeny. Of some aid in recognition are the small size and narrow shape of the ventral leaves (Figure 1C), features shared by its progenitors but different from the typically longer and wider ventral leaves of *D. tristachyum*. In life, *D. ×verecundum* has a bright, emerald green color, quite dissimilar from the yellow-green color typical of *D. digitatum*, from the dull, darkish-green to yellow-green color of *D. complanatum*, and from the glaucous blue-green color of *D. tristachyum* and its hybrids. Plants from shaded habitats are particularly difficult to assess, as are dried and pressed specimens. Therefore, the above description is based on plants from the four living populations observed, all occurring in open, sunny habitats.

Relationships in *Diphasiastrum* are unresolved and the presumed hybrid origin of taxa of intermediate morphology has not been fully demonstrated. At least some hybrids are homoploids with diploid ($2n = 46$) chromosome numbers (Hersey and Britton 1981; Wagner 1980, 1992). Although Whittier and Britton (1995) succeeded in culturing gametophytes from spores of *D.* ×*habereri*, *Diphasiastrum* is difficult to cultivate and no hybrid has been produced in culture. Stoor et al. (1996) concluded additive isozyme banding patterns (phosphoglucoisomerase and esterase) supported a hybrid origin (*D. alpinum* × *tristachyum*) for the European plant they named *D. oellgaardii*, but such patterns are not logically unequivocal for homoploid taxa (Vogel and Rumsey 1999). Unlike taxa of allopolyploid origin, in which a multiplied chromosome complement convincingly argues that progenitors must have preceded derivatives, so-called "additive" banding patterns in homoploids might indicate segregating, not hybridizing, lineages. Indeed, Vogel and Rumsey (1999) questioned the validity of the hybrid hypothesis for this reason. However, it is improbable that divergent speciation would have resulted in taxa intermediate in so many morphological characters as those observed. The group indeed presents a difficult puzzle that invites further investigation by imaginative means.

ADDITIONAL SPECIMENS: U.S.A. Maine: Aroostook Co., Haynesville, large clone at S edge of powerline corridor, just W of the village of Haynesville and just upslope of U.S. Rt. 2A, 24 Aug 2000, *Gilman 2K186* (MAINE, NEBC). Vermont: Essex Co., Concord, on old pasture land under powerlines (the adjacent areas having grown up to boreal forest), near Joslin Turn, 19 Sep 1999 et seqq. *Gilman 99220* (VT, NEBC); Lamoille Co., Wolcott, one large clone, old pasture, north of Eastman Cross Road, 19 Nov 1994 et seqq., *Gilman 94349* (VT, NEBC).

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AN OVERLOOKED HYBRID JAPANESE KNOTWEED (*POLYGONUM CUSPIDATUM* × *SACHALINENSE*; POLYGONACEAE) IN NORTH AMERICA

PETER F. ZIKA[1] AND ARTHUR L. JACOBSON

Herbarium, Department of Botany, Box 355325,
University of Washington, Seattle, WA 98195-5325
[1]e-mail: Zikap@aol.com

ABSTRACT. A new combination is provided for the hybrid between *Polygonum cuspidatum* and *P. sachalinense*. The hybrid, *Polygonum* ×*bohemicum* (J. Chrtek & A. Chrtková) P. F. Zika & A. L. Jacobson, *comb. nov.*, is widespread and invasive across North America. We illustrate the parents and hybrid, and supply a key to distinguish the three taxa.

Key Words: Polygonaceae, hybrid Japanese knotweed, *Polygonum* ×*bohemicum*, invasive plants

Polygonum cuspidatum Siebold & Zucc. and *P. sachalinense* F. Schmidt *ex* Maxim. (Polygonaceae) are common naturalized members of the flora of North America. They are native to northeastern Asia, and are noted for their large size and formation of extensive rhizomatous colonies. Their hybrid is little known, and is not even mentioned in the catalog of North American plants by Kartesz (1999), although hybrids in the group have been studied elsewhere (Bailey and Stace 1992; Bailey et al. 1996; Kim and Park 2000). However, all three taxa have a long history of economic importance—first as garden ornamentals, then as invasive adventives displacing native plants (Brock et al. 1995; Townsend 1997). In Europe *P. cuspidatum* was first cultivated in the 1840s, whereas *P. sachalinense* has been grown as an ornamental since 1864 (Bailey and Conolly 2000). Their hybrid was grown in English gardens from 1872 onward, although only recently was the parentage recognized (Bailey and Conolly 2000). Their value as ornamentals has perhaps now been surpassed by the cost of control for these three invasive and dominating taxa (Bailey et al. 1995; Sukopp and Starfinger 1995). *Polygonum cuspidatum* is widespread in North America, and classified as a noxious weed in North Carolina, California, Oregon, and Washington. *Polygonum sachalinense* is also established across the continent, and classified as a noxious weed in California and Washington (Kartesz 1999; Toney et al. 1998). In Great Britain, *P. cuspidatum* is considered the "nation's most pernicious weed" (Townsend 1997).

In our area, western Washington, the hybrid is more common in cultivation than *Polygonum cuspidatum* or *P. sachalinense*. In our field investigations we observed the hybrid had commonly escaped from ornamental plantings, and aggressively colonized riverbanks, roadsides, garden dumps, and disturbed ground. It can appear anywhere earth-moving activity might introduce a rhizome. In lowland Washington the hybrid is more abundant than either parent as a wild plant. We turned to the herbarium to determine its distribution outside of the Pacific Northwest, and we found that many specimens in this aggregate are misnamed. The hybrid is widespread in North America, yet unrecognized as such. For example, we found six publications with illustrations labeled *P. cuspidatum* that were actually the hybrid *P. cuspidatum* × *sachalinense* (Hickman 1993; Hitchcock and Cronquist 1964; Mitchell and Dean 1978; Radford et al. 1968; Strausbaugh and Core 1978; Whitson 1991).

The hybrid was first recognized, studied, and named in Europe under the segregate genera *Reynoutria* Houtt. (Chrtek and Chrtková 1983) and then *Fallopia* Adans. (Stace 1989). We agree with Bailey and Stace (1992) that *Reynoutria* must be combined with *Fallopia*; there are species transitional between the two concepts. However, in contrast to those authors who give it the rank of genus, we believe that *Fallopia* is best placed as a section of *Polygonum* L. Base chromosome numbers are similar throughout the genus *Polygonum s.l.*, excepting *Fagopyrum* Mill., but including all elements of *Fallopia* (Bailey and Stace 1992). Minor floral differences form the basis of division for most segregate genera in *Polygonum* L. (Ronse Decraene and Akeroyd 1988). The floral differences make good sectional or subgenus groupings within *Polygonum s.l.*, similar to subgeneric rankings in *Solanum* L., *Prunus* L., *Juncus* L., or *Carex* L. We consider *Fallopia* (including *Reynoutria*) a taxonomic synonym of *Polygonum*, as have virtually all North American authors (e.g., Douglas et al. 1999; Gleason and Cronquist 1991; Hickman 1993; Mitchell and Dean 1978; Voss 1985; Wolf and McNeill 1986, 1987). There is no name for this hybrid Japanese knotweed in the genus *Polygonum*, which we provide here.

Polygonum ×bohemicum (J. Chrtek & A. Chrtková) P. F. Zika & A. L. Jacobson (*P. cuspidatum* Siebold & Zucc. × *P. sachalinense* F. Schmidt *ex* Maxim.), *comb. nov. Reynoutria ×bohemica* J. Chrtek & A. Chrtková, Čas. Nár. Mus., Odd. Přír. 152(2): 120. 1983. TYPE: CZECH REPUBLIC. Province of Bohemia: District of Náchod, prope balneas Běloves, non procul ab oppido Náchod

> [near spa of Běloves, not far from Náchod], 15 Aug 1982, *J. Chrtek & A. Chrtková s.n.* (HOLOTYPE: PR!). *Fallopia* ×*bohemica* (J. Chrtek & A. Chrtková) J. P. Bailey, Watsonia 17(4): 443. 1989.

Hybrid Japanese knotweed, or Bohemian knotweed, *Polygonum* ×*bohemicum*, has leaves intermediate in size between its parents (Figure 1). The leaves of *P. sachalinense* are thin, but the leaves of *P.* ×*bohemicum* and *P. cuspidatum* are thicker and tougher. Mid-stem leaves of *P. cuspidatum* are less than 18 cm long; in *P. sachalinense* they are often more than 30 cm long. The hybrid has leaves of intermediate length, sometimes approaching the length of one or the other of the parents. The hybrid is variable in the shape of the leaf base on mid-stem leaves. Most are slightly cordate, though they can approach the deeply cordate shape of *P. sachalinense* in some extremes, and the essentially truncate leaf base of *P. cuspidatum* on other plants (Figure 1). The mid-stem leaves of *P. sachalinense* are generally evenly tapered to a blunt or short-acute tip, while the corresponding leaves of *P. cuspidatum* are abruptly cuspidate and long acuminate. The hybrid has mid-stem leaf tips intermediate, generally long acuminate but not cuspidate. Mid-stem leaves are rarely seen on herbarium specimens. Another useful character in the field is plant habit. *Polygonum sachalinense* grows to 5.3 m tall in Seattle and branches sparingly. *Polygonum cuspidatum* is usually 1.5–2 m tall, but we have seen plants 2.5 m in height. It branches profusely. The hybrid is intermediate, usually 2.5 m tall, ranging from 2–3 m tall in some clones. Both parents and the hybrid can be stunted in exposed sites on the outer coast of Washington.

The three taxa are most effectively distinguished by pubescence on the underside of the leaves, which is easiest to find early in the growing season, from June through flowering in mid-September (Figure 2; Bailey et al. 1996). Later in the growing season many of the distinctive hairs are shed. In our experience, veins on the basal half of the leaf underside are the best place to see the characteristic hairs, but many herbarium specimens are mounted inconveniently. Pubescence on the upper surface or margin of the leaves is not diagnostic. Although the hairs of *Polygonum sachalinese* and *P.* ×*bohemicum* are small, with practice they can be located with a 15–20× hand lens, by bending a fresh leaf to backlight the midvein against the sky. The swollen scabers characteristic of *P. cuspidatum* are more difficult to see without high magnification (30–40×), and are usually quite scattered. The inflorescence of *P. cuspidatum* has well-developed simple hairs. The diagnostic multi-

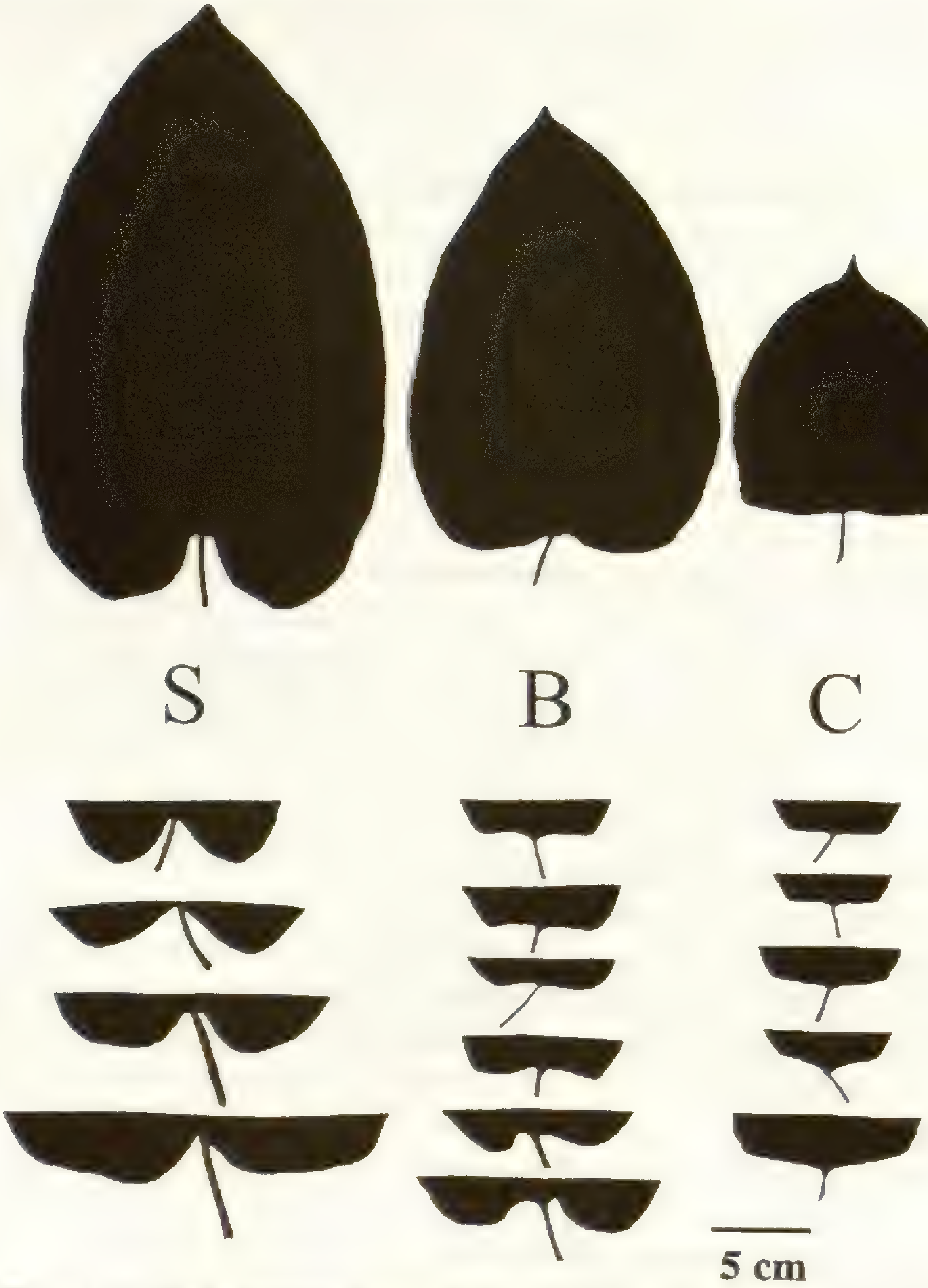
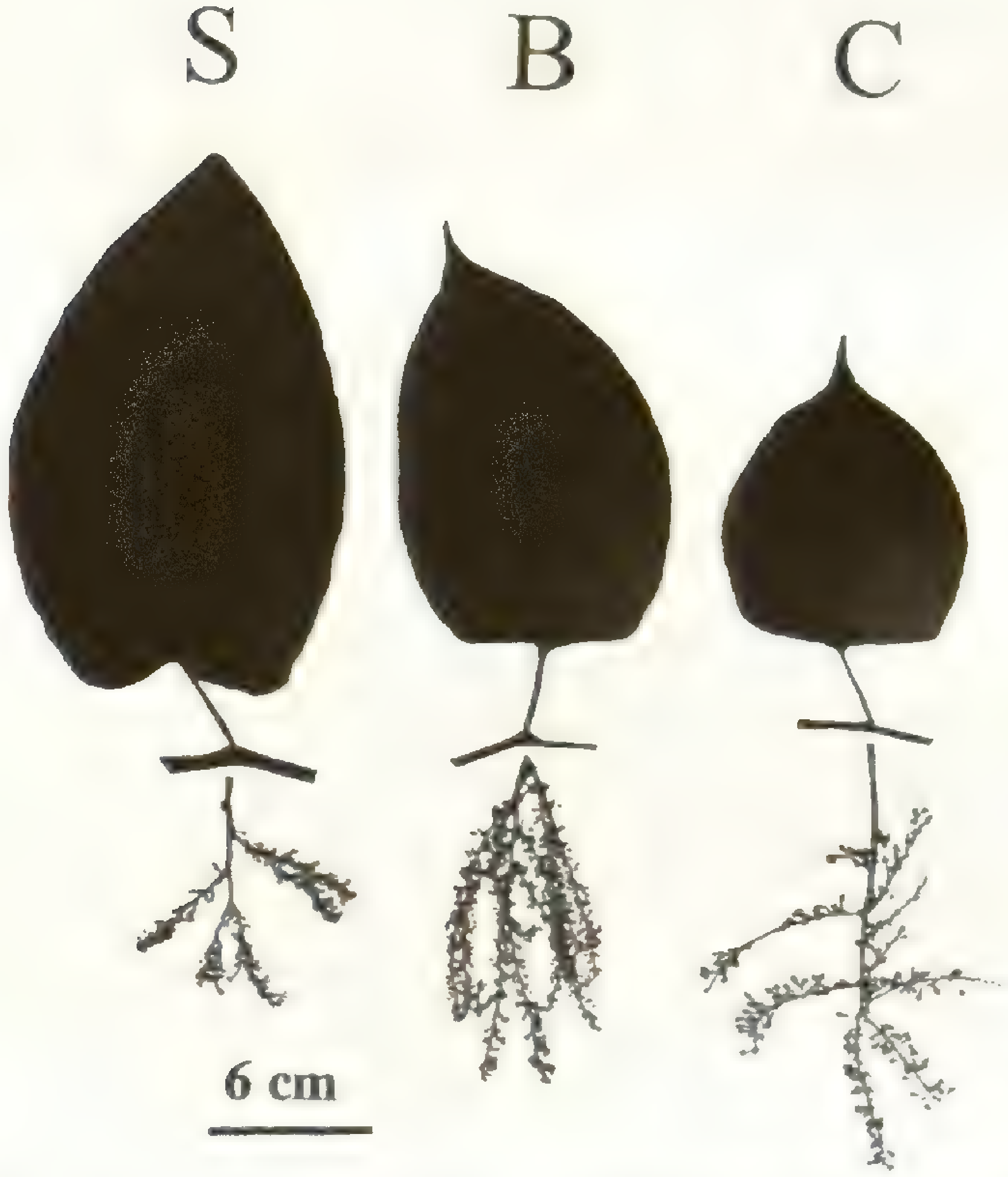


Figure 1. Leaf silhouettes for mid-stem leaves of *Polygonum*, showing variation in shape of leaf bases. S = *P. sachalinense*, note deeply cordate base, and short tip, acute to blunt (*Zika 16464*, WTU). B = *P.* ×*bohemicum*, note base varies from deeply cordate to slightly cordate or essentially truncate; leaf apex gradually tapered, acute or acuminate (*Zika 16624*, WTU). C = *P. cuspidatum*, note truncate to slightly cuneate base; apex abruptly acuminate or cuspidate (*Zika & Jacobson 16466*, WTU).

cellular hairs of *P. sachalinense* are easily seen on the leaf underside. Usually some can also be found at the base of the upper leaf surface, or on the petiole, and they are common in the inflorescence. The hybrid has hairs intermediate in size and morphology between the parents.

2

3



Figures 2–3. *Polygonum* morphology. 2. Hairs on veins of lower leaf surface. S = *P. sachalinense*, narrow-based long multicellular hairs (*Bernard B82-313*, GH). B = *P.* ×*bohemicum*, broad-based stout single-celled hairs (*Halse 4299*, GH). C = *P. cuspidatum*, blunt broad-based scabers or knobs (*MacDonald 11408*, MO). 3. Relative length of inflorescence and subtending mid-branch leaf. S = *P. sachalinense*, inflorescence < leaf (*Zika 16464*, WTU). B = *P.* ×*bohemicum*, inflorescence variable, usually ≤ leaf (*Bean 15753*, NEBC). C = *Polygonum cuspidatum*, inflorescence ≥ subtending leaf (*Zika & Jacobson 16466*, WTU).

Characteristic hairs are scattered on the larger veins of the leaf underside, are simple, not multicellular, and are swollen at the base. Inflorescence hairs are mostly simple, like *P. cuspidatum*, but in some clones it is possible to find scattered multicellular hairs derived from *P. sachalinense*.

The inflorescence of *Polygonum cuspidatum* is typically longer than the subtending mid-branch leaf, whereas the inflorescence of *P. sachalinense* is much shorter than the subtending leaf at mid-branch. The hybrid inflorescences are usually intermediate in length relative to the length of the subtending mid-branch leaf (Figure 3).

The key below is written for use with fresh flowering material. In addition, unlike most herbarium collectors, avoid leaves from the tip of the flowering branches, as they are not characteristic in shape or size.

KEY TO THE *POLYGONUM* HYBRID AND ITS PARENTS

1. Veins of leaf underside with multicellular hairs (20×; Figure 2); mid-stem leaf bases deeply cordate; inflorescence much shorter than subtending mid-branch leaf . . . . *P. sachalinense*

1. Veins of leaf underside with simple hairs, or slightly and minutely scabrous (Figure 2); mid-stem leaf bases truncate to slightly cordate or slightly cuneate; inflorescence shorter or longer than subtending mid-branch leaf 2

    2. Veins of leaf underside with scattered simple stout-based hairs; mid-branch leaf base usually slightly cordate; well-developed mid-stem leaves usually > 20 cm long . . *P. ×bohemicum*

    2. Veins of leaf underside minutely scabrous with scattered swollen cells or knobs; mid-branch leaf base truncate (rarely slightly cuneate); largest mid-stem leaves < 18 cm long . . . . *P. cuspidatum*

The reproductive biology of *Polygonum ×bohemicum* and its parents is an interesting example of gynodioecious perennials reproducing primarily by vegetative means. In England, *P. cuspidatum* (var. *cuspidatum*) is represented by a male-sterile clone, and a similar situation seems to exist in western Washington. Although this clone often sets copious fruit, viable seeds are the result of pollen donation by *P. sachalinense*, *P. ×bohemicum*, or (in England) by *P. baldschuanicum* Regel (Bailey 1994). In western Washington, we have seen many dozens of examples of wild staminate clones of *P. ×bohemicum*, and only a few examples of fruiting *P. ×bohemicum*. What are the pollen sources and vectors for the pistillate hybrid knotweed? How can backcrosses be detected? Further studies of breeding and reproduction by seed are merited. Apparently most reproduction of *P. cuspidatum*, *P. ×bohemicum*, and *P. sachalinense* is vegetative outside their native range (Bailey 1994; Bailey et al. 1995; Sukopp and Starfinger 1995). Our observations support this idea, suggesting the common *P. ×bohemicum* is not usually forming spontaneously from hybridization of the uncommon parents in lowland Washington; instead hybrids cultivated as garden ornamentals are spreading vegetatively. The hybrid and its parents regenerate from small fragments of stem or rhizome (Brock et al. 1995), and can form large exclusive stands. They are prevalent in riparian zones, where the clones are distributed by floodwaters. This suggests that planting the hybrid or its parents near river corridors should be discouraged, and that control of the three invasive taxa will be slow, expensive, and difficult.

REPRESENTATIVE SPECIMENS EXAMINED: CANADA. British Columbia: Captain's Cove, Ladner, 16 Oct 1971, *McLaren 1* (UBC); Port Hardy, Vancouver Is., 3 m, 8 Sep 1986, *Reeve s.n.* (UBC); Queen Charlotte City, Graham Is., Queen Charlotte Is., 24 Aug 1997, *Lomer & Grove 97555* (V).

U.S.A. Connecticut: Hartford Co., South Windsor, floodplain of Scantic River, 4 Oct 1989, *Mehrhoff 13114* (NEBC); Tolland Co., Willington, 9 Sep 1989, *Murray 4* (NEBC). Idaho: Bonner Co., Pack River near Pend Oreille Lake, 730 m, 28 Sep 1986, *Johnson & Brunsfield s.n.* (ID); Idaho Co., Bimerick Cr. along Lochsa River, Clearwater National Forest, 550 m, 11 Sep 1987, *Johnson 87079 & Brunsfield* (ID); Lewis Co., Nez Perce, 24 Sep 1964, *Higgins 8-64* (ID); Nez Perce Co., Garden Gulch Creek, rangeland 2 miles E of Lapwai, 415 m, 6 Jul 1993, *Lass & Carson s.n.* (ID). Illinois: Lee Co., Route 26 at Green River, 12 miles S of Dixon, 28 Sep 2000, *Ebinger 29231* (EIU); Peoria Co., Peoria Heights, waste ground, very obnoxious, 21 Aug 1950, *Chase 11432* (WTU); Richland Co., 6 miles S of Noble, 16 Jun 1999, *Edgin 3017* (EIU); Wabash Co., 2 miles N of Mesa Lake, 16 Jun 1999, *Edgin 3012* (EIU). Iowa: Jones Co., Lovell Twp., 0.5 miles NE of Monticello, 15 feet tall, 28 Aug 1955, *Cooperrider 51* (RSA); Poweshiek Co., Grinnell, 16 Sep 1921, *Wittrock s.n.* (WTU). Louisiana: Claiborne Parish, W of Aycock, 26 May 1987, *Thomas 99875* (ID, RSA, WCW); Ouachita Parish, aggressively spreading, Monroe, 13 Jul 1982, *Thomas 81951* (RSA). Maine: Franklin Co., Stetson Twp., NW shore, Kennebago Lake, 27 Aug 2000, *Sonder & Angelo s.n.* (NEBC); Sagadahoc Co., Phippsburg, 21 Jul 1948, *Bean s.n.* (NEBC); Somerset Co., Fairfield, Kennebec River island, 13 Aug 1968, *Bean & Harris 33044* (NEBC). Maryland: Baltimore Co., marsh margin, 0.6 miles W of Loch Raven Reservoir, 23 Aug 1971, *Windler & Lombardo 3773* (RSA); Calvert Co., Chesapeake Bay, Parkers Creek, 13 Sep 1965, *Meyer 9289* (WS). Massachusetts: Dukes Co., Martha's Vineyard, Chilmark, 13 Aug 1962, *MacKeever 545* (NEBC); Essex Co., Haverhill, 14 Sep 1958, *Harris 18605* (GH); Middlesex Co., Wakefield, 8 Sep 1915, *Bean 15753* (NEBC); Plymouth Co., East Gate shopping mall, Brockton, 1 Sep 1981, *Perkins s.n.* (NEBC). Nebraska: Douglas Co., Omaha, Elmwood Park, ravine, 5 Sep 1987, *Alfieri s.n.* (OSC). New York: Bronx Co., Bronx, escaped on garbage dump, abundant, 18 Aug 1946, *Moldenke 18447* (OSC). North Carolina: Madison Co., French Broad River, near Hot Springs, 23 Jul 1966, *Radford & Pence 45033* (OSC, UBC). Oregon: Lane Co., logging road, Middle Fork Willamette River, 8 Aug 1973, *Mason 9594* (ORE, UC); Linn Co., N of Albany, Gibson Hill, 6 Aug 1957, *Sims s.n.* (GH, OSC, WS); Multnomah Co., Columbia River Gorge, exit 40 on I-84, basalt cliff base, 31 m, 13 Sep 1991, *Halse 4299* (GH, MO, OSC); Wallowa Co., trail, Imnaha River, 335 m, 8 May 1991, *Zika 11094* (OSC). Pennsylvania: Cameron Co., 6 Sep 1940, *Wahl 806* (GH); Clearfield Co., Clearfield, recycling center, 17 Aug 1996, *Cook & Cook 557* (WS); Clifton Co., 2.5 miles NNW of Keating, 7 Oct 1951, *Wahl 12544* (UC); Lackawanna Co., Moosic, moist thicket, 31 Aug 1937, *Glowenke 1083* (GH). Tennessee: Polk Co., N of Copperhill, roadside denuded by copper smelter, 24 Apr 1965, *Iltis 23281 et al.* (UC). Vermont: Caledonia Co., Waterford, *Gilman 92159* (GH). Virginia: Arlington Co., roadside near Arlington Forest, 18 Aug 1973, *Fosberg 55091* (GH, RSA). Washington: Chelan Co., E of Holden Village, 1005 m, 4 Jun 1993, *Naas 5660* (WTU); Clallam Co., W of Sequim, Dungeness River, 80 m, 27 Sep 2001, *Zika 16599* (WTU); Grays Harbor Co., Moclips, 5 m, 27 Aug 2002, *Zika 17685* (WTU); Island Co., Clinton, Whidbey Is., 60 m, 6 Sep 2001, *Zika 16498* (WTU); King Co., Green River, near Fort Dent Park, 5 m, 26 Aug 2000, *Zika 15404* (WTU); Kitsap Co., Bremerton, thickets, 30 m, 5 Sep 2001, *Zika 16488* (OSC, UC, WTU); Mason Co., overgrown field, 6 m, 14 Sep 1977, *Buckingham 1517* (onp); Pacific Co., North Cove, Willapa Bay N shore, 3 m, 27 Aug 2002, *Zika 17705* (WTU); Pierce Co., Tacoma, vacant lot, 90 m, 19 Aug 1987, *Lewis s.n.* (WTU); San Juan Co., San Juan Is., Friday Harbor, 10 m, 4 Jun 1986, *Atkinson 249* (WTU); Skagit Co., I-5 near Starbird Road, 20 m, 20 Sep 2001, *Zika 16584* (WTU); Snohomish Co., Route 525, E of Lake Serene, 180 m, 6 Sep 2001, *Zika 16494* (MO, WTU); Stevens Co., Hunters Creek, Hunters, 475 m, 26 Sep 2002, *Zika 17958* (WTU); Thurston Co., Black River SE of Gate, 10 m, 18 Aug 2002, *Zika 17152* (WTU); Wahkiakum Co., Skamokawa, Brooks Slough, Columbia River, 10 m, 29 Aug 2002, *Zika 17727 & Weinmann* (WTU); Whatcom Co., 4 miles NE of Acme, 19 Sep 1962, *Heath s.n.* (WWB); Yakima Co., Yakima, wet ditch by railroad tracks, 320 m, 29 Sep 2001, *Zika 16635* (WTU). West Virginia: Kanawha Co., Ridenour Memorial Park, E end of lake, 185 m, 13 Aug 1999, *Tucker 11792* (EIU). Wisconsin: Calumet Co., Niagara escarpment, N of lime kiln ruins, 24 Jul 1970, *Nee 3130* (UC).

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THE VASCULAR FLORA OF MUD POND PEATLAND, CARROLL COUNTY, NEW HAMPSHIRE

C. ERIC HELLQUIST[1] AND GARRETT E. CROW

Department of Plant Biology, Rudman Hall, 46 College Rd.,
University of New Hampshire, Durham, NH 03824
[1]Current Address: School of Biological Sciences,
Washington State University, P.O. Box 644236, Pullman, WA 99164-4236
e-mail: ehellqui@mail.wsu.edu

ABSTRACT. Mud Pond peatland (Moultonborough, New Hampshire) is an approximately 12 ha wetland with a flora that consists of 124 vascular plant species, representing 46 families. Among the flora of Mud Pond peatland were two New Hampshire Endangered species (*Arethusa bulbosa* and *Carex diandra*), one New Hampshire Threatened species (*Lysimachia thrysiflora*), and four New Hampshire Species of Special Concern (*Calopogon tuberosus*, *Platanthera blephariglottis*, *Pogonia ophioglossoides*, and *Sarracenia purpurea*). During field reconnaissance, the vegetation of Mud Pond peatland was qualitatively classified as follows: *Nuphar variegata–Nymphaea odorata* (aquatic), *Carex lasiocarpa* (sedge fringe), *Vaccinium oxycoccos–Sarracenia purpurea* (*Sphagnum* lawn), *Picea mariana–Carex trisperma* (muskeg), *Chamaedaphne calyculata* (ericaceous scrub), *Typha latifolia–Carex lacustris* (marsh), and *Nemopanthus mucronatus–Calamagrostis canadensis* (lagg) communities. Based primarily on vegetation and basin characteristics, Mud Pond peatland can tentatively be classified as a *Sphagnum*-dominated poor fen.

Key Words: New Hampshire, Carroll County, flora, peatland, vegetation

Peatlands are wetland ecosystems characterized by the prolific deposition of organic peat (Vitt 2000). In northeastern North America, peat typically contains no less than 20% partially decayed organic matter (McQueen 1990). These organic substrates are predominantly the remains of *Sphagnum* mosses, sedges, and ericaceous shrubs (Crum 1988; Moore and Bellamy 1974; Vitt 2000). The interaction of physical (e.g., pH, nutrient levels, anoxia) and biological parameters, especially the dominance of *Sphagnum* mosses, perpetuate the deposition and accumulation of peat in these unique wetlands (Clymo and Hayward 1982; Crum 1988; Gorham 1957; Johnson 1985; McQueen 1990; van Breeman 1995; Vitt 2000).

Vegetation in peatlands is distributed along gradients of minerotrophy, pH, moisture, and light (e.g., Crum 1988; Damman and French 1987; Gignac and Vitt 1994; Gorham and Janssens 1992; McQueen 1990; Vitt and Slack 1975). Certain areas within a peatland such as a pond shoreline, the lagg bordering the upland, or networks of sunken hollows, typically have vegetation with minerotrophic affinities. Conversely, partially elevated areas on grounded mats, such as large *Sphagnum* hummocks, may be colonized by groups of species associated with comparatively oligotrophic to ombrotrophic microhabitat conditions (Crum 1988; Damman and French 1987; Glaser 1987; McQueen 1990; Schwintzer 1978; Vitt et al. 1975, 1995).

Regionally, peatlands tend to be colonized by both bryophyte and vascular taxa that are highly predictable from site to site (Gore 1983; Johnson 1985; Vitt 2000; Waterman 1926; Wheeler et al. 1983). In northern latitudes such as New England and the upper Midwest of North America, peatlands typically have a distinct boreal physiognomy characterized by *Picea* spp. and ericaceous shrubs compared to other wetlands such as swamps or marshes (Crum 1988; McQueen 1990). Peatlands provide cool, nutrient-poor habitats where species at the southern extent of their geographic range may occur (Andreas and Bryan 1990; Andreas and Host 1983; Braun 1928, Damman and French 1987; Sperduto 1997). Despite the large volume of literature on peatland ecology, there is a relatively limited number of studies that have examined peatland ecology in New England (e.g., Anderson and Davis 1997; Bubier 1991; Damman and French 1987; Dunlop 1987; Fahey and Crow 1995; Mitchell and Niering 1993; Moizuk and Livingston 1966; Motzkin and Patterson 1991; Searcy and Hickler 1999; Worley 1981).

Although studies are relatively scarce, New Hampshire peatlands have been used as sites for a variety of research ranging from assessments of peat quality to paleoecological and biogeochemical studies (e.g., Davis et al. 1980; Frolking and Crill 1994; Krauss and Kent 1944; Murray 1994; White 1941). One of the first examinations of the vegetation of a New Hampshire peatland was a description of the flora and vegetation patterns of Rochester Heath Bog (Rochester, Strafford County; Barrett 1966). Dunlop (1983, 1987) described the flora and vegetation of Mud Pond Bog (Hillsborough, Hillsborough County) while similar studies were conducted at Pequawket and Heath Pond Bogs (Ossipee, Carroll County) by Fahey (1993) and Fahey and Crow (1995). The bryophyte and vascular vegetation of Spruce Hole Bog (Durham, Strafford County) as well as the dendrochronology of conifers within the kettlehole was examined by Miller (1996).

This floristic inventory of Mud Pond peatland augments the literature describing the vegetation of New Hampshire's peatlands. The purpose of this study was to compile a vascular species inventory of the flora of Mud Pond peatland documented by herbarium voucher specimens. This study also describes the major plant communities within Mud Pond peatland in relation to other New Hampshire peatlands.

SITE DESCRIPTION

Mud Pond peatland (elevation 165 m) is located in Moultonborough, New Hampshire about 5 km west of Moultonborough Village (Carroll County), and approximately 3 km east of Center Harbor (43°43′22″N, 71°25′37″W). The approximately 12 ha peatland is located just north of Moultonborough Neck at the northern end of Lake Winnipesaukee. Mud Pond is located in the center of the peatland and has an inlet/outlet stream (Mud Pond Brook) that runs roughly from north to south through the basin (Figure 1).

The peatland is located within the Southern New England Coastal Plain and Hills Section (Sebago-Ossipee Hills and Plain subsection) according to the classification of the natural divisions of New Hampshire (Smith 1996). This region is known for its mountainous topography, glacial features, and its extensive lakes and wetlands. The forests of the surrounding upland belong to the "Hemlock–White Pine–Northern Hardwoods Region," and consists of both deciduous, coniferous, and mixed forest stands (Braun 1950). The peatland basin is situated among development that includes homes, businesses, recreation fields, and town highway department facilities.

Part of the 6 ha tract of land adjacent to the peatland where the recreation area now exists was donated to Moultonborough in 1974. This area was once the site of a gravel pit as well as the Moultonborough town garage (Anonymous 1974). The recreation facility was constructed during the late 1970s and apparently claimed parts of the western end of the peatland. The 1974 Annual Report of the Town of Moultonborough noted that the project would be completed over a two-year period and refered to earth moving and "ground drainage" at the site of the recreation area (Anonymous 1974). The 1975 Annual Report of the Town of Moultonborough noted the procurement of dredge and fill permits for the recreation area project (Anonymous 1975).

Climate. Carroll County has a climate characterized by moderate summer temperatures, cold winters, and substantial precipitation throughout the year (Diers and Vieira 1977). There is typically 107 cm of annual precipitation in the Lake Winnipesaukee vicinity and approximately 117 cm at Conway. The mean snowfall within Carroll County ranges from 191–318 cm. Snow cover lasts from early December through April. January is the coldest month of the year with average temperatures

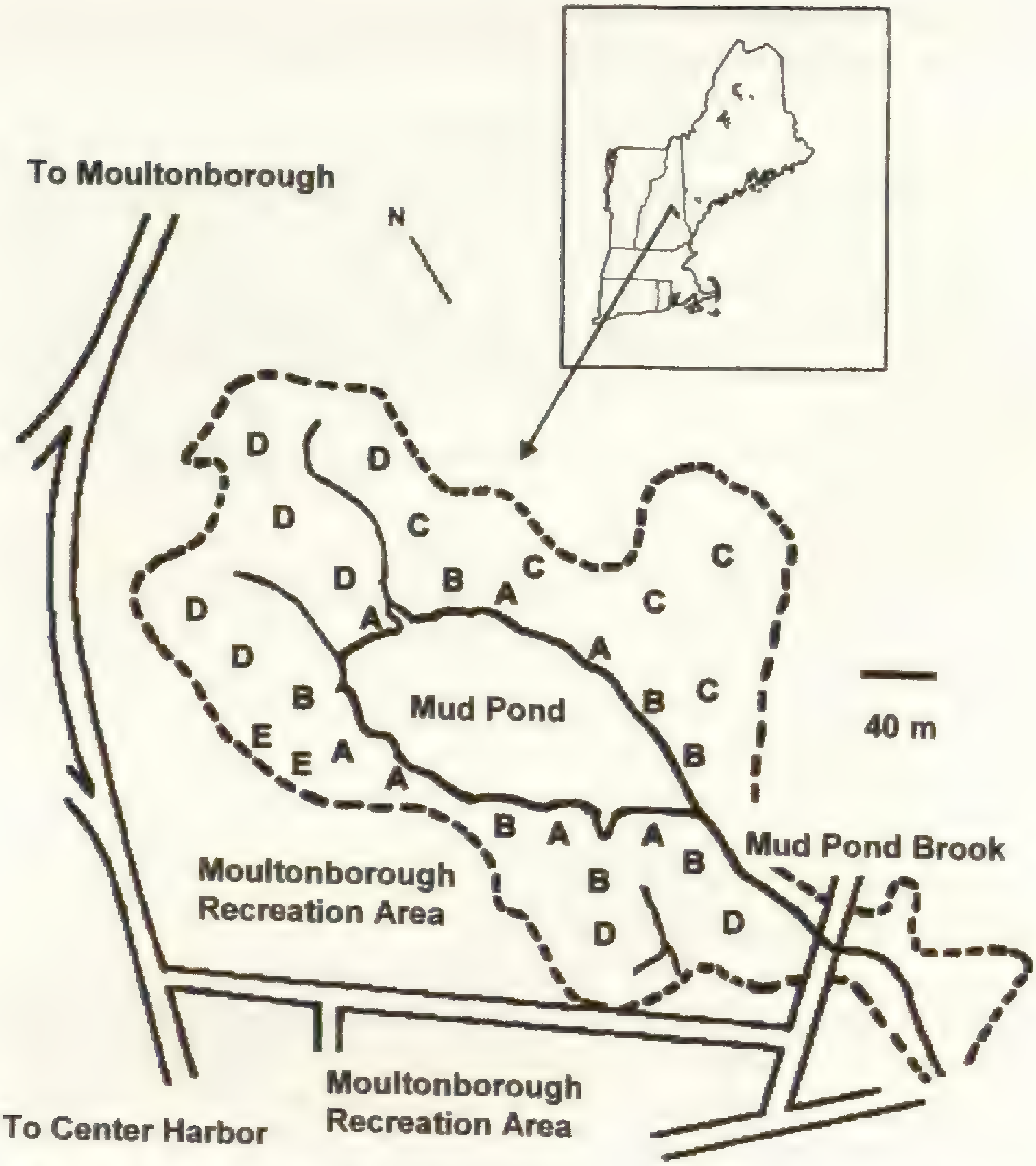

Figure 1. Map of Mud Pond peatland and surroundings. Letters indicate approximate position of selected communities. The sedge fringe and lagg communities are not noted due to their predominance along the pond shore and upland perimeter of the peatland respectively. A. *Vaccinium oxycoccos–Sarracenia purpurea* community; B. *Picea mariana–Carex trisperma* community; C. *Chamaedaphne calyculata* community; D. *Typha latifolia–Carex lacustris* community; E. Open water within the *Nemopanthus mucronatus–Calamagrostis canadensis* community. Redrawn and modified from the Town of Moultonborough Property Map by John E. O'Donnell and Associates, Auburn, ME (1973).

approximately –7°C to –5°C. July is the warmest month of the year with average temperatures approximately 15–21°C.

Soils and geology. The topography of Carroll County has been influenced by the effects of the last glaciation that receded from the area approximately 14,000 years ago (Diers and Vierra 1977). The uplands around Mud Pond peatland consist mainly of glacial tills that belong to the Hollis-Gloucester-Charlton association. These well-drained soils of sand and loam have formed at various depths over bedrock on uplands and mountains. The soils of the peatland basin are classified as "Freshwater Marsh." These soils are immersed most of the year, frost prone, and are colonized by graminoid vegetation including cattails and rushes.

The underlying bedrock of Mud Pond peatland consists of Winnipesaukee Quartz diorite, a medium-grained igneous rock composed of gray quartz and diorite. Red Hill is located immediately north of Mud Pond peatland and is characterized by alkaline geology that is an unusual feature in New Hampshire (Billings 1955; Quinn 1937).

MATERIALS AND METHODS

From May through October of 1993, a floristic inventory of the vascular vegetation of Mud Pond peatland was compiled. From June through August the peatland was surveyed at least once a week. A survey consisted of several hours in the field and at least a single circumnavigation of the peatland to ensure that the basin was consistently observed throughout the entire growing season. Botanical reconnaissance was conducted on foot and by canoe. All plant species growing on organic soils (including beaver lodges) within the topographical limits of the peatland were included in the flora. The abundance of each species was estimated using a visual abundance index (described in the Appendix). Plant communities within the peatland were described based on visual prominence of constituent species. Vascular plant communities were named according to prominent taxa and were given a synonymous habitat designation based on the physiognomy of the community.

Voucher specimens were collected and deposited at the Hodgdon Herbarium at the University of New Hampshire, Durham (NHA). Nomenclature follows Gleason and Cronquist (1991) and Crow and Hellquist (2000a, b) except for the pteridophytes, gymnosperms, and members of the Magnoliidae and Hamamelidae which follow Flora of North America Editorial Committee (1993, 1997).

RESULTS

In 1993, the vascular flora of Mud Pond peatland consisted of 124 species, representing 46 families and 83 genera (Appendix). During the floristic inventory, seven plant communities were described based on qualitative field observations. These vegetation types were visually distinct, although in many areas one community blended gradually into neighboring communities. The three most abundant vascular plant families in the peatland were the Cyperaceae (22 species), the Ericaceae (11 species), and the Rosaceae (8 species). The species within these three families represented 33% of the peatland flora. Four non-native species (*Lythrum salicaria*, *Solanum dulcamara*, *Trifolium repens*, and *Verbascum thapsus*) grew within the basin and consisted of 3.0% of the species richness of the flora. *Arethusa bulbosa* and *Carex diandra* have "endangered" status for the state of New Hampshire and *Lysimachia thrysiflora* has "threatened" status for the state (DRED 2000).

Seven plant communities (with habitat designation in parentheses) were described. These communities were the *Nuphar variegata–Nymphaea odorata* (aquatic), *Carex lasiocarpa* (sedge fringe), *Vaccinium oxycoccos–Sarracenia purpurea* (*Sphagnum* lawn), *Picea mariana–Carex trisperma* (muskeg), *Chamaedaphne calyculata* (ericaceous scrub), *Typha latifolia–Carex lacustris* (marsh), and *Nemopanthus mucronatus–Calamagrostis canadensis* (lagg) communities.

DISCUSSION

Vegetation of Mud Pond peatland. During the floristic inventory of Mud Pond peatland, vegetation patterns within the peatland became apparent. The approximate locations and characteristics (Figure 1) of the seven communities are summarized with particular emphasis on prominent plant species. These communities are described based on field observations without quantitative sampling. General comparisons of the vegetation patterns at Mud Pond to other New Hampshire peatlands are emphasized. For the purposes of clarity, Mud Pond Bog in Hillsborough, New Hampshire described by Dunlop (1983, 1987), is referred to as "Hillsborough Bog."

1. *Nuphar variegata–Nymphaea odorata* (aquatic) Community

Submersed and floating aquatic species grew within the open water of Mud Pond, the various streamlets that dissect portions of the peatland mat, Mud Pond Brook, and portions of the lagg that contain open water (Figure 1). Mud Pond has a false bottom of peat and organic detritus that is especially prominent around the perimeter of the pond. Anchored in the false bottom were aquatic macrophytes including *Nuphar variegata*, *Nymphaea odorata*, *Potamogeton amplifolius*, *P. natans*, and *Utricularia vulgaris*.

At Hillsborough Bog the aquatic community was dominated by *Nymphaea odorata* (33% coverage) and *Brasenia schreberi* J. F. Gmel. (26%), with *Nuphar variegata* and *Pontederia cordata* also prominent in some areas (Dunlop 1987). A similar, but more diverse aquatic community at Pequawket Bog was characterized by *N. odorata*, *Utricularia purpurea* Walter, and *Eleocharis robbinsii* Oakes (Fahey and Crow 1995). *Nuphar variegata*, *Potamogeton confervoides* Rchb., and *U. intermedia* were also present at Pequawket Bog. Spruce Hole Bog contained only one aquatic species, *U. geminiscapa* Benj. (Miller 1996).

2. *Carex lasiocarpa* (sedge fringe) Community

Carex lasiocarpa formed the immediate margin along the entire shore of Mud Pond. This fringe also extended to varying degrees along Mud Pond Brook where it blended with the marsh communities in northern and southern areas of the wetland. The dominance of *C. lasiocarpa* has been considered by many researchers to reflect more minerotrophic (fen-like) conditions (Crum 1988; Schwintzer 1978; Vitt and Slack 1975; Wheeler et al. 1983). Other prominent species in the sedge fringe included *Chamaedaphne calyculata*, *Cladium mariscoides*, *Myrica gale*, *Peltandra virginica*, *Triadenum virginicum*, and *Alnus incana*. The sedge fringe was also the primary habitat of *Arethusa bulbosa*. Another orchid, *Platanthera blephariglottis*, was an occasional inhabitant of the transitional area between the *C. lasiocarpa* and *Vaccinium oxycoccos–Sarracenia purpurea* communities.

A similar community was described at Pequawket Bog (Fahey and Crow 1995). At Pequawket Bog, *Carex lasiocarpa* was a dominant component of the shoreline vegetation as were *Chamaedaphne calyculata*, *Myrica gale*, and *Vaccinium macrocarpon*. Other frequently observed species in this cover type included *Peltandra virginica*, *Pogonia ophioglossoides*, *Sagittaria latifolia*, and *Triadenum virginicum*. This same suite of species also was prevalent in the *C. lasiocarpa* community at Mud Pond. No analogous community was recorded at Rochester Heath Bog (Barrett 1966), Hillsborough Bog (Dunlop 1987), Heath Pond Bog (Fahey 1993), or Spruce Hole Bog (Miller 1996).

3. *Vaccinium oxycoccos–Sarracenia purpurea* (*Sphagnum* lawn) Community

Areas of the *Vaccinium oxycoccos–Sarracenia purpurea* community were located adjacent to the *Carex lasiocarpa* community (Figure 1). These lawns are small-scale poor fens defined by an open, floating, saturated surface of *Sphagnum* species (Crum 1988). These areas were encroached upon by the *Picea mariana–C. trisperma* community and *Chamaedaphne calyculata* community in the western, southwestern, and northeastern areas of the peatland. In the northwestern and south-southeastern portions of the peatland the *Typha latifolia–Carex lacustris* community abutted *Sphagnum* lawn habitats. The *Sphagnum* lawn and sedge fringe formed the characteristic quaking mat associated with pond-border peatlands. Instead of forming extensive broad mats, these *Sphagnum* lawns were confined to pockets between neighboring communities.

Although not expansive, the *Sphagnum* lawns at Mud Pond peatland were inhabited by numerous vascular plants. *Vaccinium oxycoccos* was abundant, as were stunted individuals of *Chamaedaphne calyculata* and *Andromeda glaucophylla*. Insectivorous species such as *Sarracenia purpurea* and *Drosera rotundifolia* were also prominent. *Drosera intermedia* was uncommon and found in trough-like hollows where standing water pooled. *Calopogon tuberosus* also thrived in the open conditions of this community.

At Pequawket Bog, a similar community was characterized by a quaking mat of low *Chamaedaphne calyculata* with *Vaccinium oxycoccos* and *Eriophorum virginicum* (Fahey and Crow 1995). Dunlop (1983, 1987) designated an analagous community at Hillsborough Bog as the "*Vaccinium oxycoccos–Rhynchospora alba* subtype" of the "*C. calyculata* cover type." At Spruce Hole, the "*Sphagnum*–Sedge Lawn community" was described based on the dominance of *S. recurvum* P. Beauv., dwarf ericaceous shrubs including *C. calyculata*, *Lyonia ligustrina*, and *V. corymbosum*. Sedge species of this community included *Carex canescens*, *Eriophorum tenellum*, and *E. virginicum* (Miller 1996).

4. *Picea mariana–Carex trisperma* (muskeg) Community

A muskeg is an area of peatland dominated by *Sphagnum*, *Picea mariana*, *Larix laricina*, and ericaceous species (Heinselman 1963). Muskeg vegetation is often associated with older areas of grounded mat (Crum 1988). At Mud Pond, the most extensive areas of muskeg were at the northeast, east, and southwest ends of the peatland, with smaller pockets of *P. mariana* occurring sporadically throughout the basin. The *P. mariana–Carex trisperma* community formed stands of partially closed canopies that usually were located adjacent to the *Vaccinium oxycoccos–Sarracenia purpurea* and *Chamaedaphne calyculata* communities.

Among the stands of *Picea mariana* the flora was depauperate. The dominant herb was *Carex trisperma*, which formed an uneven carpet of hummocks from which woody species such as *Alnus incana*, *Chamaedaphne calyculata*, *Gaylussacia baccata*, *Kalmia polifolia*, and *Vaccinium myrtilloides* grew. In shallow, damper areas between hummocks, *Peltandra virginica* and *V. macrocarpon* were sometimes observed. Damman and French (1987) recognized a similar community, the "*Sphagnum magellanicum–P. mariana* forest" that is characterized by sparse to abundant individuals of *P. mariana* with an understory of ericaceous shrubs that dwindles as overstory shading increases.

In the northeastern and southwestern areas of the peatland, the muskeg community expanded into an open *Picea mariana* parkland characterized by hummock-hollow microtopography. This hummock-hollow complex eventually graded into the *Chamaedaphne calyculata* and *Typha latifolia–Carex lacustris* communities. The hummocks were dominated by *Sphagnum* species, *Eriophorum vaginatum*, and a dense turf of *C. trisperma*. Sunken hollows formed a network around the hummocks. In these saturated hollows, species such as *Calopogon tuberosus*, *Drosera rotundifolia*, *E. virginicum*, *Platanthera blephariglottis*, *Rhynchospora alba*, *Sarracenia purpurea*, and *Vaccinium oxycoccos* were abundant.

A dense population of *Picea mariana* was located at Spruce Hole Bog (Miller 1996). Due to the lack of penetrating light, there was scant ground cover in this community. The understory consisted primarily of *Carex trisperma* and *Gaultheria hispidula* (L.) Muhl. *ex* Bigelow. Despite the relative lack of vascular species richness in the understory of the *P. mariana* stands at Spruce Hole Bog, there were twelve species of bryophytes present including four *Dicranum* species, three *Sphagnum* species, and three "leafy" liverwort species. The *Dicranum* and liverwort species were limited to the *P. mariana* understory. Closed canopies of *P. mariana* were absent at Pequawket, Heath Pond, and Hillsborough peatlands (Dunlop 1987; Fahey 1993; Fahey and Crow 1995). Heath Pond Bog has an extensive open muskeg similar to areas on the southwestern side of Mud Pond (Fahey 1993; Hellquist, pers. obs.). Similar *P. mariana* communities are abundant in peatlands in upper Michigan (Vitt and Slack 1975).

At Mud Pond, the muskeg communities were impacted by beavers. In the late spring of 1993, a single beaver lodge approximately 7.0 m long, 4.5 m wide, and about 2.0 m high, existed on the northwestern edge of the peatland. By early summer, beavers had excavated a channel into a stand of *Picea mariana* at the southwestern end of the peatland and constructed a second lodge composed of mud, branches, and small trunks of *P. mariana*. Beaver activity was evident at the mouth of Mud

Pond Brook and in muskeg areas along the entire western end of the peatland. Similar harvests of *P. mariana* by beavers at Beckley Bog (Norfolk, Connecticut) have been noted by Mitchell and Niering (1993).

The presence of beaver lodges on the peatland mat was also interesting botanically. On the muddy, elevated beaver lodges grew a variety of plant species not usually associated with peatland floras. Some of these unexpected, opportunistic species restricted to beaver lodges included *Erechtites hieraciifolia*, *Fragaria virginiana*, *Impatiens capensis*, *Polygonum arifolium*, and *Verbascum thapsus*.

5. *Chamaedaphne calyculata* (ericaceous scrub) Community

The ericaceous scrub and the muskeg were found on the grounded mat of the peatland and formed the most internal communities of the peatland. The ericaceous scrub community was limited to the east and southeast areas of the basin and consisted of the most homogeneous vegetation within the peatland. This community was characterized by broad expanses of *Andromeda glaucophylla*, *Chamaedaphne calyculata*, *Kalmia angustifolia*, and *K. polifolia* growing among hummocks of *Sphagnum*.

Animal trails provided habitat for other species including *Eriophorum virginicum*, *Peltandra virginica*, and occasionally *Calla palustris* within the scrub. Another microhabitat found in the ericaceous scrub was located in areas where trees including *Larix laricina*, *Picea mariana*, or *Pinus strobus* had died, leaving large, uplifted, circular hummocks a few meters in diameter. These elevated areas provided habitat for species such as *Kalmia angustifolia*, *Rhododendron canadense*, *Vaccinium corymbosum*, and *V. myrtilloides* as well as saplings of *Acer rubrum*, *L. laricina*, and *P. strobus*.

Ericaceous scrub-dominated communities are present at Rochester Heath Bog (Barrett 1966), Hillsborough (Dunlop 1987), Heath Pond (Fahey 1993), Pequawket (Fahey and Crow 1995), and Spruce Hole (Miller 1996) bogs. In all of these peatlands, *Sphagnum* carpeted the substrate. Often sedges such as *Carex trisperma*, *Eriophorum vaginatum*, *E. virginicum*, and *Rhynchospora alba* were interspersed within the ericaceous shrubs (Dunlop 1987; Fahey and Crow 1995). Similar vegetation communities dominated by ericaceous shrubs have been documented across the Northeast (Anderson and Davis 1997; Damman and French 1987; Johnson 1985; Worley 1981) and in the Midwest (Crow 1969; Crum 1988; Gates 1942; Hellquist and Crow 1999; Schwintzer 1981; Vitt and Slack 1975).

6. *Typha latifolia–Carex lacustris* (marsh) Community

The marsh community of Mud Pond peatland was characterized by standing and moving channels of water that were surrounded by *Typha latifolia* and graminoid species. The largest expanse of the marsh occurred at the northern end of the peatland where it surrounded the inlet stream to Mud Pond. A second substantial area of marsh occurred at the southeastern end of the peatland along Mud Pond Brook (Figure 1). The southeastern marsh extends to the west behind the muskeg where it encompasses another stream that drains into a culvert across from the recreation area hockey rink.

The northern marsh area was distinguished by tussocks of *Carex stricta* that were often surrounded by water. *Utricularia intermedia* was abundant in the narrow channels of water around these tussocks. At the northern inlet to Mud Pond, the extensive expanse of *Carex* tussocks and *Typha latifolia* formed a network of channels with false bottoms. The marsh areas also were colonized by *C. lacustris*, *C. lasiocarpa*, and *C. pseudocyperus*. This vegetation is associated with moving water as well as with fen and marsh habitats (Crum 1988). Farther from the inlet, the tussock complexes contained abundant *T. latifolia* as well as *Acer rubrum* (seedlings and saplings), *Osmunda cinnamomea*, *O. regalis*, *Thelypteris palustris*, *Alnus incana*, *Calamagrostis canadensis*, *Chamaedaphne calyculata*, *Spiraea latifolia*, *Toxicodendron vernix*, *Triadenum virginicum*, and *Vaccinium macrocarpon*.

The marsh in the southwestern portion of the peatland basin was a transitional area with characteristics of both the *Typha latifolia–Carex lacustris* community and the *Chamaedaphne calyculata* community (Figure 1). At one time, this area may have been entirely ericaceous scrub. The construction of the recreation area and the apparent dredging and filling of the adjacent wetland (Anonymous 1974, 1975) may have altered the hydrology of this portion of the peatland. This disturbance could have altered the wetland enough to allow prolific *Typha* populations to invade and become established in the former ericaceous scrub community.

Lythrum salicaria was also found in the *Typha latifolia–Carex lacustris* community. *Lythrum* was limited to the southwestern portions of the peatland adjacent to the recreation area and the access road to the Moultonborough Highway Department. Due to its vigorous growth, an expansion of the *Lythrum* population may have a competitive impact on the distribution of other neighboring species.

7. *Nemopanthus mucronatus–Calamagrostis canadensis* (lagg) Community

The *Nemopanthus mucronatus–Calamagrostis canadensis* community surrounded the outermost perimeter of the peatland and immediately bordered the upland. The lagg (moat) represents a shift in substrate from peat to more mineral-rich, mucky soils. This transitional area between the peatland proper and the upland tends to be heavily shaded, collects leaf litter, and experiences seasonal variation in wetness (Crum 1988; Gore 1983). Higher concentrations of dissolved oxygen and minerals are present within lagg substrates. These subsidies support a flora characteristic of more nutrient-rich wetland environments such as marshes or swamps (Crum 1988; McQueen 1990).

The variable habitat conditions along the periphery of the peatland were reflected in the variety of vegetation patterns within the lagg. At the western edge of the peatland (Figure 1), the lagg contained standing water in which submersed species grew (e.g., *Potamogeton pusillus* and *Utricularia vulgaris*) as well as emergent species including *Sparganium americanum* and *Calla palustris*. In 1993, the eastern lagg abutting the gravel pit did not have standing water, but formed a swath of semiliquid black muck. The herbaceous cover of this area was similar to the *Eriophorum* and *Carex* lagg phases described for Spruce Hole Bog (Miller 1996).

The northern, western, and southern lagg areas were dominated by shrubs including *Ilex verticillata*, *Nemopanthus mucronatus*, *Vaccinium corymbosum*, *V. myrtilloides*, and *Viburnum nudum*. *Alnus incana*, a species found frequently in the laggs of lakefill peatlands (Crum 1988) also was abundant. The lagg community at Mud Pond shared much of its flora with the Cinnamon Fern–Highbush Blueberry Thicket community described by Damman and French (1987). At Pequawket Bog, the lagg community was dominated by tall shrubs (> 1.5 m), especially *Acer rubrum*, *V. corymbosum*, and *Lyonia ligustrina*. Other characteristic species of this zone included *Alnus incana*, *Aronia melanocarpa*, *I. verticillata*, *N. mucronatus*, and *Rhododendron canadense* (Fahey and Crow 1995). The lagg community at Pequawket Bog shared similarities with both Heath Pond Bog (Fahey 1993) and Hillsborough Bog (Dunlop 1987).

At Mud Pond, open lagg areas not shaded by tall shrubs contained a diverse flora of herbaceous species including *Calamagrostis canadensis*, *Carex pseudocyperus*, *Scirpus cyperinus*, *Cicuta bulbifera*, *Epilobium leptophyllum*, *Lycopus uniflorus*, *Scutellaria galericulata*, and *Solanum dulcamara*. At Rochester Heath Bog, peripheral areas of the basin had similar fen-like components dominated by *Carex canescens*, *Calamagrostis canadensis*, *Dulichium arundinaceum*, and *Lysimachia terrestris* (Barrett 1966).

State of New Hampshire Endangered species. Two species categorized as Endangered in the state of New Hampshire were found in Mud Pond Peatland (*Arethusa bulbosa* and *Carex diandra*). The range of *Arethusa* extends from Newfoundland to Ontario and Minnesota. *Arethusa* is rare south to New Jersey and northern Indiana, and disjunct into the mountains of North Carolina (Crow and Hellquist 2000a). *Arethusa bulbosa* was frequent throughout the sedge fringe along the perimeter of Mud Pond. Occasionally *Arethusa* was observed on tussocks along the edge of Mud Pond Brook.

The New Hampshire Natural Heritage Inventory (DRED 2000) lists twenty-one sites for *Arethusa bulbosa*. Of these twenty-one sites, only nine have been observed since 1979 (DRED 2000). Mud Pond peatland represents the fifth location for *Arethusa* in Carroll County with the majority of other records scattered over southeastern New Hampshire, especially in Rockingham County (DRED 1997). *Arethusa* is classified as "critically imperiled" within New Hampshire (DRED 2000).

The population of *Arethusa bulbosa* at Mud Pond was thriving and probably ranks as one of the largest in the state. In the northeast, populations of *A. bulbosa* have been in decline as a result of habitat loss and unscrupulous collectors (Damman and French 1987). A potential threat to *Arethusa*, and all of the endangered and threatened species at Mud Pond, is loss or alteration of habitat due to either human- or beaver-instigated manipulations of the surface hydrology. Another potential concern is the expansion of a population of *Lythrum salicaria*. *Lythrum salicaria* could conceivably colonize the sedge fringe habitats along Mud Pond and exclude individuals of *A. bulbosa*.

Carex diandra was an occasional inhabitant of the sedge fringe and marsh communities where it was found growing along channels of open water. Fernald (1950) states that *C. diandra* is found in bogs, peaty swamps, and calcareous wetlands. *Carex diandra* is a circumboreal species with a range extending south to New Jersey, Pennsylvania, Maryland, Illinois, Nebraska, Colorado, and California (Crow and Hellquist 2000a). With the exception of the Mud Pond record which represents the southernmost station for *C. diandra* in New Hampshire, the remaining localities are in western Coos County (DRED 1997).

State of New Hampshire Threatened species. *Lysimachia thrysiflora* (Swamp or Tufted loosestrife) is a circumboreal species with a range that extends south to northern New Jersey, Ohio, Illinois, Missouri, Nebraska, northern Colorado, and northern California (Crow and Hellquist 2000b). *Lysimachia thrysiflora* was relatively uncommon at Mud Pond. The largest population occurred along Mud Pond Brook at the south-southwestern end of the peatland. *Lysimachia thrysiflora* grew on tussocks along the edge of the brook in an area dissected by beaver paths and was occasionally observed in the southwestern lagg. In addition to Mud Pond peatland, there are seven documented records of *L. thrysiflora* (DRED 2000). These records are largely concentrated in Rockingham and Strafford Counties, with one record in Coos County. The Mud Pond record represents the first locality for this species in Carroll County.

Preliminary classification of Mud Pond peatland. New Hampshire peatlands tend to be small kettlehole or basin peatlands ranging in size from 0.5 ha or less to approximately 100 ha (Johnson 1985). Sperduto (1997) has presented a tentative classification of New Hampshire peatlands that is based upon Damman and French (1987), describing peatlands with regard to landform characteristics, vegetation patterns, and florisitic composition. Most peatlands in New Hampshire are topogenous, limnogenous, or a combination of both types (Sperduto 1997). Topogenous peatlands are found within low-lying parts of the landscape and receive runoff from uplands that wash over or through mineral soils. The hydrology of these peatlands is usually maintained by the water table (Damman and French 1987). Limnogenous peatlands often contain areas with emergent marsh vegetation and are distinguished by lakes and nutrient-poor streams that circulate water and nutrients within the peatland (Damman and French 1987).

Sperduto (1997) recognized five peatland vegetation communities in New Hampshire. These five physiognomic types were forests, tall shrub thickets, dwarf-shrub peatlands, sedge lawns or graminoid fens, and moss carpets/mud bottoms. The floras of most New Hampshire peatlands are indicative of acidic (poor) fens or more intermediate (oligotrophic) fens that receive limited mineral subsidies (Sperduto 1997). Of the New Hampshire peatlands that have published floras, Mud Pond peatland in Moultonborough is the most species-rich (Table 1).

The unique topography, hydrology, and flora of Mud Pond peatland does not lend the basin to a single, convenient classification. The peatland basin is composed of several discrete areas that adhere to

Table 1. Approximate area and vascular species richness of New Hampshire peatlands with existing species inventories. Data compiled from [1]Fahey 1993, [2]Dunlop 1987, [3]Miller 1996, and [4]Barrett 1966. *Mean area of peatland mat estimated by calculating approximate area from U.S.G.S. Hillsboro Upper Village topographic map and Dunlop (1987, Figure 4). **Mean area estimated from 1944, 1953, and 1962 aerial photographs of the open peatland mat.

Site	Area	Species Richness
Mud Pond Peatland, Moultonborough, Carroll Co.	12.2 ha	124
Pequawket Bog, Ossipee[1], Carroll Co.	9.9 ha	109
Mud Pond Bog, Hillsborough[2], Hillsborough Co.	10.7 ha*	107
Heath Pond Bog, Ossipee[1], Carroll Co.	16.2 ha	70
Spruce Hole Bog, Durham[3], Strafford Co.	1.0 ha	37
Rochester Heath Bog, Rochester[4], Strafford Co.	6.9 ha**	29

various aspects of the classification systems of Damman and French (1987) and Sperduto (1997). For example, Mud Pond peatland has aspects of both a topogenous and limnogenous system. Topogenous characteristics include the location of the peatland within a basin, the fringe of vegetation around the pond, the narrow *Sphagnum* lawns, and the extensive grounded mat areas.

Despite the topogenous characteristics of the basin, the northern and southern mat areas along Mud Pond Brook have characteristics of limnogenous peatlands. The peatland mat around the open water of Mud Pond classifies the system as a pond border peatland since the pond has not been entirely covered by vegetation (Damman and French 1987). The presence of the extensive *Typha latifolia–Carex lacustris* community attests to the relative minerotrophy of waters flowing through the more limnogenous areas of the peatland (Crum 1988; Damman and French 1987). Limnogenous peatlands are also characterized by *Sphagnum* spp., *C. lasiocarpa*, *Chamaedaphne calyculata*, and *Myrica gale* (Damman and French 1987).

Based on its floristic composition and the presumed chemical conditions that the flora reflects, Mud Pond peatland most resembles a poor to intermediate (oligotrophic) fen as described by Vitt (2000). Particularly telling is the dominance of *Sphagnum* in the peatland and the presence of ericaceous vegetation throughout the peatland, as well as sedges along the pond margin (Vitt 2000). Many of the taxa present at Mud Pond are considered species indicative of oligiotrophic conditions in New Hampshire peatlands. These taxa include *Sphagnum* spp., *Arethusa bulbosa*, *Calamagrostis canadensis*, *Carex lasiocarpa*, *C. trisperma*, *Decodon verticillatus*, *Drosera intermedia*, *Eriophorum tenellum*, *Lyonia ligustrina*, *Myrica gale*, *Pogonia ophioglossoides*, *Rhododendron canadense*, *Solidago uliginosa*, *Triadenum virginicum*, and *Vaccinium macrocarpon* (Sperduto 1997).

The relative minerotrophy of the Mud Pond peatland basin amidst the generally acidic conditions of the Winnipesaukee diorite bedrock may be influenced by the proximity of the peatland to Red Hill and its relatively alkaline geology. Ground water and runoff in contact with Red Hill syenite may percolate into the peatland basin through surface and subsurface hydrology and therefore could be a source of nutrient ions. An influx of nutrient-enriched groundwater may account for some of the fen-like characteristics of the peatland flora. Further investigations of local geology and hydrology, as well as quantitative ecological surveys will further elucidate the flora and vegetation patterns of Mud Pond peatland.

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APPENDIX

THE VASCULAR FLORA OF MUD POND PEATLAND

The abundance of each species was estimated using the following visual abundance index for the checklist of the vascular flora. Abundant: Dominant or codominant in at least one community; Frequent: Easily observed in one or more communities, but not dominant; Occasional: Widely distributed but generally easy to locate; Rare: Difficult to locate, limited to two or fewer localities within the peatland. The checklist cites the physiognomic name of the communities or a specific location where a species was most prevalent.

EQUISETOPHYTA (Horsetails)

EQUISETACEAE

Equisetum arvense L. – Rare; NW lagg.
Equisetum sylvaticum L. – Rare; NW lagg.

POLYPODIOPHYTA (Ferns)

DRYOPTERIDACEAE

Dryopteris cristata (L.) A. Gray – Rare; NW lagg.
Onoclea sensibilis L. – Rare; NW lagg.

OSMUNDACEAE

Osmunda cinnamomea L. – Frequent; sedge fringe, lagg.
Osmunda regalis L. – Occasional; sedge fringe, marsh.

THELYPTERIDACEAE

Thelypteris palustris Schott – Frequent; sedge fringe.

PINOPHYTA (Gymnosperms)

PINACEAE

Larix laricina (Du Roi) K. Koch – Occasional; ericaceous scrub.
Picea mariana (Mill.) Britton, Sterns & Poggenb. – Frequent; muskeg.
Pinus strobus L. – Rare; ericaceous scrub.

MAGNOLIOPHYTA (Angiosperms)

MAGNOLIOPSIDA (Dicotyledons)

ACERACEAE

Acer rubrum L. – Frequent; muskeg, marsh.

APIACEAE

Cicuta bulbifera L. – Rare; NW lagg.

ANACARDIACEAE

Toxicodendron vernix (L.) Kuntze – Frequent; sedge fringe, lagg.

AQUIFOLIACEAE

Ilex verticillata (L.) A. Gray – Frequent; lagg.
Nemopanthus mucronatus (L.) Trel. – Frequent; lagg.

ASCLEPIADACEAE

Asclepias incarnata L. – Occasional; sedge fringe.

ASTERACEAE

Aster umbellatus Mill. – Rare; W lagg.
Bidens cernua L. – Rare; W beaver lodge.
Bidens connata Muhl. *ex* Willd. – Rare; W lagg.
Erechtites hieraciifolia (L.) Raf. – Rare; W beaver lodge.
Solidago uliginosa Nutt. – Frequent; sedge fringe, marsh.

BALSAMINACEAE

Impatiens capensis Meerb. – Occasional; NW lagg, on W beaver lodge.

BETULACEAE

Alnus incana (L.) Moench subsp. *rugosa* (Du Roi) Clausen – Frequent; sedge fringe, lagg.
Betula populifolia Marshall – Frequent; muskeg, ericaceous scrub.

CAPRIFOLIACEAE

Viburnum cassinoides L. – Frequent; lagg.

CLUSIACEAE

Hypericum mutilum L. – Rare; W beaver lodge.
Triadenum virginicum (L.) Raf. – Abundant; sedge fringe, marsh.

DROSERACEAE

Drosera intermedia Hayne – Rare; Damp hollows on the *Sphagnum* lawn.
Drosera rotundifolia L. – Frequent; *Sphagnum* lawn.

ERICACEAE

Andromeda glaucophylla Link – Frequent; muskeg, ericaceous scrub.
Chamaedaphne calyculata (L.) Moench – Abundant; throughout peatland.
Gaylussacia baccata (Wangenh.) K. Koch – Abundant; muskeg.
Kalmia angustifolia L. – Frequent; muskeg, ericaceous scrub.
Kalmia polifolia Wangenh. – Occasional; muskeg, ericaceous scrub.
Lyonia ligustrina (L.) Alph. de Candolle – Frequent; marsh, lagg.
Rhododendron canadense (L.) Torr. – Occasional; ericaceous scrub.
Vaccinium corymbosum L. – Abundant; muskeg, ericaceous scrub.
Vaccinium macrocarpon Aiton – Frequent; sedge fringe, marsh.
Vaccinium myrtilloides Michx. – Occasional; muskeg, ericaceous scrub.
Vaccinium oxycoccos L. – Abundant; *Sphagnum* lawn, ericaceous scrub.

FABACEAE

Trifolium repens L. – Rare; a few plants on a beaver slide through a *Sphagnum* lawn at the NE end of Mud Pond. Introduced from Eurasia (Gleason and Cronquist 1991).

LAMIACEAE

Lycopus uniflorus Michx. – Occasional; marsh, lagg.
Scutellaria galericulata L. – Frequent; marsh, lagg.

LENTIBULARIACEAE

Utricularia gibba L. – Rare; exposed mud along Mud Pond.
Utricularia intermedia Hayne – Frequent; submersed in beaver channels throughout sedge fringe.
Utricularia vulgaris L. – Frequent; submersed in Mud Pond, occasional in open water of W lagg.

LYTHRACEAE

Decodon verticillatus (L.) Elliott – Occasional; transition area between *Sphagnum* lawn and muskeg.
Lythrum salicaria L. – Occasional; SW marsh. Introduced from Eurasia (Gleason and Cronquist 1991).

MYRICACEAE

Myrica gale L. – Abundant; sedge fringe, ericaceous scrub, marsh.

NYMPHAEACEAE

Nuphar variegata Durand – Abundant; Mud Pond.
Nymphaea odorata Aiton subsp. *odorata* – Abundant; Mud Pond.

ONAGRACEAE

Epilobium leptophyllum Raf. – Occasional; marsh, lagg.
Epilobium strictum Muhl. *ex* Spreng. – Occasional; marsh, lagg.

POLYGONACEAE

Polygonum amphibium L. – Rare; W beaver lodge.
Polygonum arifolium L. – Rare; W beaver lodge.
Polygonum punctatum Elliott – Occasional; sedge fringe along Mud Pond Brook, lagg.

PRIMULACEAE

Lysimachia terrestris (L.) Britton, Sterns & Poggenb. – Occasional; N–NE lagg.
Lysimachia thrysiflora L. – Rare; sedge fringe at mouth of Mud Pond Brook and along lagg. New Hampshire Threatened Species.

ROSACEAE

Aronia arbutifolia (L.) Elliott – Occasional; marsh.
Aronia melanocarpa (Michx.) Elliott – Frequent; muskeg, marsh.
Fragaria virginiana Duchesne – Rare; several plants on W beaver lodge.

Rosa palustris Marshall – Frequent; sedge fringe.
Rubus hispidus L. – Occasional; muskeg, marsh.
Rubus pubescens Raf. – Rare; NW lagg.
Spiraea latifolia (Aiton) Borkh. – Frequent; sedge fringe, marsh, lagg.
Spiraea tomentosa L. – Occasional; lagg.

RUBIACEAE

Galium trifidum L. – Frequent; lagg, sedge fringe bordering the mouth of Mud Pond Brook.

SALICACEAE

Salix discolor Muhl. – Occasional; NW marsh, lagg.
Salix pedicellaris Pursh – Occasional; NW lagg.

SARRACENIACEAE

Sarracenia purpurea L. – Frequent; muskeg, *Sphagnum* lawn. New Hampshire Species of Special Concern.

SCROPHULARIACEAE

Verbascum thapsus L. – Rare; single population of several plants on W beaver lodge. Introduced from Europe (Gleason and Cronquist 1991).

SOLANACEAE

Solanum dulcamara L. – Occasional; lagg. Introduced from Eurasia (Gleason and Cronquist 1991).

VIOLACEAE

Viola macloskeyi Lloyd subsp. *pallens* (Banks *ex* Ging.) M.S. Baker – Rare; sedge fringe along Mud Pond Brook, on tussocks in the marsh and lagg.

LILIOPSIDA (Monocotyledons)

ALISMATACEAE

Sagittaria latifolia Willd. – Frequent; sedge fringe, *Sphagnum* lawn.

ARACEAE

Arisaema triphyllum (L.) Schott – Rare; NW lagg.
Calla palustris L. – Frequent; lagg, animal paths in the ericaceous scrub.
Peltandra virginica (L.) Schott & Endl. – Frequent; sedge fringe.

CYPERACEAE

Carex brunnescens (Pers.) Poir. – Frequent; muskeg, marsh.
Carex diandra Shrank – Occasional; sedge fringe, marsh. New Hampshire Endangered Species.

Carex lacustris Willd. – Abundant; marsh.
Carex lasiocarpa Ehrh. – Abundant; sedge fringe, frequent in marsh.
Carex lurida Wahlenb. – Rare; W lagg.
Carex pseudocyperus L. – Frequent; marsh, lagg.
Carex scoparia Schkuhr – Rare; W lagg.
Carex stricta Lam. – Frequent; marsh, occasional in lagg.
Carex trisperma Dewey – Abundant; muskeg, occasional in ericaceous scrub.
Carex utriculata Boott – Frequent; lagg, occasional in ericaceous scrub.
Cladium mariscoides (Muhl.) Torr. – Frequent; sedge fringe.
Dulichium arundinaceum (L.) Britton – Rare; W lagg.
Eleocharis olivacea Torr. – Occasional; on exposed peat of marsh and along Mud Pond.
Eleocharis smallii Britton – Frequent; sedge fringe.
Eriophorum gracile W. D. J. Koch – Rare; W marsh.
Eriophorum tenellum Nutt. – Rare; muskeg, lagg.
Eriophorum vaginatum L. subsp. *spissum* (Fernald) Hultén – Abundant; muskeg.
Eriophorum virginicum L. – Abundant; muskeg.
Rhynchospora alba (L.) Vahl – Frequent; muskeg, sedge fringe.
Scirpus cyperinus (L.) Kunth – Rare; marsh along Mud Pond Brook.
Scirpus subterminalis Torr. – Occasional; submersed along Mud Pond shoreline.
Scirpus tabernaemontani C. C. Gmel. – Rare; S marsh near Mud Pond Brook.

ERIOCAULACEAE

Eriocaulon aquaticum (Hill) Druce – Rare; on exposed muck along Mud Pond and Mud Pond Brook.

IRIDACEAE

Iris versicolor L. – Frequent; in lagg, along animal paths in the ericaceous scrub.

JUNCACEAE

Juncus brevicaudatus (Engelm.) Fernald – Occasional; sedge fringe.
Juncus canadensis J. Gay – Occasional; lagg.
Juncus effusus L. – Occasional; lagg.
Juncus pelocarpus E. Meyer – Occasional; sedge fringe, exposed muddy areas in W marsh.

LEMNACEAE

Lemna minor L. – Occasional; floating in beaver channels in sedge fringe, also in channels around tussocks in the marsh.

ORCHIDACEAE

Arethusa bulbosa L. – Frequent; sedge fringe. New Hampshire Endangered Species.
Calopogon tuberosus (L.) Britton, Sterns & Poggenb. – Frequent; *Sphagnum* lawn. New Hampshire Species of Special Concern.
Platanthera blephariglottis (Willd.) Lindl. – Occasional; sedge fringe, muskeg. New Hampshire Species of Special Concern.

Pogonia ophioglossoides (L.) Ker Gawler – Frequent; sedge fringe. New Hampshire Species of Special Concern.

POACEAE

Agrostis hyemalis (Walter) Britton, Sterns & Poggenb. – Rare; along beaver channel in W sedge fringe.
Brachyelytrum erectum (Schreber) P. Beauv. – Rare; NW lagg.
Calamagrostis canadensis (Michx.) P. Beauv. – Abundant; lagg.
Glyceria canadenis (Michx.) Trin. – Occasional; lagg.
Leersia oryzoides (L.) Swartz – Occasional; lagg.

PONTEDERIACEAE

Pontederia cordata L. – Occasional; sedge fringe.

POTAMOGETONACEAE

Potamogeton amplifolius Tuckerman – Frequent; submersed in Mud Pond.
Potamogeton epihydrus Raf. – Rare; single population submersed near the culvert at the southern end of Mud Pond Brook.
Potamogeton natans L. – Frequent; submersed in Mud Pond.
Potamogeton pusillus L. subsp. *tenuissimus* (Mert. and W. D. J. Koch) R. R. Haynes and C. B. Hellquist – Occasional; submersed in open water of W lagg.

SPARGANIACEAE

Sparganium americanum Nutt. – Rare; W lagg.
Sparganium natans L. – Frequent; beaver channels of sedge fringe.

TYPHACEAE

Typha angustifolia L. – Occasional; N marsh.
Typha latifolia L. – Abundant; N and S marsh.

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STATUS AND ECOLOGY OF *AGALINIS KINGSII* (SCROPHULARIACEAE), A RARE ENDEMIC TO THE CAYMAN ISLANDS (CARIBBEAN SEA)

AMANDA DIOCHON

Department of Biology, St. Francis Xavier University,
Antigonish, Nova Scotia, B2G 2W5, Canada

FREDERIC J. BURTON

National Trust for the Cayman Islands,
P. O. Box 31116 SMB, Grand Cayman, British West Indies

DAVID J. GARBARY[1]

Department of Biology, St. Francis Xavier University,
Antigonish, Nova Scotia, B2G 2W5, Canada
[1]Corresponding Author; e-mail: dgarbary@stfx.ca

ABSTRACT. *Agalinis kingsii* (Scrophulariaceae) is a rare Grand Cayman species that is poorly known taxonomically and ecologically. Sampling in 1999 suggested that approximately 43,000 individuals occurred within a single 500,000 m^2 sedge wetland habitat in the Salina Reserve and that approximately 500 plants occurred in a 9 m^2 location in the Central Mangrove Wetland. For every tenth individual located during the population count in the Salina Reserve, vegetation community associations, environmental parameters, and individual morphology were noted. Based on the findings, we suggest that rarity is a consequence of habitat availability. Since both populations were found within a narrow geographic and ecological range, we conclude that this species may be sensitive to extinction via a stochastic event.

Key Words: *Agalinis kingsii*, Caribbean Sea, endemism, endangered species, Grand Cayman, Scrophulariaceae

Agalinis kingsii Proctor (Scrophulariaceae) is one of 21 endemic species of vascular plants reported from the Cayman Islands (Caribbean Sea; Proctor 1994). Proctor (1977) described *A. kingsii* based on a single collection by Kings in 1935, but the exact location of the type locality ("Forest Glen") is unknown. The species was compared with *A. albida* Britton & Pennell and *A. purpurea* (L.) Pennell, and included in the *Flora of the Cayman Islands* without further study (Proctor 1984). A small, but stable population of *A. kingsii* was later reported by Davies (1994) based on unpublished observations by Burton in 1988. Both accounts reported the species growing on drier ground in *Conocarpus erectus* L. swamps. These limited reports are the only known accounts of the species and bring to light the lack of taxonomic, biogeographic, and ecological information on *A. kingsii*.

The aforementioned *Agalinis kingsii* populations are small and found within a narrow geographic and ecological range. According to Gilfedder et al. (1997) and van Treuren et al. (1993), narrowly endemic species with small populations are vulnerable to extinction due to stochastic events. Translocation techniques are commonly used to ensure the survival of self-sustaining populations in the wild (Gilfedder et al. 1997; Watson et al. 1994), but this approach might not be suitable for *A. kingsii*. Although a botanical garden exists on Grand Cayman, habitat on this small island is rapidly disappearing (Davies 1994) and the management needs of the species are unknown. In order to effectively devise a management strategy, knowledge of the autecology of the species in its natural environment is essential (Gilfedder et al. 1997; Grigore and Tramer 1996; Lesica 1999; Watson et al. 1994).

The objectives of this study were to: 1) provide a more detailed morphological and ecological description of *Agalinis kingsii*; 2) evaluate the distribution and abundance of *A. kingsii* on Grand Cayman; 3) consider the long-term survival of *A. kingsii* in light of the impact of human activities and frequent disturbance in its primary habitat; and 4) suggest management strategies to enhance the long-term survival of *A. kingsii*.

MATERIALS AND METHODS

Study area. The Salina Reserve (hereafter referred to as the Salina) is located inland off the northeast coast of Grand Cayman, British West Indies (B.W.I.; 19°21′N, 81°07′E; Figure 1). The area was established as a nature reserve in 1988 through a Crown land grant to the National Trust for the Cayman Islands and is currently protected under strict legislation (National Trust for the Cayman Islands 1997). The relative remoteness of the location and rough terrain provide natural restrictions on public access, and fencing and dolostone karst outcrops prevent livestock grazing.

Agalinis kingsii grows in the sedge wetland on the southern side of the Salina. The wetland displays evidence of a former buttonwood (*Conocarpus erectus*) swamp, possibly brought to its present state because of fire or anthropogenic disturbance (National Trust for the Cayman Islands 1997). The wetland is a mosaic of communities, and has been likened to the Florida Everglades (Diochon, pers. obs.; National Trust for the Cayman Islands 1997).

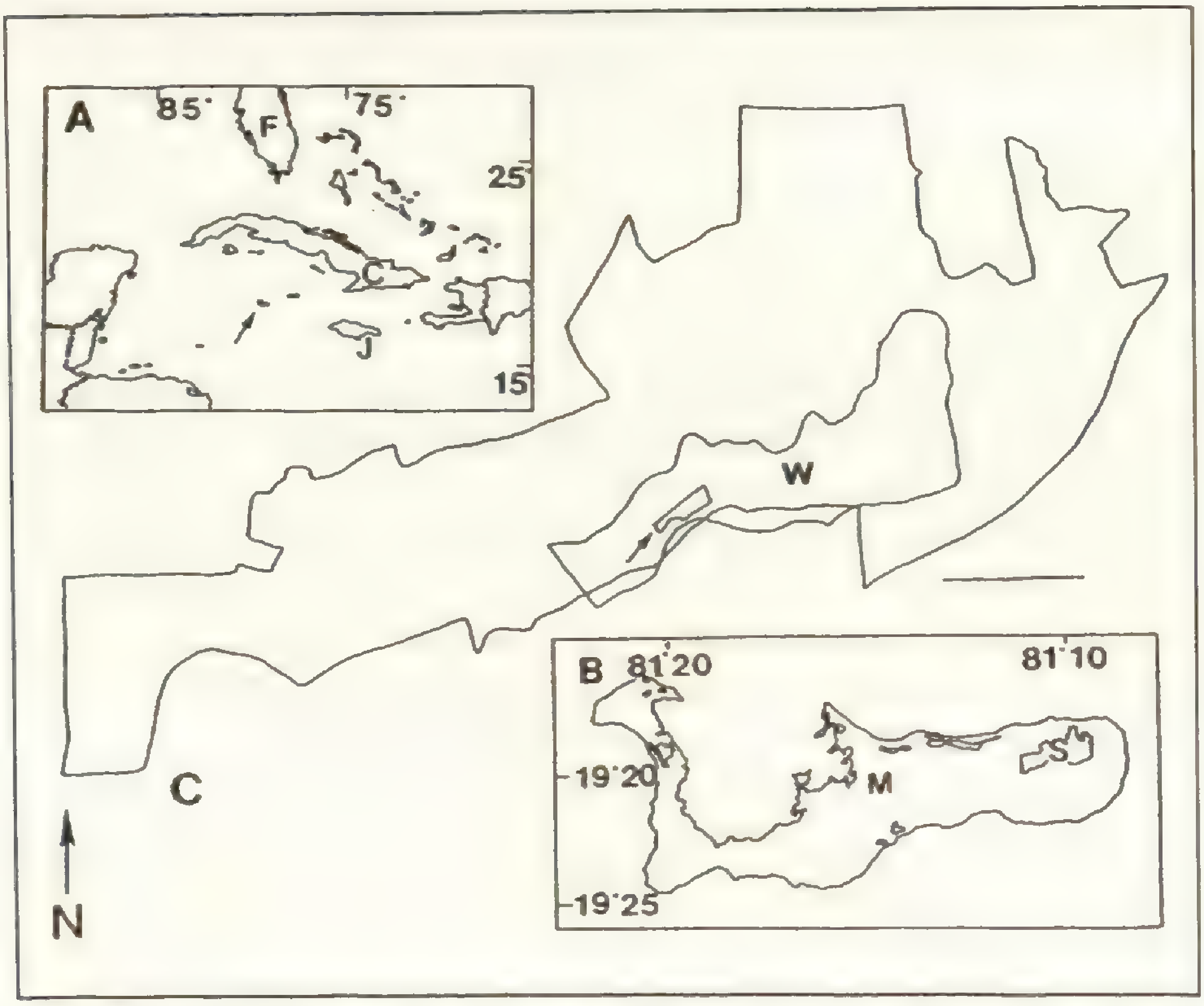


Figure 1. Location of study area. A. Map of Caribbean Sea showing location of Grand Cayman (arrow), and positions of Florida (F), Cuba (C) and Jamaica (J). B. Detail of Grand Cayman showing location of the Salina Reserve (S) and Central Mangrove Wetland (M) populations of *Agalinis kingsii*. C. Detail of Salina Reserve showing location of sedge wetland (W) and area examined for population count (arrow).

This study was conducted from May to August 1999. A population count was completed during July 1999 when the plants were most conspicuous. A portion of the sedge wetland was selected based on accessibility, and a grid was established in this area for a concurrent study on the community structure of the wetland. All plants of *Agalinis kingsii* in the grid were counted and the search was expanded into the surrounding area for *A. kingsii* individuals. Care was taken to mark the boundaries of the area examined to facilitate area calculation using a Trimble (Sunnyvale, CA) global positioning system and ArcView GIS software (ESRI, Redlands, CA).

Data collection. The relative position of every tenth *Agalinis kingsii* individual (N = 101) was noted in conjunction with the number of individuals in the immediate area (N = 1014). For every tenth individual, the following environmental and biological factors were recorded: 1) percent (%) shade at the soil surface, estimated by the percentage of biomass cover at the soil surface; 2) the distance from soil surface to the water table; 3) plant height, measured as the distance from the soil surface to tip of peduncle; 4) number of flowers on peduncle; 5) number of lateral branches; 6) average number of flowers on lateral branches; 7) associated species and % cover in a 1 m quadrat using the individual as the center; 8) community association; 9) evidence of previous generations; 10) evidence of defoliation (i.e., herbivory); and 11) the presence of ants in or on the corolla. If the tenth individual was a juvenile, no data were recorded.

Continuous monitoring for potential pollinators entering the corolla was undertaken for the duration of the study between the hours of 0730 and 1630, Monday to Saturday. A qualitative description of flower morphology was developed based on both field observations and measurements of flower structures using a dissecting microscope and a standard ruler on 20 flowers transported in alcohol. Flower structure measurements included: 1) length and position of stamens; 2) length, width, and morphology of ovary; and 3) length of style and stigma. In addition, the phenology of 20 marked individuals was monitored throughout the study. To determine if the species self-fertilized, one flower on each of 10 of these individuals was bagged with nylon mesh, and the bag was left until the flower wilted and/or detached.

Mature seeds were collected on an ongoing basis from the Salina (month/day: 06/09; 06/12; 06/16; 06/23; 07/02; 07/19; 07/16; 07/23; 07/29). Seeds were also collected from a second population in the Central Mangrove Wetland (07/22; 07/29; Figure 1). The length and width of mature seed capsules (N = 100), not yet dehisced, were measured using a dissecting microscope and a standard ruler. The number of seeds was counted from each capsule, and measurements of length and width were recorded for 50 randomly selected seeds using a dissecting microscope and ruler. Voucher specimens for seeds are deposited in the herbarium of the National Trust for the Cayman Islands (CAYM; Grand Cayman). Because of the concern over the status of *Agalinis kingsii*, whole plant specimens were not collected.

Seed morphology has been recognized for its value in the systematic analysis of *Agalinis* (Canne 1979, 1980; Musselman and Mann 1976; Pennell 1913, 1929, 1935). To provide a more detailed description of the species, surface morphology of mature seeds was examined using scanning electron microscopy (SEM). Seeds (unfixed and without critical point drying) were mounted on a sticky carbon stub, sputter-coated with gold (2–60 sec. cycles), and examined on a Joel JSM-5300 SEM.

Data were analyzed using the descriptive statistics package in SPSS 8.0 for Windows (SPSS Inc., Chicago, IL). Values given in text are ranges and means ± SE. The nomenclature used in this paper follows Proctor (1984).

RESULTS

Description of *Agalinis kingsii*. *Agalinis kingsii* individuals ranged in height from 28.0 cm to 75.0 cm. The stems were pale green, but sometimes violet, and blackened upon drying. The flowers and the leaves were decussate (Figure 2) and the pedicels were observed to ascend. All lobes of the corolla spread and were pubescent within at the base of the posterior lobes. There were between 5 and 13 flowers on the peduncle and 0–7 flowers on each lateral branch, with 0–7 lateral branches per plant.

The corolla was membranous and pink, with darker spots and two yellow lines within the anterior of the throat. The capsule was globose, and the calyx lobes were always less than the length of the tube. There were two shorter (4–5 mm) and two longer (8–9 mm) stamens that attached to the posterior of the corolla. The ovary was two-celled (1–2 mm). The style was 9–10 mm long and the stigma was 4–5 mm.

Mature seed capsules were 16.5–21 mm long and 11–13 mm wide and contained 196–205 seeds of unknown viability. Seeds were 0.6–0.9 mm long and 0.2–0.3 mm wide (Figure 2). The shape was angular and bluntly trapezoidal (Figure 3). The outer seed coat was black and reticulate, and the cells of the outer seed coat had conspicuous walls that were medium to deep relative to other species in the genus (Figure 4, 5). The wall suture between cells consisted of a trough, but this trough was shallow (Figure 5, 6). The radial walls were uniformly thickened and the surface was smooth (Figure 4). The thickenings were always smooth; however, the pattern of thickening was variable (Figure 4, 5).

Abundance and ecology. In the 17,764 m^2 area examined in the Salina, 1524 *Agalinis kingsii* individuals were located, equaling a density of $8.57\ 10^{-3}$ individuals m^{-2}. The area of the sedge wetland where *A. kingsii* occurred is 491,040 m^2 and an extrapolation of the data suggests the existence of approximately 42,000 individuals growing in the Salina during July, 1999. The second population of *A. kingsii* in the Central Mangrove Wetland (Figure 1) was much less extensive. A single dense population was observed on dry ground with < 1000 individuals in a 3×3 m open area with a few scattered individuals observed along a path to this site.

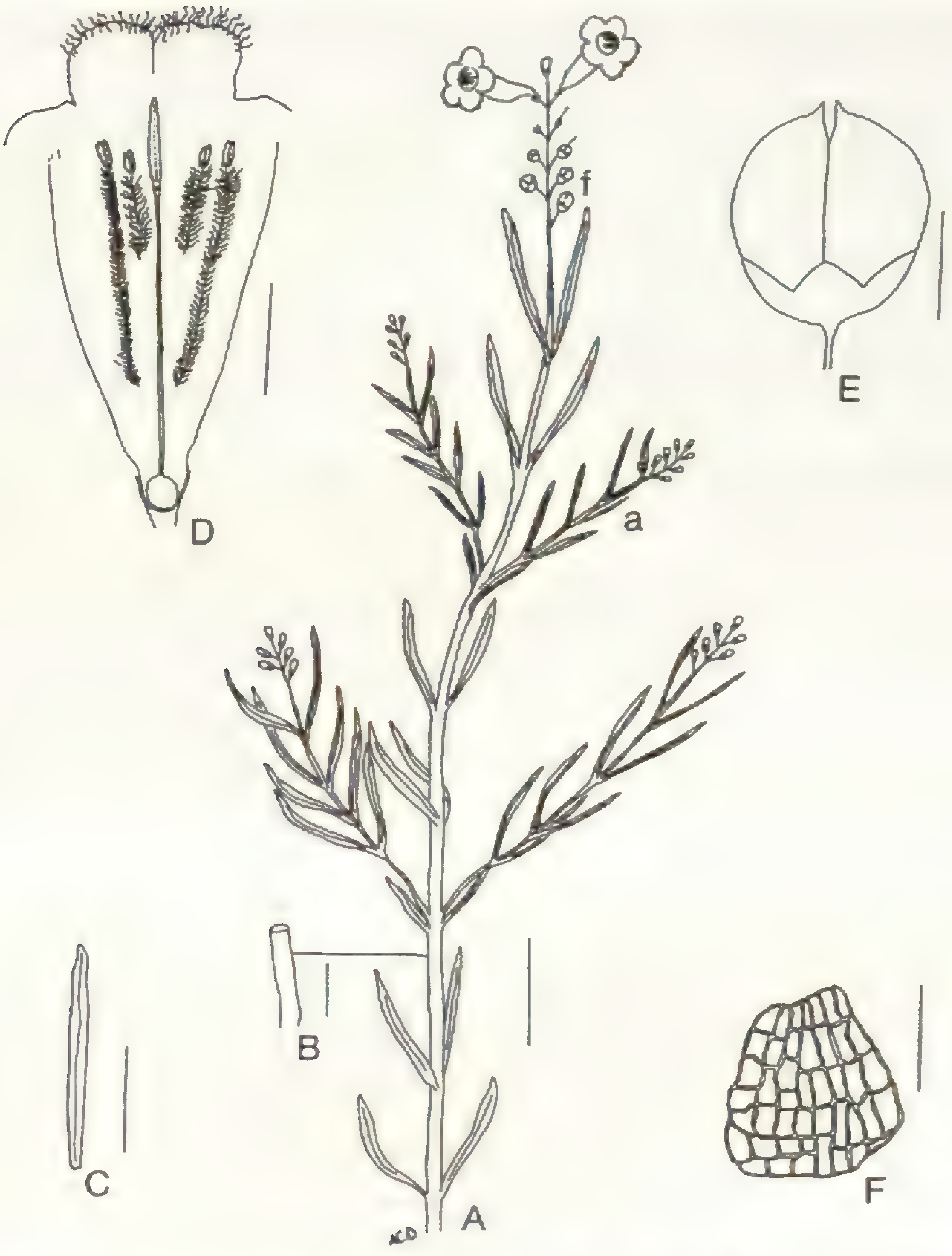
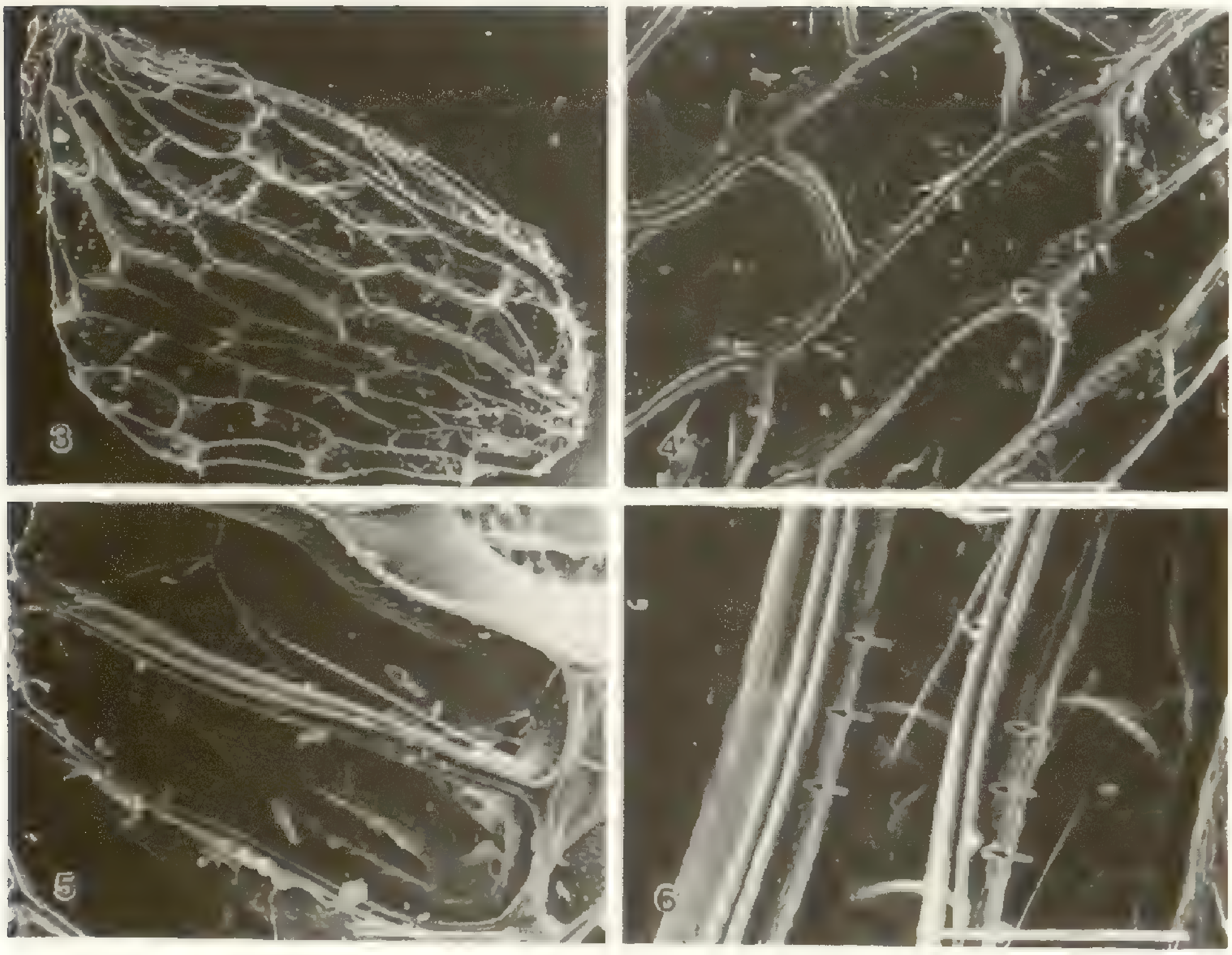


Figure 2. *Agalinis kingsii*. A. Habit of mature plant with flowers, fruits (f), and lateral branches (a). Scale = 4 cm. B. Stem section indicating terete transverse section. Scale = 0.5 cm. C. Leaf. Scale = 2 cm. D. Section of flower showing two large and two small stamens and single pistil. Note conspicuous hairs on stamens and dorsally on petal tips. Scale = 0.4 cm. E. Partially dehiscent fruit. Scale bar = 0.1 cm. F. Mature seed. Scale = 0.05 cm.

Agalinis kingsii had a clumped distribution and when located, there were 2–28 individuals in 1 m^2. In the Salina *A. kingsii* could be found with the base of the stem submerged in standing water, but was generally found 4.2 ± 0.9 cm above the water table. *Agalinis kingsii* was most commonly found growing on the sides of *Conocarpus erectus–Cladium jamaicense* Crantz tree islands and at drier, upland locations in the *C. jamaicense* community (Table 1). Individuals were located most



Figures 3–6. Scanning electron microscopy of seeds of *Agalinis kingsii*. 3. Whole seed. Scale bar = 100 μm. 4. Shape and relative depth of outer seed coat cells and pattern of wall thickening. Scale bar = 50 μm. 5. Surface features of radial walls (arrows), wall sutures, and relative depth of outer seed coat walls. Scale bar = 50 μm. 6. Detail of wall suture showing conspicuous trough (arrows). Scale bar = 50 μm.

frequently (74.3%) on the side of small (< 5 m diameter) *Conocarpus erectus–Cladium jamaicense* tree islands. *Agalinis kingsii* was found associated with *C. jamaicense* [frequency (f) = 100%], *Eleocharis cellulosa* Torr. (f = 54.5%), *Metastelma palustre* (Pursh) Schltr. (f = 18.8%), *Rhabdadenia biflora* (Jacq.) Muell.-Arg. (f = 3%), and *Acrostichum aureum* L. (f = 3%).

Growth time from emergence to flowering was 16–21 days. Flowering of each pair of buds was consecutive (1–2 days between pairs) and each pair was viable for 1 day. Accordingly, *Agalinis kingsii* probably began emerging in mid-April and continued until early September. Flowering began in early May and climaxed in July. Upon emergence, growth of the peduncle was rapid. A raceme formed and began to produce flower buds. Each pair of buds (or single for the terminal bud), flowered in the early morning, which is common in the genus (Dieringer 1991, 1992). Flowers wilted and detached in the afternoon on the day of emergence. Seed set began approximately 18

Table 1. Frequency table for presence of past year(s) individuals, ants on stem or in corolla, defoliation, and general habitat for *Agalinis kingsii*. N = 100.

Ecological Feature	Frequency (%)
Presence of past year(s) individuals	90
Presence of ants on stem or in corolla	99
Presence of defoliation	47
Presence on small tree islands (< 5 m diam.)	78
Presence on medium tree islands (5–10 m diam.)	15
Presence on large tree islands (> 10 m diam.)	6

days after pollination. The seeds were dispersed to the ground. Once all capsules had dehisced, the peduncle turned black and detached.

Individuals from the previous year(s), as evidenced by dead standing biomass, were present at 90.1% of the sites where *Agalinis kingsii* occurred (Table 1). There was evidence of defoliation on 46.5% of plants, presumably by larvae of *Junonia evarete* (Pule 1995; Smith et al. 1994; Stiling 1989). Pupae of the same species were observed on *A. kingsii* in the Central Mangrove Wetland. No winged insects were observed entering the corollas during the study. Flightless ants were the only insects observed entering the corolla and they were present in the corolla or on the stem of 99% of the individuals examined (Table 1). Ants, covered in pollen, were regularly seen exiting the corollas. Bagged flowers did not self-fertilize and the ovary detached after 1–2 days.

Several environmental factors were significantly correlated with growth, and the number of flowers per plant showed significant correlations with size. Percent shade at the soil surface correlated with individual height ($r = 0.753$, $p < 0.05$), and distance from the plant base to the water table correlated with plant height from base to tip of the peduncle ($r = 0.378$, $p < 0.05$). As well, the number of flowers on the peduncle correlated with height of the plant ($r = -0.301$, $p < 0.05$). These relationships may have significant implications for species persistence and their importance will be addressed in the forthcoming discussion.

DISCUSSION

This account of the biology and the life history of *Agalinis kingsii* will aid in designing more detailed ecological studies, as well as in developing long-term survival and management strategies for *A. kingsii* on Grand Cayman. The following discussion will focus on understanding species-environment interactions, in the context of species rarity, to further assist in the design of a management plan that will encourage persistence of the species.

The rarity of *Agalinis kingsii* on the island might be explained by the limited quantity of suitable habitat. This species was never located in an area that had 100% "forest" canopy cover. Thus habitat in the Central Mangrove Wetland that is suitable in terms of species composition may have inadequate light. *Agalinis kingsii* germinated in areas where there was 100% shade at the soil surface, but dead, overlying vegetation or dense stands of *Cladium jamaicense* typically imposed this shade. The data suggest that lower light at germination results in a taller individual at maturity. However, the taller the plant, the fewer flowers present on the peduncle. The relationship implies that, as competition for light increases, reproductive fitness of the individual decreases. If fitness is decreased, then there may be fewer individuals recruited into these small, rare populations.

Concomitantly, many rare species are known to benefit from disturbance (Grigore and Tramer 1996; Hartnett and Richardson 1989; Jacobson et al. 1991; Lesica 1999; Watson et al. 1994) and *Agalinis kingsii* does not appear to be an exception. *Agalinis kingsii* in the Salina was found in an area frequently ($<$ 10 years) affected by fire. Fire constrains the growth of woody species in the Salina and removes dead aboveground biomass, creating an adequate light environment for successful growth. The recurring fires in the Salina may be a requirement for the long-term stability of *A. kingsii* populations on Grand Cayman. The long-term survival of the *A. kingsii* population in the Central Mangrove Wetland, without recurring fires, appears more tenuous. As previously mentioned, the *A. kingsii* plants in the Central Mangrove Wetland were found in a very limited area but this area has been cleared annually by the Mosquito Research and Control Unit (MRCU) of the Cayman Islands government. Should the MRCU halt their path maintenance in this area, *A. kingsii* may be in danger of disappearing. Disturbance, especially by fire and clearance, removes litter and thereby increases seedling emergence and opens habitat that was previously unsuitable. The autecology of *A. kingsii* suggests a positive relationship with disturbance and, as such, no attempt should be made to alter the disturbance regime.

In the Salina, *Agalinis kingsii* was most often found growing in the *Conocarpus erectus–Cladium jamaicense* community. This community differs from all other communities in the sedge wetland in its soil pH, water salinity, and distance from the water table (Diochon, unpubl. data). Any commercial developments undertaken in the northeast corner of Grand Cayman have the potential to influence hydrographic features in the Salina. Alterations to the water table may have a dramatic effect on community structure, possibly similar to the alarming modifications to the vegetation structure in the Florida Everglades subsequent to development in the surrounding area (Jordan et al. 1997; Loveless 1959). Although the populations of *A. kingsii* on Grand Cayman are small, but appear stable, they may be at risk due to their narrow geographic and environmental range.

Conservation measures should be taken to ensure species survival. Such measures could include: 1) continuous monitoring of the status of the populations; 2) a continuation of current disturbance regimes in the Salina and Central Mangrove Wetland; 3) establishment of a seed bank; and 4) introduction of the species to the Queen Elizabeth II Botanic Park, located on Grand Cayman Island. The authors are hopeful that this account might encourage further systematic analysis of *Agalinis kingsii* to confirm its endemic status.

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NEW ENGLAND NOTE

A RECORD FOR *SELAGINELLA ECLIPES* (SELAGINELLACEAE) IN MASSACHUSETTS

Arthur Haines

441 Dead River Road, Bowdoin, ME 04287
e-mail: arthurhaines@gwi.net

The *Selaginella apoda* (L.) Spring *in* Mart. et al. complex contains subtly differentiated taxa in the eastern United States. The number of taxa recognized in this complex over the years has varied and the taxonomy has been considered controversial (Buck and Lucansky 1976). Buck (1977) described a new species from within this group—*S. eclipes* W. R. Buck—after examination of numerous specimens from various regions of the United States. Identification of this new species requires careful review of megaspore size, ornamentation, and surface characteristics and morphology of the upper leaf rank. Due to the lack of obvious and straightforward characteristics to separate *S. eclipes* from *S. apoda*, some regional floristic manuals have chosen to subsume the former in the latter species (Magee and Ahles 1999).

Skoda (1997) reduced *Selaginella eclipes* to a subspecies of *S. apoda*, under the name *S. apoda* subsp. *eclipes* (W. R. Buck) Skoda. This change in rank was based on the apparent lack of characters separating the two species. Skoda made the new combination as part of a review of the second volume of the *Flora of North America North of Mexico*. In the *Selaginella* contribution in this volume, Valdespino (1993) used only vegetative characters in the identification key that separated *S. apoda* and *S. eclipes* and did not provide descriptions of megaspores. Skoda's change in rank of *S. eclipes* did not appear to make use of specimen review or field surveys. It is, therefore, not followed here. There is little doubt that the *S. apoda* complex would benefit from further biosystematic study.

Selaginella eclipes and *S. apoda* are largely allopatric. The former is primarily distributed in the Midwest, Great Lakes, and St. Lawrence Seaway regions, while the latter is largely found in the eastern and southeastern United States. Buck reported only two small areas of sympatry: central New York and southeastern Missouri.

Valdespino discovered the first New England record of *Selaginella eclipes* in Canaan, Litchfield County, Connecticut (*Mehrhoff 7546*, CONN). The plants were located on the floor of an abandoned marble quarry. The record represented a significant range expansion for *S. eclipes*—central New York was the closest location reported by Buck (1977). Since the discovery, activity in the quarry has resumed and the plants have been extirpated (Les Mehrhoff, pers. comm.).

Selaginella eclipes is a target species of the Herbarium Recovery Project. The goal of this two-year research program is to locate herbarium records of rare and/or poorly known native species in New England, verify the accuracy of the determinations, and enter the corresponding label information into a database. Specimens determined as *S. apoda* from the Gray Herbarium (GH) and New England Botanical Club Herbarium (NEBC) collected from western New England were closely examined for the possibility of locating vouchers of *S. eclipes*. A single specimen was discovered from Massachusetts.

SPECIMEN CITATION: U.S.A. Massachusetts: Berkshire Co., Wet hillside, Lee, 14 Aug 1904, *Hoffman s.n.* (NEBC).

The specimen demonstrates characteristics of *Selaginella eclipes* noted by Buck (1977). The leaves of the upper rank taper to a long-attenuate, frequently recurved apex. The megaspores are ornamented with a lax reticulum comparable to specimens annotated by Buck to *S. eclipes* from the Great Lakes regions (housed at GH). Further, the megaspores are ca. 375 μm in diameter. This measurement, though not out of range for *S. apoda*, is larger than average for that species (Somers and Buck 1975) but well within the range of *S. eclipes*.

This represents the first report of *Selaginella eclipes* from Massachusetts (Angelo and Boufford 1996; Sorrie and Somers 1999). *Selaginella eclipes* is currently not afforded protection by formal listing as rare in any state of New England. It possesses a global rank of G4 (apparently secure; Natureserve 2001).

ACKNOWLEDGMENTS. Les Mehrhoff, the curators of the Harvard University Herbaria, and staff of the Botanical Libraries of Harvard University are thanked for their help with this note. The New England Wild Flower Society is also thanked for permission to use information gathered during the Herbarium Recovery Project.

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RHODORA, Vol. 105, No. 922, pp. 192–195, 2003

NEBC MEETING NEWS

January 2003. The evening began with an exceptional potluck dinner featuring a wide range of botanical edibles. Various members of the Apiaceae and Fabaceae appeared as appetizers and dips. *Spinacea oleracea* and *Lycopersicon esculentum* combined in an excellent lasagna and quiche. Most of the desserts featured *Theobroma cacao*, supported by Pam Weatherbee's outstanding apple-cranberry pie. Apples appeared again in the mulled cider. *Vitis vinifera*, *Humulus lupulus*, and various strains of yeasts contributed to the array of beverages.

The annual member's "show-and-tell" evening got off to an early start, as images of ferns from Don Lubin's website played during the announcements. Don showed slides of the fall NEBC trip to Owls Head in Vermont and Mt. Willard in Crawford Notch, featuring intrepid club members and some pteridological highlights (fertile *Pteridium aquilinum*, *Isoetes echinospora*, *Lycopodium lagopus*). Paul Somers followed with more slides of Club trips, including the Montague Plains in June, Yale Camp in August (Sue Williams teaching about mosses, Ernst Schori as chef, drenched botanists), Owls Head, and the spectacular view from Mt. Willard. Art Gilman continued the fern theme with photos of an unusual dissected *Osmunda cinnamomea*, a new tetraploid subspecies of *Phegopteris connectilis*, and *Botrychium pallidum* on Petit Manan. Art also shared pictures of a population of showy lady slippers in Vermont, with spectacular patches of albino flowers.

Marsha Salett provided a preview of her CD field guide to peatlands and acidic fens of New England. The interactive format allows students and amateurs to easily find photos of common bog species at various life stages, with information on natural history, ecology, and phenology, as well as information on peatland ecology. In the same theme, Jenn Forman shared her summer project, which documented the flora of the UMass field station on Nantucket with a "virtual nature trail" and photo gallery. Some highlights included *Vitus labrusca*, which should be known as the kudzu of Nantucket, and the invasive *Cytissus scoparius*.

Traveling farther afield, Lisa Standley showed images of her trip to Mongolia by way of Beijing. Slides featured Mongolian modes of transportation, the grassy steppes of central Mongolia, and the vast spaces and mountain ranges of the Gobi. Plants were weird and wonderful, from the tiny curlicue *Ephedra* to the tremendous diversity of *Astragalus*, *Oxytropis*, and *Iris*. Barre Hellquist also showed slides and told tales of the desert, although in the Davis Mountains of Texas rather than Central Asia. He showed images of his search for

Potamogeton clystocarpus, the extremely rare Aguha Canyon Pondweed. Barre assured us that the plant (which looks exactly like *P. pusillus*) really is a good species with a unique rhizomatous growth form, perhaps to anchor it against the turbulence of flash floods. Nancy Eyster-Smith closed the evening presentation with slides from Arizona, featuring the Biosphere site, various effects of fire in the southwest, and sunset behind the Saguaros.

—LISA STANDLEY, Recording Secretary *pro tempore*.

February 2003. The evening's scheduled speaker was unable to attend due to the snowstorm, prompting a change in the program. Kanchi Gandhi introduced Rebecca Pradhan, a visiting scholar at Harvard from the Royal Society for the Protection of Nature, Bhutan, who spoke on "Rhododendrons and Conservation in Bhutan." She showed spectacular pictures of the many plant communities of Bhutan, with emphasis on her main research taxon, the genus *Rhododendron*. Rebecca was trained as a mathematician, but also has a Diploma in Horticulture from the University of Edinburgh. She has spent the past 18 years in forest research in Bhutan, where she is a pioneer in establishing a national herbarium and in conservation education.

Ms. Pradhan introduced Bhutan as a small country with extreme ecosystem diversity, with an elevation range from 100 m to 7000 m. The country is 72.5% forested while cultivated lands cover only 8.1% of the surface. Fortunately, there is a well-established system of four National Parks, four Wildlife Sanctuaries, and one strict Nature Reserve to safeguard the outstanding flora of Bhutan. Perhaps as important, and very forward-looking, is that biological corridors linking these preserves have been established to assure connectivity of the communities over time. To date, the flora is known to include 5600 species, of which 80 are endemic. There are two endemic genera: *Chromopanax* (Araliaceae) and *Bhutantherea* (Orchidaceae).

Focusing first on the various major communities, Rebecca led us through a tour of the forests of Bhutan from subtropical to subalpine. Lowland forests feature large trees of *Terminalia*, *Morus*, and *Ficus*. There are many orchids, including showy species of *Dendrobium* and *Phaius*. Next in elevation are warm broadleaf forest and chirpine (*Pinus roxburghii*) forest. Chirpine forest, although quite dry, has many epiphytes, including *Dendrobium falconii* and *Ceropegia* sp. The *Cymbidium hookerianum*, common to this forest type, is a delicacy in Bhutanese cuisine. Moist evergreen forest features trees of the genera

Persea, *Magnolia*, *Acer*, and *Quercus*, and also large bamboos (*Borinda grossa*), used locally in making brooms and bamboo mats. Dry broadleaf forest is dominated by the oaks *Q. griffithii* and *Q. lanata*. Further up slope, conifer forests and alpine vegetation dominate, with many beautiful genera such as *Cypripedium*, *Meconopsi*, *Primula*, *Aconitum*, and *Senecio*.

Bhutan has 46 species of *Rhododendron*, of which four are endemic: *R. kesangiae* (named after the Queen Mother of Bhutan), *R. bhutanensis*, *R. pogonophyllum*, and *R. flinckii*. Only one, *R. arboreum*, occurs in lowland forests. There are 10 species in the warm broad-leaved forests, but 34 species occur in the cool broad-leaved forest, with maximum diversity at approximately 3500–4000 m. About 14 species occur in the alpine shrub community. There are at present few identified threats to rhododendrons in Bhutan. Although several have economic uses (for incense, for wood carving, even for insecticide) the level of exploitation is small. Rebecca has published a book, *Wild Rhododendrons of Bhutan*, and is helping to establish an *in situ* rhododendron garden at the Thrumshingla National Park.

—ART GILMAN, Recording Secretary *pro tempore*.

March 2003. Vice President Art Gilman introduced the evening's speaker, Kristen Porter-Utley, a Ph.D. candidate from the University of Florida at Gainesville. She began her talk, titled "The Apetalous Passionflowers: Phylogenetic Relationships within *Passiflora* Section *Cieca* (Passifloraceae)," by drawing a diagram to introduce Club members to the intricacies of *Passiflora* flower morphology.

As indicated by the title of her talk, Kristen studies passionflowers that have sepals but no petals. This is a group of 19 climbing species (4 of which are endangered) that are native to the southern U.S., Mexico, and Central and South America. Club members were introduced to the research subjects with many photos of *Passiflora* plants in flower, no less beautiful for their lack of petals. In her research, Kristen used both morphological and molecular data in order to better understand the taxonomy of *Passiflora* subgenus *Decaloba* supersection *Cieca* [note: change in rank reflects a new, unpublished classification presented at the meeting of the Botanical Congress in St. Louis in August, 2000]. She began by examining over 4000 specimens at 40 herbaria, as well as photos of species in the *P. suberosa* complex that have become naturalized in tropical regions of the Old World. After the preliminary analysis, she then scored 95 of the specimens for 330 different vegetative and floral characteristics. For the molecular analysis, she scored samples for sequence variation in three different regions of ribosomal DNA: ITS-1, ITS-2 and 5.8S. Both the morphological and molecular data were then analyzed using software that generates cladograms to show how closely related the taxa are to one another.

Supersection *Cieca* contains two problematic species complexes, *Passiflora suberosa* and *P. coriacea*. Morphological analysis of herbarium specimens of *P. suberosa*, a species known to have both polyploidy and hybridization, indicates that it has served as a "taxonomic garbage can" for at least four entities (*P. pallida*, *P. suberosa* subsp. *suberosa*, *P. suberosa* subsp. *littoralis*, and *P. tridactylites*) that cannot be assigned to any of the other members of the supersection. The molecular analyses also support this finding. *Passiflora coriacea* is another "species" that exhibits marked morphological variation over its distribution from eastern Mexico to northern South America. Evidence indicates that it contains three distinct entities: *P. coriacea*, *P. megacoriacea*, and *P. sexocellata*.

Kristen also noted that when the cladograms of morphological and genetic data were placed side by side they were completely different. Thus, the complex relationships that exist within the supersection are not yet completely understood. She concluded by saying that this work had led to revisions in the taxonomy of the genus, since the analyses showed that while members of supersection *Cieca* share a common ancestor, the *Passiflora suberosa* and *P. coriacea* subcomplexes within it are not monophyletic. Following her talk, Kristen entertained several questions from club members about the apetalous *Passiflora* species, including a query about their pollinators, which are mainly wasps and bees, and whether their fruits are edible (they are, but they tend to be small and bitter).

—JENNIFER FORMAN, Recording Secretary *pro tempore.*

THE NEW ENGLAND BOTANICAL CLUB

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NOMENCLATURAL AND TAXONOMIC REVIEW OF KNOTROOT BRISTLE GRASS (*SETARIA PARVIFLORA*, GRAMINEAE)

Kanchi N. Gandhi

Harvard University Herbaria, 22 Divinity Ave,
Cambridge, MA 02138-2094
e-mail: kgandhi@oeb.harvard.edu

Mary E. Barkworth

Intermountain Herbarium, Utah State University,
Department of Biology, Logan, UT 84322-5305
e-mail: mary@biology.usu.edu

ABSTRACT. We support Kerguélen's (1977, 1987) assertion that both Lamarck (1798) and Willdenow (1809) independently published the identical name *Panicum geniculatum* and that P. Beauvois (1812) based his *Setaria geniculata* on Willdenow's name. The type collections of Lamarck's and Willdenow's names are different, but were from the same locality and belong to the same species. Willdenow's name, which is traced to Vahl's unpublished manuscript, is a later homonym, is illegitimate, and cannot serve as a basionym. Because of the illegitimacy of *P. geniculatum* Willd., *S. geniculata* is treated as a *nom. nov.* with its priority from 1812. *Cenchrus parviflorus* Poir. (1804) is the earliest legitimate name available for this species, and therefore, *S. parviflora* (Poir.) Kerguélen (1987) is recognized.

Key Words: *Cenchrus parviflorus*, *Panicum geniculatum*, *Setaria geniculata*, *S. gracilis*, *S. parviflora*, Gramineae, knotroot bristle grass, nomenclature

The knotroot bristle grass, long known by the name *Setaria geniculata*, is widespread in the US and extends south to Chile. In the past, the authorship of *S. geniculata* was cited as: (Lam.) P. Beauv. This citation implies that Beauvois based his *S. geniculata* on *Panicum geniculatum* Lam. 1798 (vide Hitchcock 1931: 320; 1951: 949–951). In a few early botanical works, *P. geniculatum* was attributed to Poiret (Joseph Jacquin 1820: 37; Steudel 1841: 256; Trinius 1834: 222) or to Hornemann (Roemer and Schultes 1817: 491; Trinius 1826: 163). It is noted here that Hitchcock's extensive synonymy included, among others, *Cenchrus parviflorus* Poir. (in Lamarck 1804) and *S. gracilis* Kunth (1816).

Contrary to early beliefs, Beauvois did not base his *Setaria geniculata* on *Panicum geniculatum* Lam. (1798), but explicitly referred to *P. geniculatum* Willd. (1809). Willdenow did not refer to Lamarck, but referenced Hornemann (1807). Although both versions of *P. geniculatum*, Lamarck's and Willdenow's, have the same type locality ("Antilles/Guadeloupe"), the two names were published independently and have different types. Willdenow's work was generally ignored in botanical works of the 19th and 20th centuries, but it was recognized by Roemer and Schultes (1817: 491), Jacquin (1820: 37), Sprengel (1825: 304), and Steudel (1841: 256).

Perhaps unaware of P. Beauvois's publication of *Setaria geniculata*, Roemer and Schultes (1817: 491–492) published the same combination and based it on *Panicum geniculatum* Hornemann (1807) *ex* Willdenow (1809). Their comb. nov. is a later isonym (of P. Beauv. 1812). They appear to be the first to remark that *P. geniculatum* Willd. was perhaps the same as *P. geniculatum* Lam. ("An idem cum P. geniculato Poiret ..."). Jacquin (1820: 37) and Steudel (1841: 256) also treated Lamarck's (as Poiret's) and Willdenow's *P. geniculatum* as applying to a single species.

Roemer and Schultes (1817) referred to *Pennisetum geniculatum* J. Jacq. Since Jacquin's *Pennisetum geniculatum* was not published until 1820, Roemer and Schultes must have had access to Jacquin's unpublished work. For his *Pennisetum geniculatum*, Jacquin referenced Hornemann, Willdenow, and Lamarck. Since, Lamarck's publication is the earliest, we assert that Jacquin's grass name was based on Lamarck's name.

Kerguélen (1977: 344–345) was perhaps the first to emphasize the fact that Beauvois based his *Setaria geniculata* on *Panicum geniculatum* Willd. (1809: 1031). In his nomenclatural analysis, Kerguélen concluded that: 1.) *P. geniculatum* Willd. is a later homonym of *P. geniculatum* Lam. (and hence, illegitimate and does not have priority); 2.) the identities of *Cenchrus parviflorus* Poir. and of *P. geniculatum* Willd. were uncertain; and 3.) *P. geniculatum* Lam. cannot be transferred to *Setaria*, as it would create a later homonym (non *S. geniculata* P. Beauv. 1812).

Nevertheless, the name *Setaria geniculata* is legitimate, but its author is Beauvois alone (no parenthetical author), and its priority dates from Beauvois' publication in 1812, not from the publication of either Lamarck 1798 (whose work Beauvois did not cite) or Willdenow 1809 (whose name is a later homonym). Since Kerguélen was uncertain whether *Cenchrus parviflorus* belonged to the same species as *S. geniculata*, he chose to use the name *S. gracilis* Kunth (1816: 109).

Kerguélen (Feb 1987: 161–162) later, however, decided that *Cenchrus parviflorus* Poir. and *Setaria geniculata* P. Beauv. do belong to the same species as *S. gracilis* and therefore proposed the combination: *S. parviflora* (Poir.) Kerguélen, "*parviflorus*," being the earliest available epithet. He cited *S. gracilis*, among other names, as a synonym of his new combination. Webster (1987: 208), perhaps unaware of Kerguélen's 1987 work, followed Kerguélen (1977).

At the time Kerguélen (Feb 1987) made the combination *Setaria parviflora*, names of species could be conserved only if the species concerned was of major economic importance (Art. 14.2 of the Sydney Code; Voss 1983); unfortunately, *S. geniculata* (= *S. parviflora*) did not meet that criterion, so Kerguélen was not able to propose conservation of the name *S. geniculata*. In the Berlin Code (Greuter 1988), one year too late for Kerguélen, Art. 14.2 was amended to include conservation of the names of species that had been widely and persistently used (in spite of their illegitimacy or not having priority) even if the species concerned was not of major economic importance.

We considered the possibility of reviving the name *Setaria geniculata* by establishing a link between *Panicum geniculatum* Willd. and *P. geniculatum* Lam. If Willdenow were to refer to Lamarck directly or indirectly, the authorship of *S. geniculata* must be (Lam.) P. Beauv. Our analysis follows.

Both Lamarck (1744–1829) and Willdenow (1765–1812) were contemporary botanists. It puzzled us that Willdenow was not aware of Lamarck's earlier usage of the name *Panicum geniculatum*. Lamarck (1798: 727 '737') based his *P. geniculatum* on a specimen collected from Guadeloupe . . . Antilles, on deposit at P-JU. Willdenow (1809: 1031) also gave Antilles as the place of origin for his type specimen. It is unclear whether it was a coincidence that both Lamarck and Willdenow chose a specimen from the Antilles for the type specimen.

Willdenow (1809: 1031) referenced Hornemann's 1807 work ("Hornem. Cat. Hort. haf. p. 28."). Hornemann mentioned the following: "*Panicum geniculatum* Vahl." In his subsequent publication, Hornemann (1813: 81) referenced Willdenow, copied Willdenow's 1809 description, cited the locality as Antilles, and stated that this grass was introduced to the Botanical Garden at Copenhagen in 1803. He did not refer to either Lamarck or Vahl.

Both Hornemann (1770–1841) and Vahl (1749–1804) were Danish botanists and worked at the herbarium of the University of Copenhagen (C). To the best of our knowledge, Vahl did not use *Panicum geniculatum* in his published works; this makes Hornemann's reference to Vahl puzzling.

We corresponded with Peter Wagner (C), who provided the following information. Vahl had prepared an index of cards and planned to publish a revised version of *Species Plantarum* in several volumes (titled

"Enumeratio Plantarum"). Unfortunately, after the publication of the first volume in 1804, he died. After Vahl's death, the Danish king bought Vahl's herbarium and library from his widow and placed it in the botanical garden. The second volume, posthumously issued in 1805, was edited by N. Toender Lund, J. W. Hornemann, and P. Thonning using Vahl's herbarium as well as his cards (cf. TL2 6: 631, no. 15,733. 1986). In their preface (p. viii), they stated that if the volume were to find recognition among botanists, the rest of Vahl's manuscript or parts of it would be published from the cards. Unfortunately, war with England (1807–1814) and the death of Toender Lund (in 1809) probably terminated the publication.

Regarding Vahl's usage of *Panicum geniculatum*, Wagner stated that Vahl, in his unpublished portion of the index, used the name *P. geniculatum*. [This explains Hornemann's 1807 reference to Vahl on the usage of the name *P. geniculatum*.] For his *P. geniculatum* (which he at first called *P. pauciflorum*), Vahl provided a description and mentioned the habitat as Ile de France. Since the usage of the name *P. pauciflorum* was not established until 1810 by R. Brown, we speculate that Vahl realized that his plant was the same as that of Lamarck, and therefore abandoned the name *P. pauciflorum* and accepted Lamarck's name. But Vahl did not reference Lamarck; hence, it is impossible to prove that he accepted Lamarck's name. [About 10 years ago, Carlo Hansen (c) also provided the same information (i.e., Vahl's usage of *P. geniculatum* and *P. pauciflorum*) to the senior author.]

Consequently, no link can be established between Lamarck's and Willdenow's treatments, and therefore, *Setaria parviflora* is the recognized name. The paragraphs below summarize the pertinent taxonomic data.

Setaria parviflora (Poir.) Kerguélen, Lejeunia, n.s., 120: 161. 1987.

Cenchrus parviflorus Poir. *in* Lam., Encycl. 6: 52. 1804; *Chaetochloa corrugata* var. *parviflora* (Poir.) Scribn. & Merr., Bull. Div. Agrostol., U.S.D.A. 21: 24. 1900; *Setaria ventenatii* Kunth, Revis. Gramin. 1: 251, t. 37. 1830, *nom. superfl.*; *Panicum ventenatii* Steud., Nomencl. Bot., ed. 2, 2: 265. 1841; *Chamaeraphis ventenatii* Beal, Grasses N. Amer. 2: 153. 1896; *Chaetochloa ventenatii* Nash *in* Kearney, Contr. U.S. Natl. Herb. 5(6): 515. 1901. Type: Puerto Rico: *Ventenat s.n.* (p).

Panicum vulpinum L., Amoen. Acad. 4: 134. 1759 [*non S. vulpine* (Willd.) P. Beauv. 1812]. lectotype (vide Merr., Dept. Agric. & Nat. Resources, Bur. Sci. Manila Publ. 9: 91. 1917): illustration in Rumph., Herb. Amboin. 6: t. 7, f. 2, 1750, b; epitype (vide Veldkamp, Taxon 49: 253. 2000):

[INDONESIA.] Amboina: Jul–Nov 1913, *C. B. Robinson*, Plantae Rumphianae Amboinensis No. 41, L; ISOLECTOTYPE: BM.

Panicum geniculatum Lam., Encycl. 4: 727 ('737'). 1798; *Pennisetum geniculatum* (Lam.) J. Jacq., Eclog. Gram. Rar. 3–4: 37, t. 26. 1820; *Chamaeraphis glauca* var. *geniculata* (Lam.) Kuntze, Revis. Gen. Pl. 2: 767. 1891; *Chaetochloa imberbis* var. *geniculata* (Lam.) Scrib. & Merr., Bull. Div. Agrostol., U.S.D.A. 21: 12. 1900; *Setaria glauca* var. *geniculata* (Lam.) Urb., Symb. Antill. 4: 96. 1903; *Chaetochloa geniculata* (Lam.) Millsp. & Chase, Publ. Field Columbian Mus., Bot. Ser. 3: 37. 1903. TYPE: "Antilles [West Indies] and Guadelope"; LECTOTYPE (vide Kerguélen, Lejeunia, n.s., 120: 162. 1987): P, P-JU 2572.

Panicum geniculatum Hornem. [Enum. Pl. Hort. Hafn. 28. 1807, *nom. nud.*] *ex* Willd., Enum. Pl. [pt. 2]: 1031. 1809, *nom. illeg.* (*non* Lam. 1798); *Setaria geniculata* P. Beauv., Ess. Agrostogr. 51, 169, 178. 1812; Roem. & Schult., Syst. Veg. 2: 491–492. 1817. TYPE: "Antilles" [West Indies].

Setaria gracilis Kunth *in* Humb., Nov. Gen. Sp. (H.B. & K.) 1(ed. qu.): 109. 1816; R. D. Webster, Australian Paniceae 208. 1987. TYPE: "Crescit in montanis regni Quiltense, prope Chillo" *F. W. H. A. Humboldt & A. J. A. Bonpland s.n.* (P).

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Setaria affinis Schult., Mant. 2: 276. 1824. TYPE: U.S.A. Georgia and Pennsylvania: *G. H. E. ["H."] Muhlenberg 153.* [based on Muhlenberg's *Panicum* No. 4.]

Setaria berteroniana Schult., Mant. 2: 276. 1824; *Panicum berteronianum* (Schult.) Steud., Syn. Pl. Glumac. 1: 50. 1853. TYPE: DOMINICAN REPUBLIC. *C. G. L. Bertero.*

Panicum dasyurum Nees *in* Mart., Fl. Bras. Enum. Pl. 2(1): 241. 1829; *Panicum imberbe* var. *dasyurum* (Nees) Döll *in* Mart., Fl. Bras. 2(2): 157. 1877; *Setaria gracilis* var. *dasyura* (Nees) Arechav., Anales Mus. Nac. Montevideo 1(2): 165. 1894. TYPE: BRAZIL.

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Panicum penicillatum Willd. *ex* Nees *in* Mart., Fl. Bras. Enum. Pl. 2(1): 242. 1829, *nom. illeg.* (*non* Nees *ex* Trin. 1826); *Setaria penicillata* J. Presl *in* C. Presl, Reliq. Haenk. 1: 314. 1830; *Setaria glauca* var. *penicillata* (J. Presl) Griseb., Fl. Brit. W.I. 554. 1864; *Chamaeraphis glauca* var. *penicillata* (J. Presl) Kuntze, Revis. Gen. Pl. 2: 767. 1891; *Chaetochloa penicillata* (J. Presl) Scribn. *in* Scribn. & J. G. Sm., Bull. Div. Agrostol., U.S.D.A. 4(6): 39. 1897; *Chaetochloa imberbis* var. *penicillata* (J. Presl) Scribn. & Merr., Bull. Div. Agrostol., U.S.D.A. 21: 11, fig. 2. 1900; *Chamaeraphis penicillata* J. Presl *ex* Stuck., Anales Mus. Nac. Buenos Aires 13: 442. 1904; *Setaria gracilis* forma *penicillata* (J. Presl) Mez *ex* Ekman, Ark. Bot. 13: 33. 1913. TYPE: BRAZIL.

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Setaria geniculata var. *pauciseta* E. Desv. *in* Gay, Fl. Chil. 6: 248. 1853 [March 1854]; *Setaria gracilis* var. *pauciseta* (E. Desv.) B. K. Simon, Austrobaileya 2: 22. 1984. SYNTYPES: [1] CHILE. Valdivia, *C. Gay*; [2] CHILE. Concepción and Talcahuano, *J. A. Pavón y Jiménez.*

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A SYNOPSIS OF THE GENUS *CLADRASTIS* (LEGUMINOSAE)

MATTHEW L. DULEY[1] AND MICHAEL A. VINCENT

Department of Botany, Miami University,
Oxford, OH 45056
[1]e-mail: duleyml@muohio.edu

ABSTRACT. The genus *Cladrastis* (*Sophora* group, Sophoreae, Papilionoideae, Leguminosae) occurs in the southeastern United States, China, and Japan, having an eastern North America–eastern Asia disjunct distributional pattern. It comprises trees with alternate, imparipinnate leaves with alternate leaflets, lateral buds enclosed in the base of the petiole, and white flowers in paniculate inflorescences that may be erect or pendulous. A phenetic analysis of morphological characters was conducted on a subset of the 600 herbarium specimens examined from 26 herbaria worldwide. The resulting phenogram of vegetative specimens showed 4 clusters of specimens. Further analysis using flowering specimens indicated two additional clusters. Comparing these clusters with type specimens resulted in recognition of six taxa: *Cladrastis platycarpa*, *C. kentukea*, *C. wilsonii*, *C. delavayi*, *C. shikokiana*, and one new species, *C. chingii*.

Key Words: *Cladrastis*, Fabaceae, legume, Leguminosae, Papilionoideae, *Sophora* group, Sophoreae

The genus *Cladrastis* Raf. is a member of the *Sophora* group, tribe Sophoreae, subfamily Papilionoideae of Leguminosae. The *Sophora* group contains 9 genera with 72–80 species (Polhill 1978); however, on the basis of wood anatomy (Fuji et al. 1994), pollen morphology (Chung and Lee 1990; Ferguson et al. 1994), and recent DNA studies (Doyle et al. 1997; Käss and Wink 1996) the group may not be monophyletic. *Cladrastis* comprises deciduous trees 10–20 m in height with smooth grayish bark and rounded crowns. Leaves are imparipinnate, with 5–15 leaflets on short petiolules. Flowers are typically white, in erect or pendulous panicles 25–50 cm long. The fruit is a narrowly oblong, compressed legume containing 1–8 seeds. *Cladrastis* is morphologically similar to both *Sophora* L. and *Maackia* Rupr. (Andrews 1996; Spongberg and Ma 1996); however, it differs from both in having alternate leaflets and petioles that enclose the lateral buds (*Sophora* and *Maackia* have opposite leaflets and *Maackia* has exposed lateral buds). In addition, it differs from *Maackia* in having paniculate inflorescences (those of *Maackia* are racemose), and from *Sophora* in having compressed seed pods (*Sophora* has cylindrical seed pods constricted between the seeds).

Cladrastis has an eastern North America and eastern Asia disjunct distribution pattern (Fernald 1931; Hu 1980). *Cladrastis kentukea*

(Dum.Cours.) Rudd is endemic to the central and southeastern United States (Pittillo 1963). All remaining taxa are Asian, with *C. delavayi* (Franch.) Prain, *C. wilsonii* Takeda, and *C. chingii* Duley & Vincent occurring only in China, and *C. shikokiana* (Makino) Makino occurring only in Japan; *C. platycarpa* (Maxim.) Makino is found in both China and Japan. *Cladrastis* may have been in North America as early as the Eocene, based on the fossil *C. eocenica* E. W. Berry, as reported from the Wilcox flora (Berry 1930; Cain 1943), and on fossil leaves and fruits from the southeastern United States (Herendeen 1992). Oligocene fossils of the genus have been found in Oregon (Manchester and Meyer 1987; Meyer and Manchester 1997). Miocene fossils of the genus have been reported from Alaska (Wolfe and Tanai 1980), Oregon [*C. oregonensis* (Knowlt. & Cockerell) R. W. Br.; Brown 1937], and Japan (*C. aniensis* Huzioka; Tanai et al. 1963).

In North America, *Cladrastis kentukea* occurs along cliffs above rivers, and in openings of mesophytic coves, where it appears to do best in the rich, coarse-textured soils. In China, *C. wilsonii* is common in moist woods of Hubei and as far west as the eastern reaches of the Red Basin of Sichuan province. *Cladrastis delavayi* occurs between 1500 and 2500 m in the forests of western Sichuan. *Cladrastis platycarpa* is reported from provinces along the southern and eastern borders of China and throughout Japan, whereas *C. shikokiana* is restricted to the southern provinces of Japan, below 500 m.

Used as an ornamental because of its large, showy, and fragrant inflorescences (Andrews 1999; Rehder 1927), *Cladrastis kentukea* makes a good shade tree with its rounded canopy and moderately dense silhouette (Gilman 1997). It should be noted, however, that *C. kentukea* flowers profusely only every two to three years (Spongberg 1990). Its yellowish heartwood has been used to make dyes and household items, such as bowls and paneling (Harlow et al. 1991), and the hard, dense wood was used by the American settlers to make gunstocks. Three of the Asian species, *C. platycarpa*, *C. wilsonii*, and *C. delavayi*, are also listed as garden trees (Griffiths 1994) because of their smooth, gray bark and showy inflorescences.

The name *Cladrastis* was first mentioned in 1822 by Rafinesque in the *Kentucky Gazette* (Rafinesque 1822), and then in a botanical garden catalog (Rafinesque 1824a), with the species name *C. fragrans*, but without a description. Rafinesque (1824b) subsequently described that genus and species in the *Cincinnati Literary Gazette*, based on a new tree he had reported earlier as *Virgilia alba* (Rafinesque 1822). Rafinesque (1824b) stated that he had now seen the tree in bloom and it was not a *Virgilia* after all; therefore, he proposed the genus name *Cladrastis* (meaning "brittle branches") for the tree and renamed the species *C. fragrans*.

Takeda (1913) separated the genus into subgenus *Eucladrastis* (*nom. inval.*, = subg. *Cladrastis*), including *Cladrastis sinensis* (= *C. delavayi*), *C. shikokiana*, and *C. lutea* (= *C. kentukea*), and subgenus *Platyosprion* containing *C. platycarpa*. Ma (1982) recognized two sections, *Cladrastis* and *Platyosprion*; section *Platyosprion* contained three species, *C. platycarpa*, *C. scandens*, and *C. parvifolia*, while section *Cladrastis* contained *C. lutea*, *C. sinensis* (= *delavayi*), *C. shikokiana*, and *C. wilsonii*. Murray (1985) also divided the genus into two subgenera, *Cladrastis* and *Platyosprion*. He further subdivided each subgenus into sections, subsections, series, and subseries. Murray's classification may be excessive for a genus to which he attributes only four species.

Several chemical compounds (mostly phenolics and flavonoids) have been isolated from the bark of *Cladrastis platycarpa*, *C. shikokiana*, and *C. kentukea* (Imamura et al. 1972, 1974, 1975; Ohashi et al. 1974, 1976; Ohashi, Goto, and Imamura 1977; Ohashi and Imamura 1978; Ohashi, Yamada, and Imamura 1977; Van Damme et al. 1995) but they have not proven useful for differentiation of species within the genus. The only published chromosome number for the genus, $2n = 28$, is for *C. kentukea* (as *C. lutea*; Atchison 1949; Berger et al. 1958; Smith 1988).

There has been no monograph published for *Cladrastis*. While Ma (1982) provided a key and descriptions of the species that he accepted, he did not reexamine type specimens, and he left many nomenclatural problems unresolved. The purpose of this study was to determine the number of species in the genus *Cladrastis* by morphological means, and answer the numerous nomenclatural questions after study of all available type material.

MATERIALS AND METHODS

Approximately 600 herbarium sheets were examined from the following herbaria: A, B, BM, CAS, DS, E, F, GH, HAST, ILL, ILLS, IND, K, KNK, KUN, KY, KYO, LL, MAK, MICH, MO, MU, NAS, NY, P, PE, PH, S, TEX, US, and WIS. In addition to specimens, photographs of some taxa were obtained from the Royal Botanical Gardens, Kew, England (K), and photocopies from Hong Kong (HK). Of these 600 specimens, 215 were selected for analysis, representing the range of morphological and geographical variation within the genus. Specimens were selected or rejected

Table 1. Characters measured for the analysis of the genus *Cladrastis*. Qualitative character state codes are in parenthesis. Characters marked with an asterisk (*) indicate those used in the final phenetic analysis.

Plant Part	Characters
VEGETATIVE CHARACTERS	
Leaf	1. Leaf length. 2*. Number of leaflets. 3. Petiole color: yellow (3), green (4), brown (6), yellow green (7). 4. Petiole pubescence: absent (0), sparse (1), dense (2). 5. Petiole pubescence color: white (1), rusty (2), yellow (3), green (4).
Terminal leaflet	6. Shape: ovate (1), obovate (2), elliptical (3), narrow elliptical (4). 7. Length. 8. Width. 9*. Apex: emarginate (0), rounded (1), acute (2), acuminate (3). 10*. Base: rounded (1), acute (2), cuneate (3), inequilateral (4). 11. Underside pubescence: absent (0), sparse (1), dense (2). 12. Underside pubescence color: white (1), rusty (2), yellow (3), green (4). 13. Underside midrib pubescence: absent (0), sparse (1), dense (2). 14. Underside midrib pubescence color: white (1), rusty (2), yellow (3), green (4). 15. Petiolule length. 16. Petiolule color: white (1), rusty (2), yellow (3), green (4), brown (6), yellow green (7). 17. Petiolule pubescence: absent (0), sparse (1), dense (2). 18. Petiolule pubescence color: white (1), rusty (2), yellow (3), green (4).
First leaflet	19. Shape: ovate (1), obovate (2), elliptical (3), narrow elliptical (4). 20. Length. 21. Width. 22. Apex: emarginate (0), rounded (1), acute (2), acuminate (3). 23. Base: rounded (1), acute (2), cuneate (3), inequilateral (4). 24. Underside pubescence: absent (0), sparse (1), dense (2). 25. Underside pubescence color: white (1), rusty (2), yellow (3), green (4). 26. Underside midrib pubescence: absent (0), sparse (1), dense (2). 27. Underside midrib pubescence color: white (1), rusty (2), yellow (3), green (4). 28. Petiolule length. 29. Petiolule color: white (1), rusty (2), yellow (3), green (4), brown (6), yellow green (7). 30. Petiolule pubescence: absent (0), sparse (1), dense (2). 31. Petiolule pubescence color: white (1), rusty (2), yellow (3), green (4).
Stipels	32*. Stipel type: absent (0), subulate (1), branched and multiple (2).
FLORAL CHARACTERS	
Inflorescence	33. Inflorescence length. 34. Peduncle color: yellow (3), green (4), brown (6), yellow green (7). 35*. Peduncle pubescence: absent (0), sparse (1), dense (2). 36*. Peduncle pubescence color: white (1), rusty (2), yellow (3), green (4).

Table 1. Continued.

Plant Part	Characters
Calyx	37. Tube width. 38. Tube length. 39. Upper lobe width. 40. Upper lobe length. 41*. Upper lobe shape: rounded (1), acute (2). 42. Lower lobe width. 43. Lower lobe length. 44. Lower lobe shape: rounded (1), acute (2). 45. Lateral lobe width. 46. Lateral lobe length. 47. Lateral lobe shape: rounded (1), acute (2). 48*. Pubescence color: white (1), rusty (2), yellow (3), green (4). 49. Pedicel pubescence color: white (1), rusty (2), yellow (3), green (4).
Corolla	50. Upper petal width. 51. Upper petal length. 52. Upper petal claw length. 53. Lateral petal width. 54. Lateral petal length. 55. Lateral petal claw length. 56. Lower petal width. 57. Lower petal length. 58. Lower petal claw length. 59. Anther width. 60. Anther length. 61. Ovary length. 62. Ovary width. 63*. Ovary pubescence color: white (1), rusty (2), yellow (3). 64. Style length.
Fruit	65*. Base shape: rounded (1), acute (2). 66*. Pod winged: yes (1), no (0).

based on whether they were complete for either vegetative or floral characters. The 215 herbarium sheets were assigned unique numeric codes and served as operational taxonomic units (OTUs), of which 66 vegetative/fruiting and 13 floral sheets were used in the final phenetic analysis.

The OTUs were divided into floral and vegetative/fruiting subsets to eliminate age-related phenotypic variation (e.g., the underside of the terminal leaf is pubescent when the tree is in flower, but glabrous later in the growing season). Sheets were coded as floral if they contained flowers or if the collection date was prior to July, and as vegetative/fruiting if they contained fruits or if the collection date was between July and October.

Fifty-one vegetative/fruiting and fifty-one floral characters were scored for each OTU. Quantitative character states were coded as continuous data, and qualitative character states were coded as discrete values. The character states were coded as in Table 1. For a detailed explanation of how each character was measured, or to see the complete data matrix, see Duley (1998).

Data were entered into Excel (1997, Microsoft Corp., Redmond, WA) and then imported into NTSYS-pc 2.01 (Exeter Software, Setauket, NY) for computerized phenetic analysis. The default options were used to standardize the data. This resulted in the typical standardization of a data matrix used in numerical taxonomy (Rohlf 1997). Distance coefficients were computed using the similarity interval command, SIMINT (correlation coefficient code, CORR). The sequential, agglomerative, hierarchical, and nested clustering method (SAHN) with the default, unweighted pair group method using arithmetic averaging (UPGMA), was used to construct a phenogram. To test how well the phenogram represented the original standardized data matrix, cophenetic values were computed, returning a cophenetic correlation coefficient r. These analyses were repeated for each subset of the data set and the phenograms were compared for variation. Principal Components Analyses (PCA) were also performed using NTSYS-pc 2.01 to help define the structure of these data sets.

RESULTS AND DISCUSSION

Based on the phenetic analysis of overall morphology, we recognize six species in the genus. The differences among the species do not warrant any infrageneric classification; previous authors (Ma 1982; Takeda 1913) subdivided the genus based on the presence or absence of winged fruits, and our analyses do not support this distinction. *Cladrastis kentukea* is endemic to central and southeastern United States. All remaining taxa are Asian, with *C. chingii*, *C. delavayi*, and *C. wilsonii* occurring only in China, and *C. shikokiana* restricted to Japan. *Cladrastis platycarpa* is found in both China and Japan.

The phenogram for the quantitative, vegetative data set (Figure 1) is used here to illustrate the most informative clustering result obtained. It also serves as a framework onto which other characters can be mapped to further illustrate interspecific differences. Figure 1 shows two major (A and B) and four minor (1–4) clusters. The first major cluster contains all of the North American specimens, representing *Cladrastis kentukea*, and a mix of Chinese and Japanese specimens, representing *C. wilsonii* and *C. shikokiana*. The second major cluster contains Chinese and Japanese specimens, representing *C. delavayi* and a complex of *C. platycarpa* and another taxon.

Within the first major cluster, several smaller clusters can be seen. However, it should be noted that the North American specimens tend to group together as do the Asian specimens. When qualitative characters such as leaf color, pubescence color, and geographical distribution are taken into consideration, a clear distinction between the North American species and the Asian species can be drawn. Observation of the

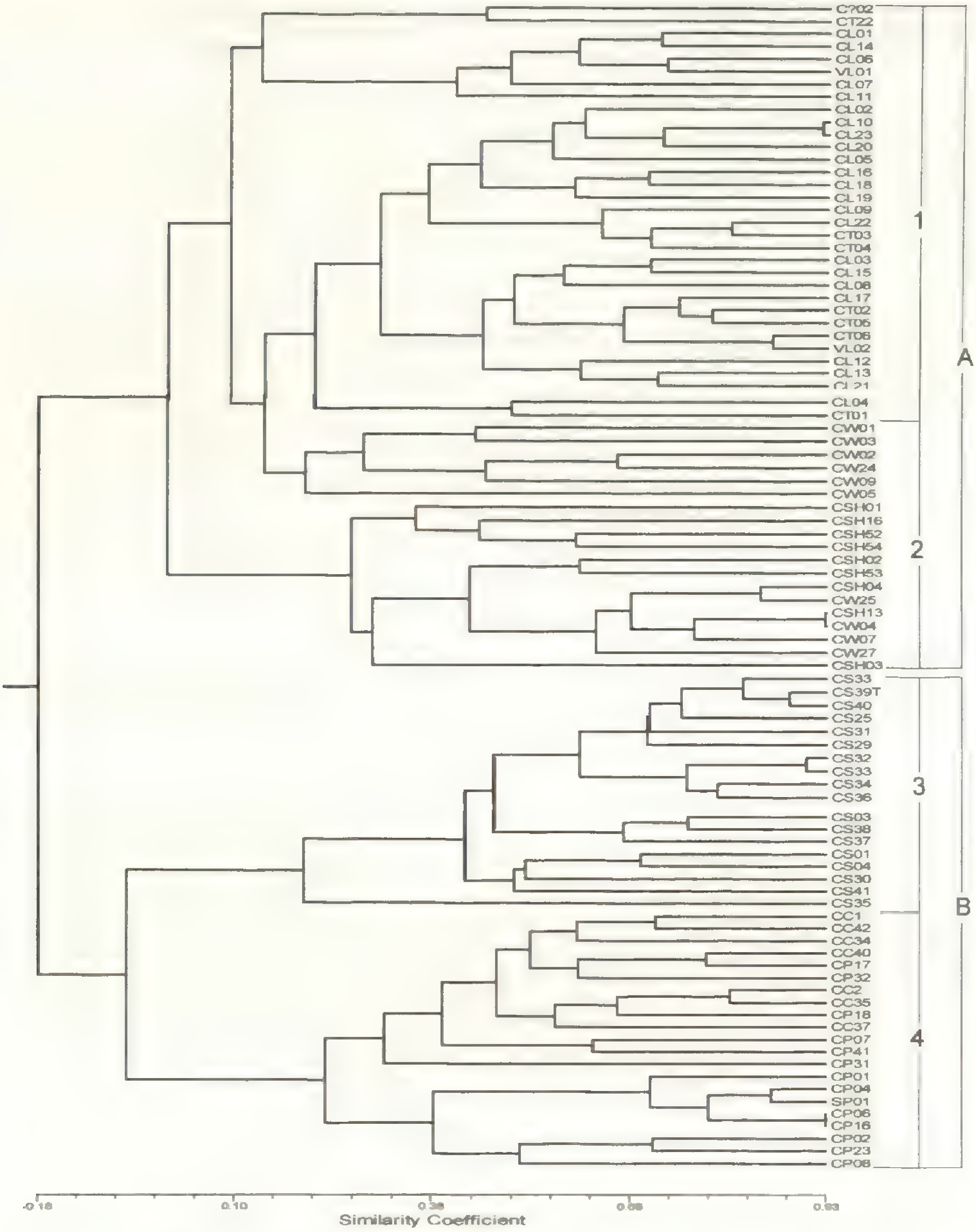

Figure 1. Phenogram derived from vegetative characters showing 2 major (A & B) and four minor (1–4) clusters. OTUs are identified as follows: CT, CL, VL, and C? = *Cladrastis kentukea*; CW = *C. wilsonii*; CSH = *C. shikokiana*; CS = *C. delavayi*; CC = *C. chingii*; CP, SP = *C. platycarpa*.

herbarium sheets suggested that OTUs CW01 through CW05 and CW09 should not be included with Cluster 1 (North American specimens) but with Cluster 2 (Asian specimens). Cluster 1 then contains all North American specimens of *Cladrastis kentukea*. Cluster 2 contains a mix of Chinese and Japanese specimens and represents the species *C. wilsonii*

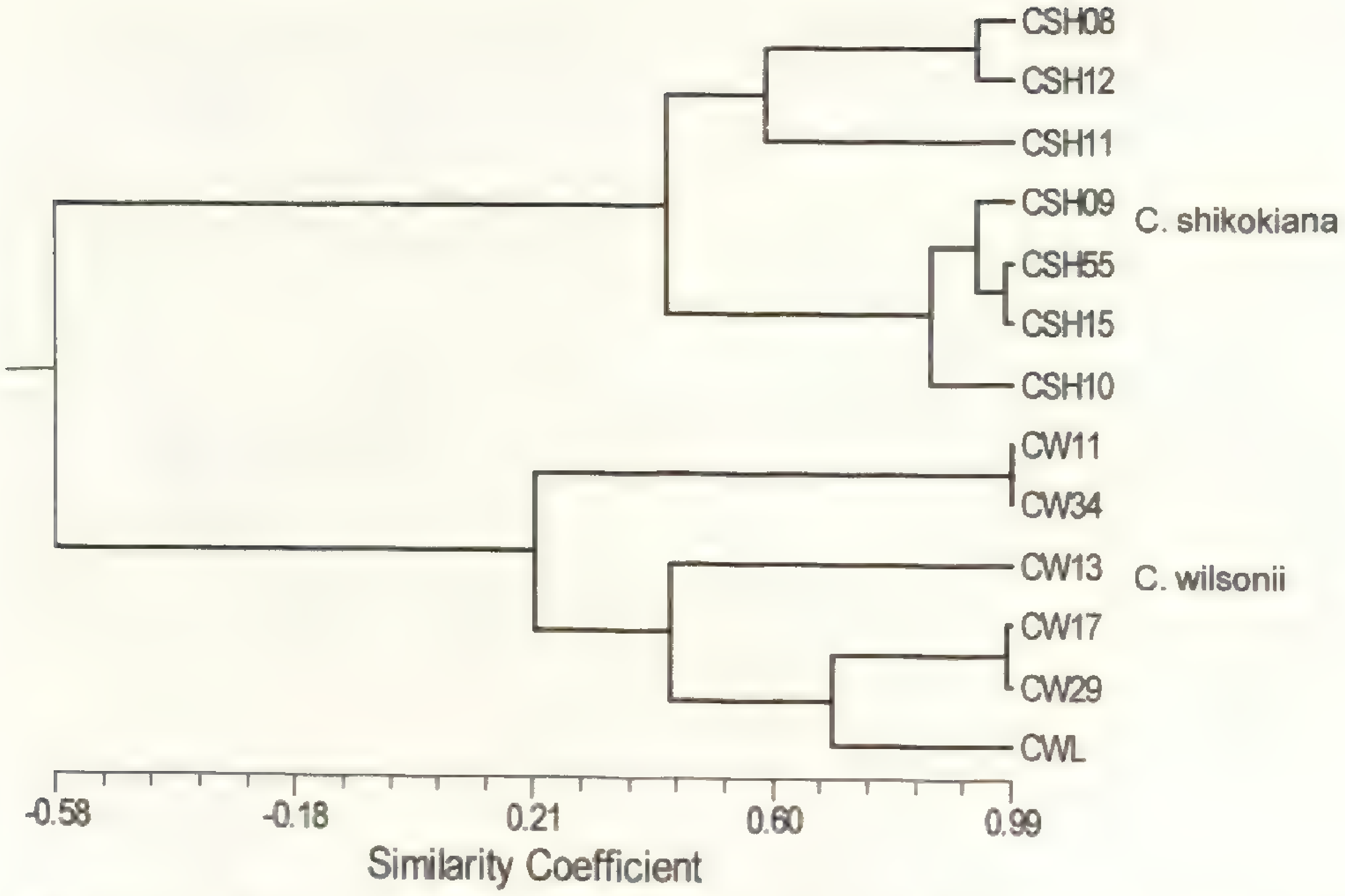

Figure 2. The top portion of the phenogram for the floral data set shows the separation of *Cladrastis wilsonii* and *C. shikokiana* into different clusters.

and *C. shikokiana*. *Cladrastis wilsonii* and *C. shikokiana* can be difficult to distinguish vegetatively. It had been observed that the best way to distinguish between these two species (Cluster 2) is with floral characters, such as the color of the pedicel/calyx pubescence: the hairs of *C. wilsonii* are green, while those of *C. shikokiana* are rusty brown. Analysis of other floral characters revealed overall clustering similar to the vegetative data set but showed clear separation between *C. wilsonii* and *C. shikokiana* (Figure 2).

Within the second major cluster, two additional smaller clusters can be seen. Cluster 3 contains only Chinese specimens and represents *Cladrastis delavayi*. Cluster 4 contains a mix of Chinese and Japanese specimens, and represents the *C. platycarpa* complex. Originally for specimens of the *C. platycarpa* complex, stipels were coded simply as being present or absent. However, there are two distinct types of stipels in this group, and stipel type appears to be linked to geography. All specimens from Japan had one awn-shaped stipel on either side of the base of the pulvinus of the leaflet. Those from China had stipels that were either like those of the Japanese specimens, or stipels that were multiple or branched on either side of the base of the pulvinus. A separate analysis performed on the OTUs in this cluster after recoding the stipel data as to type, not merely presence/absence (Figure 3),

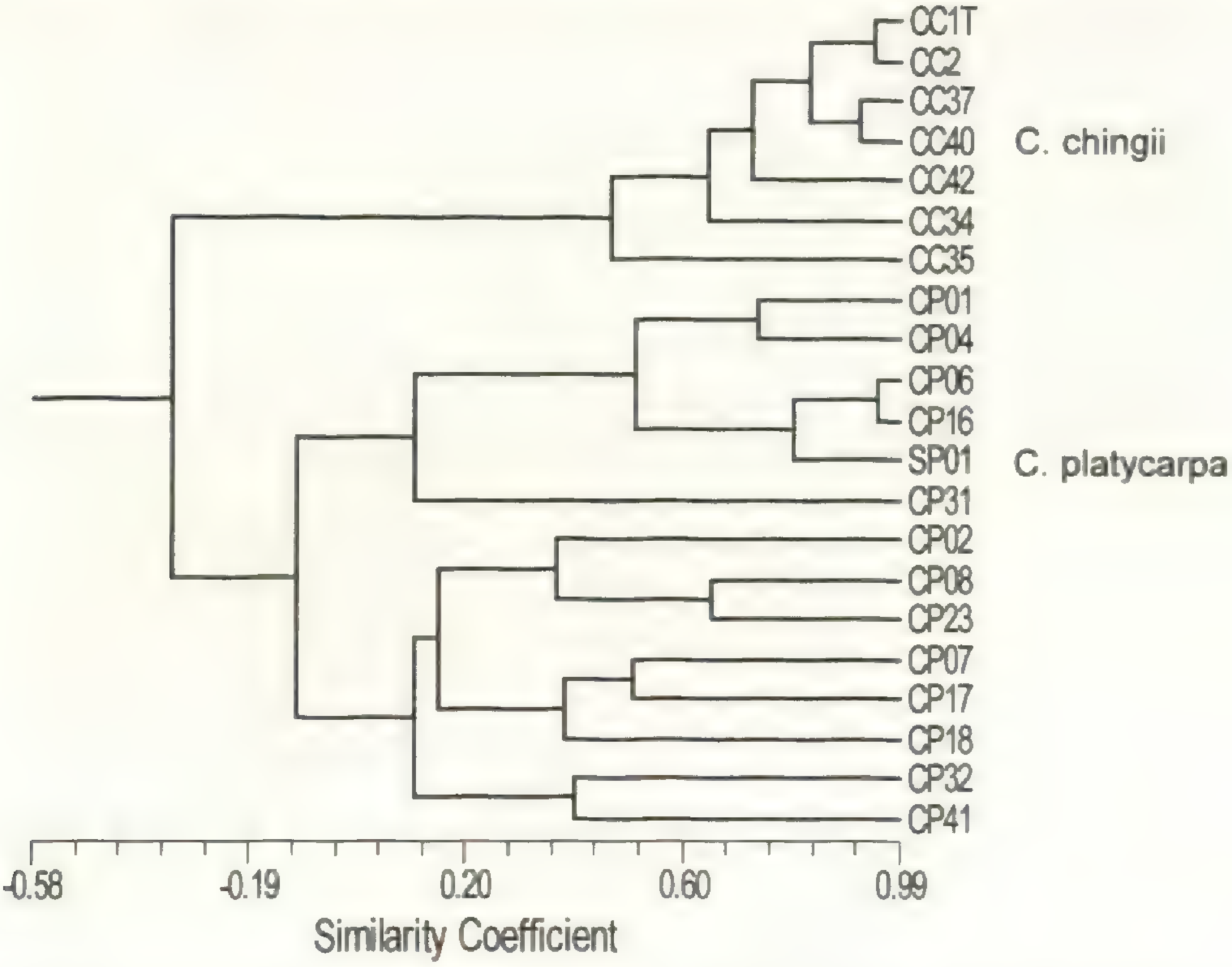

Figure 3. *Cladrastis chingii/platycarpa* complex after recoding stipel type. *Cladrastis chingii* has branched or multiple stipels; *C. platycarpa* has one pair of awn-shaped stipels.

resulted in a clear separation between *C. platycarpa* and another taxon, which we now recognize as *C. chingii*.

TAXONOMIC TREATMENT

Cladrastis Raf., Cincinnati Lit. Gaz. 1(8): 60. 1824. TYPE: *C. fragrans* Raf. *Platyosprion* (Maxim.) Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 22: 263. 1877. *Sophora* subgen. *Platyosprion* Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 18: 398. 1873.

Trees, deciduous; bark smooth, thin. Axillary buds enclosed in petiole base. Leaves alternate, odd-pinnately compound, estipulate; leaflets alternate, margins entire. Inflorescence terminal, paniculate, erect or pendulous. Flowers perfect, zygomorphic. Perianth hypogynous; calyx tubular, 5-lobed, fused basally for half its length; corolla white, sometimes pinkish, papillionoid. Stamens monadelphous, unequal, fused only slightly at base, anthers dorsifixed, dehiscence introrse via longitudinal slits. Ovary with 6–13 ovules, pubescent; style subulate;

stigma terminal, glabrous, minute. Fruit a compressed legume, with or without wings. Seeds oblong, compressed, testa brown.

Six species: temperate eastern Asia; central and southeastern United States.

KEY TO SPECIES OF *CLADRASTIS*

1. Leaflets with stipels at the base of pulvinus; fruit winged . . . . (2)
    2. Stipels simple, subulate, single on each side of pulvinus; fruit apex and base acute; leaves typically with 11 or more leaflets . . . . 1. *C. platycarpa*
    2. Stipels branched, and/or two or more on each side of pulvinus; fruit apex and base rounded; leaves typically with 9 or fewer leaflets . . . . 2. *C. chingii*
1. Leaflets without stipels at the base of pulvinus; fruit not winged . . . . (3)
    3. Leaves typically with 9 or fewer leaflets . . . . (4)
        4. Terminal leaflet nearly as wide as long; calyx pubescence white to yellow; lower calyx tooth acute, upper and lateral calyx teeth rounded . . . . 3. *C. kentukea*
        4. Terminal leaflet half as wide as long; calyx pubescence white to yellow to green; all calyx teeth acute . . . . 4. *C. wilsonii*
    3. Leaves typically with 11 or more leaflets . . . . (5)
        5. Terminal leaflet base rounded (rarely acute), apex emarginate; inflorescence erect . . . . 5. *C. delavayi*
        5. Terminal leaflet base acute, apex acuminate; inflorescence pendulous . . . . 6. *C. shikokiana*

1. Cladrastis platycarpa (Maxim.) Makino, Bot. Mag. (Tokyo) 15: 62. 1901. *Sophora platycarpa* Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg. 18: 398. 1873. *Platyosprion platycarpum* (Maxim.) Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 22: 263. 1877. TYPE: JAPAN. Fudjiyama. 1864. *Tschonoski s.n.* (HOLOTYPE: LE; ISOTYPES: BM!, GH!, K!, P!, S!). Figure 4.

Cladrastis yungchunii Xiang-W. Li & G.-S. Fan, Bull. Bot. Res. Harbin 14(4): 347-348. 1994. TYPE: CHINA. Yunnan, Luxi. *Li Xiang-Wang 919028* (HOLOTYPE: SWFC). (*ex char.*)

Tree to 20 m. Leaves (17.4–) 24.4 (–31.7) cm; petiole (1.2–) 2.0 (–3.4) cm, green to greenish brown, glabrous to sparsely white pubescent;

Figure 4. Isotype of *Cladrastis platycarpa* (*Tschonoski s.n.*, 1864, P). Inset shows awn-shaped stipels.

leaflets (7–) 13 (–15); first leaflet: pulvinus sparsely white to yellow to rusty pubescent; stipels simple, subulate, positioned singly on either side of the petiole base; lamina (2.5–) 4.9 (–9) × (1.0–) 2.3 (–3.5) cm, ovate, base rounded, apex acute to acuminate, upper surface glabrous to sparsely white pubescent on veins, lower surface sparsely white pubescent near midrib; terminal leaflet: sparsely to densely white pubescent; stipels paired, subulate; lamina (4.6–) 6.8 (–8.7) × (2.1–) 3.2 (–4.1) cm, elliptical to ovate, base acute, apex acuminate, upper surface glabrous to sparsely white pubescent on veins, lower surface glabrous to sparsely white pubescent on or near midrib. Inflorescence (9.6–) 18.6 (–27.7) cm, erect; peduncle (1.0–) 2.2 (–5.2) cm, green, glabrous or isolated white to rusty pubescent near stem; pedicel 0.7–1.1 cm, sparsely to densely rusty pubescent. Calyx (1.6–) 5.6 (–6.7) × (9.1–) 9.5 (–12.0) mm, densely white to yellow pubescent, upper teeth (0.8–) 1.2 (–1.9) × (1.6) 1.8 (–3.0) mm, rounded, lateral teeth (0.8–) 1.1 (–1.3) × (1.3–) 1.8 (–2.4) mm, rounded to acute, lower tooth (1.1–) 1.3 (–1.6) × (1.6–) 2.1 (–2.7) mm, acute. Corolla white with yellow spot in throat; banner petal (5.3–) 6.8 (–8.2) × (5.3–) 6.3 (–8.5) mm, reflexed, orbicular, base acute to cuneate, claw (1.2–) 3.5 (4.8) mm; wing petals (5.9–) 7.5 (–9.3) × (3.2–) 4.1 (–5.4) mm, lanceolate, base auriculate, claw (2.9–) 3.8 (–5.1) mm; keel petals (6.4–) 8.1 (–9.9) × (3.5–) 4.6 (–5.9) mm, lanceolate, base auriculate, margins overlapping and folded together. Anthers (0.5–) 0.7 (–0.8) × (0.3–) 0.5 (–0.8) mm. Ovary (4.5–) 5.4 (–6.4) × (0.6–) 1.0 (–1.1) mm, densely white to yellow pubescent; style (2.6–) 3.3 (–4.8) mm; ovules 6–7. Fruit 5–8 cm, winged, apex and base acute; seeds 1–3.

DISTRIBUTION AND PHENOLOGY. *Cladrastis platycarpa* was believed to be restricted to Japan (Brickell and Zuk 1996; Krüssmann 1976; Rehder 1927). However, it has been reported from China (Li and Fan 1994; Ma 1982) and several specimens were seen from the southern and southeastern provinces of China, including Zhejiang, Guangxi, and Guizhou (Figures 5 and 6).

Cladrastis platycarpa flowers in June after the leaves have emerged. Fruit set immediately follows flowering, and fruits remain on the tree through leaf drop.

Li and Fan (1994) published a new species, *Cladrastis yungchunii* Xiang-W. Li & G.-S. Fan, reporting it to be similar to *C. platycarpa*, with winged fruits, non-stipellate leaves, and glabrous leaflets and petiolules. The type specimen was not available for this study. Based on

Figure 5. Distribution of *Cladrastis* in China.

the winged fruit and the ephemeral nature of the stipels of *C. platycarpa*, *C. yungchunii* is tentatively placed in synonomy with *C. platycarpa*.

This species is most similar to *Cladrastis chingii*, but the leaves of *C. platycarpa* are thinner and more membranous in texture, and the stipels of *C. platycarpa* are awn-shaped and single on either side of the base of the pulvinus of the leaflet.

Representative specimens: CHINA. Guizhou: Chengfeng, *Tsiang 4452* (NY). Guangxi: Yanshan Park, *Guilin Team 70123* (CAS). Zhejiang: Tung-yung hsien, *King 929* (A).

JAPAN. Fukui: Ichi-no-tani Valley, *Ueda 794* (A, K, MAK, MO, NY). Kagawa: *Wilson 7522* (A). Kumamoto: *Wilson 1653* (A). Nagano: Suwa City, *Mizushima 17376* (S). Tokushima: *Makino s.n.* (CAS). Tokyo: Hachiou City, Mt. Takao, *Makino s.n.* (A). Yamanashi: *Togashi & Tateishi s.n.* (K).

2. **Cladrastis chingii** Duley & Vincent, *sp. nov.* Type: CHINA: Guangxi, Luchen, Tang Gior Poo, 23 May 1928, *R. C. Ching 5230* (HOLOTYPE: NY!; ISOTYPE: A!). Figure 7.

Figure 6. Distribution of *Cladrastis* in Japan.

Species nova *Cladrastis platycarpae* proxima differt vero foliola crassiusculus paucibus (9 vice 13); stipellae ramosus vel plures (vice subulatus et singularis); legumen apex et base rotundatis.

Tree, ca. 13 m. Leaves (18.5–) 21.8 (–23.5) cm, petiole (2.4–) 3.4 (–4.3) cm, green to greenish brown, glabrous to sparsely white pubescent, leaflets 9 or fewer; first leaflet: pulvinus sparsely white to rusty pubescent; stipels branched and/or multiple; lamina (3.9–) 4.8 (–6.1) × (1.2–) 2.1 (–2.8) cm, ovate, base rounded, apex acuminate, upper

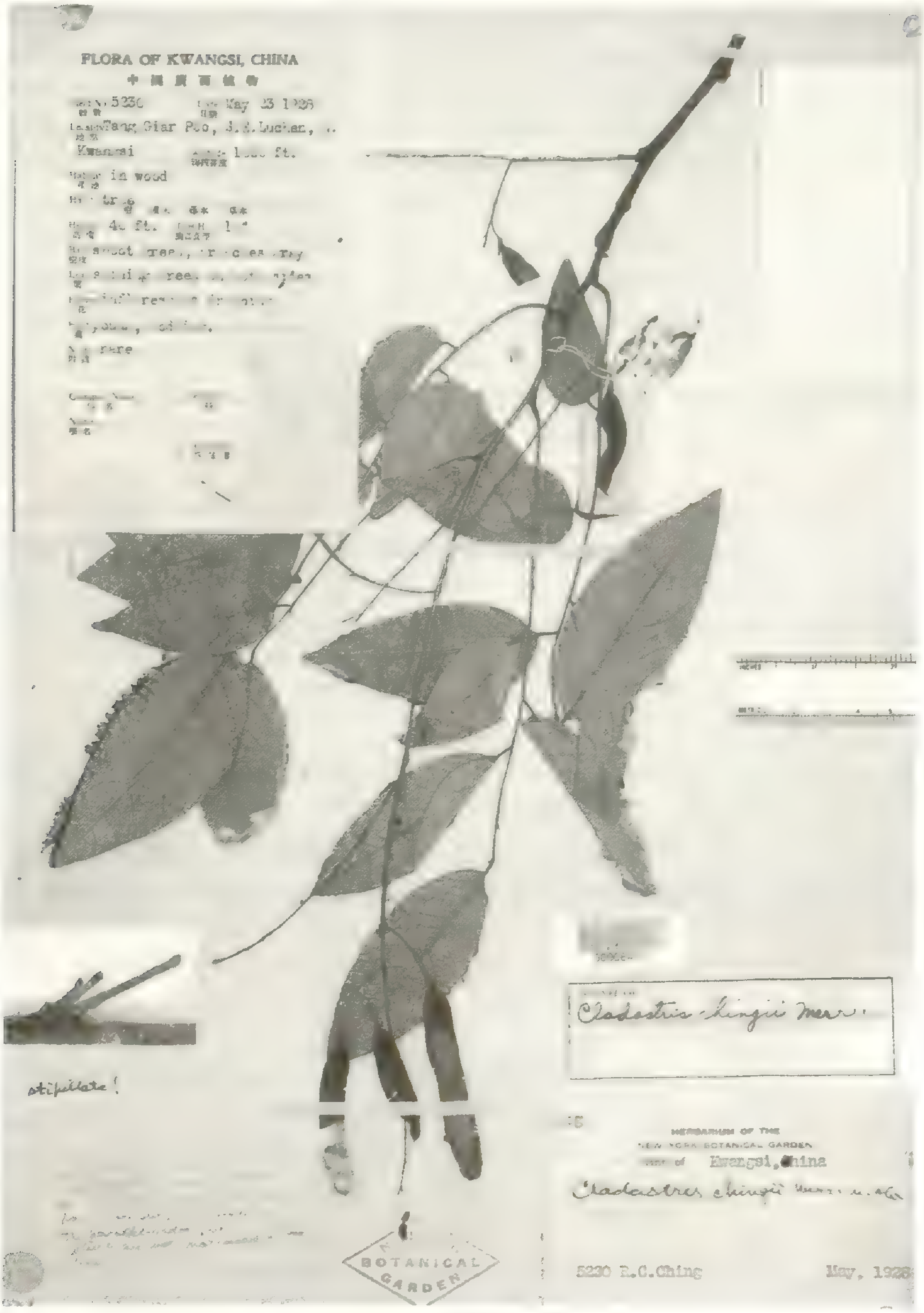

Figure 7. Holotype of *Cladrastis chingii* (*Ching 5230*, NY). Inset shows multiple/branched stipels characteristic of this species.

surface glabrous, lower surface glabrous to sparsely white pubescent on or near mid rib; terminal leaflet: pulvinus glabrous to sparsely white pubescent; stipels branched and/or multiple; lamina (5.3–) 7.0 (–7.8) × (2.5–) 3.1 (–3.5) cm, elliptical, base rounded to acute, apex acuminate, upper surface glabrous, lower surface glabrous to sparsely white to rusty pubescent on or near midrib. Inflorescence to 30.5 cm, erect; peduncle 3 cm, brown, glabrous to isolated rusty pubescent; pedicel 0.4–1.1 cm, densely rusty pubescent. Calyx 4.5–4.8 × 7.8–8.2 mm, densely rusty pubescent, upper teeth 1.3 × 1.0–1.8 mm, rounded, lateral teeth 1.1–1.4 × 1.9–2.1 mm, rounded, lower tooth 1.1–1.3 × 1.9–2.1 mm, acute. Corolla (data based on one available flower): petals white; banner petal 5.6 × 5.1 mm, reflexed, orbicular, base acute to cuneate, claw 1.4 mm; wing petals 6.2 × 3.4 mm, lanceolate, base auriculate, claw 1.8 mm; keel petals 6.1 × 3.4 mm, lanceolate, base auriculate, margins overlapping and folded together, claw 1.9 mm. Anthers 0.6–0.8 × 0.3–0.5 mm. Ovary 4.3–4.8 × 1.4 mm, densely white pubescent; style 2.1–2.6 mm, glabrous; ovules 3–6. Fruit 6–8 cm, winged, apex and base rounded to acute; seeds 1–3.

DISTRIBUTION AND PHENOLOGY. Specimens of this species have been seen from southern and eastern China in Guangxi, Hunan, Yunnan, and Zhejiang provinces (Figure 5).

Only two herbarium sheets of flowering specimens were available. Both were collected in early to mid-May and the flowers had begun to lose their petals. In addition, herbarium sheets of fruiting specimens examined were dated from late May through the end of June. Therefore, it is probable that flowering occurs in late April or early May.

NOTES. *Cladrastis chingii* is named in honor of its collector, R. C. Ching (Ching 1988; Ching et al. 1999). The type specimen was cited by Chun (1934) as *C. platycarpa*. The specimen at Harvard (A) was labeled as a duplicate distributed by the Lingnan University herbarium in 1954, which had been previously distributed from the Metropolitan Museum of Natural History, Nanking. There may be isotypes in those herbaria, as well.

Vegetatively, this species is very similar to *Cladrastis platycarpa* except for the stipel type and leaf texture. *Cladrastis chingii* has a very distinctive stipel that is branched, or, if unbranched, there are multiple stipels on either side of the base of the pulvinus. Leaves of *C. chingii* are thicker and more coriaceous than those of *C. platycarpa*. In addition, the base of the terminal leaf showed variation from rounded to acute, while the terminal leaf base in *C. platycarpa* is typically acute with very little variation. There are also major differences between this species and *C. platycarpa* regarding fruit characteristics. The pod is 5–8 cm long for both species; however, the fruit of *C. chingii* is 4–5 times longer than wide with a more rounded apex and base, while that of *C. platycarpa* is 2–3 times longer than wide with an acute apex and base.

Ten collections were available of this species, only two of which were flowering.

PARATYPES: CHINA. Guangxi: *Chen 62–66* (MU), *Li Lin F349* (MU). Hunan: *Liang Baohan 83155* (MO). Guangdong: *Tso 20959* (A), *Gao Xipeng 52588* (MO), *Tan Peixiang 59058* (MO, MU). Yunnan: *Feng 12608* (KUN). Zhejiang: *King 923* (A), *Yu 29203* (MO).

3. Cladrastis kentukea (Dum.Cours.) Rudd, Phytologia 21: 327. 1971. (as "*C. kentuckea*"). *Sophora kentukea* Dum.Cours., Bot. Cult. (ed. 2) 6: 56. 1811. *Virgilia dumontii* Raf., Kentucky Gaz., Vol. 36 (new series 45(1): 2, Thursday, 7 November). 1822. *Virgilia kentukea* (Dum.Cours.) Raf., Neogenyton 1. 1825 (as "*V. kentukensis*"). *Cladrastis kentukea* (Dum.Cours.) Raf. *ex* B. D. Jacks., Index Kew. 1: 552. 1893 (as "*C. kentukensis*"; *pro. syn., nom. inval.* Art. 34.1c). TYPE: North Carolina: Jackson County, 16 May 1999, *K. D. Heafner & J. F. Barcelona s.n.* (NEOTYPE here designated: MU!; ISONEOTYPES: K!, MO!, US!). Figure 8.

Virgilia lutea Michx. f., Hist. Arbr. Forest. 3: 266, pl. 3. 1813. *Cladrastis lutea* (Michx. f.) K. Koch, Dendrologie 1: 6. 1869. TYPE: *A. Michaux s.n.* (HOLOTYPE: P; ISOTYPE: P!).

Virgilia fragilis Raf., Kentucky Gaz., Vol. 36 (new series 45(1): 2, Thursday, 7 November). 1822. TYPE: Kentucky: 1842, *C. W. Short s.n.* (NEOTYPE here designated: NY!; ISONEOTYPES: NY!, NY!).

Virgilia alba Raf., Kentucky Gaz. 1822, *fide* Raf. Cincinnati Lit. Gaz. 1(8): 60. 1824. TYPE: Kentucky: banks of Kentucky River, May 1833, *R. Peter s.n.* (NEOTYPE here designated: NY!; ISONEOTYPE: NY!).

Cladrastis fragrans Raf., Cincinnati Lit. Gaz. 1(8): 60. 1824. TYPE: Kentucky: 1831, *Rafinesque s.n.* (NEOTYPE here designated: NY!).

Cladrastis tinctoria Raf., Neogenyton 1. 1825. *Cladrastis albiflora* Raf., New Fl. (Rafinesque) 3: 83. 1838. (*pro syn.*). TYPE: Kentucky: Kentucky River, Cumberland, *s.d.*, *Rafinesque s.n.* (NEOTYPE here designated: PH!).

Cladrastis lutea f. *tomentosa* Steyerm., Rhodora 40: 487. 1938. *C. kentukea* f. *tomentosa* (Steyerm.) Spongberg *in* Spongberg and J. Ma, Int. Dendrol. Soc. Year. Book (1996): 29. 1996. TYPE: Alabama: Tuscaloosa Co., *E. J. Palmer 35387* (HOLOTYPE: F!; ISOTYPE: US!).

Tree 10–20 m, canopy broad, rounded, to 16 m wide. Bark gray to gray-brown, on new stems reddish brown. Buds rusty-pubescent. Leaves

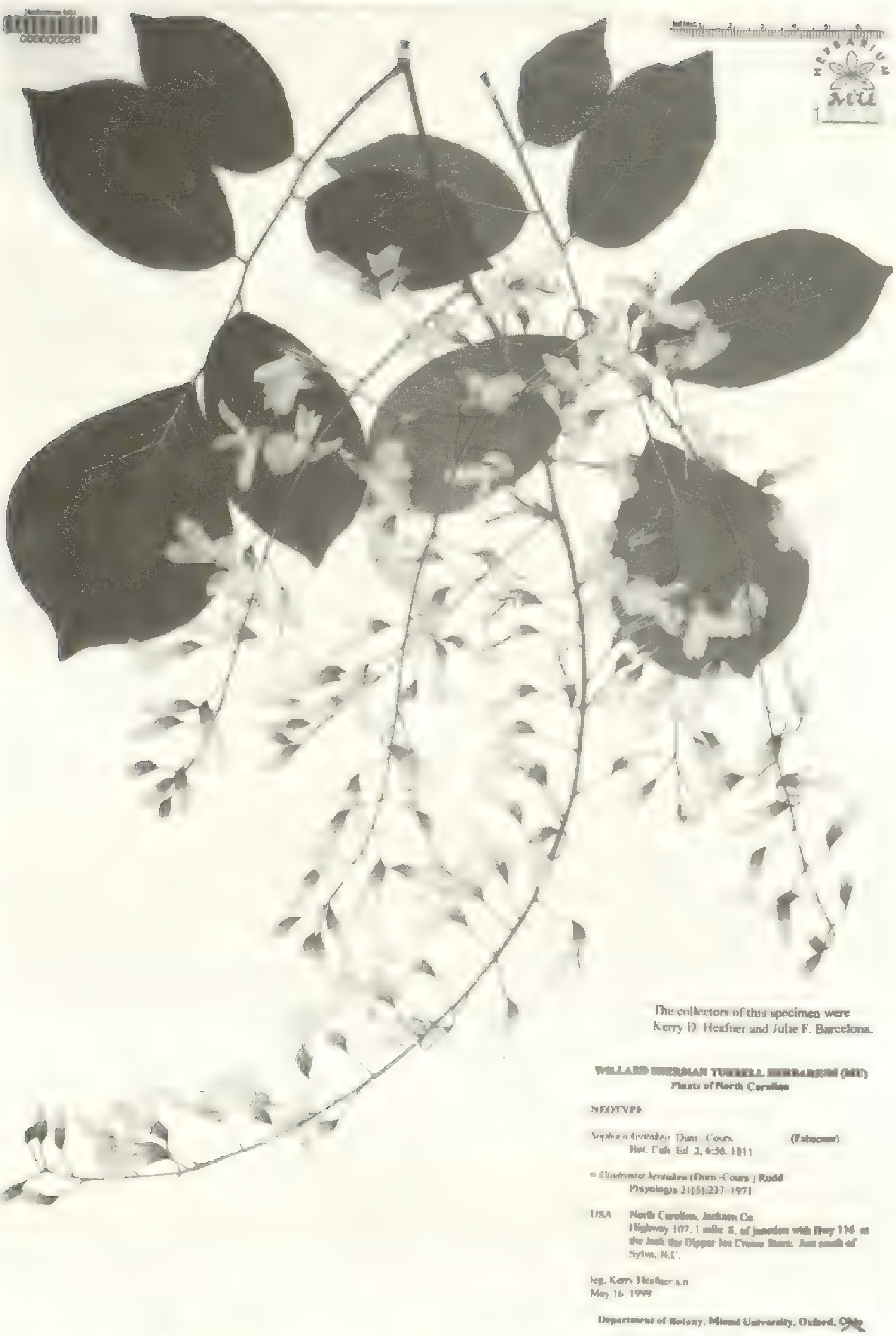

Figure 8. Neotype of *Sophora kentukea* (= *Cladrastis kentukea*; *Heafner & Barcelona s.n.*, MU).

(17–) 26 (–34) cm, petiole (1.0–) 3.3 (–5.0) cm, green to greenish brown, glabrous, leaflets (5–) 7 (–9); first leaflet: pulvinus sparsely yellow to rusty pubescent; stipels absent; lamina (3.0–) 6.0 (–9.5) × (2.5–) 3.9 (–6.0) cm, ovate, base rounded, apex acuminate, upper surface glabrous, lower surface sparsely to densely white pubescent at base near midrib; terminal leaflet: pulvinus glabrous to sparsely yellow to rusty pubescent, stipels absent, lamina (6.0–) 7.0 (–17.0) × (5.0–) 7.2 (–11.0) cm, obovate to ovate to elliptical to broadly elliptical, base acute, apex acuminate, upper surface glabrous, lower surface glabrous to sparsely white pubescent on or near midrib. Inflorescence (20–) 25 (–50) × 7–22 cm, pendulous; peduncle (1.5–) 2.8 (–8.0) cm, green, glabrous or sparsely yellow to rusty pubescent proximally; pedicel 1–2 cm, sparsely to densely white to yellow pubescent. Calyx (7.2–) 7.4 (–11.2) × (9.6–) 12.5 (–14.9) mm, densely white to yellow pubescent; upper teeth (1.0–) 1.5 (–2.4) × (2.4–) 3.8 (–6.7) mm, rounded; lateral teeth (1.1–) 1.6 (–2.5) × (2.2–) 2.7 (–3.2) mm, rounded; lower tooth (0.4–) 1.5 (–2.4) × (0.9–) 1.9 (–2.7) mm, acute. Corolla white (rarely pink); banner petal (12.3–) 15.9 (–18.3) × (10.0–) 13.0 (–15.7) mm, reflexed, orbicular, base acute to cuneate, claw 4–7 mm; wing petals (12.0–) 15.3 (–18.9) × (5.1–) 6.4 (–7.7) mm, lanceolate, base auriculate, claw 5–8 mm; keel petals (10.7–) 14.2 (–18.2) × (6.1–) 6.8 (–9.0) mm, lanceolate, base auriculate, margins overlapping and folded together. Anthers (0.8–) 1.3 (–1.6) × (.5–) 0.9 (–1.3) mm. Ovary (3.8–) 7.2 (–9.4) × (0.6–) 0.9 (–1.3) mm, densely white to yellow pubescent; style (3.5–) 4.0 (–4.8) mm; ovules 8–13. Fruit 7–8 cm, not winged, apex and base acute; seeds 5–8. Chromosome number $2n = 28$ (Atchison 1949).

DISTRIBUTION AND HABITAT. *Cladrastis kentukea* is endemic to North America (Figure 9). It is found in two separate geographic areas in the United States: 1) North and South Carolina, Tennessee, Kentucky, Alabama, and Georgia, and 2) Illinois, Indiana, Missouri, Arkansas, and Oklahoma (Pittillo 1963). Populations in Brown County State Park in Brown County, Indiana, and the Yellowwood State Forest in Indiana are the northernmost occurrences of the species (Huffman 1986). Spongberg and Ma (1996) reported *Cladrastis* from Brown County, Ohio, though Cooperrider et al. (2001) considered it as introduced in that state.

The habitat of *Cladrastis kentukea* is variable across its range, but it is typically found along river bluffs and in openings in mesophytic cove forests in association with major drainage areas (Huffman 1986; Pittillo 1963). Sargent (1949) reported that *Cladrastis* only grew in limestone soils but other researchers have reported it in areas where the parent

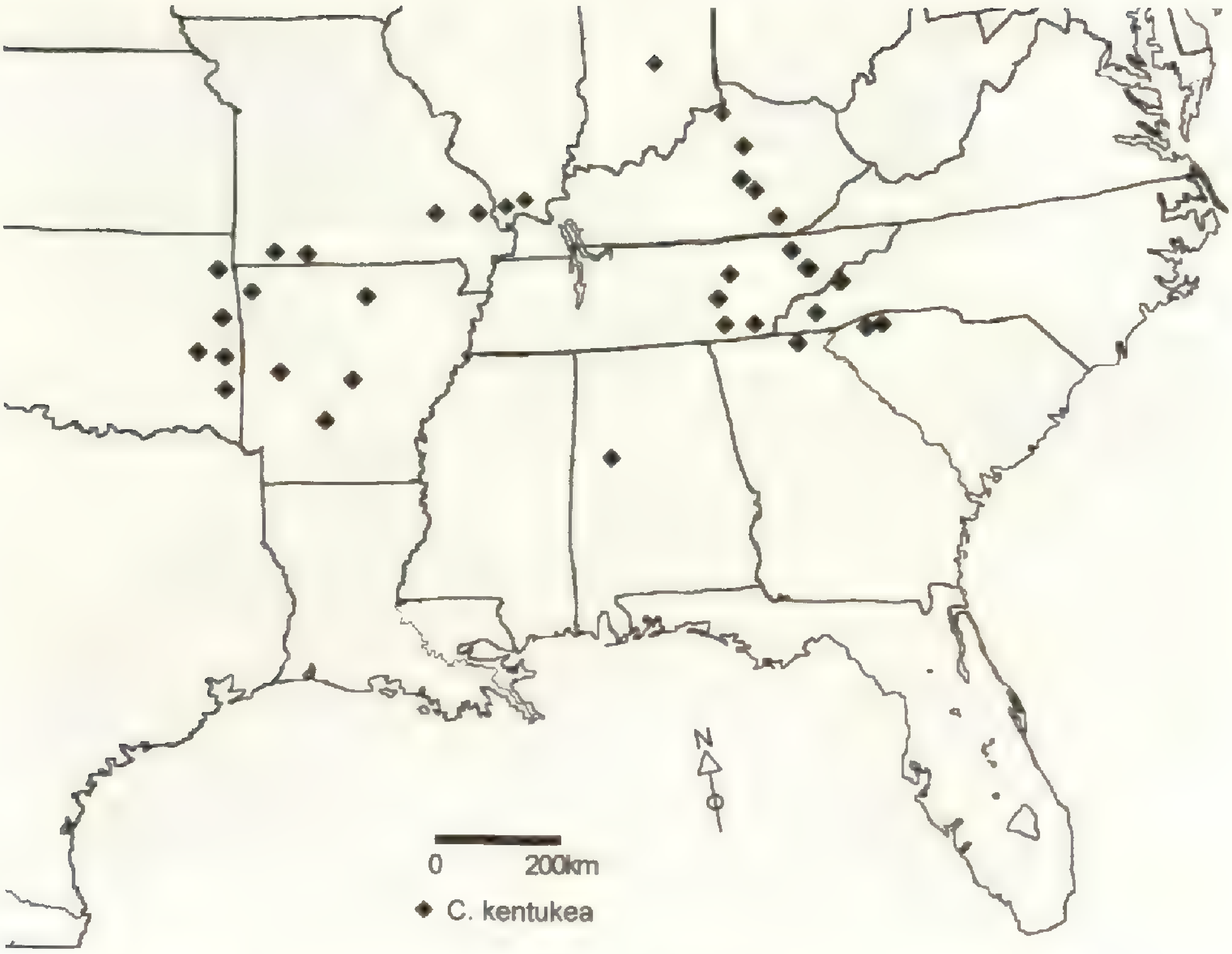

Figure 9. Distribution of *Cladrastis kentukea* in the United States.

material is other than limestone, such as shale (Palmer and Steyermark 1935).

PHENOLOGY. Flowering commences in mid-May, after the leaves have emerged, and is generally finished by the end of May. Trees become fertile after 6–8 years and generally flower every two to three years (Hershey 1977). Fruit set immediately follows flowering and the fruits remain on the trees through leaf drop (Robertson 1977).

NOTES. The specimen designated as the neotype for *Cladrastis fragrans*, *Rafinesque s.n.* 1831 (NY), has been determined by R. L. Stuckey to be a Rafinesque specimen. It is believed to be one of only two surviving *Cladrastis* specimens from Rafinesque's herbarium (Stuckey 1971a, b). We have chosen the other specimen, labeled "*Cladrastis riparia*" (an unpublished name) in Rafinesque's script, as neotype of *Cladrastis tinctoria*; the specimen is mounted on the upper right corner of a sheet with a collection by C. W. Short.

Cladrastis kentukea is not a common tree in the wild but it can be propagated by root cuttings or from seed (Robertson 1977) and it is widely cultivated (Gilman 1997; Griffiths 1994; Hershey 1977;

Krüssmann 1976). However, unlike many other species in the subfamily Papilionoideae, *C. kentukea* does not fix nitrogen with rhizobia (Graves and van de Poll 1992) so those wishing to grow this species should not rely on rhizobia to provide the plant with nitrogen. A pink-flowered tree is on the grounds of the Perkins School for the Blind in Watertown, Massachusetts. The origin of this tree is unknown; however, cuttings have been successfully cultivated by the Arnold Arboretum; Brimfield Nurseries in Connecticut; The Barnes Foundation in Marion, PA; the Dawes Arboretum in Newark, OH; and the Morton Arboretum in Lisle, IL (Hershey 1977; Robertson 1977). Specimens of the pink-flowered form are sold by nurseries under the horticultural name 'Rosea.' A pubescent form was described by Steyermark (1938). However, the type is of a young flowering plant, and since *Cladrastis* is somewhat pubescent early and becomes glabrous later in the season, the form name is not warranted.

Rafinesque published seven names for this taxon, and this has resulted in much confusion. The first mention he made of this plant was in the *Kentucky Gazette* (Rafinesque 1822), in a note in which he distinguished *Virgilia lutea* Michx. from *V. fragilis* (found in Kentucky) and from *V. dumonti* (also found in Kentucky). He proposed the latter name as a replacement for *Sophora kentukea* Dum.Cours. In *Neogenyton*, Rafinesque (1825) used the name *Cladrastis tinctoria* (replacing *C. fragrans*) as a synonym for both *V. lutea* Michx. and *V. kentukensis* Dum.Cours. It is thought that Rafinesque meant Dumont de Courset's *S. kentukea* instead of *V. kentukensis*, since *V. kentukensis* had apparently never been published. In his *New Sylva*, Rafinesque (1838) equated *C. albiflora* with *C. tinctoria*. Koch (1869) made the combination *C. lutea*. Finally, Rudd (1971) made the combination *C. kentuckea* [*sic*] based on a note in the 1893 Index Kewensis that *S. kentukea* and *V. kentukensis* were synonyms. The name *C. kentukea* (Dum.Cours.) Raf. *ex* B. D. Jackson (Index Kew. 1: 552. 1893; as "C. kentukensis") is not validly published as per Art. 34.1c of the 2000 International Code of Botanical Nomenclature and therefore does not have priority over *C. kentukea* (Dum.Cours.) Rudd. The original description of Dumont de Courset's *S. kentukea* clearly represents this taxon; the spelling of the epithet should be *kentukea*, not the incorrect spelling *kentuckea*.

Of the thirteen names associated with this species, only two, *Virgilia lutea* Michx. f. and *Cladrastis lutea* forma *tomentosa* Steyermark had holotypes specified in the protologues. Neotypes for *Sophora kentukea* and *C. fragrans* are designated here, as no original material is known to exist for either epithet. The Rafinesque specimen is designated neotype rather than lectotype because there is no date on the specimen and it is impossible to ascertain when and where it was collected. The specimen was labeled, in Rafinesque's script, as *Cladrastis*. The need for neotypification of many of Rafinesque's names is borne out by the fact that very few of his specimens still exist, and much of his botanical collection was destroyed or sold as waste paper after his death (Call 1895; Stuckey 1971a, b).

REPRESENTATIVE SPECIMENS: UNITED STATES. Alabama: Tuscaloosa Co., Warrior River near lock 14, *Palmer 35387* (A, MO, PH). Arkansas: Benton Co., *Demaree 6613* (A, F, MO, NY, TEX). Georgia: Towns Co., 1.5 mi. E, 10° S of Titus, Hightower Bald region, *Duncan 7644* (B, GH, KY, LL, MO, NY, PENN, TEX, US). Illinois: Alexander Co., NW slope of Wolf Creek Hill, SE 1/4 sec. 17, T14S, R2W, Thebes quad, SW of Diswood, *Busar 5420* (ILL). Indiana: Brown Co., Brown Co. State Game Preserve, *Deam 54279* (A, F, GH, IND, MO, PH, NY, US). Kentucky: Along Kentucky River, *Short s.n.* (E, GH, NY). Missouri: Taney Co., Forsyth, common on rocky bluffs, *Bush 84* (F, GH, IND, MO, NY, US). North Carolina: Haywood Co., Pigeon River Gorge, 2.1 km E of TN state line on I-40, *Pittillo 5120* (BM, GH, KY, NY, TEX). Oklahoma: Cherokee, Wooded base of Keyough Bluffs, 2 mi. N of Ft. Gibson, *Wallis 6896* (GH, TEX). South Carolina: Greenville Co., Saluda River valley between reservoir and Benfield, *Hill 25031* (GH, MO, NY, TEX). Tennessee: Davidson Co., Hills around Nashville, *Gattinger 703* (BM, F, GH, K, MO, NY, PA).

4. Cladrastis wilsonii Takeda, Notes Roy. Bot. Gard. Edinburgh 8(37): 103. 1913. [LECTOTYPE here designated: CHINA. Patung Hsien woodlands, alt. 1500–1600 m, Jul and Sep 1907, *E. H. Wilson 1102* in part (A!)]. Figure 10.

C. lichuanensis Q. W. Yao & G. G. Tang *in* G. G. Tang, Bull Bot. Res. Harbin 8(3): 157. 1988. *C. lichuanensis* Q. W. Yao & G. G. Tang, Chinese Trees and Wood 2: 1335–1336. 1985, *nom. nud.* TYPE: CHINA. Hupeh, Lichuanxian Shindoshan, *s.d., G.G. Tang & X. H. Song 633* (HOLOTYPE: Nanjing Forestry University Herbarium).

Tree 4–16 m. Bark gray to yellowish gray, on new stems reddish gray. Leaves (20.4–) 26.4 (–34.6) cm, petiole (1.4–) 2.4 (–3.9) cm, green to greenish brown, glabrous, leaflets (8–) 9 (–11); first leaflet: pulvinus glabrous to sparsely white to yellow pubescent; stipels absent; lamina (3.5–) 6.2 (–8.7) × (1.8–) 2.8 (–3.7) cm, ovate, base rounded, apex acuminate, upper surface glabrous; lower surface glabrous; terminal leaflet: pulvinus glabrous; stipels absent; lamina (6.0–) 9.3 (–14.3) × (2.7–) 4.6 (–6.5) cm, elliptical to ovate, base acute, apex acuminate, upper surface glabrous, lower surface glabrous when mature, (early leaves sparsely white pubescent on or near midrib). Inflorescence (13.3–) 22.3 (–28.4) cm, pendulous; peduncle (1.5–) 2.2 (–4.3) cm, green to

Figure 10. Lectotype of *Cladrastis wilsonii* (*Wilson 1102*, in part, A).

brown, glabrous to sparsely white to yellow pubescent; pedicel (0.5–) 0.8 (–1.1) cm, sparsely to densely white to yellow to pale green pubescent. Calyx (7.2–) 7.7 (–8.0) × (10.4–) 12.3 (–14.4) mm, densely white to yellow to pale green pubescent; upper teeth (1.3–) 1.9 (–2.8) × (1.9–) 2.3 (–2.7) mm, acute; lateral teeth (1.9–) 2.2 (–2.6) × (2.1–) 2.7 (–3.2) mm, acute; lower tooth (1.6–) 2.1 (–2.7) × (1.6–) 2.2 (–2.9) mm, acute. Corolla white; banner petal (9.3–) 12.9 (–15.2) mm × (9.6–) 11.6 (–13.4) mm, reflexed, orbicular, base acute to cuneate, claw (2.3–) 3.6 (–5.1) mm; wing petals (9.3–) 13.4 (–14.4) × (3.8–) 5.7 (6.7) mm, lanceolate, base auriculate, claw (4.0–) 5.0 (–5.9) mm; keel petals (8.8–) 14.0 (–14.9) × (4.8–) 6.0 (–7.2) mm, lanceolate, base auriculate, margins overlapping and folded together. Anthers (0.8–) 1.1 (–1.6) × (0.6–) 0.7 (–1.0) mm. Ovary (5.0–) 7.9 (–8.0) × (1.1–) 1.4 (–1.6) mm, densely white to yellow pubescent; style (3.2–) 5.1 (–7.2) mm; ovules (1–) 3 (–5). Fruit 4.5 cm, apex and base acute; seeds 1–5.

DISTRIBUTION AND PHENOLOGY. *Cladrastis wilsonii* is found throughout central China (Figure 5). It is fairly common in the moist woods of western Hubei province (Takeda 1914) and is known from Yunnan province in the south, north through Guangxi and Hunan, east to the Jiangxi, Fujian, and Zhejiang provinces, and as far north as Anhui province. The eastern edge of the Red Basin in Sichuan province appears to be the western limit of the range of *C. wilsonii.*

Cladrastis wilsonii flowers in mid-May in the southern extent of its range with flowering time moving into mid-July in Hubei and Sichuan provinces farther north. Flowering is preceded by the emergence of the leaves, and seed set immediately follows. The fruits remain on the trees through leaf drop in September and October.

NOTES. The designation "*Wilson 1102*" appears to have been a field number for the species, rather than an actual collection number, since many different dates and localities are listed on different sheets with this number on them. *Cladrastis wilsonii* is cultivated, although the inflorescences are not as large as nor as showy as those of either *C. delavayi* or *C. kentukea*. The species may be susceptible to frost damage when young (Krüssmann 1976). The leaves of *C. wilsonii* are similar to those of *C. shikokiana*; however, the underside of the young leaves of *C. wilsonii* are sparsely white to yellowish pubescent when young, becoming glabrous, whereas the underside of the leaves of *C. shikokiana* are brown pubescent. *Cladastis wilsonii* is sympatric on the western edge of its range with *C. delavayi. Cladrastis delavayi* differs from

C. wilsonii by its larger number of leaflets that are narrower with rounded bases and emarginate apices. The leaves of *C. delavayi* are also a darker green and may be slightly glaucous underneath.

Tang (1988) reported a new species, *Cladrastis lichuanensis* Q. W. Yao & G. G. Tang, as similar to *C. wilsonii* but differing in the underside of the leaflet being a paler green, and the petiole, leaf rachis, and legume densely rusty pubescent (all characters of *C. delavayi*). Examination of the type specimen, *Tang & Song 633*, located in the Nanjing Forestry University, was not possible. However, when we read the original article, it became clear that two different species, *C. delavayi* and *C. wilsonii*, were inadvertently used in writing the species' description. The illustration given with the protologue is of *C. wilsonii*, and at least one of the paratypes (*C. T. Hwa 417*, A!) is *C. delavayi*.

REPRESENTATIVE SPECIMENS: CHINA. Anhui: Wang shan, *Ching 2958* (A, K, S). Zhejiang: King Yuan, *Ching 2535* (BM, E, GH, NY). Hubei: *Wilson 1102* (BM, E, F, A, K, MO, P, US). Hunan: Wukang, *Handel-Mazzetti 702* (A). Jiangxi: *Wilson 1535* (A); Kuling, 1 Aug 1907, *Wilson 1535* (A, syntype). Guangxi: *Steward & Cheo 375* (BM, GH, NY, P, S). Sichuan: *Cheng 2885* (BM, E). Yunnan: *s.d., McLaren s.n.,* (K); Changyang Hsien woods, alt. 1600–200. m, 19 May 1907, *Wilson 1102* in part (*n.v.*, syntype). Fang Hsien woodlands, alt. 2000 m, 19 May 1907, *Wilson 1102* in part (A, syntype); Changlo Hsien, woods, alt. 1600–2000 m, Jul 1907, *Wilson 1102* in part (A, syntype); Wushan Hsien woods, alt. 1600–2000 m, Oct 1907, *Wilson 1102*, in part (A, BM, MO, syntypes).

5. Cladrastis delavayi (Franch.) Prain, Ann. Roy. Bot. Gard. (Calcutta). 10(1): 109. 1904. *Dalbergia delavayi* Franch., Pl. Delav. (1): 186–187. 1888. TYPE: CHINA: Yunnan Province: Pou-sy, Pien-kio, 16 Jul 1888, *P. J. M. Delavay s.n.* (HOLOTYPE: P!). Figure 11.

Cladrastis sinensis Hemsl., J. Linn. Soc., Bot. 29: 304. 1892. TYPE: CHINA. Szechuan: Tachienlu, *s.d., A. E. Pratt 129* (HOLOTYPE: K!; ISOTYPES: BM!, E!, GH!, K!, P!).

Tree to 15 m. Bark grayish. Leaves (15–) 23 (–33) cm, petiole (1.2–) 2.5 (–3.0) cm, yellow to green to greenish brown, glabrous to sparsely yellow pubescent, leaflets (9–) 11 (–13); first leaflet: pulvinus densely yellow pubescent; stipels absent; lamina (3.9–) 5.1 (–6.6) × (1.7–) 2.2 (–2.8) cm, ovate, base rounded, apex emarginate, upper surface glabrous, lower surface glabrous to sparsely white to yellow pubescent near midrib; terminal leaflet: pulvinus glabrous to sparsely yellow to rusty pubescent; stipels absent; lamina (5.6–) 7.6 (–11.3) × (2.2–) 3.2 (–3.8) cm, elliptical to narrowly elliptical, base rounded (rarely acute), apex emarginate, upper surface glabrous, lower surface glabrous to sparsely white pubescent on or near midrib. Inflorescence (11.8–) 21.9 (–29.3)

Figure 11. Holotype of *Cladrastis delavayi* (*Delavay s.n.*, P).

cm, erect; peduncle (1.1–) 2.7 (–5.3) cm, green to brown, sparsely rusty pubescent proximally; pedicel (0.4–) 0.6 (–0.8) cm, densely rusty pubescent. Calyx (4.6–) 5.9 (–6.9) × (7.7–) 9.5 (–10.9) mm, densely white to rusty pubescent; upper teeth (0.8–) 1.7 (–1.8) × (1.4–) 2.0 (–2.6) mm, acute; lateral teeth (0.6–) 1.4 (–2.1) × (1.6–) 2.1 (–2.7) mm, acute; lower tooth (0.8–) 1.4 (–1.9) × (1.4–) 1.8 (–2.4) mm, acute. Corolla white (rarely pink); banner petal (6.4–) 9.0 (–14.4) × (5.4–) 7.3 (–9.3) mm, reflexed, orbicular, base acute to cuneate, claw (0.6–) 2.4 (–3.2) mm; wing petals (6.4–) 8.3 (–9.6) × (3.0–) 3.9 (–4.8) mm, lanceolate, base auriculate, claw (2.1–) 3.2 (–4.0) mm; keel petals (6.2–) 9.3 (–10.5) × (3.8–) 4.8 (–5.6) mm, lanceolate, base auriculate, margins overlapping and folded together. Anthers (0.5–) 0.8 (–1.1) × (0.3–) 0.6 (–0.8) mm. Ovary (4.0–) 5.5 (–7.2) × (0.8–) 0.7 (–1.3) mm, densely white to yellow pubescent; style (1.1–) 2.8 (–3.5) mm; ovules (7–) 10 (–15). Fruit 3–6 cm, apex and base acute; seeds 1–3.

DISTRIBUTION AND PHENOLOGY. *Cladrastis delavayi* occurs in western and central China (Figure 5). It is found in western Sichuan, Yunnan, Hunan, and Hubei provinces primarily in wooded habitats between 1500 and 2500 m.

Flowering begins mid-June, after the leaves have emerged, and is generally finished by mid- to late July. Fruit set immediately follows flowering and the fruits remain on the trees through leaf drop.

NOTES. *Cladrastis delavayi* has been cultivated in the United States and Europe (Cullen 1995) and, like *C. kentukea*, has a pink-flowered horticultural form, 'Rosea.' In China, the range of *C. delavayi* overlaps somewhat with another Chinese species, *C. wilsonii*. In the field, the two species can be easily distinguished when they are in flower, since *C. delavayi* has an erect inflorescence, whereas the inflorescence of *C. wilsonii* is pendulous. In addition, *C. delavayi* is the only *Cladrastis* species with an emarginate leaflet apex.

All references seen cite the name *Cladrastis sinensis* Hemsl. as the correct name for this species. However, Franchet (1889) reported a new species as *Dalbergia delavayi* and cited a Delavay specimen collected 16 July 1888 as the type. Prain (1904) excluded *D. delavayi* from his *Dalbergia* treatment and correctly placed it in *Cladrastis*. Takeda (1913) stated he had not seen the specimen but, according to the description, he believed it was not a *Cladrastis* and placed *C. delavayi* in his excluded species. The specimen Franchet cited as the holotype represents the same species as *C. sinensis* Hemsl. According to the International Code of Botanical Nomenclature, *delavayi*, as the older specific epithet, has priority over *sinensis*. Therefore, the correct name is *C. delavayi* (Franch.) Prain.

REPRESENTATIVE SPECIMENS: CHINA. Hubei: *Wilson 2398* (A, NY); Hubei/Sichuan border near *Metasequoia* area, *Hwa 417* (A). Hunan: *Henry 10784* (A, E, MO, S). Sichuan: *Forrest 7827* (A, E). Yunnan: *Maire 686* (E).

6. Cladrastis shikokiana (Makino) Makino, Bot. Mag. (Tokyo) 15: 62. 1901. *Sophora shikokiana* Makino, Bot. Mag. (Tokyo) 14: 34–35. 1900. *Sophora shikokiana* Makino, Bot. Mag. (Tokyo) 6: 53. 1892. *nom. nud.* (LECTOTYPE here designated: MAK 133710!). Figure 12.

Tree, 15 m. Leaves (19.8–) 24.7 (–34.8) cm, petiole (2.0–) 2.7 (–4.2) cm, green to greenish brown, glabrous, leaflets (9–) 11 (–13); first leaflet: pulvinus glabrous to isolated yellow pubescent; stipels absent; lamina (4.2–) 5.7 (–6.9) × (1.6–) 2.6 (–3.3) cm, ovate, base rounded, apex acuminate, upper surface glabrous, lower surface glabrous to sparsely white to yellow pubescent at base near midrib; terminal leaflet: pulvinus glabrous; stipels absent; lamina (5.3–) 9.2 (–12.4) × (2.5–) 4.2 (–5.3) cm, elliptical, base acute, apex acuminate, upper surface glabrous, lower surface glabrous. Inflorescence (14.0–) 19.4 (–27.2) cm, pendulous; peduncle (1.7–) 2.6 (–4.6) cm, green, glabrous; pedicel, densely rusty pubescent. Calyx (7.4–) 8.5 (–9.6) × (11.5–) 12.9 (–14.9) mm in circumference, densely rusty pubescent; upper teeth (1.6–) 1.8 (–1.9) × (1.9–) 2.6 (–3.2) mm, acute; lateral teeth (1.9–) 2.2 (–2.4) × (2.4–) 2.7 (–3.2) mm, acute; lower tooth (1.9–) 2.1 (–2.6) × (2.1–) 2.5 (–3.2) mm, acute. Corolla white; banner petal (9.3–) 12.7 (–14.4) × (10.2–) 11.0 (–12.0) mm, reflexed, orbicular, base acute to cuneate, claw (2.9–) 3.7 (–4.0) mm; wing petals (9.3–) 12.2 (–14.4) × (3.8–) 5.7 (–6.7) mm, lanceolate, base auriculate, claw (4.0–) 5.3 (–5.6) mm; keel petals (8.8–) 12.2 (–14.4) × (4.8–) 5.9 (–7.2) mm, lanceolate, base auriculate, margins overlapping and folded together. Anthers (0.8–) 1.2 (–1.6) × (0.6–) 0.7 (–0.9) mm. Ovary (4.8–) 6.7 (–7.2) × (1.1–) 1.4 (–1.6) mm; densely white to yellow pubescent; style (3.2–) 4.9 (–6.4) mm; ovules 11–14. Fruit 6–7 cm, not winged, apex and base acute; seeds 4–6.

DISTRIBUTION AND PHENOLOGY. *Cladrastis shikokiana* is restricted to the southern half of Japan (Figure 6), from as far south as Hondo in the Kumamoto prefecture on the island of Kyushu, north to Ehime prefecture on the island of Shikoku, and then the southern half of the island of Honshu. There, it is found in Shimane, Hyogo, Kyoto, Wakayama, Shiga, Aichi, and Yamanashi prefectures, and as far north as

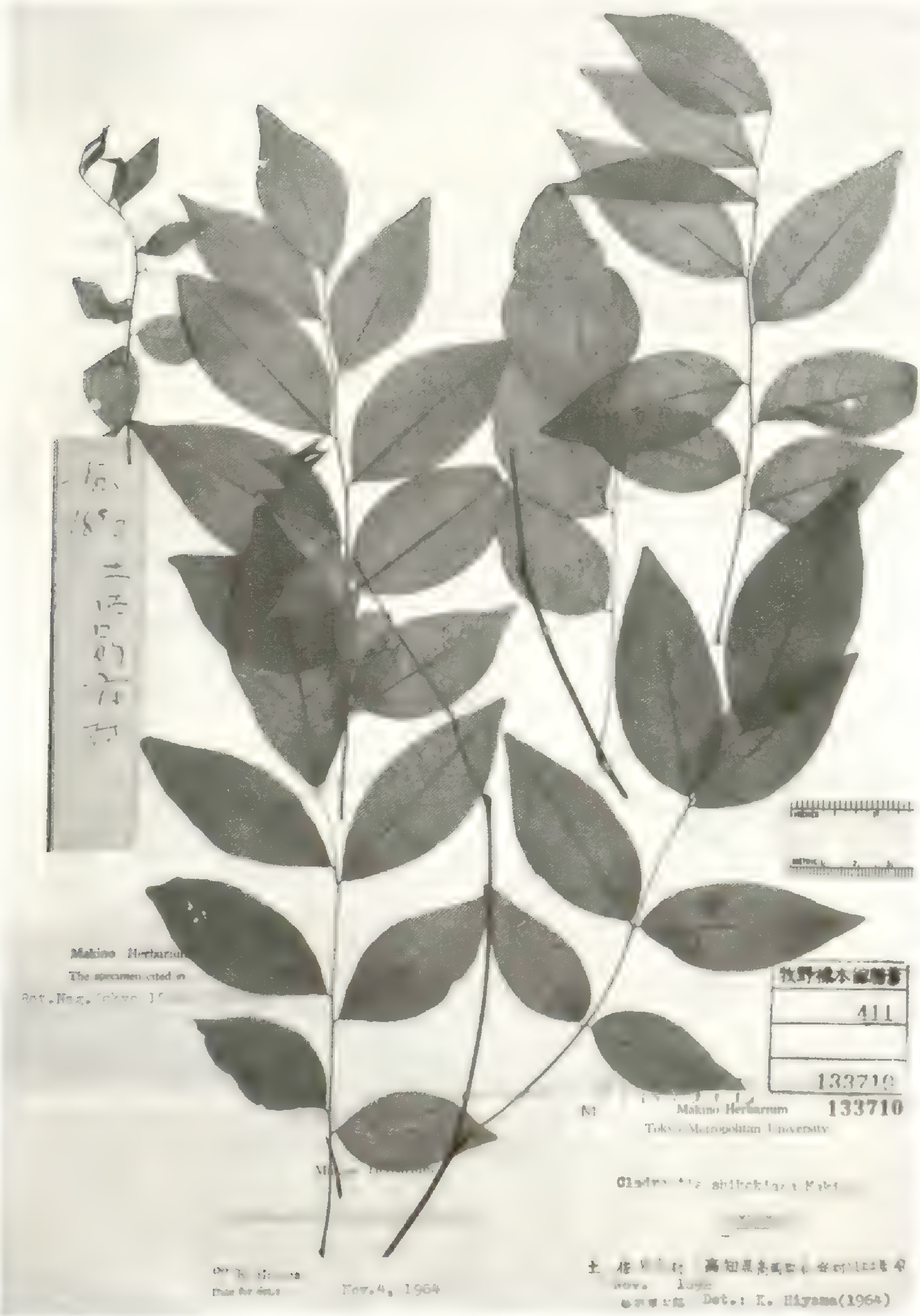

Figure 12. Lectotype of *Cladrastis shikokiana* (MAK 133710).

Tokyo prefecture. In all instances, it appears to be found at elevations of less than 500 m.

Cladrastis shikokiana flowers between May and June, after the emergence of the leaves.

NOTES. There is very little written about *Cladrastis shikokiana*. It appears to be rare in occurrence (Makino 1901; Ohwi 1965; Satake 1989), its distribution is limited, and it is not listed in the literature as being cultivated.

REPRESENTATIVE SPECIMENS: JAPAN. Ehime: *Yamanaka s.n.* (MO). Hyogo: Harima province, *Faruse s.n.* (NY). Kumamoto: *Kobayashi 14293* (S). Kyoto: *Tsugarwu & Sawada 19101* (A, MO). Shiga: W side of Mt. Hira san, *Tateishi & Hoshi 9149* (MO). Shimane: *Oka 990* (P, NY). Wakayama: Mt. Keya, *Makino s.n.* (A, MO). Yamanashi: near junction of Taba & Komuro rivers, *Tateishi & Hoshi 8701* (MO).

QUESTIONABLE TAXA

Ma (1982) reported two new *Cladrastis* species, *C. scandens* and *C. parvifolia*, in China. The type specimens of these two species were repeatedly requested from the herbaria cited in the protologue, with no response. It was subsequently discovered that the types were not at the herbaria indicated in the protologue (C. Y. Ma, pers. comm.). According to Dr. Ma, the type of *C. scandens* Ma is in the Hebarium, Institute of Botany, Academia Sinica, Beijing (PE), and the type of *C. parvifolia* Ma is in the Herbarium, Department of Taxonomy, South China Institute of Botany, Academia Sinica, Guangzhou (IBSC). We were unable to obtain these specimens on loan.

Cladrastis scandens C. Y. Ma, Bull. Bot. Res., Harbin 2(1): 112–113. 1982. TYPE: CHINA. Guizhou, Anlong, Renli, May 1960, *Y. T. Chang & Z. S. Chang 3547* (HOLOTYPE: PE, *n.v.*). (*ex char.*)

From the description, it is highly probable that *C. scandens* is synonymous with *C. platycarpa*. Ma stated that the only difference between the two is the scandent habit of *C. scandens*. There is no clear indication as to how the habit was determined.

Cladrastis parvifolia C. Y. Ma, Bull. Bot. Res., Harbin 2(1): 110–111. 1982. TYPE: CHINA. Guangxi: Linggui, Chaotian Tangjiacun, Oct 1950, *C. H. Tsoong 808659* (HOLOTYPE: IBSC, *n.v.*). (*ex char.*)

Without having seen the type of *C. parvifolia*, it is impossible to ascertain if it belongs in the genus *Cladrastis*. Information on the axillary bud location (whether or not it is enclosed by the petiole) is missing (Ma 1994). The smaller size of the leaflets, 2–4 × <2 cm versus (2.5–) 4.9 (–9) × (1–) 2.3 (–3.5) cm in other *Cladrastis* species, the smaller inflorescence length, 5–10 cm versus (9.6–) 18.6 (–27.7) cm in other *Cladrastis*, and the fact that it flowers in October rather than in the spring suggest it may not belong in this genus. Based on the descriptions of *C. parvifolia* and *Maackia fauriei* (Takeda 1913), *C. parvifolia* may be synonymous with *M. fauriei*.

EXCLUDED TAXA

Cladrastis amurensis (Rupr.) Benth. *ex* Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 18: 400. 1873. ≡ *Maackia amurensis* Rupr., Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 15: 128, 143. 1856. TYPE: CHINA. Manchuria: *s.d.*, *R. Maack s.n.* (HOLOTYPE: LE; ISOTYPE: K!, P!).

Cladrastis australis Dunn, Bull. Misc. Inform. 10: 86–87. 1912. ≡ *Maackia australis* (Dunn) Takeda, Notes Roy. Bot. Gard. Edinburgh 8: 102. 1913. TYPE: CHINA. "*Sophora* from China, Hort. Soc. Hort. London." 1838, *Millett s.n.* (SYNTYPE: K!).

Cladrastis buergeri (Maxim.) Kom., Trudy Imp. S.-Petersburgsk. Bot. Sada 22: 571. 1904. *Amorpha fruticosa* Thunb., Fl. Jap. 278. 1784. *Buergeria floribunda* Miq., Ann. Mus. Bot. Lugduno- Batavi 3: 53. 1867. *Cladrastis amurensis* var. *buergeri* Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 18: 400. 1873. *Maackia amurensis* var. *buergeri* (Maxim.) C. K. Schneider, Ill. Handb. Laubh. 2: 16. 1907. *Maackia buergeri* (Maxim.) Tatew., Trans. Sapporo Nat. Hist. Soc. 16: 4. 1939. *Maackia amurensis* subsp. *buergeri* (Maxim.) Kitam., Acta Phytotax. Geobot. 25(2–3): 44. 1972. (*ex char.*)

Based on the descriptions, *C. buergeri* (Maxim.) Kom. should be placed in *Maackia*, not *Cladrastis*. It is not possible to say whether it merits specific rank without a complete revision of the genus *Maackia*.

Cladrastis fauriei H. Lev., Repert. Spec. Nov. Regni Veg. 7: 230. 1909. ≡ *Maackia fauriei* (H. Lev.) Takeda, Notes Roy. Bot. Gard. Edinburgh 8: 101. 1913. TYPE: KOREA: Hallaisan, Quelpaert, Aug 1907, *U. Faurie 1692* (HOLOTYPE: E!).

Cladrastis secundiflora (Ortega) Raf., Neogenyton Sect. 1: 1. 1825. ≡ *Sophora secundiflora* (Ortega) DC., Cat. Pl. Horti Monsp. 148. 1813. (Isely 1998).

Cladrastis tashiroi Yatabe, Bot. Mag. (Tokyo) 6: 345. 1892. ≡ *Maackia tashiroi* (Yatabe) Makino, Bot. Mag. (Tokyo) 16: 34. 1902. TYPE: JAPAN. Osumi, Oshima Island, Sep 1887, *Y. Tashiro s.n.* (*n.v.*). (*ex char.*)

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A REAPPRAISAL OF *PASPALUM PILOSUM* AND *P. PEREGRINUM* (POACEAE: PANICOIDEAE: PANICEAE)

SILVIA S. DENHAM AND SANDRA S. ALISCIONI

Instituto de Botánica Darwinion, Casilla de Correo 22, B1642HYD San Isidro,
Buenos Aires, Argentina
e-mail: sdenham@darwin.edu.ar

ABSTRACT. *Paspalum pilosum* and *P. peregrinum* are members of the informal Decumbentes group of *Paspalum*, and grow from Mexico and Mesoamerica to Brazil and Bolivia in South America. *Paspalum pilosum* is characterized by its erect to decumbent culms, glabrous to pilose sheaths and blades, one or two racemes in terminal inflorescences, glabrous spikelets arranged in pairs in 2 irregular series on the rachis, dimorphic lower glumes in the pair of spikelets, longitudinally sulcate lower lemmas, and glabrous gynoecium. *Paspalum peregrinum* has sheaths and blades densely pilose, racemes occasionally branched, hairy spikelets arranged in 1 to 4 series on the rachis, and a hairy gynoecium. These modifications in the morphology of *P. peregrinum* are due to a fungal infection. Another species, *Thrasya venezuelana*, known only from the type collection, is the same taxon as *P. peregrinum*. We conclude that *P. peregrinum* and *T. venezuelana* are in fact abnormal specimens of *P. pilosum*, whose morphology is modified by the fungal infection. Therefore, both species are reduced to the synonymy of *P. pilosum*. This constitutes two new incidents of erroneous interpretation of abnormal morphology caused by fungi, and the first in the tribe Paniceae.

Key Words: *Paspalum*, Paniceae, Poaceae, abnormal morphology, fungal infection

Paspalum pilosum Lam. is a member of the informal group Decumbentes of *Paspalum* L. (Chase 1929). It grows from southern Mexico and Mesoamerica to Bolivia and southern Brazil (Figure 1), inhabiting open fields, savannas, and wooded slopes. It is frequent in grazed places, from 60 to 1700 m elevation.

In a revision of the genus *Thrasya* Kunth, Burman (1987) excluded *T. villosa* Hitchc. from the genus and placed it in *Paspalum*, in the informal group Decumbentes under the new name *P. peregrinum* A. G. Burm. & Filg., since *P. villosum* was pre-occupied by *P. villosum* Thunb. The specimens studied by Burman were from Panama and central Brazil, and the specific epithet *peregrinum* refers to the unusual pattern of disjunction exhibited by the specimens. The type specimen, *Pittier 5363*, is from Panama.

During our revision of the Decumbentes group of *Paspalum*, we found that *Thrasya venezuelana* Chase is the same as *P. peregrinum*. The analysis of new collections from Venezuela and Brazil, in addition

Figure 1. Distribution of *Paspalum pilosum.*

to field observations made by Dr. O. Morrone (pers. comm.), led us to consider *P. peregrinum* as a doubtful species, similar to *P. pilosum.* A detailed morphologic study of both species was performed in order to analyze diagnostic characters and to recircumscribe both species.

MATERIALS AND METHODS

Material studied came from: BM, G, K, LPB, MEXU, MO, P, SI, US, and W (Appendix). Specimens of *Paspalum peregrinum* included some of the material seen by Burman (*Partch 69133* and *Hammel 5506*) and new material from Venezuela (*Trejos 45102*) and Brazil (*Filgueiras 2219* and *Filgueiras & Zuloaga 2101*). The type, *Pittier 5363*, was not seen. The type collection of *Thrasya venezuelana, Chase 12407*, was examined.

Scanning electron microphotographs of the upper anthecium and gynoecium were prepared following Soderstrom and Zuloaga (1989). The specimens were viewed in a Zeiss 940 A scanning electron microscope at the Darwinion institute, operating at 10–20 kV.

The specific histochemical test for chitin was carried out in order to detect fungal hyphae walls using an aqueous solution of 1% aniline-blue and 85% lactic acid (Clark et al. 1983).

RESULTS

The material determined as *Paspalum pilosum* includes short-rhizomatous, perennial plants, 40–100 cm tall, with erect to decumbent culms. The sheaths and blades are glabrous to scarcely pilose. The terminal inflorescences have 1–2 unbranched racemes that are 4–15 (–20) cm long. The last sheath usually subtends a cymose system of 1–3 axillary inflorescences, each with a single raceme; other axillary inflorescences commonly occur at the middle nodes. The rachis is glabrous adaxially and hispid abaxially, the margins are glabrous to sparcely pilose. The spikelets are glabrous, 2.2–3.0 mm long, arranged in pairs, in two irregular series on the rachis. The lower glumes are dimorphic when comparing this bract in the upper and lower spikelets of a pair: in the upper spikelet the lower glume is generally reduced, up to 1/6 the length of the spikelet, while in the lower spikelet, the lower glume is well-developed, up to 3/4 the length of the spikelet, and eccentric. The lower lemma is 5-nerved with a longitudinally sulcate and finely papillose back. The lower palea is well-developed and the lower flower is usually absent. The upper anthecium is papillose and glabrous. The gynoecium is glabrous.

The specimens of *Paspalum peregrinum* differ from *P. pilosum* by their shorter culms (25–35 cm tall), sheaths and blades that are densely pilose on both surfaces and margins, shorter racemes (3–6 cm long) that are sometimes branched, and rachis of the racemes that are pilose on both surfaces and margins. The spikelets are pilose, 2.5–3.5 mm long, and irregularly arranged in 1 to 4 series on the rachis. The upper anthecium is papillose and pilose toward the apex. The gynoecium is pilose or rarely glabrous (Table 1). Hairs of the ovary are unicellular, 90–330 μm long, with a rounded or dome-shaped apex and with a basal constriction (Figure 2). Characters shared by the two species are: the terminal inflorescences with 1–2 racemes and the axillary ones with a single raceme; the dimorphic lower glumes in the two spikelets of a pair; the 5-nerved, longitudinally sulcate and finely papillose lower lemma; the well-developed lower palea; and the absence of the lower flower.

The specimen *Filgueiras 2219* (MO) presents tillers with the morphology of *Paspalum peregrinum* and tillers with the morphology

Table 1. Comparison of *Paspalum pilosum* and *P. peregrinum.*

Plant part	*P. pilosum*	*P. peregrinum*
Culms	40–100 cm tall	25–35 cm tall
Sheaths and blades	Glabrous to scarcely pilose	Densely pilose
Racemes	14–15 (–20) cm long, never branched	3–6 cm long, occasionally branched
Rachis of the racemes	Adaxial surface glabrous, abaxial surface hispid, and margins glabrous to scarcely pilose	Both surfaces and margins pilose
Spikelets	Glabrous, 2.2–3 mm long	Pilose, 2.5–3.5 mm long
Spikelets on the rachis	In 2 irregular series	In 1 to 4 irregular series
Upper anthecium	Glabrous	Pilose toward the apex
Gynoecium	Glabrous	Hairy, rarely glabrous

of *P. pilosum* in the same plant. By using a histochemical reaction to detect chitin, we verified the presence of fungal hyphae on the reproductive structures of the tillers with features of *P. peregrinum.* Fungal hyphae were also detected on reproductive structures of the rest of the specimens of *P. peregrinum.*

Thrasya venezuelana is only known from the type, *Chase 12407*, from Venezuela. This specimen matches the morphology of *Paspalum peregrinum*, with sheaths, blades, and rachis of the racemes densely pilose; pilose spikelets, 3.5–3.7 (–4) mm long; the upper anthecium papillose and pilose toward the apex; and the gynoecium densely pilose.

DISCUSSION

The presence of a hairy gynoecium is a frequent feature within the subfamily Pooideae; it can be hairy throughout its surface or only near the top, sometimes as a fleshy hairy appendage (Clayton and Renvoize 1986). A hairy gynoecium is present in some species of *Festuca* L., *Megalachne* Steud., and *Vulpia* C. C. Gmel. of the tribe Poeae; *Avena* L., *Arrhenatherum* P. Beauv., and *Gaudinia* P. Beauv. of the tribe Aveneae; and *Elymus* L. and *Agropyron* Gaertn. of the tribe Triticeae. In contrast, a hairy gynoecium is unusual within the subfamily Panicoideae. Within the tribe Paniceae, Watson and Dallwitz (1992) cited the presence of a hairy ovary only for the African genus *Chaetopoa* C. E. Hubb., although there is no reference of this character in the original description of the genus.

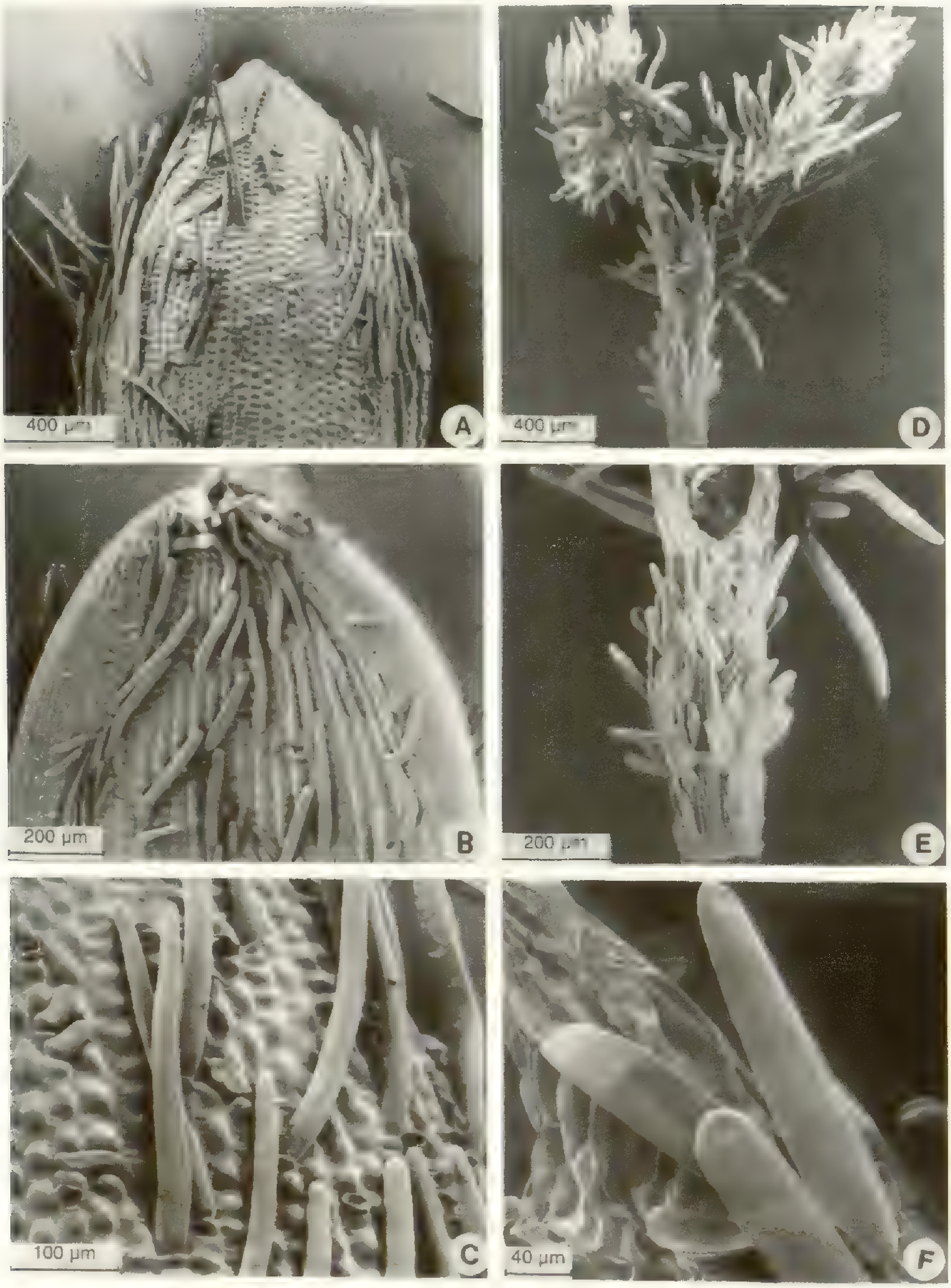

Figure 2. Scanning electron microphotographs of *Paspalum pilosum*. All microphotographs are based on the abnormal specimen *Filgueiras & Zuloaga 2101* (SI). A. Upper anthecium, lemma side. B. Upper anthecium, palea side. C. Detail of lemma of upper anthecium showing hairs. D. Hairy gynoecium. E. Ovary zone. F. Detail of ovary showing hairs.

Structural modifications on vegetative and reproductive parts of the plants, such as culm length, branching at vegetative axes and inflorescences, and proliferation and size of the spikelets, have been cited as malformations caused by fungal infections (Fischer and Holton 1957). Examples of morphological changes caused by fungi in other grass taxa are well documented in *Ichnanthus* P. Beauv. (Stieber 1982), growing in tropical America, Asia, Africa, and Australia; *Streptostachys* Desv. (Zuloaga and Soderstrom 1985), which grows from Venezuela to Brazil and Paraguay; and *Holcus* L. (Menezes de Sequeira and Almaraz 2001), native from Eurasia, but introduced in another areas. Another species of the Decumbentes group of *Paspalum*, *P. unispicatum* (Scribn. & Merr.) Nash, which grows from Texas to Argentina, has been reported by Chase (1929) as being frequently affected by a fungus that distorts the inflorescense. The discovery of specimens such as *Filgueiras 2219*, which presents tillers with normal and abnormal morphology on the same plant, allows us to conclude that the specimens that Burman (1987) recognized as *P. peregrinum* represent affected plants, constituted only by tillers with the abnormal morphology.

In contrast, we have no evidence that pilosity on sheaths, blades, axis, and bracts of the spikelets may be caused by fungal pathogens. Uphof (1962) reported that it is plausible that mutations can cause glabrous and pubescent varieties of a species. In her treatment of *Paspalum pilosum*, Chase (unpubl. manuscript) mentioned specimens collected in grazed or trodden places in Brazil, with short culms, blades densely pilose, racemes 4–8 cm long, spikelets densely hispid with glistening hairs, and stamens and gynoecium abnormal. She described these plants as being affected by a fungus, probably belonging to the genus *Balansia*. Also, she noticed plants with both affected and normal culms. Even though the abnormal morphology of the specimens of *P. peregrinum* is evidently caused by a fungal infection, we were unable to identify the pathogen due to the lack of living material. However, White (1987), Clay (1988), and Clay and Leuchtmann (1989) have pointed out that the Poaceae are commonly infected by fungal endophytes of the family Clavicipitaceae (Ascomycetes).

Examples of "taxa" based on infected specimens include *Holcus mollis* L. var. *parviflorus* Parn., which was synonymized under *Holcus mollis* L. by Menezes de Sequeira and Almaraz (2001), and *Agrostis pumila* L., which Roemer and Schultes (1817) included as an infraspecific category of *A. vulgaris* With. *Paspalum peregrinum* and *Thrasya venezuelana* represent two new incidents of taxa that are based on characters resulting from a fungal infection, and the first in the tribe Paniceae. The remaining species of the Decumbentes group of *Paspalum*, approximately 17 species, have been examined for this phenomenon and no infection was detected.

In short, the abnormal morphology observed in the studied specimens of *Paspalum peregrinum* and in *Thrasya venezuelana* represent pathological deformations that cannot be treated as taxonomic differences. For this reason, we propose the reduction of *P. peregrinum* and *T. venezuelana* to synonymy under *P. pilosum*.

The following nomenclatural treatment should be adopted:

Paspalum pilosum Lam., Tabl. Encycl. 1: 175. 1791. *Dimorphostachys pilosa* (Lam.) E. Fourn., Mexic. Pl. 2: 14. 1886. TYPE: America Tropical, *Richard s.n.* (HOLOTYPE: P-LA!; ISOTYPE: US!).

Thrasya villosa Hitchc., *syn. nov.*, Proc. Biol. Soc. Wash. 40: 84. 1927. *Paspalum peregrinum* A. G. Burm. & Filg., Acta Bot. Venez. 14(4): 91. 1987. TYPE: PANAMÁ. Cerro Vaca, eastern Chiriquí, 25–28 Dec 1911, *Pittier 5363* (HOLOTYPE: US not seen).

Thrasya venezuelana Chase, *syn. nov.*, J. Wash. Acad. Sci. 42(4): 122. 1952, non *Paspalum villosum* Thunb., 1784. *Paspalum venezuelanum* (Chase) A. G. Burm., Acta Bot. Venez. 14(4): 90. 1987. TYPE: VENEZUELA. Federal District, 11 Mar 1940, *Chase 12407* (HOLOTYPE: US-1762130!; ISOTYPE: VEN not seen).

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APPENDIX

SPECIMENS EXAMINED.

Specimens previously treated as *Paspalum peregrinum* A. G. Burman & Filg. are identified with an asterisk.

BELIZE. Stann Creek, Possum Point Biological Station, 23 Jun 1993, *Vincent et al. 6184* (MO).

BOLIVIA. La Paz: Franz Tamayo, Apolo, 52 km hacia Charasani, 1550 m, 7 Jun 1990, *Beck & Foster 18538* (K, LPB, SI); Nor-Yungas: camino Yolosa-Caranavi, desvío a Coroico, a 9 km de Yolosa, 1 Jun 1993, *Rúgolo & Villavicencio 1936* (SI). Santa Cruz: Velasco, Parque Nacional Noel Kempff M., Catarata Ahlfeld, 300 m, 24 Apr 1993, *Killeen et al. 5451* (MEXU, MO, SI).

BRAZIL. Bahía: 24 km SW of Belmonte on road to Itapebi, 24 Mar 1974, *Harley et al. 17387* (K, MO); Serra do Rio de Contas, *Harley et al. 15330* (K, MO, P); Mocugé, de Mocugé a Barra de Estiva, 15 Mar 1999, *Zuloaga & Morrone 6959* (SI). Distrito Federal: W of Taguatinga, 1200 m, 25 Nov 1965, *Irwin et al. 10652* (MO); D.F. 205, entre Sobradinho y Corregom d'Ouro, 15 km W de Sobradinho, 22 Feb 1992, *Filgueiras & Zuloaga 2101** (SI). Goiás: Padre Bernardo, entre Padre Bernardo e Curralinho, ca. 20 km N de Curralinho, 28 Feb 1992, *Filgueiras 2219** (MO); 15 km N of Corumbá de Goiás on road to Niquelandia, ca. 1150 m, 15 Jan 1968, *Irwin et al. 18610* (MO); Chapada dos Veadeiros, 10 km south of Cavalcante, 1000 m, 10 Mar 1969, *Irwin et al. 24239* (US); Padre Bernardo, entre Padre Bernardo e Curralinho, ca. 20 km N de Curralinho, 28 Feb 1992, *Filgueiras 2219* (MO); Pirinopolis, Pirineus, 17 Feb 1956, *without collector 4375* (SI); Serra do Pirineus, 9 km S of Corumbá de Goiás, 1000 m, 1 Dec 1965, *Irwin et al. 10892* (US); without locality, 1894–1895, *Glaziou 22434* (G, K, P, W). Minas Gerais: 13 Jan 1951, *Pires et al. 2907* (US); ca.11 km E of Campanha along Hwy. 267 to Caxabu, 960 m, *Davidse & Ramamoorthy 10609* (MO); ca. 22 km S of Padre Paraíso along Hwy. BR-116, 700 m, 29 Mar 1976, *Davidse et al. 11516* (MO). Pará: Belém, 10 Nov 1964, *Soderstrom & Carvalho 1158* (MO). Paraná: Itararé, 20 Jan 1915, *Dusén 13507* (SI); Jaguariaiva, Parque Estadual do Cerrado, 13 Dec 1992, *Rúgolo et al. 1725* (MO). Rio de Janeiro: Macieiras, Serra de Itatiaia, 1000 m, 18 Jan 1925, *Chase 8346* (US). Sao Paulo: Piracununga, 31 Dec 1964, *Clayton 4104* (US); São Paulo, Parque Estadual das Fontes do Ipiranga, 13 Jan 1976, *da Silva 235* (MO).

COLOMBIA. Buenaventura: 13 Jun 1923, *Hitchcock 19909* (US). Cauca: Around Calí, western side of Cauca valley, 1000–1200 m, Dec 1905, *Pittier 659* (US); carretera Calipopayan, entre Madomo y Pescador, 1630 m, 26 Jun 1989, *Zuloaga & Londoño 4190* (MO, SI); Cauca Valley, Río Sucio, W of Popayan, 1500–1700 m, 3 Jul 1922, *Pennel et al. 8164* (US); La Esmeralda near Jamundí, Cauca Valley, 1200 m, Jan 1906, *Pittier 1539* (US). Chocó: Hoya del Río San Juan, Andagoya, 12 Apr 1979, *Forero et al. 5117* (MO). Cundinamarca: 4 km SW of Fusagusuga, 1450 m, 8 Jan 1974, *Davidse et al. 5556* (MO). Santander: Mesa de Los Santos, 1500 m, 11–15 Dec 1926, *Killip & Smith 15112* (US). Without locality, 1846, *Moritz 650* (BM, G).

COSTA RICA. Guanacaste: Parque Nacional Rincon de La Vieja, 900–1200 m, 27–28 Jan 1983, *Davidse et al. 23441* (MO). Puntarenas: Buenos Aires, 380 m, 17 Jul 1966, *Pohl & Calderón 10075* (MO). San José: 1 km S of Rivas, 6 km NE of San Isidro del General, 725 m, 14 Jul 1966, *Pohl & Calderón 10050* (MEXU).

EL SALVADOR. Chalatenango: along Hwy. 4, 4 km SSE of La Palma, 950 m, 11 Jun 1970, *Pohl & Davidse 11896* (MO).

FRENCH GUIANA. Cayenne: 1835, *Leprieur s.n.* (G, P).

GUATEMALA. Chiquimula: 3 km S of Quezaltepeque on CA-10, 8 Dec 1970, *Harmon & Dwyer 3690* (MO).

HONDURAS. Comayagua: along new Hwy., 10 km NW of Siguatepeque, 1080 m, 14 Aug 1971, *Pohl 12762* (MO). Cortes Lago de Yojoa: 60 km SE de San Pedro Sula, 21 Feb 1982, *Izaguirre 148* (MO). El Paraiso: along Hwy. 4, 25 km E of El Zamorano, 600 m, 14 Jun 1970, *Pohl & Davidse 11921* (MO); Quebrada Honda, por la carretera entre Manzaragua y San Lucas, 1100 m, 11 Oct 1994, *Linares & Metsger 1805* (MEXU). Morazán: 800 m, Nov 1943, *Rodriguez 1561* (MEXU); ca. 16 km SW of Talanga along the road to Tegucigalpa (Hwy. 3), 750 m, 4 Oct 1986, *Davidse & Pilz 31554* (MEXU, MO). Olancho: 6 km SW of Dulce Nombre de Culmí, along Hwy. 3, 550 m, 23 Jul 1970, *Pohl & Davidse 12443* (MO); Vaguada del río de Culmí, 500 m, 17–22 Jul 1978, *Nelson & Romero 4703* (MEXU).

MEXICO. Tabasco: Huimanguillo, 10 Oct 1980, *Cowan et al. 3249* (MEXU).

NICARAGUA. Comarca Del Cabo: Puente Pozo Azul, 10 Jul 1972, *Seymour 5802* (MO). Zelaya: between Waspan and Ulwas, 12 Jul 1970, *Pohl & Davidse 12287* (MO).

PANAMÁ. Chiriqui: Alto Boquete, 1125 m, 25 Jan 1969, *Partch 69133** (MO); Foothills, vicinity of El Boquete, 1000–1300 m, 28 Sep–7 Oct 1911, *Hitchcock 8192* (SI). Panamá: Altos de Campana, a unos 85 km del Moel Sulín, 11 Jun 1977, *Méndez 39* (MO); Cerro Campana, 1000 m, 9 Nov 1978, *Hammel 5506** (MO); Chorrera, 16 Sep 1911, *Hitchcock 8130* (SI); Veraguas, along road to radio tower on Cerro San Cristobla, near Pam. Am. Hwy., 9 km W of bridge over Río Cobre, 450 m, 25 Feb 1974, *Nee 10163* (MO). Zona del Canal: Ancón Hill, 26 Nov–9 Dec 1923, *Standley 25205* (MO).

PERU. Ayacucho: Aina, between Huanta and Río Apurimac, 750–1000 m, 7–17 May 1929, *Killip & Smith 22528* (US).

TRINIDAD Y TOBAGO. Port of Spain, 26 Nov 1912, *Hitchcock 9987* (US); Aripo Savanna, northeast of Cumuto Village, 18 Jun 1963, *Soderstrom 980* (US); Aripo

Savanna, Cumutu Station, 5 Dec 1912, *Hitchcock 10075* (US); St. Joseph, 23 Dec 1912, *Hitchcock 10189* (US).

VENEZUELA. Amazonas: Rio Negro, Solano, along the Brazo Casiquiare, 75 m, 26 Jun 1984, *Davidse & Miller 26655* (MO). Anzoátegui: Bolivar, 1100 m, 24 Nov 1981, *Davidse & Gonzalez 19389* (SI). Anzoátegui: Freites, Burro trail between San Durrial and Los Pajaritos, 1200–1400 m, 1 Dec 1981, *Davidse & González 19794* (MO, SI). Atures: near Capuana, E bank of the Río Orinoco, 90 m, 27 Apr 1979, *Davidse et al. 16795* (MO). Bolivar: a 4 km al N de Santa Elena de Uairen, 900 m, 14 Aug 1989, *Zuloaga et al. 4441* (MO); Roscio, Hato La Divina Pastora, approx. 8 km al N de Santa Elena de Uairén, 830 m, 25 Jul 1983, *Huber & Alarcon 7831* (MO); Sifontes, sector La Hoyada, 7 km al W de Sta. Elena de Uairén, 850–1100 m, 23 Oct 1986, *Aymard 4797* (MO). Distrito Federal: El Avila, 1600 m, Oct 1959, *Trejos 45102** (MO). Guárico: Estación Biológica Los Llanos, 10 km SSE of Calabozo, 60 m, 9 Nov 1971, *Davidse 2917* (MO). Monagas: via cueva del Guacharo, 19 Aug 1983, *Montes 1661* (MO).

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WHAT IS THE CORRECT NAME FOR THE BRISTLY GREENBRIER?

ROBERT L. WILBUR

Department of Biology, Duke University, Durham, NC 27708
e-mail: rwilbur@duke.edu

ABSTRACT. The scientific name of Bristly Greenbrier, a widespread species in eastern North America, has been unsettled for at least the past six decades with *Smilax tamnoides* and *S. hispida* both strongly competing for acceptance in scores of books, papers, and checklists. Neither binomial as currently employed can withstand nomenclatural scrutiny. The correct name determined in the present study is *S. hispida* Raf., a binomial with three years priority over *S. hispida* Muhl. *ex* Torrey.

Key Words: *Smilax tamnoides*, *S. hispida*, *S. pandurata*, Bristly Greenbrier, Smilacaceae

In eastern North American floras, checklists, and atlases, two different binomials are widely employed to designate the common and widespread Bristly Smilax or Greenbrier. Both *Smilax tamnoides* and *S. hispida* have received strong support, as shown by the sampling of the literature listed in the following paragraph. However, neither of these binomials, as employed for the past six decades, withstands close examination.

Publications employing the binomial *Smilax tamnoides* L. to designate the Bristly Greenbrier include Alford (2001), Clewell (1985), Diggs et al. (1999), Duncan (1967, 1975), Duncan and Kartesz (1981), Fernald (1944, 1950), Godfrey (1988), Godfrey and Wooten (1979), Harvill et al. (1986), Judd (1998), Kartesz (1994), Kartesz and Kartesz (1980), Radford et al. (1968), Smith (1988), Steyermark (1962), Voss (1972; although expressing considerable doubt), Wofford (1989), Wofford and Kral (1993), Wunderlin (1982, 1998), and Yates and Duncan (1970). Those who accepted the binomial *S. hispida* as the name for the Bristly Greenbrier include Braun (1943), Browne and Athey (1992), Clausen (1951), Coker (1944), Correll and Johnston (1970), Deam (1940), Gleason (1952), Gleason and Cronquist (1963, 1991), The Great Plains Flora Association (1977, 1986), Holmgren (1998), Jones and Coile (1979, 1988), Jones and Fuller (1955), Mitchell (1986), Mohlenbrock (1970), Mohlenbrock and Ladd (1978), Ownbey and Morley (1991), Rehder (1949), Rhoades and Klein (1993), Small (1933), Strausbaugh and Core (1952, 1978), Tatnall (1946), Thomas and Allen (1993), Van Bruggen (1976, 1985), Wetter et al. (2001), Wherry et al. (1979), Wilbur (1990), Yatskievych (1999), and Yatskievych and

Turner (1990). MacRoberts (1984, p. 38) listed the binomials of both *S. tamnoides* and *S. hispida* as part of the flora of Louisiana. Although more authors have employed the binomial *S. hispida* than *S. tamnoides* over the past six decades, a very strong minority has adopted the binomial *S. tamnoides* as the name for the widespread Bristly Greenbrier. Clearly the application of the two different binomials for the same species leads to confusion and is contrary to Principle IV of the International Code (Greuter et al. 2000).

Although Linnaeus had had little contact with either specimens or prior published accounts or illustrations of what became his *Smilax tamnoides* prior to the publication of its protologue, that binomial then got off to a muddled start and the confusion has persisted for 250 years. Linnaeus's descriptive polynomial included the information that the stem was armed, as did Catesby's polynomial included in the synonomy. Nothing in the protologue pointed to any of the nonwoody smilaxes. The binomial initially was based in part upon a recently received specimen of Pehr Kalm's, then and now preserved in the Linnaean herbarium, originating from the mid-Atlantic area, perhaps New Jersey or Delaware (Fernald 1944, p. 33), and in addition upon the description together with the illustration of Mark Catesby of plants probably encountered in South Carolina. Kalm's specimen was a member of the herbaceous-stemmed section whose members always lack prickles, while Catesby's plant was from the woody section, often with prickly stems and/or leaves. Cauline prickles are clearly indicated in Catesby's published plate (1730, 1: t. 52.). The binomial *S. tamnoides* was grouped by Linnaeus with four other lianoid species all possessing perennial, armed stems, the group designated by Linnaeus as "*Caule aculeato, tereti*." The only specimen in the Linnaean herbarium named *S. tamnoides* has proven, according to Fernald (1944, p. 33), to be an unarmed herbaceous species that Linnaeus actually named, in the same publication and based on another specimen, as *S. pseudo-china*. Obviously Kalm's specimen was misplaced in Linnaeus's account and belonged under the heading "*Caule inermi, tereti*" and had nothing to do with the woody, prickly stemmed species being discussed in this note. Although not included in the Linnaean protologue of *S. tamnoides*, Kalm's specimen of *S. pseudo-china* in the Linnaean herbarium did add to the confusion surrounding *S. tamnoides*. Michaux (1803) did not include *S. tamnoides* in any manner. Pursh (1814) treated *S. tamnoides* as an herbaceous-stemmed species, citing both Wildenow (1806, 4: 780) and Catesby (1730, 1: t. 52.) in its synonymy, even though both described their plants as woody and spiny, as did Linneaus. It is to be remembered that Pursh wrote his flora while living in London where he had access to the Linnaean Herbarium. The Kalm specimen there was identified as *S. tamnoides*, a woody species, including that misidentified specimen of Kalm's masquerading as *S. tamnoides*, although that specimen was actually *S. tamnifolia* Michx. (= *S. pseudo-china*). Elliott (1824), publishing a decade after Pursh (1814), was not misled by Pursh's interpretation of the Linnaean binomial but instead treated *S. tamnoides* as applying to a prickly, woody-stemmed species.

After chiding Linnaeus for failing to understand his own species, *Smilax tamnoides*, Fernald (1944) pointed out that "there can be no question that the type of *S. tamnoides* was the Catesby plate" (i.e., 1: t. 52 together with the accompanying descriptive material on the page opposite the plate). Howard and Staples (1983, p. 517) stated that "a specimen obtained by Kalm (LINN 1132.10) is preferable as lectotype" of *S. tamnoides*. Fernald (1944, pp. 33–34, 38) had earlier identified the only specimen in the Linnaean Herbarium, originally labeled as *S. tamnoides*, to be the herbaceous-stemmed, nonprickly *S. pseudo-china*. Clearly, Howard and Staples overlooked this fact in suggesting that the annual-stemmed specimen in the Linnaean Herbarium would be a better lectotype for *S. tamnoides* than the Catesby plate, even with its obvious deficiencies in biological depiction. Although the Kalm specimen was available to Linnaeus prior to the publication of *Species Plantarum*, Kalm's collection was not cited by Linnaeus. In fact, because the herbaceous-stemmed plant in the Linnaean Herbarium conflicts strongly with the characteristics included by Linnaeus in the protologue of the species, the lectotype suggested by Howard and Staples for *S. tamnoides* would reestablish the misapplication of the name. Elliott (1824, p. 701) considered *S. tamnoides* to be a prickly, woody-stemmed vine with slightly panduriform, 5-nerved leaves. He included in its synonymy *S. panduratus* (sic!) Pursh, even though that species was described by Pursh as three-nerved.

Clausen (1951) criticized Fernald's acceptance of Catesby's illustration that Fernald (1944, p. 38) had stated "was a beautiful match for the terete stemmed plant, with relatively thin though firm, and delicately veined, often panduriform leaves, and elongate, arching and finally drooping peduncles (up to 6.5 cm long) and long pedicels . . ." Coker (1944, p. 30) reached a different conclusion as to the identity of Catesby's plate 1: 52, claiming that it "illustrates the herbaceous *S.* (*Nemexia*) *tamnifolia*." To reach such a conclusion, Coker would have had to overlook the prominent prickles clearly displayed in Catesby's rather crude illustration and whose presence is clearly stated in

Catesby's accompanying Latin polynomial. Clausen challenged Fernald's conclusion that Catesby's illustration was a perfect match for the Bristly Greenbrier "since it has the long peduncles and clusters of 25–32 fruits characteristic of *S. Psuedo-China*, but prickles and leaves as in *S. Bona-nox*. The prickles are sparse, slender, broadest at the base, and green, quite unlike the abundant black bristles of *S. hispida*." Coker (1944, pp. 30, 46) also noted that Catesby erred in attributing tuberous underground parts to the species that Linnaeus named *S. tamnoides*. Coker, whose studies especially focused on the differences in the underground organs of *Smilax*, pointed out that that species does not have tubers. Coker then suggested that the tubers discussed by Catesby must belong to either *S. lanceolata* L. or *S. auriculata* Walter. Clausen stated that the features illustrated or described in Catesby's account were derived from several species and that probably no species existed with the combination of characteristics described or illustrated by Catesby. Clausen found that it was impossible to identify Catesby's account of *Smilax bryoniae nigrae foliis; caule spinoso, baccis nigris*, the sole cited synonym of Linnaeus's protologue of *S. tamnoides* (1753, 2: 1030). Clausen concluded his analysis by proposing that *S. tamnoides* be treated as an ambiguous name and doubtless his recommendation is the reason that a majority of the publications of the later half of the twentieth century took up the binomial *S. hispida*. I agree that Linnaeus's account of *S. tamnoides* is not a reasonable match for the Bristly Greenbrier.

Clearly it would be no easy task to select a lectotype for *Smilax tamnoides* considering its very confused history. It surely would have been better if Fernald had followed his own convictions (1944, p. 41): "One sometimes doubts the wisdom of starting our nomenclature of American plants with Linnaeus (1753). It is almost an exceptional North American species about which he was not hopelessly confused." Still, the International Code of Botanical Nomenclature now gives us almost *carte blanche* to salvage almost any name by lectotypification or to reject it completely in order to maintain stability in nomenclature. Obviously such license is to be used judiciously, and fortunately the published proposed resolution is reviewed in succession by at least two international committees.

During the first four decades of the twentieth century, authors almost universally employed the binomial *Smilax hispida*, as was the practice for much of the previous century. However, during the last half of the twentieth century, as is shown in the second paragraph of this paper, authors were strongly divided in usage between *S. tamnoides* and *S. hispida*. Since there are clearly very serious nomenclatural problems with *S. tamnoides*, we ought now to examine the history of *S. hispida*. It was first published in Muhlenberg's *Catalogue* (1813) but, like almost all new binomials in that publication, it appeared there as a *nomen nudum*, and hence the name was not validly published (Greuter et al. 2000; Merrill and Hu 1949). Muhlenberg's binomial still appears in the literature as *S. hispida* Muhl., and also as *S. hispida* Muhl. *ex* Willd. and *S. hispida* Muhl. *ex* Torr. (1843). The first version attributes the valid publication of the binomial to Muhlenberg who, as we have seen, merely published a binomial without either a diagnosis or a reference to a validly published diagnosis (Merrill and Hu 1949). I have never found a reference to a valid publication of the binomial *S. hispida* Muhl. *ex* Willd. The third version, *S. hispida* Muhl. *ex* Torr., would be correct except that Rafinesque (1840) had earlier validly published *S. hispida* Raf. with no reference to Muhlenberg. Rafinesque's binomial is certainly the same species as that intended by Muhlenberg. Rafinesque's descriptive account is sufficient, as shown below, and can be identified with certainty.

> 925. *Smilax O. hispida* Raf. ramis striatis hispidis basi teretis, apice angulatis, fol. cordatis petiol tenuis concolor acutis 5 nervis reticul. laevigatis margine scabris.—West Kentucky, very distinct by many flexible bristles instead of prickles, leaves very thin, well cordate, 2 or 3 inches long, edges very rough.

The "*O.*" appearing between the generic name and the specific epithet in Rafinesque's description is explained by him in his preceding paragraph: "… the real *Smilax* includes 2 subg. *Oplax* more or less aculeate, *Luiste* inerme." Unfortunately, as with so many of Rafinesque's binomials, no one has yet found authentic material. In spite of this deficiency, I believe Rafinesque's description certainly can be applied only to the same species that Muhlenberg intended to so name but failed to describe. Rafinesque's publication (1840) of *S. hispida* has three years' priority over the publication *S. hispida* Muhl. *ex* Torr. It is somewhat ironic to find Rafinesque claiming *S. hispida* as his own species, since he bitterly and repeatedly criticized Pursh for publishing *Drosera filiformis* as his own species and not attributing it to Rafinesque, who had originally collected the species and described it prior to Pursh's account. Rafinesque (1840) made no mention in publishing *S. hispida* Raf. that Muhlenberg (1813) had published the same binomial, although without a description.

An even earlier name that remains unaccounted for is *Smilax pandurata* Pursh (1814, as *panduratus*). Elliott (1824, p. 701) placed

Pursh's binomial in the synonymy of the woody vine *S. tamnoides*, although Pursh originally described *S. pandurata* as having 3-nerved leaves while Elliott stated that *S. tamnoides* had 5-nerved leaves. In contrast, Morong (1895) included *S. pandurata* in the synonymy of *S. bona-nox* L. and Alphonse de Candolle (1878) treated Pursh's species as a subspecies of *S. bona-nox*. Without authentic material of Pursh of this *Smilax* it is impossible to determine precisely what Pursh had, as the protologue of *S. pandurata* does not provide the information that one must have to determine which species Pursh was describing. Pursh's account is presented in full below. It appeared under the second of the three species groupings employed by Pursh: "***Caule fruticoso; ramis teretibus*."

> 14. S. aculeata; foliis ovato-panduraeformibus acuminatis *panduratus.*
> 3-nervibus, pedunculo communi petiolo duplo longiore.
> In sandy woods: New Jersey to Carolina. ___ July. v.v.
> Leaves smooth and shining on both sides.

It seems unlikely that authentic material of Pursh's *Smilax pandurata* will ever be found. Ewan (1979) indicated in the introductory essay for the Cramer reprint of Pursh's *Flora*, that he had sought widely for the specimens upon which Pursh based his *Flora*, both in Philadelphia, as well as elsewhere in the United States and Europe, with limited success. He had no success in finding authentic material for *S. pandurata*, stating: "*S. panduratus* (251) not located. Fernald [1944, p. 39] = "*S. tamnoides* L." Fernald (1944, p. 39) was as usual for him, positively certain as to the identity of "*S. panduratus*" Pursh: "Pursh's brief description could have applied only to typical *S. tamnoides*."

Pursh's failure to describe the unique bristly trichomes on the lower stems of the Bristly Smilax and his description of the 3-nerved leaves (instead of 5-nerved as usually noted for that species) make me much less certain of the identity of Pursh's *Smilax paniculata* than was Fernald. The rounded branchlets noted by Pursh for *S. paniculata* match well with those of the Bristly Greenbrier as does the described ratio of peduncle length to the subtending petiole length. However, without authentic specimens or type material, it seems impossible to establish the identity of *S. pandurata* Pursh with any certainty. Consequently it seems we have no recourse but to leave Pursh's binomial with the rather lengthy list of *Smilax* names impossible to place in synonymy (i.e., the listings of *Nomina Dubia*). The Rafinesque binomial also lacks a type specimen, but its description seems unquestionably to apply to the Bristly Greenbrier.

The synonymy of the Bristly Greenbrier hence appears to be as follows:

Smilax hispida Raf., Autikon Bot. 125. 1840.
S. hispida Muhl. *ex* Torr., Fl. N. York 2: 302. 1843.
S. grandifolia Buckley, Amer. J. Sci. Ser. 1. 45: 171. 1843.
S. hispida [rankless] *australis* Small, Man. S. E. Fl. 312. 1933.
S. tamnoides var. *hispida* Fernald, Rhodora 46: 38. 1944.
S. hispida var. *australis* (Small) Coker, J. Elisha Mitchell Sci. Soc. 60: 48. 1944.
S. hispida Muhl., Cat. Pl. Amer. Sept. (ed. 1) 92. 1813. *nom. invalid.*, Art. 32.1c.
S. hispida var. *montana* Coker, J. Elisha Mitchell Sci. Soc. 60: 49. 1944. *nom. invalid.*, Art. 36.

It has been suggested that the above synonyms ought to have their types indicated or, if the types are lost, to provide neotypes. I am not prepared to do so at this time. It would be easy to name one of my own collections as a neotype of Rafinesque's species as we can be rather certain that a type will not be found. It would seem to better serve systematics to choose a neotype after making a broad survey of herbaria and then to choose a specimen that had numerous duplicates and those widely distributed. I think the above synonymy is useful and that the suggested typifications can be more judiciously selected at a later time.

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CONSPECTUS AND NOTES ON THE GENUS *AMARANTHUS* IN CANADA

MIHAI COSTEA[1] AND FRANÇOIS J. TARDIF[2]
Department of Plant Agriculture, University of Guelph,
Guelph, Ontario, N1G 2W1, Canada
e-mail: [1]coste_amihai@hotmail.com; [2]ftardif@uoguelph.ca

ABSTRACT. The *Amaranthus* spp. collections from the largest Canadian herbaria were reviewed and a conspectus was prepared. The genus is represented in Canada by 14 species (eight naturalized, four cultivated, and two rare adventive) and by six hybrids. New records for the Canadian flora include: *Amaranthus caudatus*, *A. powellii* subsp. *bouchonii*, *A. hybridus* subsp. *quitensis*, *A. blitum* subsp. *emarginatus*, *A. tricolor*, *A. powellii* × *A. hybridus*, *A. powellii* × *A. tuberculatus*, and *A. albus* × *A. blitoides*. The presence of the previously reported dioecious species *A. palmeri* and *A. cannabinus* is not confirmed by herbarium material. The taxonomy of the most problematic taxa is discussed and a key is provided for all Canadian species and subspecies. Morphology of fruits, seeds, and pollen belonging to *A. albus* and *A. californicus* was compared and their taxonomic relationship discussed. The infraspecific variability of *A. tuberculatus* was analyzed and a new nomenclatural combination proposed—*A. tuberculatus* var. *rudis*.

Key Words: *Amaranthus*, Canada, weeds, exotic plants

The genus *Amaranthus* comprises about 70 species, many of them economically important. Some are among the world's worst weeds (Holm et al. 1997) while others are cultivated as cereals, vegetables, and ornamentals (Brenner et al. 2000). The genus is considered difficult by taxonomists, weed scientists, and horticulturists because its taxa are extremely polymorphic and often not easy to identify; additionally the genus has many nomenclatural problems. In Canada, all the species are cultivated or adventive and the genus has never been reviewed. The purpose of this paper is to provide a list of *Amaranthus* species that occur in Canada and to discuss their taxonomy. The most important weed species of the genus in Canada have been treated in detail for the "Biology of Canadian Weeds" series. They include: *A. albus*, *A. blitoides*, and *A. blitum* (Costea and Tardif, in press) and *A. retroflexus*, *A. powellii*, and *A. hybridus* (Costea et al., unpubl. manuscript). Distribution maps as well as relevant biological and ecological information have been included in these papers.

MATERIAL AND METHODS

The following Canadian herbaria were surveyed: ACAD, ALTA, BRS, DAO, HAM, LRS, MMMN, MT, MTMG, NBM, NFLD, NSPM, OAC, OTT, QFA, QK, QUE, SASK, SFS, TRT, TRTE, TUP, UAC, UBC, UNB, USAS, UWO, UWPG, V, WAT, and WIN. Furthermore, the Canadian collections deposited in more than 40 herbaria in the United States (Costea, Sanders, and Waines 2001) were also examined. Detailed notes on the nomenclature and descriptions for most of the species can be found in Sauer (1950, 1955, 1967); Costea, Sanders, and Waines (2001); and Costea, Waines, and Sanders (2001). The morphology of fruits and seeds belonging to *Amaranthus californicus* and *A. albus* was comparatively studied from Canadian herbarium specimens (Appendix). Furthermore, accessions from the U.S.D.A., ARS germplasm collection were examined as well: *A. albus*—Ames 137 888 and Ames 18499; *A. californicus*—PI 595319 (U.S.D.A., ARS 2002). The Scanning Electron Microscopy (SEM) was done with a Hitachi S-570 at 10 and 15 kV, using an Anatech Hummer VII sputter-coater. Twenty-five fruits and seeds were collected from each herbarium specimen or per accession examined (Appendix). The same number of pollen grains per herbarium specimen (25) was analyzed in order to assess the morphology of the pollen grains in the two species (Appendix). A list of representative specimens examined was included in the Appendix for the most problematical taxa. Plants with mature fruits are necessary for accurate determinations. It is important to distinguish between tepals and bracteoles, and floral parts should be examined at magnifications higher than 30×. In the key "tepals" refers to those of female flowers only.

RESULTS AND DISCUSSION

The Canadian species of the genus *Amaranthus*. Based on the herbarium collections surveyed, in Canada there are eight naturalized, four cultivated, and two rare adventive species of *Amaranthus*. The number of *Amaranthus* spp. in Canada is fewer than in floras of significantly smaller countries from the same latitude in Europe. For example, Karlsson (2001) listed approximately 25 *Amaranthus* spp. from cool-temperate northern countries such as Sweden, Denmark, and Norway. The low number of species in Canada may be explained in two ways. Firstly, in Canada the disturbed habitats in which amaranths thrive are not as common comparative to European countries, where the density of human settlements is higher. Secondly, amaranths in Canada are undercollected; the total number of Canadian specimens deposited in Canadian and United States herbaria does not exceed 3000. Therefore, the number of *Amaranthus* spp. and their inferred distribution from the available herbarium material is probably incomplete, especially if one takes into account that there are about 40 species reported from the United States (U.S.D.A., NRCS 2002).

The dioecious amaranths, *Amaranthus palmeri* S. Watson and *A. cannabinus* (L.) Sauer are mentioned by Scoggan (1978) and might occur in Canada, but their presence is not confirmed by any herbarium evidence. Some monoecious species that are widely distributed in the United States and Europe, such as *A. deflexus* L., if not already introduced in Canada, are very likely to be found in the future.

KEY TO THE *AMARANTHUS* SPECIES OCCURRING IN CANADA

1. Plants dioecious . . . . 1. *A. tuberculatus*
1. Plants monoecious . . . . (2)
  2. Flowers in a terminal spiciform or paniculiform inflorescence (axillary clusters may be present as well) . . . . (3)
    3. Axils of stem leaves bearing a pair of spines; female flowers distributed only at the base of each inflorescence branch . . . . 8. *A. spinosus*
    3. Axils of stem leaves without spines; female flowers evenly distributed in the inflorescence . . . . (4)
      4. Tepals 3 . . . . (5)
        5. Tepals longer than the fruit, with a long, pale awn . . . . 14. *A. tricolor*
        5. Tepals shorter or equaling the fruit, without an awn . . . . (6)
          6. Leaves acute; tepals somewhat shorter than or equaling the brownish, strongly muricate fruit . . . . 13. *A. viridis*
          6. Leaves emarginate to bilobed; tepals much shorter than the green, almost smooth fruit . . . . 12. *A. blitum*
            7. Leaves not fleshy, deeply emarginate to bilobed at apex; terminal inflorescence long, thin and flexuous; fruit 1.2–1.8 mm long; seeds 0.8–1.1 mm in diameter . . . . 12b. *A. blitum* subsp. *emarginatus*

7. Leaves fleshy, emarginate but never bilobed; terminal inflorescence short, thick and dense; fruit 1.7–2.6 (–3) mm long; seeds 1–1.2 mm in diameter . . . . 12a. *A. blitum* subsp. *blitum*

4. Tepals 3–5 on the same plant, or constantly 5 . . . . . . (8)

8. Tepals spathulate to obovate . . . .(9)

9. Cultivated ornamentals or cereals, sometimes escaped in ruderal places, with large and conspicuous red, yellow, or whitish inflorescences; bracteoles shorter than stigma branches; tepals shorter than fruit . . . . (10)

10. Inflorescence with a terminal part 10–30 (–40) cm long, thick and pendent; tepals wide-obovate to spathulate, the outer ones overlapping laterally and ± outcurved; fruit gradually narrowed toward apex; stigma branches spreading . . . . 2. *A. caudatus*

10. Inflorescence usually with many lateral, patent (± perpendicular on inflorescence axis) or ascendant, thin branches; tepals narrow-obovate, straight and not overlapping; fruit abruptly narrowed toward apex in a thin rostrum; stigma branches erect . . . . 3. *A. cruentus*

9. Weeds with green inflorescences; bracteoles longer than stigma branches; tepals longer than the fruit . . . . (11)

11. Stem sparsely hairy below inflorescence; inflorescence with many lateral, patent, thin branches; tepal midribs extending beyond apex into the mucro . . . . 4b. *A. hybridus* subsp. *quitensis*

11. Stem densely hairy below inflorescence; inflorescence usually with short, thick, ascendant or erect branches; tepal midribs ending below apex (although apex often mucronate). . . . . 7. *A. retroflexus*

8. Tepals oblong-linear to lanceolate . . . .(12)

12. Cultivated ornamentals or cereals, sometimes escaped in ruderal places, with large and

conspicuous red inflorescences; pericarp with 3–4 cell layers; bracteoles shorter than stigma branches . . . . (13)

13. Fruit abruptly narrowed toward apex in a thin rostrum; stigma branches parallel, erect; inflorescence usually with many lateral, patent or ascendant, thin branches . . . . 3. *A. cruentus*

13. Fruit apex truncated, rostrum absent, stigma branches divergent from the base; inflorescence usually stiff, with thick, erect or ascendant branches. . . . . 5. *A. hypochondriacus*

12. Weeds with green inflorescences; pericarp with 2–3 cell layers; the bracteoles surpassing the stigma branches . . . . (14)

14. Inflorescence with a few rigid, erect, and widely spaced branches or with many ascendant or erect, thick branches; leaves broadly elliptic to rhombic or lanceolate; tepals 3–5, very unequal with yellowish midveins; fruit apex gradually narrowed . . . . (15)

15. Inflorescence stiff and erect, ± unbranched or with a few widely spaced, long branches; bracteoles 5–7.5 (–8) mm long; fruit circumcissile, irregularly wrinkled above the dehiscence line . . . . 6a. *A. powellii* subsp. *powellii*

15. Inflorescence not strictly erect, more lax, with many lateral branches; bracteoles 3.5–5 mm long; fruit indehiscent or irregularly dehiscent, ± smooth . . . . 6b. *A. powellii* subsp. *bouchonii*

14. Inflorescence usually with many patent, short and thin branches or with only a few thin, flexuous and long branches; leaves broadly ovate to rhombic-ovate; tepals 5, subequal with green mid veins; fruit apex abruptly narrowed . . . . (16)

16. Tepals erect, shorter than the fruit . . . . 4a. *A. hybridus* subsp. *hybridus*

16. Tepals erect or outcurved, longer than the fruit . . . . 4b. *A. hybridus* subsp. *quitensis*

2. All flowers in axillary cymose clusters, terminal inflorescence absent . . . . (17)

17. Perianth with (4–) 5 tepals . . . . 11. *A. blitoides*

17. Perianth with 3 tepals or reduced to 1–2 tepals . . . . . . (18)

18. Leaves emarginate or slightly bilobed; bracteoles foliaceous; fruit indehiscent . . . . (19)

19. Fruit 1.7–2.6 (–3) mm long, pericarp 4-layered; seeds 1–1.2 mm in diameter. . . . . 12a. *A. blitum* subsp. *blitum*

19. Fruit 1.2–1.8 mm, pericarp 3-layered; seeds 0.8–1.1 mm in diameter . . . . 12b. *A. blitum* subsp. *emarginatus*

18. Leaves not emarginate; bracteoles spinescent; fruit circumcissile . . . . (20)

20. Stems many from the base, prostrate and mat forming, sometimes ascendant; stem and leaves glabrescent, often fleshy-turgescent; male flowers with 1–2 stamens; bracteoles short, thin, equaling the fruit; perianth of female flowers with 1 linear-lanceolate, membranous tepal and 1 (–2) tepals that are reduced or absent . . . . 10. *A. californicus*

20. Stems usually single, divaricately branched, ascendant to erect, rigid, bone-like, usually scurfy villous or pubescent; leaves not fleshy; male flowers with (2–) 3 stamens; bracteoles 1.5–2× longer than fruits, spinescent, subulate, rigid; female flowers perianth with 3 membranous tepals . . . . 9. *A. albus*

TAXONOMIC TREATMENT

I. Subgenus *Acnida* (L.) Aellen *ex* K. R. Robertson, J. Arnold Arbor. 62: 283. 1981.

1. *Amaranthus tuberculatus* (Moq.) J. D. Sauer, Madroño 13: 18. 1955; incl. *A. rudis* J. D. Sauer, Madroño 21: 428. 1972.

Pratt and Clark (2001) showed that *Amaranthus tuberculatus* and *A. rudis* as defined by Sauer (1955) are the morphological extremes of a single variable waterhemp species continuum. However, the authors admitted that the morphologic variation of female flowers exhibits a geographical separation, which follows Sauer's concept of two waterhemp entities (Sauer 1955). The western specimens correspond to the *A. rudis* race, while northern and eastern North American populations can be ascribed to typical *A. tuberculatus*. The two forms have a different ecology. Sauer (1955) observed that although they grow in similar habitats (e.g., margins of inland bodies of water), *A. rudis* (= *A. tamariscinus*) has "a very definite weedy tendency" compared to *A. tuberculatus*. Furthermore, the pericarp of the indehiscent fruits (in typical *A. tuberculatus*) is provided with extensive intercellular air spaces allowing a more effective water dispersal of the seeds than of the plants having circumcissile fruits (in typical *A. rudis*; Costea et al., unpubl. data). Only in the midwestern populations (Iowa, Illinois, and Missouri) might diagnostic traits segregate in populations and form a unique and inseparable morphological, isoenzymatical (Pratt and Clark 2001; Sauer 1955) and, most probably, ecological complex. Uline and Bray (1895) also combined the two waterhemps in a single species, *Acnida tamariscina* (Nutt.) A. W. Wood, but the authors recognized them as varieties. The latter solution seems to be the most appropriate because it would allow a distinction of the two entities (based on the morphology of the female flowers and their ecology) outside the Midwest.

1a. *Amaranthus tuberculatus* var. *tuberculatus*.

Female flowers with one or two lanceolate or linear tepals; the fruit is indehiscent. It has been collected since the last century from Ontario and Québec, where it is native. It grows along lake shores, ponds, and rivers (Appendix).

1b. **Amaranthus tuberculatus** var. **rudis** (J. D. Sauer) Costea & Tardif, *comb. nov. Amaranthus rudis* J. D. Sauer, Madroño 21: 428. TYPE: U.S.A. Kansas: Riley Co., 6 Aug 1895, *J. B. Norton 428* (HOLOTYPE: MO 1740436!).

Female flowers with absent or vestigial tepals; the fruit is dehiscent. This invasive weed, often resistant to various herbicides, has been recently introduced in southern Ontario, in Lambton County, and a few specimens were collected from ruderal places in Burnaby, British Columbia (Appendix).

II. Subgenus *Amaranthus*.

The most problematic group of species in this subgenus is referred to in the literature as the *Amaranthus hybridus* aggregate. It includes six extensively studied species, today almost cosmopolitan in distribution (*A. hybridus*, *A. powellii*, *A. hypochondriacus*, *A. cruentus*, *A. caudatus*, and *A. quitensis*), and a number of other species, poorly known, restricted to the southern parts of North America and to Central and South America (Costea, Sanders, and Waines 2001; Sauer 1950, 1967). *Amaranthus retroflexus* is usually separated from this complex. In our opinion, it should be included here as well because it hybridizes readily with all of the above-mentioned species. Cytological studies indicate a close genomic homology between *A. retroflexus* and other members of the *A. hybridus* complex (e.g., *A. cruentus* and *A. powellii*; Pandey 1999). Molecular (Xu and Sun 2001) and morphological studies (Costea and DeMason 2001; Costea, Sanders, and Waines 2001) have, in general, proved the distinction of the six (seven with *Amaranthus retroflexus*) species. However, such studies have necessarily based their conclusions on a limited number of populations and/or accessions. A worldwide survey of thousands of *Amaranthus* herbarium specimens has revealed that, especially in some subtropical and tropical regions, an overlapping pattern of variation may occur between species (Costea, unpubl. data). Nonetheless, including these six (or seven) species in a broadly defined *A. hybridus* may be a premature solution. Other concepts of *A. hybridus* in which only one or several species are included in *A. hybridus*, while the others are separately maintained or combined in various ways, are also unacceptable because they provide an arbitrary classification. Therefore, until the pattern of variation within this group, including the less known species, is properly understood, the best solution is to maintain them at specific rank.

2. *Amaranthus caudatus* L., Sp. Pl. 990. 1753.

This distinctive South American species, reported here for the first time in Canada, is sometimes cultivated as an ornamental (Appendix). The grain amaranths—*Amaranthus caudatus*, *A. hypochondriacus*, and *A. cruentus*—have generated a great interest in recent years as agricultural crops in the United States and other regions of the world, due to the exceptionally high nutritional value of their seeds and leaves. For a comprehensive review of the genetic and breeding resources of these species, see Brenner et al. (2000).

3. *Amaranthus cruentus* L., Syst. Nat. ed. 10, 1269. 1759.

This species is native from Central America, and in Canada the name has been frequently misapplied to *Amaranthus hypochondriacus*. It is cultivated as an ornamental (but less frequently than *A. hypochondriacus*) and sometimes it escapes in ruderal places in Alberta, Ontario, and Québec (Appendix). In Canada, it has usually been treated as a variety of *A. hybridus* (Boivin 1966; Scoggan 1978).

4. *Amaranthus hybridus* L., Sp. Pl. 990. 1753.

4a. *Amaranthus hybridus* subsp. *hybridus*. *A. patulus* Bertol., Comment. Itin. Neapol. 19. 1837. *A. incurvatus* Timeroy *ex* Gren. & Godr., Fl. France Prosp. 8. 1846.

Originally from eastern North America, Mexico, and Central America, this taxon is now widespread all over the world as a weed in cultivated or ruderal places. In Canada, it is confined to southwestern Ontario (Appendix). Scoggan (1978) also mentioned that it was recorded in western Québec, and that a specimen was found in Winnipeg (Scoggan 1957). We were unable to prove this from herbarium material, although the presence of this taxon in other provinces is likely to be expected.

4b. *Amaranthus hybridus* subsp. *quitensis* (Kunth) Costea & Carretero, Sida 19: 955. 2001. *A. quitensis* Kunth, Humb., Bonpl. & Kunth, Nov. Gen. Sp. 2, folio: 156; ed. 4: 194. 1817.

This is a new record for Canada, based on a single collection: Toronto, Bull grounds, 10 Sep 1904, *W. Scott s.n.* (TRT). A native of tropical South America, where it is a noxious weed, this plant tends to be more restricted to warm climates than subsp. *hybridus*, and it is unlikely to become a permanent part of the Canadian flora in the future.

5. *Amaranthus hypochondriacus* L., Sp. Pl. 991. 1753. *A. hybridus* L. subsp. *hypochondriacus* (L.) Thell. [rankless] *erythrostachys* (Moq.) Thell., Asch. & Graebn., Syn. Mitteleur. Fl. 5: 241. 1914.

In Canada, *Amaranthus hypochondriacus* has been considered a synonym of *A. hybridus*, but the description of the latter species (e.g., Scoggan 1978) did not include the characteristics of the former. It is the most frequent grain amaranth cultivated in Canada and sometimes it escapes in ruderal places in British Columbia, Alberta, Manitoba, Ontario, and Québec (Appendix).

6. *Amaranthus powellii* S. Watson, Proc. Amer. Acad. Arts. 10: 347. 1875.

6a. *Amaranthus powellii* subsp. *powellii*. *A. retroflexus* var. *powellii* (S. Watson) B. Boivin, Naturaliste Canad. 93: 641. 1966.

This subspecies is native to North and South America and has previously been shown to be frequent in Québec and Ontario (Doyon et al. 1986; Frost 1971). The subspecies was also reported from British Columbia to Saskatchewan, and from Prince Edward Island (Boivin 1966). Moss (1983) mentioned that *Amaranthus powellii* was "rare on waste ground" in Alberta. Based on the early reports of this species in British Columbia and Alberta (which date from the late 1800s), *A. powellii* may be much more frequent in these provinces than is currently believed and the same situation may occur in Saskatchewan, Nova Scotia, and New Brunswick. A few specimens of *A. powellii*, previously identified as *A. retroflexus*, were examined from these provinces.

6b. *Amaranthus powellii* subsp. *bouchonii* (Thell.) Costea & Carretero, Sida 19: 964. 2001; *A. bouchonii* Thell., Monde Pl. 27(160): 4. 1926.

This first record for Canada was described from France (Thellung 1926), but it has spread as an agrestal weed in several western and central European countries, where it has frequently been accepted at the specific rank. In Europe, *Amaranthus bouchonii* is thought to have evolved as a colonist of nitrophilous river banks because of the water dispersal advantage conferred by its indehiscent fruits. Afterwards, it has invaded irrigated fields, where it may compete efficiently with other amaranths such as *A. retroflexus*. Costea, Waines, and Sanders (2001) reported it from the United States and, based on its morphology, reduced it to a subspecies of *A. powellii*. The latter authors suggested two hypotheses regarding its presence in North America. The first one suggests that *A. powellii* subsp. *bouchonii* was introduced from Europe; the second hypothesis assumes that the indehiscence character had developed simultaneously in both North America and Europe. This second hypothesis is supported by the early records and by the wide and scattered distribution observed for these plants in North America (Costea, Sanders, and Waines 2001; Appendix). However, this taxon has apparently not acquired here the consistency observed in Europe. A study using molecular markers would be necessary to clarify the relationships between these two subspecies using both European and North American source material.

7. *Amaranthus retroflexus* L., Sp. Pl. 991. 1753.

This is the most common species of the genus and is distributed in all the Canadian provinces. *Amaranthus retroflexus* was probably the first species of the genus introduced to Canada by the early colonists from the more southern regions of America, between the 17th and 18th centuries. Evidence for this includes the macrofossil seeds of *A. retroflexus* excavated from various sites in Québec, which are estimated to be approximately 250 years old (Richard 2001).

8. *Amaranthus spinosus* L., Sp. Pl. 991. 1753.

This distinctive tropical species is not naturalized in Canada and is unlikely to be in the future because of its cold sensitivity. Its presence in Canada is based on two collections from Manitoba (Fort Garry, 14 Jul 1931, *Hutchinson s.n.*, DAO) and Ontario (Swansea, 23 Aug 1912, *A. L. Bennes s.n.*, DAO).

III. Subgenus *Albersia* (Kunth) Gren. & Godr., Fl. France (Grenier) 3: 3. 1856.

9. *Amaranthus albus* L., Syst. Nat. ed. 10: 1268. 1759. *A. graecizans* auct., non L.

This species is a common weed, native to the plains of central North America. In Canada it occurs in all provinces except the coldest ones: Yukon Territory, Northwestern Territories, Nunavut, Newfoundland, and Labrador. It grows in both ruderal and agrestal habitats, and it is the second most frequent species after *Amaranthus retroflexus*.

10. *Amaranthus californicus* (Moq.) S. Watson, Bot. California 2: 42. 1880.

This species is a native of the western United States, but was also reported from Nebraska, Wyoming, and Texas; in Canada it is known from southern Alberta and western Saskatchewan (Boivin 1966; Scoggan 1978). *Amaranthus californicus* has been misidentified in herbaria as *A. albus* (and vice versa) and the relationship between the two taxa needs resolution. Besides the differences already mentioned in the key, the SEM study of the fruits and seeds revealed the following:

1. Fruit abruptly narrowed in a beak toward the stigma branches, with more or less smooth pericarp; stigma branches thin, erect (Figure

1C); seeds obovate, with the radicle zone prominent (Figure 1A) . . . . *A. californicus*

1. Fruit gradually narrowed and truncated toward the stigma branches, with the pericarp coarsely wrinkled; stigma branches thick, spreading from the base (Figure 1D); seeds round to nearly round, with the radicle zone not prominent (Figure 1B) . . . . *A. albus*

These differences (including those mentioned in the general key) represent the extremes between which intermediates may occur. Thellung (1914) described in *Amaranthus albus* the form *monosepalus* based on a "forme aotomnale" observed by Sennen in Barcelona, Spain. Occasionally we examined specimens of *A. albus* with a reduced perianth formed of 1 (2) tepals from Europe and eastern North America (where *A. californicus* does not occur). The morphology of bracteoles can also vary in the populations of *A. albus* located outside the distribution range of *A. californicus*; sporadically, individuals with short, thin bracteoles may be encountered. The morphology of fruits and seeds examined on Canadian specimens, although often reliable in differentiating the two taxa, may also show an overlapping pattern in some cases (e.g., round seeds and/or wrinkled fruits in *A. californicus* and obovate seeds and/or smooth pericarp in *A. albus*). These observations suggest that the normal range of variation in *A. albus* may include many of the differentiating characteristics of *A. californicus*. Howell (1970) observed that typical plants of *A. californicus* at Alpine Lake, California were growing together with a similar amaranth, which differed in having female flowers with 3 tepals. The author suggested that these forms might represent a hybrid between *A. californicus* and *A. albus*.

Costea, Waines, and Sanders (2001) and Costea, Sanders, and Waines (2001) found differences in pollen morphology among the taxa of *Amaranthus hybridus* and *A. blitum* complexes. The specimens of *A. albus* and *A. californicus* examined (Appendix) were identical with respect to their pollen morphology, suggesting a close relationship. The pollen grains are pantoporate, apolar, 18–28 μm in diameter, with 22–36 uniformly distributed apertures, and the tectum is provided with granules.

It is probable that *Amaranthus californicus* evolved from *A. albus* in western North America as an ecological segregate of moist mud or sand and in beds of dried-up lakes around ponds and lake shores, habitats from which it has been recorded by all authors (Abrams 1944; Correll and Johnston 1970; Hickman 1993; Hitchcock and Cronquist 1964; Moss 1983; Munz and Keck 1959). The

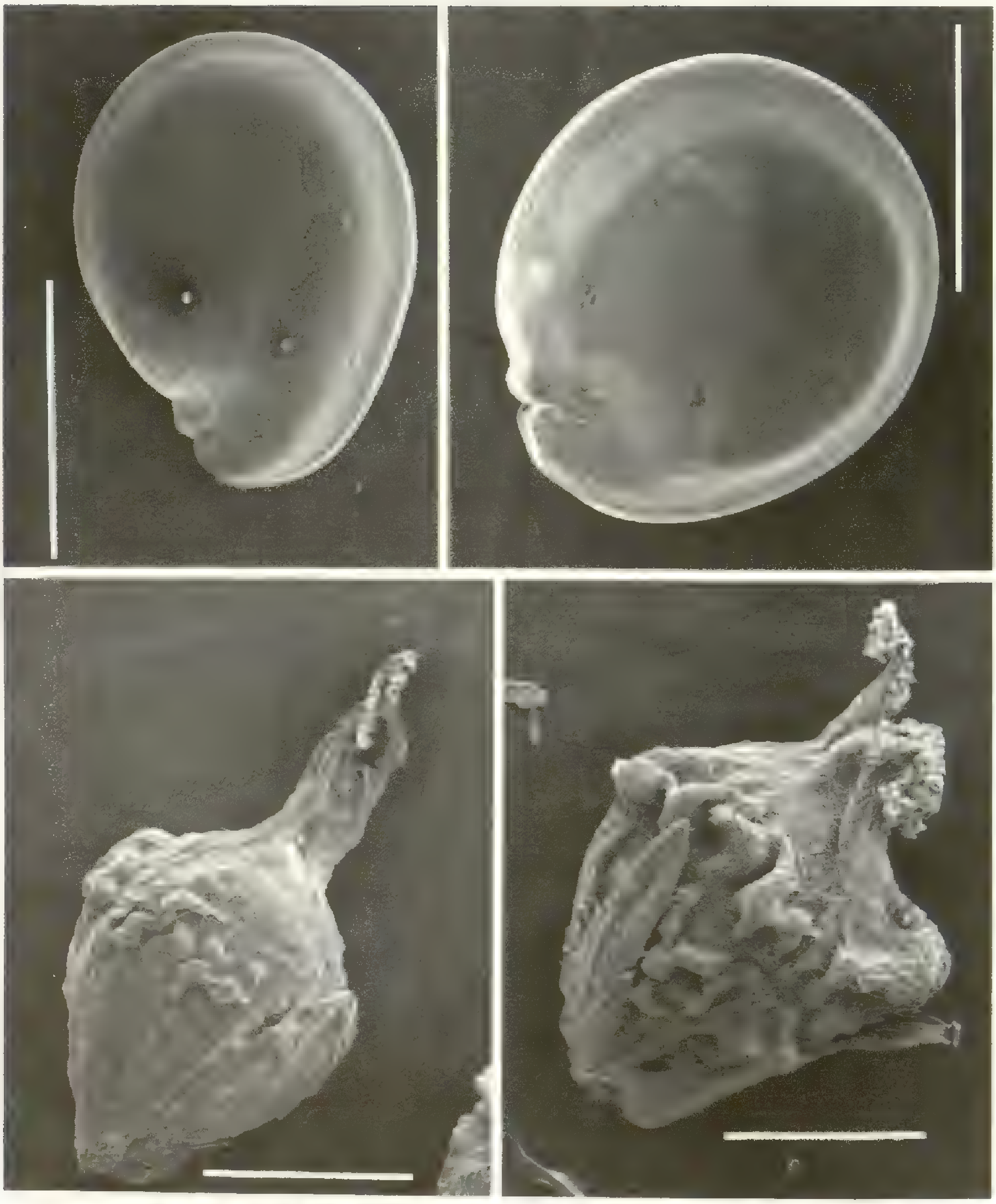

Figure 1. Morphology of seeds and fruits of *Amaranthus californicus* (left) and *A. albus* (right). Scale bar = 0.50 mm for seeds and 0.60 mm for fruits.

expansion of *A. californicus* to disturbed habitats with *A. albus* might eventually obscure the limits between the two taxa. For example, Hartman and Nelson (2000) included both *A. californicus* and *A. albus* on the list of invasive species in Wyoming. *Amaranthus californicus* in Canada often occurs in ruderal places where *A. albus* has been long-established. Nevertheless, the change in rank of *A. californicus* to an infraspecific taxon (subspecies) of *A. albus* would require more study of the United States populations. Until then it should retain its current status at specific rank.

11. *Amaranthus blitoides* S. Watson, Proc. Amer. Acad. Arts 12: 273. 1877. *A. graecizans* auct., non L.

This species is considered by most authors to be a native of western North America. In Canada it occurs with *Amaranthus albus* in many of its habitats. The provinces where it was not documented by herbarium material were Yukon Territory, Northwestern Territories, Nunavut, Newfoundland, Nova Scotia, New Brunswick, and Prince Edward Island. The binomial *A. graecizans* has been widely misapplied in North America to either *A. albus* or *A. blitoides*. *Amaranthus graecizans* (subsp. *graecizans*) is a taxon native to Europe, North Africa, and Asia that superficially resembles *A. blitoides* var. *reverchoni* Uline & Bray (Costea, Waines, and Sanders 2001).

12. *Amaranthus blitum* L., Sp. Pl. 990. 1753.

This species has been known in North America as *Amaranthus lividus* L. (for details on nomenclature see Costea, Waines, and Sanders 2001). Two of the three subspecies of *A. blitum* (Costea, Waines, and Sanders 2001) occur in Canada.

12a. *Amaranthus blitum* subsp. *blitum*; *A. lividus* L. subsp. *ascendens* (Loisel.) Thell. *ex* Wachter, Heukels, Geill. Schoolfl. Nederl., ed. 11, 169. 1934.

This subspecies is native to the Mediterranean region, Eurasia, and North Africa where it is a frequent weed in vegetable gardens and in ruderal places. In the United States, *Amaranthus blitum* subsp. *blitum* occurs as a rare adventive (Costea, Waines, and Sanders 2001) and the same situation seems to exist in Canada. A few specimens of this subspecies were collected from Ontario and Québec (Appendix).

12b. *Amaranthus blitum* subsp. *emarginatus* (Moq. *ex* Uline & Bray) Carretero, Munoz Garm. & Pedrol, Anales Jard. Bot. Madrid 44: 599. 1987; *Amaranthus emarginatus* Moq. *ex* Uline & Bray, Bot. Gaz. (Crawfordsville) 19: 319. 1894.

This subspecies is native to and very widespread in the tropics, but it has also been introduced into the temperate regions of North America and Europe. It is a thermophyte, which prefers humid, nitrophilous alluvial sands (on river banks, lakes) or fertile light horticultural substrates. It is naturalized as a ruderal and agrestal weed in the United States (Costea, Waines, and Sanders 2001). In Canada, *Amaranthus blitum* subsp. *emarginatus* is a new record and it appears to be naturalized in British Columbia and Québec (Appendix).

13. *Amaranthus viridis* L., Sp. Pl. (ed. 2) 1405. 1763.

According to the majority of authors, this species is native to South America. Previous records of this species from Canada were based on misidentifications of *Amaranthus blitum*. The only valid Canadian specimen is from Québec, Cté. de Rouville, St-Césaire, champ de tomates, 25 Jul 1983, *D. Tanguay 83-703* (QUE).

14. *Amaranthus tricolor* L., Sp. Pl. 989. 1753.

This distinctive species is native to Asia, where it is widely cultivated as a vegetable. In Canada we encountered it in Ontario as an ornamental. The most frequent cultivated ornamental forms are 0.6–1 (–1.5) m tall and their leaves are green or variegated, displaying bright white, purple-red, or yellow shades.

Hybrids. Hybridization is one of the most important sources of taxonomic difficulty in *Amaranthus*. Hybrids are known to occur naturally between the species within each of the three subgenera and also between the species of the subgenera *Amaranthus* and *Acnida*. Hybridization between the species of subgenera *Amaranthus* and *Albersia* or between *Acnida* and *Albersia* is unknown. Introgression rates have been reported only for the grain amaranths and they vary between 3.5–34%, depending on the environmental factors (Costea, Sanders, and Waines 2001). Experimental hybridizations have shown that F_1 hybrids are usually 89–90% sterile (Greizerstein and Poggio 1992; Greizerstein et al. 1997; Murray 1940). The introgression rates explain the formation of hybrid swarms, while the predominant inbreeding nature of amaranths may account for the relative stability of the hybrid products.

The F_1 hybrids within the subgenus *Amaranthus* are often not morphologically intermediate between the two parents. They have abnormally shaped inflorescences with very dense, crowded (and sometimes twisted or fan-shaped) branches. They can easily be recognized by the great number of densely packed and larger bracteoles that subtend the sterile female flowers. The best way to identify them is to note which potential parent species are present in the field where the hybrids were collected and to perform molecular tests. Franssen et al. (2001) showed that the hybrids between monoecious and dioecious species have an intermediate number of apertures in the pollen grains. The F_1 hybrids within the subgenus *Albersia* are usually morphologically intermediate between the two parents. The survey of Canadian herbarium specimens revealed the following F_1 hybrids:

1. *Amaranthus* ×*soproniensis* Priszter & Karpati, Index Horti Bot. Univ. Budapest. 7: 140. 1949 (*A. retroflexus* × *A. powellii*).

The plants are often purplish-colored, with the leaves resembling those of *Amaranthus powellii* in shape. Most commonly, the terminal inflorescence has many crowded, thin branches (occasionally fan-shaped, or a long and pendent terminal inflorescence may be encountered). The tepals of the female flowers are obovate or spathulate and much longer than the sterile ovaries (as in *A. retroflexus*; Appendix).

2. *Amaranthus* ×*ozanonii* Thell., Asch. & Graebn., Syn. Mitteleur. Fl. 5: 263. 1914 (*A. retroflexus* × *A. hybridus*).

The plants are usually green-gray. The inflorescence has many thick lateral branches, and the tepals of female flowers are like those of *Amaranthus retroflexus* (Appendix).

3. *Amaranthus hybridus* × *A. powellii* (the hybrid has not been formally named).

This hybrid is a new record for Canada. Plants are monoecious with the leaves resembling those of *Amaranthus powellii* in shape. The inflorescence has many ascendant branches. The bracteoles are thin, acicular, and 3–4.5 mm long (Appendix).

4. *Amaranthus hybridus* × *A. tuberculatus* var. *tuberculatus* (the hybrid has not been formally named).

The plants are monoecious. The inflorescence is very branched, and has many thin and patent branches. The female flowers have reduced tepals and long stigma branches, as in *Amaranthus tuberculatus* (Appendix).

5. *Amaranthus powellii* × *A. tuberculatus* var. *rudis* (the hybrid has not been formally named).

This hybrid is a new record for Canada. The plants are monoecious, they are somewhat intermediate between the parents, and they have a much more branched inflorescence than *Amaranthus powellii*, but the many, thin branches are rigid (as in the latter). The bracteoles are spinescent and 2.5–3.5 mm long. The female flowers have 1–3 tepals and long stigma branches (Appendix).

6. *Amaranthus ×budensis* Priszter, Index Horti Bot. Univ. Budapest. 7: 125. 1949 (*A. albus* × *A. blitoides*).

This hybrid is reported here for the first time in Canada. It is more or less intermediate between its parents. It differs from *Amaranthus albus* by its shorter bracts and larger fruits and seeds, and from *A. blitoides* by its ascendant or erect stems, the longer bracts, and the smaller fruits and seeds (Appendix).

The presence of *Amaranthus retroflexus* × *A. tuberculatus* is also possible in Canada. The hybridization between the species examined in the present account and the grain amaranths (*A. caudatus*, *A. cruentus*, and *A. hypochondriacus*) in Canada is feasible but improbable due to the infrequent cultivation of the grain species.

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APPENDIX

REPRESENTATIVE SPECIMENS EXAMINED.

1a. *Amaranthus tuberculatus* var. *tuberculatus*. Ontario: Essex Co., Pelee Twp., Middle Island, on the shore of Lake Erie, 27 Jul 1988, *M. J. Oldham et al. 8416* (DAO, MICH, TRTE); Haldimand Co., waste ground by Lake Erie, 21 Aug 1960, *H. J. Scoggan 14935* (MTMG); Hastings Co., Salmon River, 1 Oct 1865, *J. Macoun s.n.* (MTMG); Middlesex Co., Lobo Twp., 2 km S of Komoka, Komoka Swamp, 31 Aug 1993, *M. J. Oldham 15550* (QFA, MICH); Ottawa Co., Ottawa, 20 Aug 1892, *W. Scott s.n.* (DAO); Ottawa, Rockcliffe Park, on the shoreline of Ottawa River, 1 Sep 1951, *J. J. Basset & D. R. Lindsay 3061* (DAO). Québec: Cté. Jacques Cartier, Mount Royal, 11 Sep 1960, *G. & P. H. Du Boulay 1636* (HAM); Montréal, Pointe St-Charles, 24 Aug 1976, *J.-P. Bernard B 76-736* (DAO, QFA, MTMG); Cté. Missisquois, Stanbridge Station, 10 Sep 1959, *J.-P. Bernard 59-316* (DAO, QFA, QUE).

1b. *Amaranthus tuberculatus* var. *rudis*. British Columbia: Greater Vancouver Regional Distr., Burnaby, growing between rails of railroad tracks in ballast, 18 Oct 1992 and 3 Nov 1992, *F. Lomer 92-317* (UBC). Ontario: Lambton Co., Petrolia, 15 Sep 2002, *M. Costea & F. Tardif 8638–8643* (OAC).

2. *Amaranthus caudatus*. Saskatchewan: Regina Distr., Regina, 2352 Athol Street, 8 Sep 2001, *G. F. Ledingham 13980* (USAS). Ontario: Welland Co., Stamford, summer 1940, *W. R. Ellis 1844* (OAC). Québec: Cté. Laval, Laval University, cultivated, 5 Aug 1968, *R. Van den Hendle 068-265* (OAC); Cté. Portneuf, Deschambault, 16 Sep 1983, *R. Neron 83-3020* (QUE).

3. *Amaranthus cruentus*. Alberta: Edmonton Distr., Fort Saskatchewan, grown as ornamental, 2 Sep 1945, *G. H. Turner 4716* (ALTA). Ontario: Middlesex Co., London, Watson Street, "dump", 2 Sep 1950, *J. F. Calvert s.n.* (WAT); Waterloo, Beechwood estate, waste sandy ground, 20 Aug 1969, *J. K. Morton 3298* (WAT); Ottawa Co., Ottawa, 46°26′30″N 75°40′W, rubble and sand of basement ruins, 14 Oct 1991, *D. F. Brunton 11025* (TRT). Québec: Cté. de Vaudreuil, Ile Perrot, 26 Jul 1937, *Fr. Cléonique 9385* (MT); Montréal, cultivated, 29 Sep 1947, *J.-P. Bernard 44468* (MT).

4. *Amaranthus hybridus* subsp. *hybridus*. Ontario: Brant Co., S of New Scotland, 43°21′N 81°51′W, corn field, 29 Sep 1973, *A. Reznicek 2619* (TRTE); Elgin Co., 5 mi. NW of Dutton, weed of soybean with *A. powellii*, 29 Aug 1967, *R. A. Frost 36* (DAO, UWO); Essex Co., Pelee Island, 27 Sep 1988, *M. J. Oldham 8844, 8853* (DAO, TRTE); Leamington, 0.4 mi. Mersea Twp., field survey 725, tomato field, 23 Sep 1969, *J. F. Alex 4221* (DAO, OAC, TRT); Elgin Co., 2 mi. E of Westhome, weed of tobacco field, 29 Aug 1967, *R. A. Frost 36* (DAO, UWO); Lambton Co., Sarnia, 6 Sep 1960, *L. O. Gaiser 2884* (DAO); Kent Co., Ridgetown, 43°23′N 81°55′W, bean field, 18 Sep 1966, *R. A. Frost 23* (UWO); Dresden, Camden Twp., 43°35′N 82°11′W, 18 Sep 1977, *P. M. Catling s.n.* (TRTE).

5. *Amaranthus hypochondriacus*. British Columbia: Greater Vancouver Regional Distr., Burnaby, near Brenwood Mall, 8 Nov 1993, *F. Lomer 93-334* (UBC). Alberta: Edmonton Distr., Fort Saskatchewan, "flower garden," 4 Aug 1936, *G. H. Turner 337* (ALTA). Manitoba: Winnipeg, Aug 1921, *J. F. Higham s.n.* (WIN). Ontario: Elgin Co., St. Thomas, spreading after cultivation, 1 Sep 1958, *L. E. James 3281, 3163, 3164* (DAO, UWO); Hastings Co., 15 Aug 1875, *J. Macoun s.n.* (MTMG); Huron Co., Wingham, roadsides and gardens, Sep 1890, *J. A. Morton s.n.* (UWO); Middlesex Co., London, "fields", 8 Aug 1880, *T. J. W. Burgess & J. Macoun s.n.* (MTMG); Ottawa Co., Ottawa, School grounds, Aug 1891, *W. Scott s.n.* (DAO); Rideau River bank below White Bridge, 10 Aug 1954, *W. G. Dore & D. Erskine 15253* (DAO). Québec: Cté. Charlevoix, St-Joseph, "naturalisé depuis un an ou deux à la suite de cultures", 100 m, 22 Jul 1937, *B. Boivin 1612* (DAO); Cté. Hyacinthe, St. Damase, 3 Sep 1958, *L. Cinq-Mars & G. Samoisette 198* (QFA); Cté. Labelle, Nominingue, 1 Aug 1932, *E. Roy 2667* (MT); Cté. Laval, Bout-De-L'Ile, fossé de la route 2, 3 Sep 1937, *B. Boivin 1612* (MT).

6a. *Amaranthus powellii* subsp. *powellii*. British Columbia: Greater Vancouver Regional Distr., Vancouver, 49°16′N 123°15′W, 24 Sep 1978, *P. Bowen s.n.* (UBC); Okanagan Valley, 12 mi. NW of Penticton, fairly common in irrigated orchards, 5 Aug 1955, *G. A. Mulligan & W. Woodbury 1926* (DAO); 27 mi. of Osoyoos, fairly common in grain field, 11 Aug 1955, *G. A. Mulligan & W. Woodbury 1927* (DAO); Popcum Distr., N of Agassiz, sandy banks, 2 Sep 1912, *W. Taylor s.n.* (UBC). Saskatchewan: Regina Distr., Melford, 15 Sep 1946, *H. Groh 3182* (DAO). Ontario: Essex Co., 4 mi. SE of Leamington, weed in tomato, 30 Jul 1965, *J. F. Alex 765*

(DAO, OAC); Haldimand-Lambton Co., Forest, along James Street, 2 Oct 1963, *L. O. Gaiser 3373, 3374* (MTMG); Norfolk Co., Rock Point Provincial Park, 17 Sep 1988, *M. J. Oldham 8244* (DAO, TRTE); Middlesex Co., London, 0.5 mi. W of Hwy. 4, 24 Sep 1966, *R. A. Frost & P. B. Cavers 30* (UWO); Greater Toronto Region, Mississauga, 43°34′N 79°38′W, on clay, 22 Aug 1980, *J. M. Webber 3082* (DAO, TRTE); Ottawa Co., Ottawa, 300 m SE of Woodroffe High School, 45°22′N 75°46′W, 5 Oct 1984, *D. F. Bruno & C. Franckton 5373* (DAO). Québec: Cté. Missisquois, Clarenceville, 18 Aug 1976, *J.-P. Bernard 76-701* (DAO, QFA); Cté. Ste-Foy, Ste-Foy (Québec City), Laval University, 46°47′N 71°16′30″W, 12 Sep 1977, *J.-P. Bernard 77-772* (QFA). Nova Scotia: Kings Co., Wolville, 13 Sep 1968, *Taschereau 317* (NSPM); Lunenburg, Martin Brook Settlement, 21 Sep 1968, *Taschereau 332* (NSPM). Prince Edward Island: Queens Co., near Stanhope, on reddish sandy loam, 4 Aug 1950, *J. J. Basset s.n.* (DAO).

6b. *Amaranthus powellii* subsp. *bouchonii*. British Columbia: Greater Vancouver Regional Distr., Vancouver, Locarno Park, 21 Sep 1937, *J. W. Eastham s.n.* (UBC); Kootenays Valley, 2 mi. NW of Creston, 15 Aug 1955, *G. A. Mulligan & W. Woodbury 2051* (DAO). Ontario: Bruce Co., Walkerton, 2 Aug 1944, *H. Groh 2282* (DAO); Hulton Co., Burlington, clay disturbed area, 5 Aug 1984, *W. J. Crins 6549* (TRTE); Peel Co., Streetsville, 25 Aug 1957, *A. F. Coventry 57-155* (TRTE). Québec: Cté. L' Assomption, Ville-des-Laurentides, pommes de terre, 19 Aug 1984, *R. Néron 84-3006* (QUE); Cté. Bellechasse, St-Gervais, sur sable graveleux pierreux, 31 Aug 1984, *J.-G. Denis & L. Guay 84-443, 84-447* (QUE); Cté. Laval, Ile-Jésus, 15 Sep 1999, *R. Néron 99-250, 99-246* (QUE); Cté. Napierville, Sherrington, oignons, terre noire, 27 Aug 1981, *R. Néron 81-610-5* (QUE).

9. *Amaranthus albus*—specimens used for the SEM study. Alberta: Peace River Distr., Spirit River, 13 Sep 1939, *H. Groh 970* (DAO); Watino, 14 Sep 1939, *H. Groh 988* (DAO). Saskatchewan: Saskatoon, 15 Sep 1979, *J. H. Hudson 3859* (DAO); Asquith, Rice Lake, 23 Sep 1979, *J. H. Hudson 3868* (DAO). Manitoba: Marquette Distr., Rivers Twp., 21 Aug 1957, *I. J. Basset & J. W. Kemp 3674* (DAO). Ontario: Dundas Co., Winchester, Railroad Station, 1 Sep 1954, *W. Shumovich & G. McCann 1523* (OAC); Essex Co., 13 mi. SE of Leamington, 23 Sep 1969, *J. F. Alex 4197* (OAC); Lambton Co., Squirrel Island, 2 Oct 1957, *L. O. Gaiser & C. Gaiser s.n.* (OAC); Middlesex Co., Dorchester, tobacco field behind high school, 6 Aug 1973, *C. & B. Chamberlain 88* (OAC). Québec: Montréal, 2 Sep 1962, *G. & P. H. Du Boulay 2827* (DAO). Nova Scotia: Pictou Co., New Glasgow, 14 Sep 1951, *E. G. Anderson 1593* (DAO).

10. *Amaranthus californicus*—specimens used for the SEM study. Alberta: Herraton, 7 Aug 1933, *H. Groh s.n.* (DAO); Manyberries, 1928, *S. C. Clarke s.n.* (DAO). Saskatchewan: Cypress Distr. Cypress Hills, roadside, 20 Aug 1947, *A. J. Breitung 5695* (DAO); Grassland National Park, 10 mi. SE of Val Marie, disturbed area near Frenchman River, 6 Aug 1989, *E. R. Hooper & G. F. Ledingham 10851* (USAS); Moose Distr., 3 mi. W and 4 mi. S of Rockglen, with *Rorippa tenerrima*, prostrate on the trampled shore of stock-watering pond, 14 Sep 1984, *G. F. Ledingham 8919* (USAS); Regina Distr., 20 mi. N of Regina, dry depression in native prairie, top of south bank of Qu'Appelle Valley, 25 Jul 1988, *G. F. Ledingham 10397* (USAS); Saskatoon Distr., Dundurn, farm garden, 17 Aug 1974, *E. W. Sullivan s.n.* (USAS).

12a. *Amaranthus blitum* subsp. *blitum*. Ontario: Simcoe Co., Muck Research Station, Holland Marsh, 20 Sep 1970, *J. F. Alex 4428* (OAC). Québec: Montréal, sur le Mont-Royal, 4 Sep 1938, *Frère Cléonique 11423* (MT); Ile de Montréal, Jul 1890, *Soeur Amélie s.n.* (MT).

12b. *Amaranthus blitum* subsp. *emarginatus*. British Columbia: Coquitlam, waste sandy ground landfill, old Terra Nova dump site, 12 Aug 1993, *F. Lomer s.n.* (UBC); Greater Vancouver Region, Annacis Island, "many plants", 15 Aug 1990, *F. Lomer 90-113* (UBC). Québec: Cté. de Brome-Missisquoi, Quest, 45°04′N 73°06′W, 16 Sep 1989, *A. Sabourin & D. Paquette 363* (MT); Cté. de Chambly, Richelieu, 20 Aug 1988, *P. Guertin 3296* (QFA); Cté. de Missisquoi, Lac Selby, 15 Sep 1987, *P. Guertin 3015* (QFA); Cté. de Papineau, Montebello, 51 Rue Notre-Dame, 31 Aug 1972, *J. E. Charlebois s.n.* (QFA); Ile aux Bois Blanc, Sain-Laurent River, sect. alluviale à l'est de Montréal, 22 Aug 1966, *L. Deschamps 1374* (QFA); Francheville, Pointe-du-Lac, Saint-Laurent River, 46°17′N 72°42′W, dans le sable du rivage humide, 5 Oct 1999, *M. Blondeau 99028* (QFA); Saint-Lambert, oblique de la Voie Maritime du côté du fleuve, près des écluses, rivage graveleux, 29 Sep 2001, *S. G. Hay 01-055* (MT).

Hybrids. 1. *Amaranthus* ×*soproniensis*. Ontario: Elgin Co., 5 mi. N of Rodney, apparently sterile plant as weed of corn with *A. retroflexus* and *A. powellii*, 5 Sep 1967, *R. A. Frost 45* (DAO, UWO). Québec: Cté. Laval, Laval, Ile Jésus, *R. Neron 99-250a* (QUE); Cté. de Lac-St-Jean, Métabetchouan, Ferme Antoine Langevin, 26 route 168, champ de mais sucré, *R. Neron 83-2795*, 7 Sep 1983 (QUE).

2. *Amaranthus* ×*ozanonii* Thell. Ontario: Essex Co., N of Leamington, in vegetable gardens with *A. hybridus* and *A. retroflexus*, 26 Sep 2002, *M. Costea 8991* (OAC).

3. *Amaranthus hybridus* × *A. powellii*. Ontario: Essex Co., N of Leamington, in vegetable gardens with *A. hybridus* and *A. powellii*, 26 Sep 2002, *M. Costea 8998* (GH, OAC, QUE).

4. *Amaranthus hybridus* × *A. tuberculatus* var. *tuberculatus*. Ontario: Essex Co., Kingsville beach, ca. 0.5 km W of harbour, 29 Sep 1988, *M. J. Oldham 8882* (DAO).

5. *Amaranthus hybridus* × *A. tuberculatus* var. *rudis*. Ontario: Lambton Co., Petrolia, in soybeans infested with *A. powellii* and *A. rudis*; a few plants in the whole field, 13 Sep 2002, *M. Costea 8880* (GH, OAC, QUE).

6. *Amaranthus* ×*budensis*. British Columbia: Greater Vancouver Distr., Fraser Surrey Docks, Surrey, 17 Oct 1993, *F. Lomer s.n.* (UBC).

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NEW ENGLAND NOTE

SAGITTARIA TERES (ALISMATACEAE) IN NEW HAMPSHIRE

LIZ HARVEY

New Hampshire Natural Heritage Bureau,
P.O. Box 1856, Concord, NH 03302
lharvey@dred.state.nh.us

ARTHUR HAINES

441 Dead River Road,
Bowdoin, ME 04287
arthurhaines@gwi.net

Sagittaria teres S. Watson is a geographically restricted aquatic tracheophyte endemic to the northeastern coastal plain of the United States. It is apparently most closely related to *S. isoetiformis* J. G. Sm., a species of the southeastern coastal plain, with which it shares phyllodial leaves and CAM photosynthesis (Haynes and Hellquist 2001). Plants are typically found on acid, nutrient-poor pond shores, submerged along shallow bottoms or lower shores or emersed, usually later in the season as water volume declines.

The majority of world occurrences of *Sagittaria teres* are in New England (Sorrie 1994). Within this region, it primarily occurs on the coastal plain of Massachusetts and Rhode Island, with disjunct inland populations in the Connecticut River Valley of Massachusetts. *Sagittaria teres* is listed as Division 1 (i.e., globally rare taxa) in "*Flora Conservanda*: New England" (Brumback and Mehrhoff et al. 1996). It is also provided a global rank of G3 (i.e., less than 100 global occurrences; NatureServe 2002) and is thought to formerly have occurred from New Jersey north to Massachusetts (Haynes and Hellquist 2001). The discovery of a disjunct New Hampshire population expands the known range northward by approximately 75 km from the northernmost population in Massachusetts.

Sagittaria teres was first discovered in New Hampshire in 1991 by the first author while performing a floristic inventory of Lake Massabesic, Manchester, New Hampshire. At that time a flowering specimen was collected (*Harvey 434*, NHA). Shortly thereafter, the specimen was annotated to *S. subulata* (L.) Buchenau. In 2002, the *Sagittaria* collections at the Hodgdon Herbarium (NHA) were examined as part of the New

England Wild Flower Society's Herbarium Recovery Project, a program aimed at collecting information for New England rare tracheophytes through surveys of regional herbaria. The Lake Massabesic specimen was re-determined as *S. teres* on the basis of pubescent filaments, pedicellate carpellate flowers, and phyllodial leaves with nearly terete cross-section (then somewhat compressed in drying).

The importance of the collection prompted field surveys to re-locate the population. Visits were made on 16 August and 9 September 2002 to the stretch of shoreline along the western lobe of the lake where *Sagittaria teres* was first observed in 1991. The population was found to be extant and to extend over approximately 400 meters of shoreline. Although no flowering plants were found, vegetative plants were identified by white, prominently septate roots and thick, phyllodial leaves with elliptic to nearly terete cross-section. The first plants observed on 16 August 2002 were found detached, either floating or washed up on shore by the waves. Rooted rosettes were completely submerged in 10–100 cm of water.

By the 9 September visit, the lake water level had dropped nearly 20 cm since 16 August, and rooted plants were more visible. The northern half of the population, though largely submersed, consisted of a fair number of emersed individuals occurring on a relatively broad, mucky-silty-sand shelf. Associated plant species in this area included *Juncus militaris* Bigelow, *Eriocaulon aquaticum* (Hill) Druce, *Eleocharis robbinsii* Oakes, *Pontederia cordata* L., *Gratiola aurea* Pursh, *Nymphaea odorata* Aiton, *Sagittaria latifolia* Willd., and *Utricularia cornuta* Michx.

The southern half of the population was mostly submerged in 10–80 cm of water. The shoreline along this section consisted of a relatively narrow shelf of cobble and sand, bordered by a rocky edge and a shrub layer consisting primarily of *Vaccinium corymbosum* L. and *Clethra alnifolia* L. which abruptly transitioned into a mainly mixed pine upland forest. Associated plant species in this area included *Eriocaulon aquaticum*, *Lobelia dortmanna* L., *Juncus militaris*, *Sparganium angustifolium* Michx., and *Sagittaria graminea* Michx.

Lake Massabesic is a relatively shallow lake covering approximately 1008 ha that spans two townships (i.e., Manchester and Auburn) in southeastern New Hampshire. Measurements of pH taken in 2000 ranged from 6.4 to 6.7 (New Hampshire Department of Environmental Services 2001). The lake is impounded in order to supply municipal drinking water for seven towns: Auburn, Bedford, Derry, Goffstown, Hooksett, Londonderry, and Manchester. Of the 107 km^2 drainage area of Lake Massabesic, approximately 3226 ha is protected in some fashion (City of Manchester New Hampshire 2003).

Sagittaria teres appears, in the short term, to be secure on Lake Massabesic. However, plants remain largely vegetative, persisting as rosettes of phyllodial leaves under the artificially maintained lake level. This may pose a long-term threat to the population since only emersed plants appear to flower and reproduce sexually (Sorrie 1994). This may have ramifications for lasting genetic variability in this isolated population. Sorrie notes, however, that some populations of this species in deeper ponds rarely flower. Study of genetic variation between sites with different hydrologic regimes may be warranted to understand how *S. teres* copes with altered water levels.

The introduction of *Myriophyllum heterophyllum* Michx., an invasive aquatic plant species, into Lake Massabesic presents a potentially significant threat to aquatic flora of the lake. Though the current population does not immediately threaten the *Sagittaria teres*, elimination efforts have not thus far been effective and prove especially difficult due to the lake's use as a public water supply (New Hampshire Department of Environmental Services 2002).

We are unaware of any previous reports of *Sagittaria teres* in New Hampshire (Fernald 1950; Gleason and Cronquist 1991; Haynes and Hellquist 2001; Seymour 1982). The presence of *S. teres* at Lake Massabesic further emphasizes the recognized affinities of New Hampshire's coastal plain pond shore flora to the greater northeastern coastal plain (Sperduto 2000). While investigating these affinities, Sperduto also documented another disjunct coastal plain pond shore species previously unknown in New Hampshire with the discovery of *Scleria reticularis* Michx. in Litchfield (Sperduto 1996).

ACKNOWLEDGMENTS. The following persons assisted with this research and are thanked: Chris Mattrick, Dan Sperduto, Sherry Godlewski, Chris Kane, and Barre Hellquist.

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NOTE

THE ASIAN WEED *FATOUA VILLOSA* (MORACEAE) IN NEW YORK STATE AND MASSACHUSETTS

NORTON G. MILLER
Biological Survey, New York State Museum,
Albany, NY 12230-0001
e-mail: nmiller2@mail.nysed.gov

CARROLL E. WOOD, JR.
Arnold Arboretum of Harvard University,
22 Divinity Avenue,
Cambridge, MA 02138

About 50 years have lapsed since mulberry weed, *Fatoua villosa* (Thunb.) Nakai (Moraceae; Figures 1–9), a native of eastern Asia, was first recognized as an adventive plant in North America. Thieret (1964) reported its discovery in Lafayette, Louisiana, in the early 1960s, and mentioned that plants had also been seen in New Orleans during the previous 15 years. Numerous papers and notes published since 1964 recorded its presence as a weed in all of the southeastern United States (Massey 1975; Vincent 1993, and references cited therein). As summarized by Wunderlin (1997), *F. villosa* is known in an area from Florida west to eastern Texas and north to Oklahoma, Arkansas, Tennessee, Kentucky, southern Ohio, and Virginia. However, it has continued to spread and establish rapidly, and stations north of this area have recently been reported from Missouri (Yatskievych and Raveill 2001) and Michigan (Reznicek 2001). To these, we now add localities in upstate New York and eastern Massachusetts.

SPECIMEN CITATION: U.S.A. New York State: Rensselaer Co., Town of Brunswick, backyard of home on Pennyroyal Lane, 6 mi. east of Troy city center, 42°43′20.4″N, 73°32′58.9″W (GPS-NAD27), 207 m alt.; gravel beneath low deck attached to house, with *Pilea pumila*, *Veronica serpyllifolia*, *Glechoma hederacea*, *Taraxacum* sp., *Oxalis* sp., *Plantago* sp., 3 Sep 2002, *N. G. Miller 14261* (NYS); 21 Oct 2002, *N. G. Miller 14415* (BKL, BH, GH, NY, NYS).

The origin of the New York population is unknown. When first observed, it consisted of about 50 plants growing in an area of 1.5 × 3 m. Six weeks later near the end of October another 10 plants had appeared.

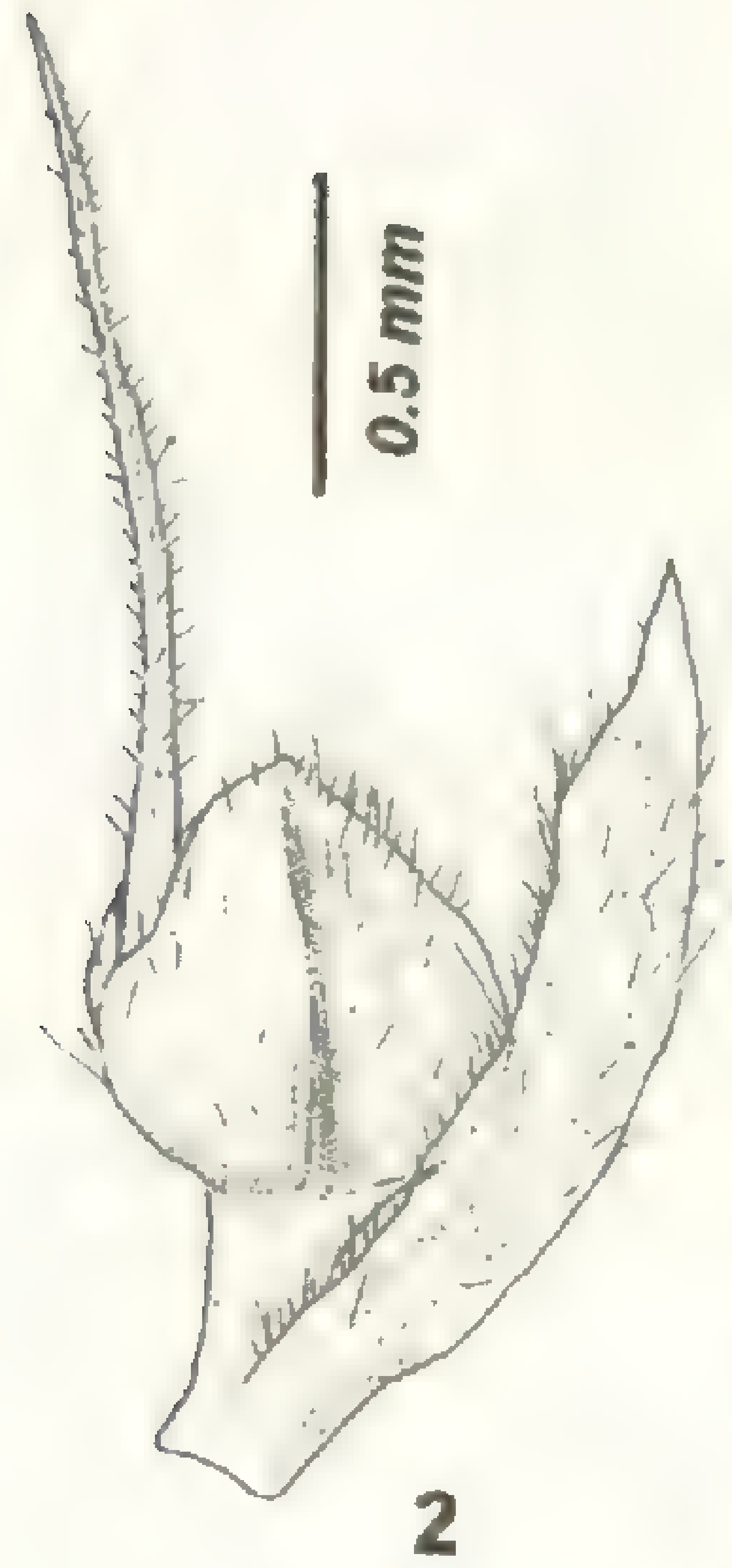
The large size of the population suggests establishment prior to 2002. The deck under which the plants grew is sometimes used as a potting bench, and "seeds" may have been spread from soil associated with nursery stock purchased for outdoor or indoor gardening. It was surprising, however, that *Fatoua* grew nowhere else on the property or indoors with houseplants. Thus the method of introduction of this population remains a mystery.

SPECIMEN CITATION: U.S.A. Massachusetts: Suffolk Co., Boston, South End neighborhood, backyard of home, 64 West Rutland Square, 42°20′30″N, 71°4′42″W (United States Geological Survey, 1:25,000 South Boston Quadrangle), plants from seedlings appearing at base of potted plant of *Crassula argentea* brought from Martha's Vineyard, Dukes Co., Massachusetts, and placed out-of-doors on patio in summer of 1993, exserted stigmas violet, 18 Oct 1994, *C. E. Wood, Jr.* (NEBC).

The source of the Boston plants is perhaps somewhat clearer. The minute endocarps of *Fatoua* definitely arrived at this Boston locality in the 8-inch pot of a jadeplant where they germinated after the plant was set outside in sunlight and kept well watered in the summer of 1993. Whether *Fatoua* came with the *Crassula* in its original soil from wherever it was propagated, or from potting soil added later, or from plants of *Fatoua* already present on Martha's Vineyard is not known. Insofar as could be determined, the *Crassula* had been grown indoors for several years but had been set outside in summer. It is conceivable that if *Fatoua* came to Martha's Vineyard with the *Crassula*, mulberry weed may now be naturalized there.

In 1994, seedlings of *Fatoua* appeared in pots of *Hippeastrum* that had been outside near the *Crassula* on the backyard patio in 1993. Subsequently, seedlings have germinated in pots of houseplants placed out in summer and also between the bricks of the patio, along with seedlings of *Viola, Astilbe, Hosta, Polygonum, Plantago, Senecio vulgaris*, and *Taraxacum* from the surrounding garden and elsewhere. *Fatoua* has not spread to the garden but continues to appear in potted plants. Seedlings appearing in the patio are being removed to prevent further possible spread of this weed that has invaded so widely in the southern United States.

In general habit, *Fatoua villosa* (Figure 1) resembles plants of *Urtica*, or it may be mistaken for young plants of mulberry (*Morus* spp.). The alternate leaves (vs. opposite in *Urtica*) bear scattered, stiff, slender, tapering, hollow, translucent trichomes that arise from the epidermis. Distal portions of the trichome chamber are occluded with a semiopaque substance. Trichomes of this type are most abundant on the upper (Figure 9) and lower leaf surfaces and are similar in general



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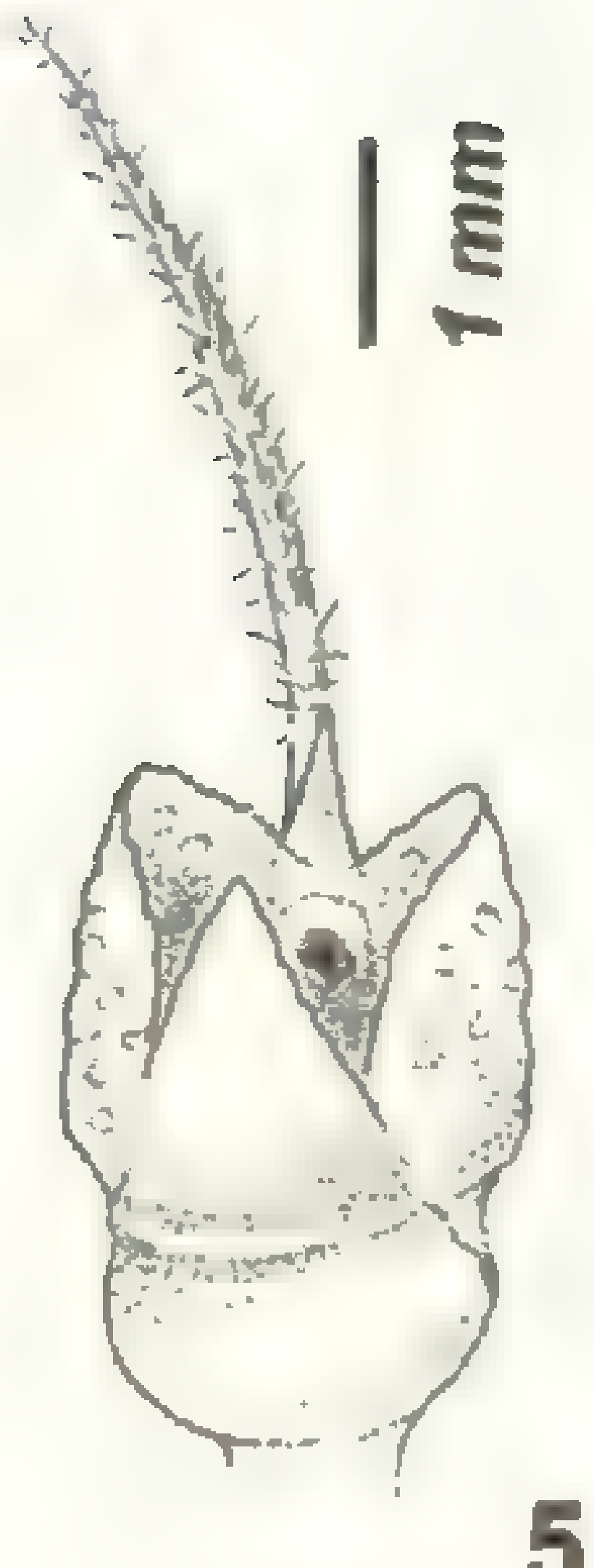

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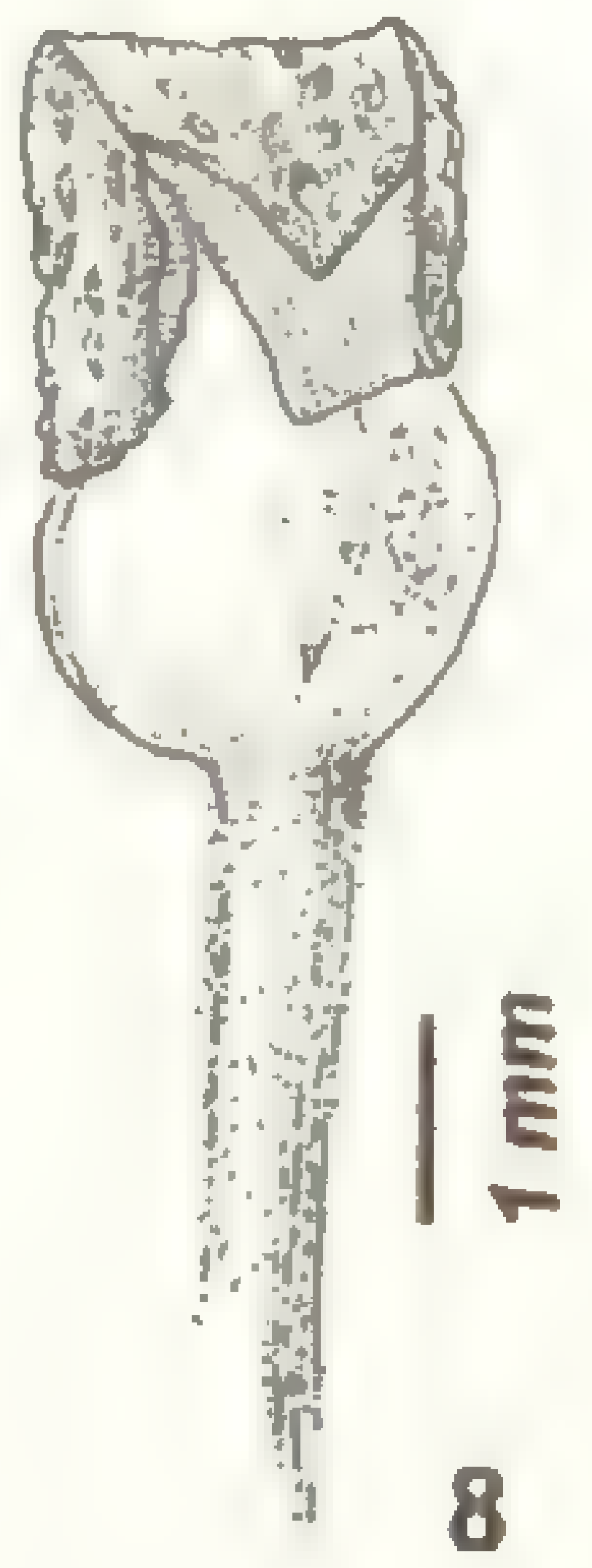

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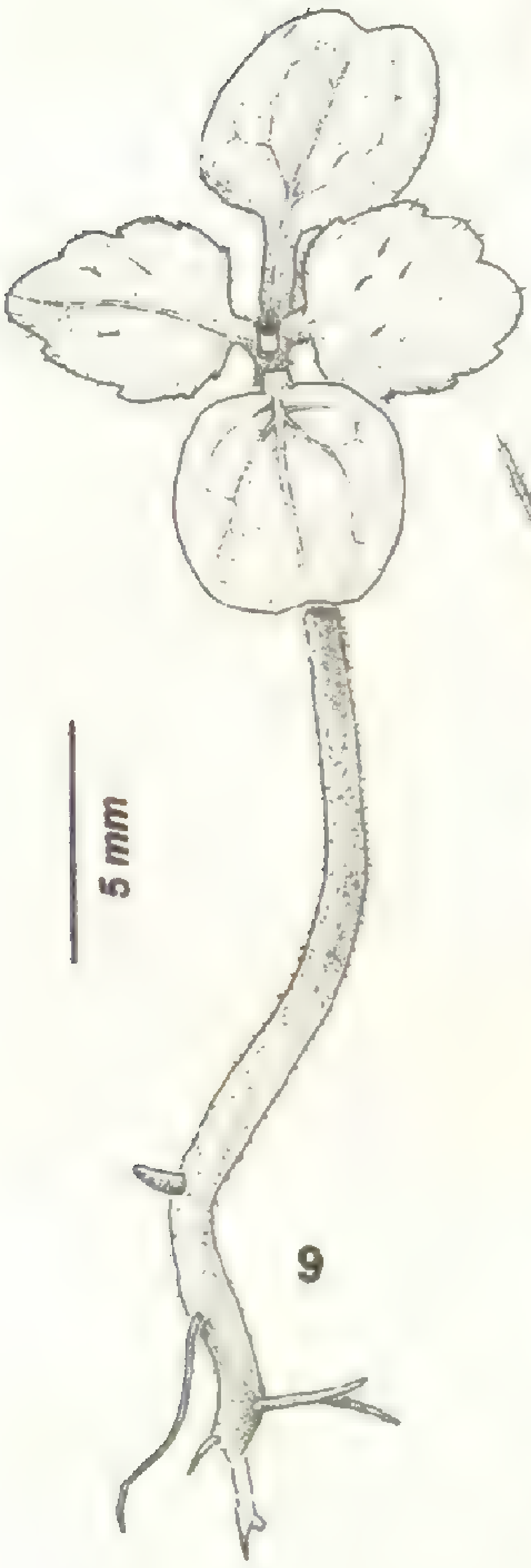

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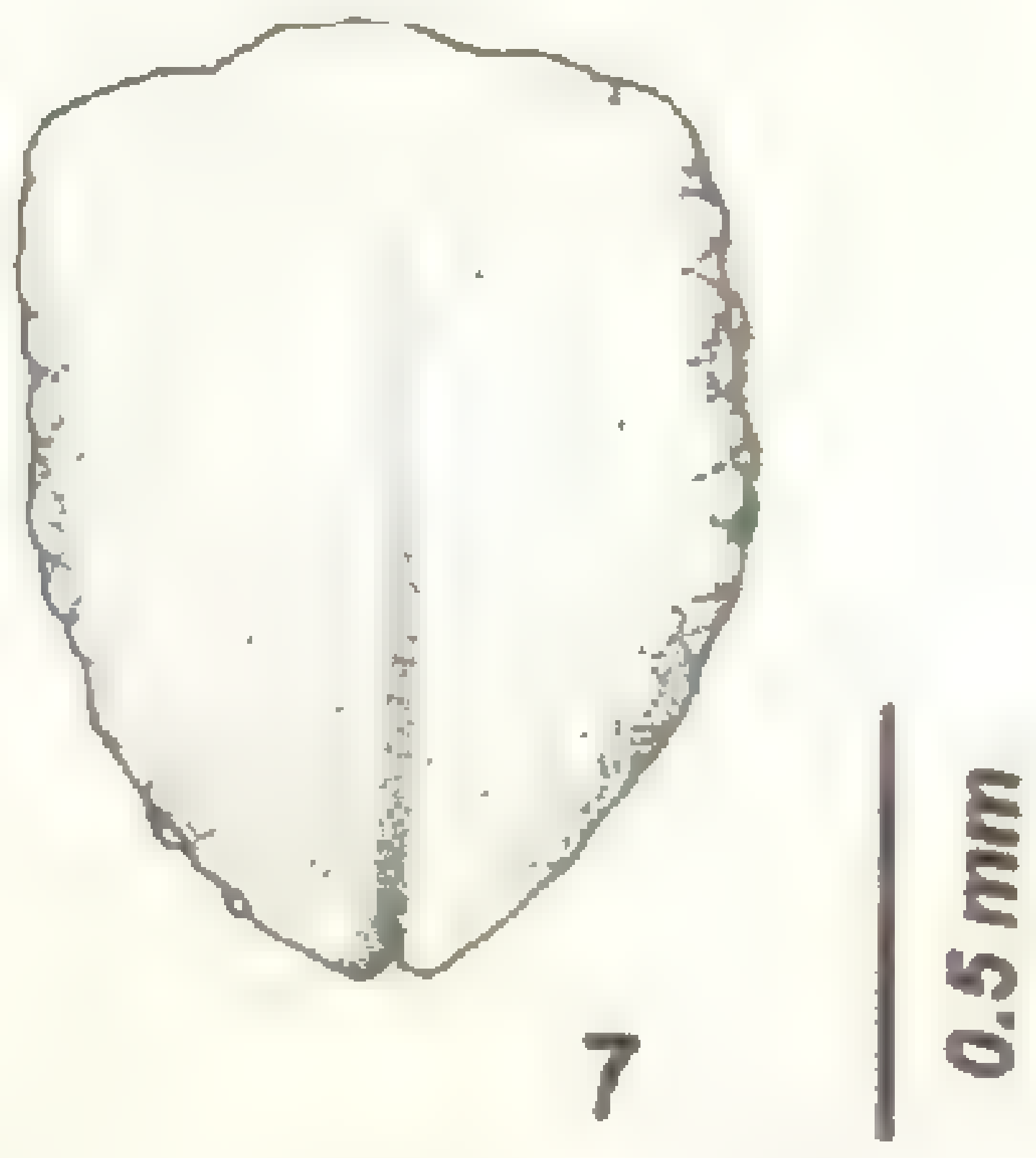

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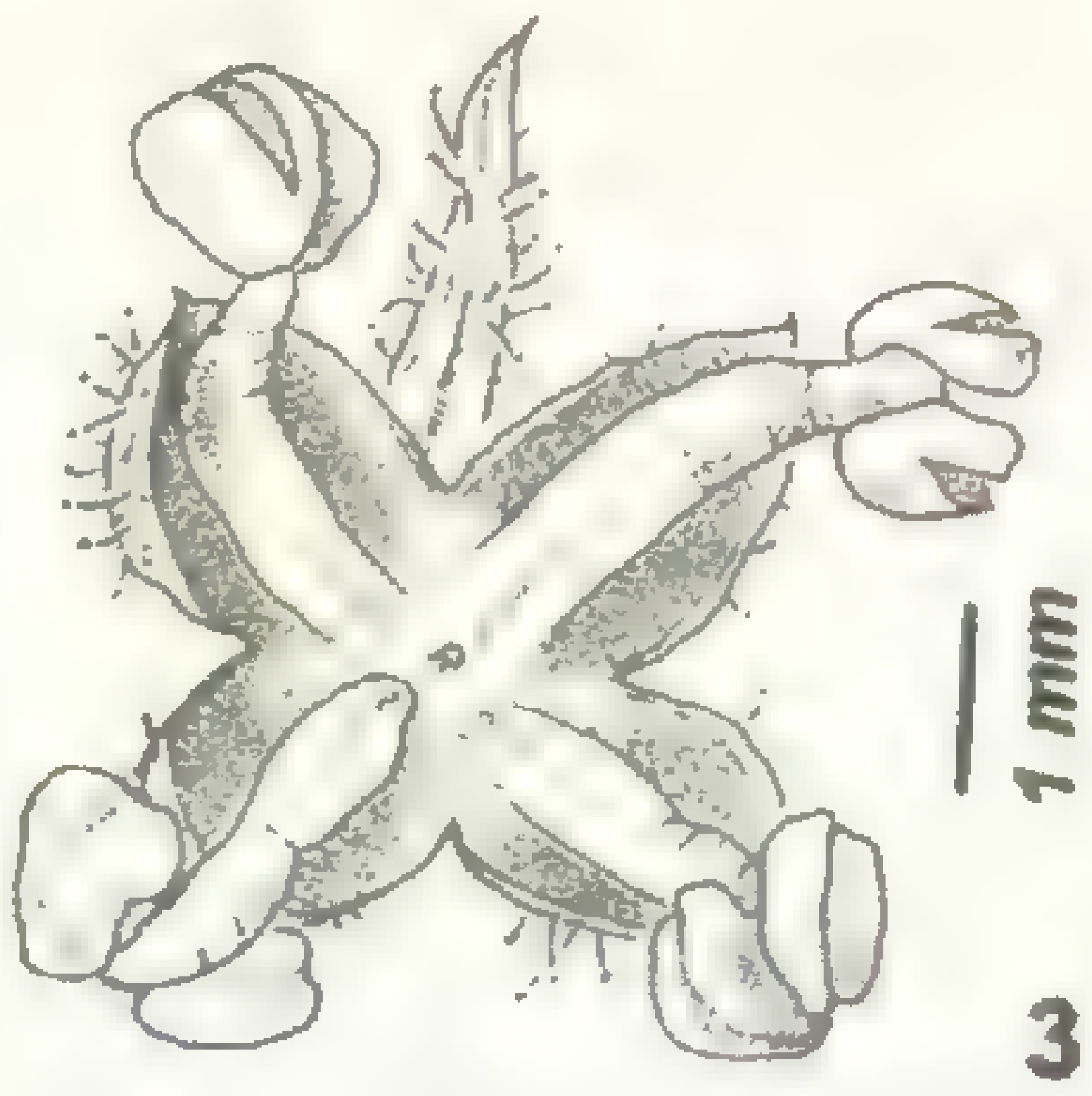

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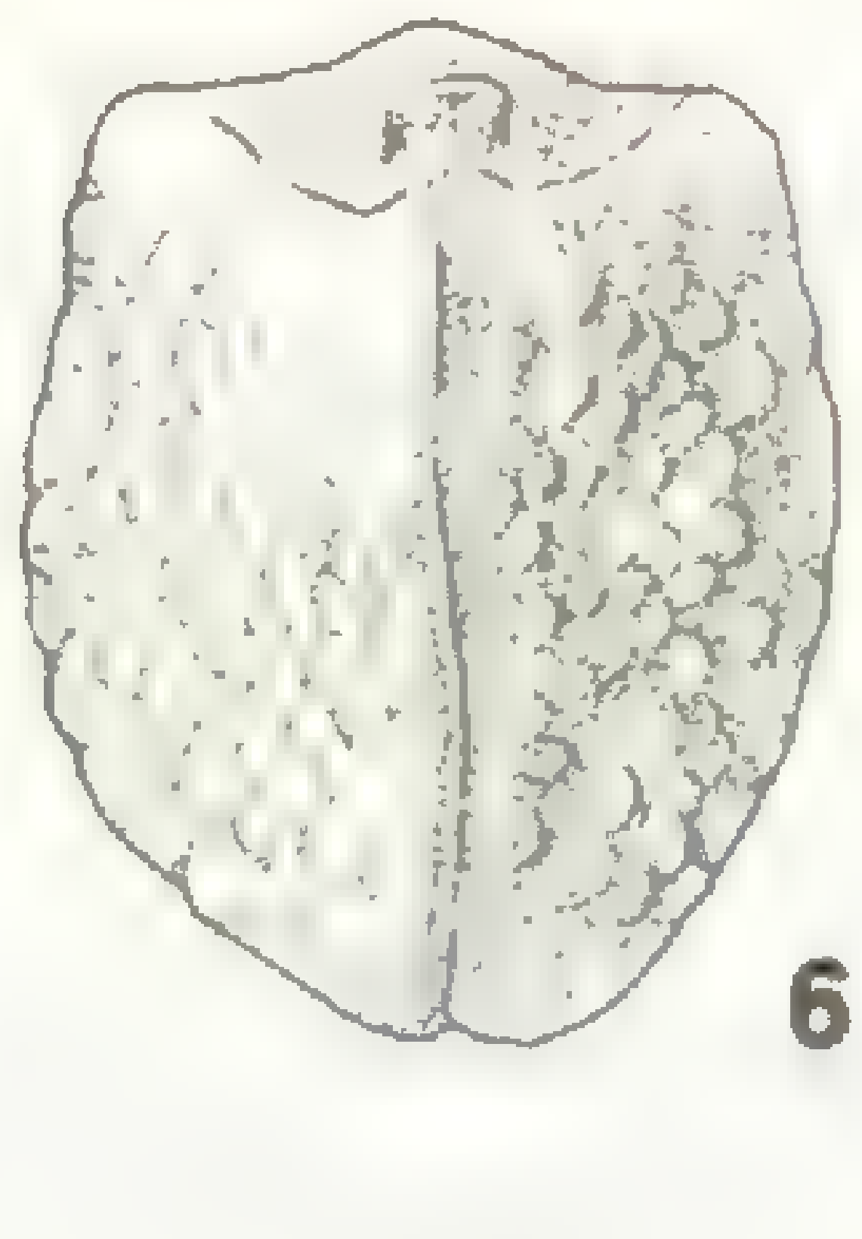

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appearance to the urticating hairs of stinging nettles (*Urtica* spp.). Although in *Fatoua* hairs of this type do not sting, they misleadingly suggest an urticaceous relationship. Careful dissection of the minute carpellate flower will show that the stigma consists of two arms, one short and inconspicuous, the other long and extending beyond a four-part perianth (Figures 2, 4). Members of the Urticaceae, in contrast, have one stigma. Stems of *F. villosa* have one to three-celled hooked hairs, and small glandular trichomes occur on flower and inflorescence parts (Figures 2, 3).

Several other points of biological interest are presented here to supplement the incomplete description of this plant in floras and other sources. The inflorescences are congested axillary cymes in which bracteate staminate (Figure 3) and carpellate (Figure 2) flowers occur intermingled. Staminate flowers appear to discharge pollen explosively, although we have not seen this in action. Liquid-preserved flowers at pre- and post-anthesis show that filament orientation changes from inwardly arched to reflexed in opened flowers. This configuration and the presence of transverse creases on adaxial surfaces of filaments (Figure 3) is paralleled in flowers of various Urticaceae in which explosive pollen discharge is well known (Mosebach 1932; see also illustrations in Miller 1971).

Fruit development is poorly understood in this plant. Fertile carpellate flowers produce one seedlike reproductive unit inside an ovary that develops unequally. The base of the ovary wall at maturity is a fleshy, saddle-shaped gynobase in which the endocarp rests (Figure 4). Above and lateral to the gynobase, the ovary wall is thin and translucent and remains closely appressed to the endocarp until the lateral walls separate along an apical suture to release the endocarp (Figure 5), which contains

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Figures 1–9. *Fatoua villosa*. 1. Habit of plant in flower, note axillary congested cymules. 2. Carpellate flower near or at anthesis, two of four valvate tepals shown. 3. Staminate flower immediately after anthesis, constrictions in filaments suggest that pollen is explosively dispersed. 4. Immature ovary, showing fleshy gynobase and thin apical ovary wall appressed to developing tuberculate endocarp, note short stigma arm. 5. Ovary immediately after release of endocarp, gynobase saddle-shaped, thin dehiscent ovary walls lateral, perianth not shown. 6. Endocarp, abaxial view, "seed" scar at top, note tuberculate walls. 7. Same endocarp, adaxial view. 8. Seedling at germination, cotyledons emerging from endocarp and seed coat. 9. Young seedling. (Illustrations by Patricia Kernan, New York State Museum: 1–7 from living or liquid-preserved material vouchered by *Miller 14415*; 8 & 9 from plants collected by C. E. Wood, Jr., in Boston, Massachusetts.)

a single seed. Sanders (1996) indicated that endocarp release is explosive. We have not confirmed this, but note that in liquid-preserved material the shape and size of the gynobase does not change after the endocarp is lost. If forceful release does occur, evidence of the mechanism should be apparent in the gynobase. The seed coat is thin (Yamazaki 1982) and can be seen beneath the wall of the endocarp during cotyledon emergence (Figure 8). We consider the seedlike disseminules of *Fatuoa* (Figures 6, 7) to be single-seeded endocarps.

Fatoua villosa has spread rapidly northward in the eastern United States mainly in association with the transportation of nursery stock from southern sources. While widespread throughout the eastern United States, *Fatoua* appears at present to be of local occurrence. The invasive potential of the species, however, remains uncertain (Yatskievych and Raveill 2001), at least in the North. Because frost kills plants of *Fatoua*, persistence out-of-doors in the northern United States depends on the rapid buildup of seed banks. Our observations in New York and Massachusetts indicate that populations can persist for some years, overwintering as dispersed seedlike endocarps. *Fatoua villosa* is a short-day annual that fruits in abundance beginning late in the summer and continuing until the first killing frost. Young plants as short as 8 cm can be found with inflorescences early in the autumn.

The species is an acknowledged pest in commercial greenhouses and nurseries in the southeastern United States (Wright 1988), where plants established in gardens are also frequently reported. Its weedy tendencies in outdoor plantings are apparent. However, with the exception of discoveries of plants growing in a mesic forest in Missouri (Yatskievych and Raveill 2001) and a construction site (Wright 1988), the species does not yet appear to have spread widely from plantings or gardens. It will be worthwhile to continue tracking the spread of *Fatoua villosa* in the southeastern United States in places where the climate is favorable to its growth, and to establish whether northern populations can persist outdoors.

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BOOK REVIEW

Vascular Flora of Illinois by Robert H. Mohlenbrock. 2002. x + 490 pp. ISBN 0-8093-2421-0 $50.00 (paperback). Southern Illinois University Press, Carbondale, IL.

When I moved to Illinois nearly seven years ago, I began to develop and teach a Plant Taxonomy course. Students were expected to collect, identify, and label 75 vascular plant specimens. We had two references available for Illinois: *The Flora of Illinois* (Jones 1963) and *Guide to the Flora of Illinois* (Mohlenbrock 1986). Both were traditional-style floras, with keys to families, genera, and species, and succinct information on phenology, habitat, and distribution within Illinois. My students generally found the format of Jones easier to work with, especially because of the indented keys.

It is gratifying to see Mohlenbrock's flora back in print, in a updated and improved format. The layout of the descriptive flora is alphabetical within higher taxonomic groupings: pteridophytes followed by gymnosperms and angiosperms (dicots preceding monocots). There is no indication of the sequence either in the table of contents or with headings in the text, but the reader will quickly catch on. It is peculiar, though, to see Selaginellaceae, Thelypteridaceae, Pinaceae, and Cupressaceae on facing pages without any indication that one is looking at representatives of different taxonomic divisions (*sensu* Cronquist).

Mohlenbrock does not appear to follow any one standard for overall taxonomic concept. The spore-bearing plants are in line with *Flora of North America, Volume* 2 (Flora of North America Editorial Committee 1993), but the rest of the text is a sort of "à la carte" approach. The Asteraceae shows a puzzling proliferation of genera. Mohlenbrock provides a note at the beginning of *Eupatorium* (*sensu stricto*) advising the user to check the segregate genera as well. Such helpful notes are scattered throughout the text. *Aster* is treated in a traditional sense, following Gleason and Cronquist (1991) and others, to include such segregates as *Doellingeria*, *Eurybia*, *Ionactis*, *Oclemena*, *Sericocarpus*, and *Symphyotrichum*. With *Eupatorium*, however, the segregates *Ageratina*, *Conoclinium*, and *Eupatoriadelphus* are recognized, an approach that follows neither Gleason and Cronquist nor the U.S.D.A. Plants Database (U.S.D.A., NRCS 2002). Not to neglect the monocots, *Scirpus* is divided into *Schoenoplectus*, *Bolboschoenus*, *Trichophorum*, and *Scirpus (sensu stricto)*, following *Flora of North America, Volume* 23 (which appeared at about the same time as this book; Flora of

North America Editorial Committee 2002). However, Mohlenbrock seemingly missed a new genus in the Araceae, *Landoltia*, represented by *L. punctata* (*Spirodela punctata*) in Illinois (Flora of North America Editorial Committee 2000).

This is not a definitive accounting of the state's flora, as Jones and Fuller (1955) was. However, Mohlenbrock has done a good job of including new records for the state. I noted that all the new records from Tucker (2000) were included. However, significant distribution records within the state are not, in my opinion, well covered. Species distributions seem little different from Mohlenbrock and Ladd (1978); since then, literally hundreds of county records and significant range extensions have been found by botanists in all parts of the state. For example, *Pueraria lobata*, kudzu, is noted to be sometimes escaping in the southern counties. In fact, it has been found as far north as Rock Island County and is now the object of control efforts by the Illinois Department of Natural Resources. *Acalypha deamii* is recorded from four counties by Mohlenbrock and Ladd; the herbarium at Eastern Illinois University (EIU) alone has specimens from ten counties. Other examples could be cited. In the preface, Mohlenbrock states that he has spent time in herbaria to verify species reports, but he was evidently not able to give much time to distribution records within the state.

A feature of the book continued from earlier editions is The Natural Divisions of Illinois, by Mohlenbrock student John Schwegman. This summary of the state's 14 natural regions and their geological and biological features occupies pages 1–35 and provides a summary of the state's biodiversity. Scientific names in this section, unfortunately, were not updated to match those used in the descriptive flora. An astonishing omission seems to be a references section. Many botanists have contributed to our knowledge of the flora of Illinois, for example the late Floyd Swink and Gerould Wilhelm, icons of northern Illinois botany (Swink and Wilhelm 1994). Several new combinations are made at various points in the text, but these are not valid because they lack references to the places of publication of their basionyms. I hope the author will take care of this oversight promptly so the names can be used.

In closing, we in Illinois are fortunate to have an updated identification guide for our state's flora. Any taxonomist can find something to quibble over in another taxonomist's work. Bottom line: the indented format of the keys is appreciated, the alphabetic arrangement is handy, and any field-oriented botanist will want a copy and will get a great deal of use out of it. Get a brick or a cookbook holder to keep it open. The paperback binding will not lie flat and it's impractical to hold it open and dissect grass spikelets (or capitula of Asteraceae, if you prefer) at the same time!

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—GORDON C. TUCKER, Stover-Ebinger Herbarium, Department of Biological Sciences, Eastern Illinois University, Charleston IL 61920. [e-mail: cfgct@eiu.edu]

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NEW BOOKS

Anatomy of the Monocotyledons, Volume IX. Acoraceae and Araceae by R. C. Keating, edited by M. Gregory and D. F. Cutler. 2002. xi + 327 pp. black & white photos. ISBN 0-19-854535-5 $231.50 (hardcover). Clarendon/Oxford University Press, Oxford. [www.oup.com]

Cape Cod Wildflowers: A Vanishing Heritage by M. J. DiGregorio and J. Wallner. 2003. xiv + 169 pp. map, color photos. ISBN 1-58465-319-1 $19.95 (softcover). University Press of New England, Lebanon, NH. [www.upne.com]

Flora of North America, Volume 25: Magnoliophyta: Commelinidae (in part): Poaceae, part 2 by Flora of North America Editorial Committee, eds. (volume editors M. E. Barkworth, K. M. Capels, S. Long, and M. B. Piep). 2003. xxv + 783 pp. line drawings, distribution maps. ISBN 0-19-516748-1 $120.00 (hardcover). Oxford University Press, New York and Oxford. [www.oup.com]

The Herbaceous Layer in Forests of Eastern North America by F. S. Gilliam and M. R. Roberts, eds. 2003. xvi + 408 pp. illus. ISBN 0-19-514088-5. $85.00 (hardcover). Oxford University Press, New York. [www.oup-usa.org]

The Role of Chromosomal Change in Plant Evolution by D. A. Levin. 2002. 240 pp. black & white photos, line drawings. ISBN 0-19-513859-7 $75.00 (hardcover), 0-19513860-0 $35.00 (softcover). Oxford University Press, Oxford. [www.oup.com]

Weeds in My Garden: Observations on Some Misunderstood Plants by C. B. Heiser. 2003. 260 pp. color photos, line drawings. ISBN 0-88192-562-4 $22.95 (hardcover). Timber Press, Portland, OR. [www.timberpress.com]

The Wild Orchids of North America, North of Mexico by P. M. Brown. 2003. x + 236 pp. line drawings, color photos. ISBN 0-8130-2572-9 $27.95 (softcover). University Press of Florida, Gainesville, FL. [www.upf.com]

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NEBC MEETING NEWS

April 2003. Vice President Art Gilman introduced the evening's speaker, Dr. Jianhua Li from the Arnold Arboretum of Harvard University. Jianhua's talk was entitled "Botanic Expeditions in Guizhou, China—In Search of Natural Populations of Ginkgo." *Ginkgo biloba* is the only member of Ginkgoales, one of the five major lineages of seed plants (the others are Coniferales, Angiospermae, Gnetales, and Cycadales). It is considered by many to be found only in cultivation. The species is dioecious, and in China male plants produce pollen cones in April, while female plants produce ovules later in the season.

In the U.S., *Ginkgo biloba* is commonly used in herbal medicine, and the males are often planted as street trees (the seed-bearing females are considered unattractive as ornamentals). In China, where the species is widely distributed, it is the females that are planted most often, for their edible seeds are an important source of food. Jianhua remarked that the seeds, which need to be processed carefully before being eaten due to the presence of toxins, have the consistency of a "chewy peanut."

With Dr. Peter Del Tredici from the Arnold Arboretum, Jianhua traveled to southwestern China and met up with researchers from Zhejiang University and Guizhou University, including members of the Chinese Ginkgo Society. Together the team members visited several sites where *Ginkgo biloba* was known to grow, measured the diameter and height of the trees, and collected DNA samples for a genetic analysis that will help determine whether there is heterogeneity among Chinese ginkgo populations.

The team visited ancient *Ginkgo biloba* trees in the province of Zhejiang, from a thousand-year-old tree perched next to a temple on the summit of Mt. Wuyun, to a 30 m tall male tree in Fuyang County observed to have a few branches bearing female cones. In Fuquan, Guizhou, they visited a ginkgo tree marked by a sign claiming it was in the *Guinness Book of World Records*, a remarkable 35 m tall specimen with a diameter of 4.5 m. The tree had four main branches, most likely the result of sucker production. Jianhua reported that the tree had a hollow spot in the center that was so large that a farmer once lived there with his cow and pig.

The best candidates for natural *Ginkgo biloba* populations were groups of 20 or more trees observed in Wuchuan County, Guizhou, near valleys and mountain slopes where rice, corn, and other crops are cultivated. In these seemingly relic, natural plant communities, there were many big ginkgo trees growing together with other Tertiary relics such as *Liquidambar formosana*, *Cupressus funebris*, and *Taxus chinensis*. These ginkgo populations had regenerative structures with seedlings and young individuals, and there were both males and females present. The sites where the ginkgo populations were found were mostly rocky slopes with little topsoil. To survive in these habitats, the trees anchored themselves with lignotubers that could grasp rocks and grow down into the soil layer.

The team also visited a "Ginkgo Village," located in Letuo, Panxian County. The sale of ginkgo seeds as a food source was a large part of the village's economy, and each tree there was individually owned. Though there were 1500 ginkgo trees in the village, there was only one male tree. To produce seeds on the females, pollen was collected from the male, mixed with water, and sprayed on the female trees. The ginkgo trees in Letuo village were large and quite tall, but had many low-growing branches, indicative of cultivated plants.

Jianhua concluded his talk by answering questions from club members about how to prepare ginkgo nuts for consumption and about the other uses of the plant in China, which include ginkgo-leaf tea and ornamental planting. He also spoke briefly about future projects, including his molecular analysis of ginkgo populations in China.

May 2003. The May meeting was held at the New England Wild Flower Society's Garden in the Woods in Framingham, Massachusetts. Karen Searcy introduced the evening's speaker, Dr. Peter Alpert from the University of Massachusetts—Amherst. Peter, who was inspired very early in his life to study plants, spoke about "Clonal Plants and Invasive Species: Combining Curiosity-driven and Problem-directed Research." Peter has done several investigative studies of clonal plant reproduction, using the aquatic herb *Eichhornia crassipes* (water hyacinth). *Eichhornia crassipes* is a South American species that was first introduced to North America in the late nineteenth century and is now invasive in many parts of the world. While known for its pale purple inflorescences, the species can also quickly and easily produce new clones via horizontal stems known as stolons. Peter noted that the advantages of clonal reproduction include the opportunity to control placement of offspring, the ability to share resources via nutrient transport, and the ability to signal attached clones to instigate plastic responses to environmental conditions. To test whether *E. crassipes* uses any of these mechanisms to succeed, Peter set up experiments exposing populations to combinations of sun and shade. When parent plants were shaded but their clonal offspring were in the light, new stolons from the parent plant grew longer before touching the water and growing into new offspring. Speculating that awareness of the wavelengths of light and whether or not a plant is producing the shade could help *E. crassipes* avoid self-competition, Peter noted that plants in the center of a mat of clones tended not to produce stolons and to grow taller than their neighbors.

Peter also works with *Fragaria chiloensis* (beach strawberry), one of the wild progenitors of cultivated strawberries. *Fragaria chiloensis* also reproduces by stolons, producing a new plant at every other node. Using populations at Año Nuevo State Reserve in California, Peter demonstrated the transport of carbon and nitrogen between attached plants using radioactive and heavy isotopes of those key nutrients. Tests also showed that if a plant was not watered but remained attached to a watered plant, it grew as well as if it had been watered itself. To test what could be controlling the transfer of nutrients between clonal individuals of *F. chiloensis*, Peter looked closely at hormonal signals. Following the application of auxin, only the plants that started out with low concentrations of nitrogen or carbon increased the import of those nutrients. Also, data are currently being analyzed to see if there is a division of labor among attached plants within clones to make populations as a whole more efficient.

As a further investigation of the signals that occur between clonal plants, Peter looked at plant response to herbivore attack. The two-spotted spider mite (*Tetranychus urticae*) commonly infests commercial strawberry plants. The mites were first released on one *Fragaria chiloensis* plant, then later released on an attached clonal plant. While the initial clones showed much herbivore damage following the release of the mites, the clones that were attacked later were somehow "warned," making them better able to defend themselves against the mites, and to keep down the number of mites per plant. Finally, Peter demonstrated that attached *F. chiloensis* plants are better able to avoid competition from each other than separated clones. Two clonal plants were grown in the same pot, and were dyed either red or green to distinguish the two. Attached plants had clear root segregation between clones, while unattached clones did not. Another experiment that further prevented competition between root systems suggested that root segregation enables clones to reduce root competition and increase clonal performance.

—JENNIFER FORMAN, Recording Secretary.

June 2003. The June "away" meeting was held at Split Rock Camp in Ashburnham, Massachusetts. The Friday evening speaker was Dr. Matthew G. Hickler of the University of Massachusetts—Amherst. Matt spoke on the topic "Vegetation Patterns and Species Diversity: Floodplain Ponds of the Nashua River."

The floodplain of the Nashua River at Fort Devens, Worcester County, Massachusetts has numerous ponds that were formed when meanders were cut off and became isolated. Matt, assisted by the "hippo-squad," studied fifteen of the floodplain ponds ranging in size from 0.25 to 2.5 hectares. This is a dynamic ecosystem. Spring floods can scour ponds or deposit sediment providing new habitat and altering old habitats. Although not dated, individual ponds last decades to a few hundred years. Hickler suspected that equilibrium models such as hydrarch succession would not be useful in understanding this ecosystem.

As a first step in understanding vegetation patterns and species diversity, the vegetation of each pond was sampled and species lists compiled. The ponds showed a marked zonation. Ponds typically had a central zone of open water characterized by *Spirodela polyrrhiza*, *Lemna minor*, *Wolffia brasiliensis*, and either *Ceratophyllum echinatum* or *C. demersum*, but not both. Additional common species included *Potamogeton natans* and *Nuphar variegata*. A deep marsh zone frequently followed the open water zone in the floodplain ponds. Common species in this zone included *Pontederia cordata* and *Sparganium americanum*. *Sparganium natans*, an endangered species in Massachusetts, was found on one pond in this zone. In 10 of the 15 ponds there was a zone of *Cephalanthus occidentalis* that formed a dense band along the shore. *Bidens discoidea*, a Massachusetts watchlist species, was observed as an epiphyte on the stems of this plant. Finally, 7 of the 15 ponds included a wet meadow. This zone was periodically flooded and was the most diverse, with a point diversity as high as 25–30 species/m^2. Species composition was highly variable but typically included an assortment of grasses and sedges mixed with a variety of herbaceous species including many annuals. *Scirpus cyperinus*, *S. tabernaemontani*, *Carex lacustris*, and *Typha latifolia* also contributed to diversity of this zone in some ponds.

Hickler found the floodplain ponds to be unexpectedly diverse relative to the surrounding area. Approximately 20% of the flora of former Fort Devens was found in the floodplain ponds even though they made up a fraction of 1% of the total fort area. One component of floodplain pond diversity was the difference in species composition between ponds, or beta-diversity. Of the 151 species recorded, 65 were found in only one or two ponds while only 2 species were found in all ponds. Using Jaccard's coefficient of similarity, basically the percent of shared species, there was about a 34% similarity between any two ponds; thus the floras of the ponds tended to be unique. However, the diversity pattern was more complex since diversity was not evenly distributed among ponds. Twelve of the ponds were relatively species-poor with about 45 species per pond while 3 ponds were species-rich with about 90–100 species per pond. In addition, the three richest ponds had about 25% of species that occurred only once or twice, while species-poor ponds had about 10% of their species in this group.

Hickler concluded that, indeed, diversity patterns in the ponds did not fit equilibrium models of biodiversity. For example, the model of island biogeography predicts that large ponds should be species-rich, while smaller ponds should be species-poor. Instead, for the Fort Devens floodplain ponds there was no significant relationship between pond size and species number. Instead, a major factor in determining species richness appeared to be whether or not the pond was connected to the river. All species-rich ponds were connected to the Nashua River while none of the species-poor ponds were. The connected ponds followed the water level of the river. High water in the spring was followed by a rapid decline as the season progressed. The occasional heavy summer rain filled the connected ponds but these drained quickly and within a few days they regained their lower water, summer level. In contrast, for the ponds that were not connected, water levels dropped more slowly in the spring and perhaps more importantly, following heavy summer rain, low-diversity ponds remained flooded for some time.

Hickler concluded that the best way to understand the Fort Devens floodplain ponds was to view them as non-equilibrium systems. With sufficient disturbance, species could not establish competitive dominance so diversity was high irrespective of pond size. In addition, differences between richness levels could probably be attributed to the effect of summer floods, a disturbance that reduced diversity in isolated but not connected ponds.

—KAREN B. SEARCY, Recording Secretary, *pro tempore.*

June 6–8 Field Trips. Over 50 Club members and other naturalists joined together in Ashburnham, Massachusetts in order to survey the flora and fauna of several sites in the town. Assisting NEBC in hosting the event were members of the Ashburnham Conservation Trust, the Campaign for Watatic, and the Athol Bird and Nature Club. Camp Split

Rock in Ashburnham served as the headquarters for meetings, meals, field trips, and species identification. Camp chef for the weekend was Ernie Schori, who had served the Club so well in this capacity at the August 2002 Yale Camp outing in Connecticut.

On Friday afternoon, the group explored the Lincoln Pond area led by Paul Somers and Chris Gagnon, a local conservationist. Lincoln Pond is a pristine site with an extensive bog. While half the group hiked around the pond and bog, the other half explored the bog itself as well as the upland and spruce swamp on its western side. All were impressed by the numerous shrubs of *Rhododendron prinophyllum* and *Vaccinium myrtilloides* in the woods adjacent the bog, as well as the flowering *Calla palustris*, *Ledum groenlandicum*, *Kalmia polifolia*, *Chamaedaphne calyculata*, and *Rhododendron canadense* present in the bog. One uncommon sedge in Massachusetts, *Carex limosa*, was reported by those who visited the bog. While exploring an area of black spruce-dominated forest, a small contingent of botanists encountered clumps of tussock cottongrass, *Eriophorum vaginatum* subsp. *spissum*, a relatively uncommon species in the state. The best find of the day was not a plant, but *Williamsonia fletcheri*, an Ebony Boghaunter dragonfly. It was discovered by Michael Veit, and is the first record of this state endangered species from Ashburnham.

Saturday was dedicated to surveying Mt. Watatic. Local guides Dwight Horan, Diane Wright, Eugene Dionne, and Bob Leary, all from Ashby, and David Hilbrook, David Leary, and Dick Lampula, residents of Ashburnham, led hikes up the mountain. The groups made their approaches from different sides of the mountain so that the many different ecological communities could be observed. Although the day got rainier hour by hour, the naturalists returned to camp excited about their findings, which included a *Betula lenta* tree with a DBH of 113 cm. Some other botanical highlights: Don Lubin found the first record of *Dryopteris campyloptera* for Mt. Watatic, Art Gilman reported seeing *Lycopodium lagopus*, and Alice Schori spotted *Corallorhiza trifida* during a trek through a hemlock-dominated swamp on the western side of the mountain. In the evening, while some of the participants logged findings or gathered around scopes to examine their specimens, the musically inclined joined Lois Somers in performing folk tunes into the night.

Sunday morning, the naturalists set out with local guides Dan and Woody Johnson, Brian Mulroy, Bob Feen, and Howard LeVaux to survey portions of a 450-acre tract of land that the Ashburnham Conservation Trust and other conservation groups are working to conserve. Three outings occurred simultaneously to cover as much ground as possible. Species lists for these surveys were compiled by Robert Bertin, Georgia Hall, Paul Somers, Lisa Standley, Art Gilman, Melanie Schori, Don Lubin, David Lovejoy, Sue Williams (bryophytes), Noah Siegel (fungi), and Jacob Morris-Siegel (birds). Discovery of *Botrychium matricariaefolium*, only known currently from a handful of sites in Massachusetts, was one of the highlights. Hemlock-dominated swamps in the lowlands were explored, yielding *Dalibarda repens*, and rock outcrops on uplands of Bush Hill provided habitat for species such as *Carex platyphylla*, *Oryzopsis asperifolia*, *Corydalis sempervirens*, *Schizachne purpurascens*, and *Poa saltuensis*. While only a small percentage of the tract was surveyed, it was evident that the native species diversity was relatively high and that the number of non-native species was extremely low due to the largely natural surrounding landscape. Art Gilman noted that the site appeared to be important moose-wintering habitat due to the heavy browsing of *Viburnum lantanoides*.

More complete accounts of some of the outings were recorded during the weekend. These journal accounts as well as the species lists compiled are posted on the NEBC website [www.huh.harvard.edu/nebc/].

—PAUL AND LOIS SOMERS, Recording Secretaries, *pro tempore*.

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IN MEMORIAM

WESLEY NEWELL TIFFNEY, JR.
1940–2003

Wesley Newell Tiffney, Jr., was born in Springfield, Massachusetts, the son of Wesley Newell Tiffney, Sr. and Sarah Cousins Tiffney, both botanists. A graduate of Rivers Country Day School and Boston University, he received his Ph.D. in botany from the University of New Hampshire. His doctoral research on arctic-alpine plants and snow-cover relationships was conducted on the summit of Mount Washington in New Hampshire's Presidential Range. During his years in the White Mountains he taught public education programs in field botany for the Appalachian Mountain Club, and participated in mountain search and rescue.

In 1967, he joined the biology faculty of the University of Massachusetts at Boston, and began the first summer courses, research opportunities for undergraduates, and field trips using the university's newly acquired property on Nantucket Island. In 1969, he was appointed the first and founding director of the Nantucket Field Station, a position he held for 33 years. Under his leadership, the Field Station became a year-round institution responsible for the environmental education of thousands of students, from preschool children to doctoral candidates in the sciences. He dedicated the Field Station to supporting the research, education, and conservation management initiatives of island organizations including the Nantucket Conservation Foundation, the Maria Mitchell Science Center, the Nantucket Land Council, island schools, and the Town of Nantucket. As director, he provided vital support to the Nantucket research efforts of many internationally renowned scientific institutions, including NASA, the Woods Hole Oceanographic Institution, the U.S. Army Corps of Engineers, and Harvard University.

In addition to UMass—Boston's summer ecology courses, he lectured and conducted field trips for the interdisciplinary programs of the many colleges and universities using the Field Station, including Northeastern University's geology and environmental policy courses, the Rhode Island School of Design's landscape architecture seminar, and the Williams College—Mystic Seaport Maritime Studies program. A believer in interdisciplinary education, he was unusual among Field Station directors in making the facility available to students and researchers interested in the arts and in subjects related to Nantucket's human history.

His research specialties included the ecology and conservation management of heaths, and he brought scientists from as far away as Britain and The Netherlands to Nantucket to share their knowledge of the subject. He studied global warming, sea level rise, and the erosion of Nantucket's shores, and was passionate in defending the island's coast from inappropriate development and from costly, ineffective, and environmentally damaging coastal defense structures. He was also passionate about protecting Georges Bank from offshore oil development. Believing that education and science-based decision-making are more effective than political rhetoric, he brought industry, government, and academic scientists together on Nantucket in 1982 to share research results in a closed conference that helped, in part, to end plans for drilling in this environmentally sensitive area. He served many years on the board of the Harbor Fuel Corporation, and was a Vice President of the American Society for Environmental Education, the Nantucket Lifesaving Museum, and the Maria Mitchell Science Center.

A large man with a deep voice, a raunchy sense of humor, and a flair for puns and outrageous statements, he was at heart a gentle person who loved all creatures and plants. At the time of his death, he had been retired for less than a year to a new home in coastal Maine, where he was enjoying exploring the area and studying the history and ecology of the Kennebec region. He is survived by his wife of 20 years, Susan Beegel of Phippsburg, Maine; and his brother Bruce Tiffney, sister-in-law Robin Gowen Tiffney, and niece Theora, of Santa Barbara, California.

ANNOUNCEMENT

NEW ENGLAND BOTANICAL CLUB
GRADUATE STUDENT RESEARCH AWARD

The New England Botanical Club will offer up to $2,000 in support of botanical research to be conducted by graduate students in 2004. This award is made annually to stimulate and encourage botanical research on the New England flora, and to make possible visits to the New England region by those who would not otherwise be able to do so. It is anticipated that two awards will be given, although the actual number and amount of awards will depend on the proposals received.

The award will be given to the graduate student(s) submitting the best research proposal dealing with systematic botany, biosystematics, plant ecology, or plant conservation biology. Members of the NEBC will be given preference if competing proposals are judged to be of equal merit. Papers based on the research funded must acknowledge the NEBC's support. Submission of manuscripts to the Club's journal, *Rhodora*, is strongly encouraged.

Applicants must submit three paper copies of each of the following: proposal of no more than three double-spaced pages, one-page literature cited, one-page budget with brief justification, and 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. Reference letters, but not proposals, may be sent by e-mail or FAX to the committee chair, who is listed on the NEBC web page. Proposals and supporting letters must be received no later than Monday, March 1, 2004. The recipient(s) will be notified by April 30, 2004.

This year the Graduate Awards Committee is pleased to announce two recipients of the Graduate Student Research Awards. Jesse Bellemare of Cornell University received support for his proposal entitled "The influence of life history traits on patterns of Holocene migration and geographic distribution of forest herbs in the Berberidaceae, Liliaceae, and Ranunculaceae" and Julie Dragon of the University of Vermont received support for her proposal "The systematics and phylogeny of *Carex lenticularis* and its allies, section *Phacocystis* (Cyperaceae)." For abstracts of these research proposals and a listing of the awards from 1985 to the present, consult the Club's web page (http://www.huh.harvard.edu/nebc/).

ANNOUNCEMENT

MERRITT LYNDON FERNALD AWARD

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

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

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

The first recipient of the Merritt Lyndon Fernald Award is Robert I. Bertin of the College of the Holy Cross in Worcester, Massachusetts, for his paper entitled "Losses of native plant species from Worcester, Massachusetts" (*Rhodora* 104: 325–349. 2002). The committee chose this paper as an outstanding example of the spirit of the Club's mission. Bertin had taken a traditional floristic approach in his earlier publication *Vascular Flora of Worcester, Massachusetts* (Special Publication of the New England Botanical Club, copyright 2000) and in the winning paper built upon those data to document and analyze changes in the flora. The winning paper, comprehensive in its consideration of habitat change and species loss, combined field, herbarium, and literature research to document and analyze floristic change and to put trends in a global context.

THE NEW ENGLAND BOTANICAL CLUB

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A REEXAMINATION OF THE APOGAMOUS TETRAPLOID *PHEGOPTERIS* (THELYPTERIDACEAE) FROM NORTHEASTERN NORTH AMERICA

HEATHER E. DRISCOLL AND DAVID S. BARRINGTON
Department of Botany and Agricultural Biochemistry,
University of Vermont, Burlington, VT 05405
e-mail: Heather.Driscoll@uvm.edu

ARTHUR V. GILMAN
William D. Countryman Environmental Assessment and Planning
868 Winch Hill Road, Northfield, VT 05663

ABSTRACT. Populations of apogamous, tetraploid plants of the beech fern genus, *Phegopteris*, have been discovered in northern New England, prompting an investigation of their putative origin as a hybrid between apogamous, triploid *P. connectilis* and sexual, diploid *P. hexagonoptera*. The present study combined evidence from morphometric analysis and isozyme electrophoresis to determine if *P. hexagonoptera* and *P. connectilis* both contribute to the tetraploid genome. Fifteen morphological characters and six gene loci representing five enzyme systems were evaluated. While our results reveal an affinity between the genomes of *P. connectilis* and the tetraploid *Phegopteris*, they do not support *P. hexagonoptera* as a progenitor of the apogamous tetraploid lineage.

Key Words: fern, apogamy, hybrid, isozyme, *Phegopteris*, polyploidy, evolutionary origin

The beech fern genus, *Phegopteris* Fée, comprises three species widely distributed in the Northern Hemisphere. *Phegopteris hexagonoptera* (Michx.) Fée is a sexual diploid ($n = 30$, $2n = 60$) of temperate eastern North America. *Phegopteris decursivepinnata* (van Hall) Fée includes three cytotypes: a sexual diploid ($n = 30$, $2n = 60$), a sexual tetraploid ($n = 60$, $2n = 120$) and a triploid hybrid ($n = 90$), all in temperate Asia (Mitui 1970, as cited in Masuyama 1979). *Phegopteris connectilis* (Michx.) Watt includes two cytotypes: an apogamous triploid ($n = 90$, $2n = 90$) and a sexual diploid ($n = 30$, $2n = 60$). Triploid *P. connectilis* has a circumboreal distribution with extensions into the Appalachian Mountains at high altitudes, but the diploid race has been reported only from the Japanese Alps of central Honshu, Japan (Matsumoto 1982).

Mulligan et al. (1972) described an apogamous tetraploid *Phegopteris* ($n = 120$, $2n = 120$) from Rougemont, Québec. They speculated that the tetraploid arose via a fertilization event involving an unreduced triploid sperm from apogamous *P. connectilis* and a haploid egg from *P. hexagonoptera*. Their conclusion about the hybrid nature of the tetraploid was supported by a lack of chromosome pairing at meiotic metaphase, chromosome numbers and breeding behavior of the putative progenitors, and by a perceived morphological similarity between the tetraploid, *P. connectilis*, and *P. hexagonoptera*.

Later, Mulligan and Cody (1979) reported additional populations of the apogamous tetraploid from New Brunswick and Nova Scotia. Since *Phegopteris hexagonoptera* does not now occur in that area, Mulligan and Cody (1979) surmised that multiple populations of the tetraploid arose when *P. hexagonoptera* was more widely distributed than today. Recently, one of us (A.V.G.) has discovered additional populations of this plant in northern Vermont (Figure 1; Tables 1 and 2). Contrary to Mulligan et al. (1972), Gilman observed, upon close examination of these plants, a lack of morphological intermediacy between *P. connectilis* and *P. hexagonoptera*. This prompted us to further investigate the hybrid hypothesis in the current study.

Although morphological intermediacy is common in pteridophyte hybrids (Wagner 1983), several authors (e.g., Barrington et al. 1989; Rieseberg and Carney 1998) warn that hybrids are not restricted to intermediate character expression and commonly exhibit parental and transgressive (falling outside the parental range) morphological character states. Since postulation of a hybrid origin based on morphological characters may be unreliable, other approaches, including isozyme analysis, may be used to test hypotheses of hybridization. Isozyme electrophoresis is a valuable technique to investigate plant hybrids and polyploid taxa, as co-dominant inheritance of discrete marker bands (allozymes) allows the detection of additive profiles in hybrid taxa where parental taxa are fixed for different alleles or where allele frequencies differ significantly (Roose and Gottlieb 1976; Werth 1989).

To test the hybrid hypothesis of Mulligan et al. (1972), we reexamined their data, evaluated additional morphological characters, and surveyed isozymes to assess a genetic component of variation. Specifically we sought to determine whether morphological characters and isozyme banding patterns were consistent with a hybrid origin of the tetraploid from *Phegopteris hexagonoptera* and *P. connectilis*.

MATERIALS AND METHODS

Field work. Whole leaves from natural populations of *Phegopteris connectilis* and the putative interspecific hybrid (hereafter *the unknown*)

Figure 1. Sporophyte of apogamous tetraploid *Phegopteris* from Cabot, Vermont (*A. V. Gilman 01141*, VT).

Table 1. Locality data for collections providing material for electrophoretic analyses. Vouchers of all collections deposited in VT.

Collection Details
Phegopteris hexagonoptera
Maine
Washington Co., 5 Jul 2000, *A. V. Gilman 97127*
Vermont
Chittenden Co., Burlington, Ethan Allen Park, 5 Jul 2000, *A. V. Gilman s.n.*
Chittenden Co., Charlotte, Lost Forest, 9 Oct 2001, *H. E. Driscoll 61, 62*
Chittenden Co., Charlotte, Thompson's Point, 5 Jul 2000, *A. V. Gilman 2K082*, with *D. S. Barrington, C. A. Paris & P. Hope*
Chittenden Co., Shelburne, Wake Robin, 5 Jul 2000, *D. S. Barrington s.n.*
Phegopteris connectilis
Vermont
Caledonia Co., St. Johnsbury, 18 Aug 2001, *A. V. Gilman & H. E. Driscoll 2, 3, 5*
Caledonia Co., Waterford, 18 Aug 2001, *A. V. Gilman & H. E. Driscoll 7, 9*
Washington Co., Cabot, 1 Oct 2001, *H. E. Driscoll 24, 25, 28, 30–39, 43–51, 54, 55*
Washington Co., Northfield, 29 Aug 2001, *A. V. Gilman & H. E. Driscoll 11, 13–15*
Unknown species
Vermont
Caledonia Co., St. Johnsbury, 18 Aug 2001, *A. V. Gilman & H. E. Driscoll 1, 4, 10.*
Caledonia Co., Waterford, 18 Aug 2001, *A. V. Gilman & H. E. Driscoll 6, 8*
Washington Co., Cabot, 1 Oct 2001, *H. E. Driscoll 23, 27, 29, 40, 41–42*
Washington Co., Montpelier, 29 Aug 2001, *A. V. Gilman & H. E. Driscoll 18–22, 56, 57*
Washington Co., Northfield, 29 Aug 2001, *A. V. Gilman & H. E. Driscoll 12, 16, 17*

were collected from five localities in northern Vermont between 1997 and 2001 for inclusion in the isozyme analysis (Table 1). Samples of *P. hexagonoptera* were also collected from four Vermont localities and one site in Maine for use in isozyme investigations. Material for the morphological analysis was collected from some of these localities as well as some unique areas (Table 2). Herbarium vouchers are deposited at the University of Vermont (VT). Leaves used in the isozyme analysis were kept in individual plastic bags and refrigerated for no more than two weeks, after which the samples were fixed with liquid nitrogen and stored in an ultra-cold freezer (–80°C). Material stored in this way is useful for at least three years.

Table 2. Locality data for collections providing material for morphological analyses. Vouchers of all collections deposited in VT.

Collection Details
Phegopteris hexagonoptera
Maine
Knox Co., Washington Twp., Patrick Mtn., 11 Jul 1997, *A. V. Gilman 97127*
Vermont
Chittenden Co., Charlotte, Mt. Philo, 14 Jul 1993, *A. V. Gilman 93145 & Briggs*
Chittenden Co., Charlotte, Thompson's Point, 5 Jul 2000, *A. V. Gilman 2K082* with *D. S. Barrington, C. A. Paris & P. Hope*
Chittenden Co., Charlotte, Thompson's Point, 5 Jul 2000, *A. V. Gilman 2K083* with *D. S. Barrington, C. A. Paris & P. Hope*
Phegopteris connectilis
Vermont
Caledonia Co., Danville, near Keiser Pond, 15 Jul 1997, *A. V. Gilman 97237*
Caledonia Co., Peacham, Peacham Corner, 23 Jul 2000, *A. V. Gilman 2K124*
Orange Co., Brookfield, Northfield Gulf, 17 Jul 1996, *A. V. Gilman 96132*
Washington Co., Cabot, Hooker Mtn., 23 Jul 2000, *A. V. Gilman 2K126*
Unknown
Vermont
Caledonia Co., St. Johnsbury, near Sleeper River, 21 Jun 1996, *A. V. Gilman 96061*
Caledonia Co., Waterford, Passumpsic, 17 Aug 1996, *A. V. Gilman 96248*
Washington Co., Cabot, Hooker Mtn., 3 Sep 2001, *A. V. Gilman 01141*
Washington Co., Northfield, Paine Mtn., 2 Sep 1993, *A. V. Gilman 93257*

Morphological analysis. The unknown was identified with reference to the description and Figure 3 in Mulligan et al. (1972); one clone (*A. V. Gilman 96248*) was cytologically determined as a tetraploid using standard techniques. Frond-shape measurements were taken from pressed, dried fronds of four clones of each taxon. Three fronds of each clone were scored.

We scored five quantitative frond-shape characters: 1) width to length ratio of lowest pinna, 2) ratio of length of lowest pinna to adjacent pinna, 3) which (xth from rachis) basiscopic pinnule on the lowest pinna is the longest, 4) which (xth from base) pinna is equivalent in length to the longest basiscopic pinnule, and 5) average width of abaxial costal scales in number of cells at the widest point (for this analysis, a total of five scales from five separate fronds of one clone of each taxon was scored). To test the hypothesis that the ratio of the genomic contribution ($3n$ *Phegopteris connectilis*: $1n$ *P. hexagonoptera*) skews the morphology of the putative hybrid towards *P. connectilis*, quantitatively scored

Table 3. Morphological analysis of *Phegopteris connectilis*, *P. hexagonoptera*, and the tetraploid plant, for comparison with predicted intermediate quantitative scores of a putative hybrid assuming 3:1 genomic contributions of possible parents, *P. connectilis* and *P. hexagonoptera*. We determined (fully explained in text) characters 1–5.

Character	*P. hexagonoptera*	*P. connectilis*	Unknown	Predicted
1. Width:length of basal pinnae	0.303	0.241	0.218	0.256
2. Basal and adjacent pinna ratio	1.071	1.093	1.096	1.087
3. Longest basiscopic pinnule is xth from rachis	5.33	6.25	6.33	6.02
4. Pinna equal to longest basiscopic pinnule	8.91	13.25	14.17	12.17
5. Width of abaxial scales in cells	6.1	22.2	19.8	18.2

characters of the tetraploid were compared to values interpolated from the putative parents using the 3:1 ratio (Table 3).

We also reexamined data presented by Mulligan et al. (1972; Table 4), in which they compared nine qualitative morphological characters: 1) surface ornamentation of spores, 2) shape of fronds, 3) size of fronds, 4) position of lowest pair of pinnae, 5) shape of lower pinnae, 6) presence or absence of wing along rachis connecting two lowest pinna pairs, 7) shape and color of scales on lower leaf surface, 8) nature of hairs on surface of pinnae, and 9) branching of hairs in notch between pinnae.

Isozyme electrophoresis. Samples were surveyed for electrophoretically detectable isozyme variation using 12% pH-buffered hydrolyzed starch gels. Because isozymes had not previously been used in systematic studies of *Phegopteris*, we tested a variety of extraction, gel, and electrode buffer systems for optimum band resolution on all three taxa. Small portions of fresh leaves were ground in cold vegetative-extraction buffer II (Cheliak and Pitel 1984) and the homogenate was absorbed into Whatman 3mm chromotography paper wicks. Saturated wicks were stored at –80°C until inserted into gels. The following eight enzymes were resolved: isocitrate dehydrogenase (IDH), glucose-6-phosphate dehydrogenase (G6PDH), malate dehydrogenase (MDH), 6-phosphogluconate dehydrogenase (6-PGD), phosphoglucoisomerase (PGI), phosphoglucomutase (PGM), shikimate dehydrogenase (SkDH), and triosephosphate isomerase (TPI). The enzymes G6PDH and 6-PGD were resolved on gel and electrode buffer system 5 of Soltis et al.

(1983). The enzymes IDH, MDH, PGM, and SkDH gave clearest band expression with gel and electrode buffer system 11 of Soltis et al. (1983). The enzymes TPI and PGI were resolved most clearly using gel and electrode buffer systems 6 and 8, respectively, of Soltis et al. (1983). Standard staining schedules were followed (Soltis et al. 1983). Although eight enzymes were resolved, only the five (PGM, PGI, TPI, MDH, and SkDH) that provided taxon-specific genetic markers for *P. connectilis*, *P. hexagonoptera*, and the unknown are considered here.

Genetic control of isozyme banding patterns was inferred based on the typical subunit structure and subcellular compartmentalization of the enzymes (Gottlieb 1981). All enzymes migrated anodally. When more than one isozyme was present for an enzyme, they were numbered sequentially with the most anodally migrating isozyme designated 1. Alleles were designated using relative mobilities of the allozymes they encode. The most common allele across all taxa for each isozyme was assigned a mobility value of 100, and all other alleles were assigned numbers representing the percent anodal migration relative to the 100 allele.

RESULTS

Morphological analysis. Morphological differences between the unknown and *Phegopteris hexagonoptera* were pronounced, but the unknown showed a morphological similarity to *P. connectilis* (Tables 3 and 4). For four of five quantitative characters (all except width of abaxial scales in number of cells), the scores for the tetraploid actually fell outside the range determined by the two other taxa on the *P. connectilis* end of the scale. Width of abaxial scales in number of cells was not transgressive, but was closer to *P. connectilis* than would be predicted by interpolation; it actually fell about halfway between *P. connectilis* and the predicted score.

We reevaluated and confirmed most of the nine qualitative scores given by Mulligan et al. (1972). Of these, only one (size of fronds, "large") was shared with *Phegopteris hexagonoptera*. Five characters (surface ornamentation of spores, absence of wing along rachis connecting two lowest pinna pairs, shape and color of scales on lower leaf surface, nature of hairs on surface of pinnae, and branching of hairs in notch between pinnae) scored with *P. connectilis*. Only two qualitative characters (shape of fronds and position of lowest pair of pinnae) had intermediate scores. We did not confirm one character: width:length ratio of basal pinnae was actually transgressive (Table 3, No. 1); the basal

Table 4. Qualitative morphological analysis for *Phegopteris* adopted from Mulligan et al. (1972) as confirmed by our observations. The fourth row is our assessment of the unknown's relation to the two progenitors proposed by Mulligan et al. (1972).

Character	Qualitative Description
1. Surface of fertile spores	
P. hexagonoptera	Blunt verrucate granules
P. connectilis	Irregular thread-shaped fibers
Unknown	Irregular thread-shaped fibers
Unknown relationship	Similar to *P. connectilis*
2. Shape of fronds	
P. hexagonoptera	Usually broader than long
P. connectilis	Usually longer than broad
Unknown	Usually slightly longer than broad
Unknown relationship	Intermediate
3. Size of fronds	
P. hexagonoptera	"Large"
P. connectilis	"Small"
Unknown	"Large"
Unknown relationship	Similar to *P. hexagonoptera*
4. Position of lowest pinnae	
P. hexagonoptera	Slightly or not at all projected downward
P. connectilis	Usual prominently projected downward
Unknown	Slightly projected downward
Unknown relationship	Intermediate
5. Shape of lower pinnae	
P. hexagonoptera	Broadly lanceolate to narrowly rhombic, abruptly contracted towards base
P. connectilis	Lanceolate, gradually narrowed from just above the middle to the base
Unknown	Lanceolate, gradually narrowed from just below the middle to the base
Unknown relationship	Narrower than either *P. connectilis* or *P. hexagonoptera*
6. Wings of rachis	
P. hexagonoptera	Present
P. connectilis	Absent
Unknown	Absent
Unknown relationship	Similar to *P. connectilis*
7. Scales on lower leaf surface	
P. hexagonoptera	Narrowly lanceolate, nearly colorless
P. connectilis	Lanceolate, brownish
Unknown	Lanceolate, brownish
Unknown relationship	Similar to *P. connectilis*

Table 4. Continued.

Character	Qualitative Description
8. Hairs on surface of pinnae	
P. hexagonoptera	Copiously glandular-puberulent beneath, scattered strigose-pubescent
P. connectilis	Sometimes slightly glandular-puberulent beneath, copiously strigose-pubescent
Unknown	Sometimes slightly glandular-puberulent beneath, copiously strigose-pubescent
Unknown relationship	Similar to *P. connectilis*
9. Branching of hairs in notch between pinnae	
P. hexagonoptera	Unbranched
P. connectilis	Branched
Unknown	Branched
Unknown relationship	Similar to *P. connectilis*

pinnae were in fact relatively narrower than those of the other two taxa, not intermediate as scored by Mulligan et al. (1972).

Isozyme electrophoresis. Ten presumed gene loci representing five enzyme systems were resolved. Six of the ten loci were consistently interpretable across all species studied and could be used for interspecific comparison: *Pgm-1*, *Pgm-2*, *Skdh*, *Tpi-1*, *Pgi-2*, and *Mdh-2*. Table 5 reports inferred isozyme genotypes interpreted from isozyme banding patterns.

The monomeric enzyme PGM was represented in all species by two well-separated sets of bands that we interpret as encoded by two loci, *Pgm-1* and *Pgm-2*. Both loci were monomorphic in *Phegopteris connectilis*, for alleles *Pgm-1*^{100} and *Pgm-2*^{100}. The unknown had a phenotype identical to *P. connectilis* for *Pgm-1*, but at *Pgm-2* it possessed a two-banded phenotype for alleles *Pgm-2*$^{100\ 115}$, interpreted as heterozygous. In *P. hexagonoptera*, *Pgm-1* was represented by a different single invariant band, *Pgm-1*^{86}, while *Pgm-2* had two phenotypes. Individuals with a single-banded phenotype for allele *Pgm-2*^{76} and those with a two-banded phenotype for alleles *Pgm-2*$^{76\ 115}$ are interpreted as homozygotes and heterozygotes, respectively.

The monomeric enzyme SkDH was represented by a single locus. All taxa exhibited a phenotype with one band, interpretable as homozygotes.

Table 5. Inferred genotype frequencies for informative isozyme loci in *Phegopteris* (not all plants expressed for all isozymes).

	P. hexagonoptera (n = 8)		*P. connectilis* (n = 34)		Unknown (n = 21)	
Locus	Mobility	Frequency	Mobility	Frequency	Mobility	Frequency
Pgm-1	86:86	1.00	100:100:100	1.00	100:100:100:100	1.00
Pgm-2	76:76 76:115	0.67 0.33	100:100:100	1.00	100:100:115:115	1.00
Skdh	71:71	1.00	100:100:100	1.00	100:100:100:100	1.00
Tpi-1	84:84	1.00	100:100:100	1.00	100:100:100:100	1.00
Pgi-2	114:114 91:114 73:95	0.60 0.20 0.20	56:77:100	1.00	56:56:100:100	1.00
Mdh-2	45:45	1.00	100:100:100	1.00	100:100:100:100	1.00

Phegopteris connectilis and the unknown shared the allele *Skdh*^{100}, whereas *P. hexagonoptera* was fixed for the allele *Skdh*^{71}.

Expression of TPI, a dimeric enzyme, was segregated into two regions. Locus *Tpi-2*, represented by a single invariant band, *Tpi-2*^{100}, exhibited identical mobility in all taxa. A single band, *Tpi-1*^{100}, characterized that locus for both *Phegopteris connectilis* and the unknown, while *P. hexagonoptera* was fixed for a different allele, *Tpi-1*^{84}.

There were two loci for PGI, each with complex banding patterns. Resolution of *Pgi-1* was inferior to *Pgi-2*, and so that locus was not included in the analysis. Individuals of the unknown possessed a phenotype with three well-marked bands, *Pgi-2*^{56}, *Pgi-2*^{77}, and *Pgi-2*^{100}, interpreted as two-allele heterozygotes for this dimeric enzyme. All individuals of *Phegopteris connectilis* had a five-banded phenotype comprising bands *Pgi-2*^{56}, *Pgi-2*^{68}, *Pgi-2*^{77}, *Pgi-2*^{91}, and *Pgi-2*^{100}. These triploid individuals were interpreted as three-allele heterozygotes. *Phegopteris hexagonoptera* was polymorphic at *Pgi-2*. One phenotype was a broad single band at *Pgi-2*^{114}. Another had three bands, *Pgi-2*^{91}, *Pgi-2*^{100}, and *Pgi-2*^{114}. These two phenotypes for *P. hexagonoptera* were interpreted as homozygous and heterozygous, respectively. A third banding pattern in *P. hexagonoptera* was a tight triplet comprising alleles *Pgi-2*^{73}, *Pgi-2*^{82}, and *Pgi-2*^{95}. None of the *P. hexagonoptera* alleles was shared with either of the apogamous taxa.

In our sample of MDH, a dimeric enzyme, all plants that resolved shared the same three most anodal bands; *Phegopteris hexagonoptera* was unique in expressing an additional, most cathodal band. We inferred from the observed phenotypes that there are two MDH isozymes expressed in the taxa in this study. All individuals had a non-segregating, asymmetrically stained, three-banded phenotype at anodally migrating locus *Mdh-1* and a one-banded pattern at cathodally migrating locus *Mdh-2*. We followed Gastony (1988) in positing a fixed three-banded pattern at *Mdh-1* attributed to post-translational modification. Under this interpretation, all taxa were inferred to be homozygotes at *Mdh-1*: allele *Mdh-1*^{100} produced both unmodified allozyme *Mdh-1*^{100} and modified allozyme *Mdh-1*^{50}; the two interacted to produce a heterodimeric third band *Mdh-1*^{73}. Allozyme *Mdh-2*^{100} co-migrated with the modified variant *Mdh-1*^{50} in *P. connectilis* and the unknown, but migrated more slowly in *P. hexagonoptera*, as *Mdh-2*^{45}.

An isozyme probe of two cultivated individuals of *Phegopteris decursivepinnata* revealed little overlap in bands with our study plants.

DISCUSSION

This study has tested the hybrid hypothesis of Mulligan et al. (1972), which proposed that the apogamous triploid *Phegopteris connectilis* had crossed with the sexual diploid *P. hexagonoptera* to give rise to the tetraploid unknown. We have found that the weight of morphological and electrophoretic evidence precludes involvement of *P. hexagonoptera* in the origin of the apogamous tetraploid plants included in the present study. Results from an isozyme probe of *P. decursivepinnata* suggest that this taxon is also unlikely to have been involved in the history of the apogamous lineage.

Our morphological analysis indicates that the tetraploid plants resemble *Phegopteris connectilis* quite closely and that resemblance to *P. hexagonoptera* is superficial. Quantitative scores were in all cases close to *P. connectilis* and in four of five instances (all except scale width) were closer to *P. connectilis* than to predicted interpolated values. Indeed, four of five metrics were not only closer to *P. connectilis* but were actually transgressive. Qualitative characters showed a similar pattern, with six of nine scoring with *P. connectilis*, only one with *P. hexagonoptera*, and two intermediate. Although mindful that hybrids are not morphologically intermediate in every character, we nevertheless found no convincing morphological evidence that *P. hexagonoptera* was a progenitor of the unknown.

The isozyme data provide six independent tests of the hybrid hypothesis of Mulligan et al. (1972). At *Pgm-1*, *Skdh*, *Tpi-1*, *Pgi-2*, and *Mdh-2*, the allozymes fixed in *Phegopteris hexagonoptera* were absent from the unknown. At *Pgm-2*, the more common allele in *P. hexagonoptera*, $Pgm\text{-}2^{76}$ was absent in the unknown, although the rarer allele was present. Thus considering the six loci (*Pgm-1*, *Pgm-2*, *Skdh*, *Tpi-1*, *Pgi-2*, and *Mdh-2*) that are relevant to judging the ancestry of the unknown, five argue against the involvement of *P. hexagonoptera* and one is consistent with *P. hexagonoptera* not being involved; no locus argues for its inclusion. Therefore, the isozyme evidence leads us to reject the hypothesis that apogamous *P. connectilis* had crossed with sexual *P. hexagonoptera* to give rise to the tetraploid unknown.

The isozyme data also offer insight about the relationship of the apogamous taxa. Of the six variable loci in our sample, four were fixed for the same allele in *Phegopteris connectilis* and the unknown. *Phegopteris connectilis* could be distinguished from the unknown at two loci, *Pgm-2* and *Pgi-2*. Locus *Pgm-2* was fixed for an allele in *P. connectilis* that was one member of the fixed heterozygote band pattern in the unknown. At *Pgi-2*, the two apomicts shared two out of three alleles; *P. connectilis* had an additional unique allele. Thus, each apomict had distinct allozymes that the other did not. Despite similarities between the genomes of *P. connectilis* and the unknown, the combination of obligately apogamous lifestyles and the presence of unique alleles at *Pgm-2* and *Pgi-2* suggest that the apomicts have different histories.

The progenitors of the apogamous unknown and apogamous *Phegopteris connectilis* remain to be discovered. An isozyme analysis that includes the diploid and presumably sexual cytotype of *P. connectilis* from Honshu, Japan would help bring to light whether this diploid race was involved in the origins of the apogamous *Phegopteris* lineages. The possibility also exists that sexual cytotypes of *P. connectilis* remain undiscovered in North America.

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AN EVALUATION OF TAXONOMIC BOUNDARIES IN *PLATANTHERA DILATATA* (ORCHIDACEAE) BASED ON MORPHOLOGICAL AND MOLECULAR VARIATION

Lisa E. Wallace

Department of Evolution, Ecology, and Organismal Biology,
The Ohio State University, Columbus, OH 43230
Current Address: Department of Biology, University of South Dakota,
Vermillion, SD 57069
e-mail: lwallace@usd.edu

ABSTRACT. *Platanthera dilatata* (Orchidaceae) is a morphologically variable species encompassing three varieties: *dilatata*, *albiflora*, and *leucostachys*. Spur length and geographic distribution are commonly used to distinguish the varieties, but these characters overlap and are not useful for distinguishing the taxa in all instances. In this study, taxonomic boundaries within *P. dilatata* are reevaluated using variation in 16 morphological traits, six ISSR primers, four RAPD primers, and RFLPs of two chloroplast regions. Morphological, ISSR, and RAPD markers revealed groupings that loosely corresponded to the three recognized varieties, but there was a substantial amount of overlap among the taxa, and no markers alone reliably distinguished the varieties. Some variation was detected in the two chloroplast regions, but it did not correspond well with taxonomy or geography. These data also revealed a surprisingly strong degree of divergence between eastern and western populations of var. *dilatata* at ISSR and RAPD loci, but not in morphological or chloroplast markers. Collectively, these results suggest a relatively recent divergence among the three varieties and among populations of var. *dilatata*. Furthermore, these taxa are likely still in a very active state of evolution due to a combination of geographic isolation and selection by pollinators. Because each of the varieties is generally distinguishable by a set of floral traits and molecular markers, their recognition at the subspecific level is supported. Taxonomic revision within var. *dilatata* is not recommended until morphological and molecular variation is examined in populations throughout its range.

Key Words: *Platanthera dilatata*, Orchidaceae, morphology, ISSR, RAPD, PCR-RFLP, *rpl*16 intron, *trn*T-F

Taxonomic classification of *Platanthera* section *Limnorchis* has been a point of contention among orchidologists for more than a century. An inability to classify species due to extensive intraspecific morphological variation and the apparent presence of interspecific hybrids has resulted in little agreement on the number of or defining characters for species (e.g., Ames 1910; Rydberg 1901; Schrenk 1978; Sheviak 1999). Within section *Limnorchis*, *P. dilatata* (Pursh) Lindl. *ex* Beck is easily distinguished among the many green-flowered forms by having white flowers. However, examination of this species throughout its range revealed a great deal of variation in floral and vegetative traits. Several authors have noted this variation and named specific or subspecific taxa. For example, Rydberg (1901) recognized nine white-flowered species in *Limnorchis*. By contrast, Ames (1910) and others combined all white-flowered plants of section *Limnorchis* together in one or a few taxa. Luer (1975), in the most recent taxonomic treatment of the white-flowered forms, considered a single species, *P. dilatata*, and three varieties, *dilatata* (Pursh) Lindl. *ex* Beck, *albiflora* (Cham.) Ledeberg, and *leucostachys* (Lindl.) Luer. These taxa are distinguished primarily by geographical distribution and floral structure. The distribution of var. *dilatata* encompasses the ranges of the other varieties, which occur throughout western North America. The nominate variety occurs as far west as Alaska, and as far east as Newfoundland. Its southern boundary is approximately New Mexico in the West, and New England in the East. Populations of var. *dilatata* are not abundant in the midwestern United States and Canada. Variety *albiflora* occurs at higher elevations in the Rocky Mountains and other Pacific ranges, and its distribution extends from Alaska to Colorado. Variety *leucostachys* also occurs in the Rocky Mountains and throughout much of the Pacific Northwest, California, Nevada, and Arizona. No consistent differences in habitat type have been noted, with the possible exception of var. *albiflora* favoring higher elevations (Luer 1975). All three varieties are commonly found in mesic sites that are mid-successional or routinely disturbed, have calcareous soils, and receive full sun. Common habitats include roadside ditches, mountain meadows, stream banks, lake shores, and fens.

The flowers of *Platanthera dilatata* are small (1–2 cm wide) and white, occasionally with greenish sepals and ovaries. Flowers occur in inflorescences containing fewer than 20 flowers to more than 75 flowers. The lips of the flowers are strongly basally dilated in all three varieties. The varieties are most readily distinguished by the length of their floral spur. In var. *dilatata* the spur is approximately equal to the length of the lip, in var. *albiflora* the spur is one quarter to one half as long as the lip, and in var. *leucostachys* the spur is approximately twice as long as the lip. The apparent differences in spur size are thought to directly influence the effectiveness of pollinators servicing the flowers. Large noctuid moths (Kipping 1971) and swallowtail butterflies (L. Wallace, pers. obs.) are confirmed pollinators of var. *leucostachys*, and a skipper and several noctuid moths are confirmed pollinators of var. *dilatata* (Boland 1993). Lastly, viscidium (i.e., the sticky pad at the base of a pollinarium) shape may also be helpful for distinguishing among the varieties (Sheviak 1999). The utility of this character is investigated in this study.

Despite numerous anecdotal accounts of morphological variation in *Platanthera dilatata*, surprisingly few studies have quantified intraspecific variation in floral or vegetative characters across multiple populations. Studies that have reported on morphological variation (e.g., Boland 1993; Catling and Catling 1997; Reddoch and Reddoch 1997) have only examined var. *dilatata* at small regional scales. Additionally, phylogenetic analyses of section *Limnorchis* based on sequences of nuclear rDNA loci did not reveal much variation among the varieties (Wallace 2002), despite the morphological distinctions that are apparent. Thus, the current taxonomy of the white-flowered forms of section *Limnorchis* is still debatable. In this study, individuals were initially assigned to a group corresponding to the gross morphological features described by Luer (1975). This taxonomic classification is evaluated by comparing variation in additional morphological characters with variation at molecular loci using data from random amplified polymorphic DNA (RAPD) loci, inter-simple sequence repeat (ISSR) loci, and restriction fragment length polymorphisms (RFLP) isolated from the *rpl*16 intron and *trn*T-F intergenic region of the chloroplast genome.

MATERIALS AND METHODS

Morphological variation. Morphological diversity was assessed from 122 individuals in a total of 30 populations (Table 1). Floral morphological measurements were taken on up to five individuals per population. Flowers were chosen from the middle of the inflorescence to minimize potential placement effects on floral morphology. Field-collected flowers were preserved in FAA (45% EtOH, 45% water, 5% glacial acetic acid, and 5% formalin) and morphological measurements were taken from preserved flowers. Voucher specimens for populations are deposited at OS. Preserved flowers from all populations remain with the author (complete data set of morphological measurements is available upon request from the author). Twelve quantitative traits were assessed on one flower from each plant included in the survey (Table 2). Floral characters included minimum and maximum lip width, lip length from the tip to the point of attachment to the rest of the flower, spur length from the opening to the tip, width of the anther at the apex and base (i.e., where the viscidia are held), dorsal sepal length and width at the widest point, lateral sepal length and width at the widest point, and lateral petal length and width at the widest point. Viscidium shape and lip shape were also noted

Table 1. Location information for populations of *Platanthera dilatata* vars. *dilatata* from the East (E Dil) or the West (W Dil), *albiflora* (Alb), and *leucostachys* (Leu) included in this study. Populations for which morphological and molecular data were collected are indicated by an asterisk (*). Vouchers deposited at OS are indicated by their collection number.

Variety	Location	Voucher ID
E Dil	Fen, Ontario, Canada*	*L. E. Wallace 233*
E Dil	Fen, Ontario, Canada	*L. E. Wallace 234*
E Dil	Beach bog, Ontario, Canada	*L. E. Wallace 232*
E Dil	Bog, Aroostook Co., ME*	*L. E. Wallace 228*
E Dil	Swamp, Herkimer Co., NY*	*L. E. Wallace 220*
E Dil	Fen, Caledonia Co., VT*	*L. E. Wallace 224*
W Dil	Meadow on Kenai Peninsula, AK*	*J. V. Freudenstein 2635a #13–26*
W Dil	Roadside ditch, Park Co., MT*	*L. E. Wallace 246*
W Dil	Seeping roadside, Ravalli Co., MT*	*L. E. Wallace 237*
W Dil	Stream bank, Sublette Co., WY*	*L. E. Wallace 258*
W Dil	Around a lake, Sublette Co., WY*	*L. E. Wallace 259*
Alb	Stream bank, Beaverhead Co., MT*	*L. E. Wallace 241*
Alb	Wet meadow, Ravalli Co., MT*	*L. E. Wallace 238*
Alb	Stream bank, Fremont Co., WY*	*L. E. Wallace 256*
Alb	Wet meadow, Teton Co., WY*	*L. E. Wallace 252*
Alb	Stream bank, Teton Co., WY*	*L. E. Wallace 261*
Alb	Stream bank, Teton Co., WY*	*L. E. Wallace 263*
Leu	Roadside ditch, Idaho Co., ID	*L. E. Wallace 204*
Leu	Roadside ditch, Idaho Co., ID	*L. E. Wallace 205*
Leu	Roadside ditch, Flathead Co., MT*	*L. E. Wallace 214*
Leu	Roadside ditch, Flathead Co., MT	*L. E. Wallace 217*
Leu	Wet forest, Flathead Co., MT	*L. E. Wallace 208*
Leu	Roadside ditch, Missoula Co., MT*	*L. E. Wallace 213*
Leu	Stream bank, Lake Co., MT	*L. E. Wallace 212*
Leu	Roadside ditch, Lake Co., MT	*L. E. Wallace 216*
Leu	Around a lake, Ravalli Co., MT*	*L. E. Wallace 236*
Leu	Roadside ditch, Klamath Co., OR*	*L. E. Wallace 231*
Leu	Wet meadow, Wallowa Co., OR*	*L. E. Wallace 201*
Leu	Roadside ditch, Wallowa Co., OR	*L. E. Wallace 206*
Leu	Roadside ditch, Wallowa Co., OR	*L. E. Wallace 207*

for all flowers. While collecting samples, some differences in the sizes of plants and flowers were noticed between eastern and western populations of var. *dilatata*. Thus, in the statistical analysis, samples of var. *dilatata* were divided into eastern (east of the Mississippi River) and western (west of the Mississippi River) groups for comparison across the range of this taxon. Kruskal-Wallis non-parametric tests (Zar 1996) were used to detect global significance. Dunn's multiple comparisons tests (Zar 1996)

Table 2. Mean (± 1 SD) of 12 quantitative morphological characters (in mm) measured on *Platanthera dilatata* var. *dilatata* from the East (E Dil) or the West (W Dil), var. *albiflora* (Alb), and var. *leucostachys* (Leu). Dunn's multiple comparisons tests were used to compare mean differences across the groups designated. A significant difference ($P < 0.05$) for a trait between groupings is indicated by unlike letters. Sample sizes (n) are indicated for each grouping.

	Mean Size (mm)			
Floral Trait	E Dil (n = 30)	W Dil (n = 25)	Alb (n = 30)	Leu (n = 37)
Lip max width	2.07 ± 0.420^{ab}	2.42 ± 0.476^{b}	1.98 ± 0.301^{a}	2.21 ± 0.438^{ab}
Lip min width	1.07 ± 0.215^{a}	1.09 ± 0.245^{a}	0.98 ± 0.202^{a}	1.03 ± 0.270^{a}
Lip length	5.20 ± 0.890^{ab}	4.18 ± 0.924^{ac}	4.46 ± 0.551^{c}	5.94 ± 1.112^{b}
Spur length	5.15 ± 0.708^{a}	4.40 ± 0.913^{a}	3.11 ± 0.569^{c}	8.79 ± 1.794^{b}
Dorsal sepal length	4.41 ± 0.783^{a}	4.01 ± 0.542^{ab}	3.84 ± 0.459^{b}	5.07 ± 0.927^{c}
Dorsal sepal width	2.50 ± 0.472^{a}	1.92 ± 0.716^{b}	1.36 ± 0.249^{c}	1.68 ± 0.622^{bc}
Lateral sepal length	5.12 ± 1.035^{a}	4.53 ± 0.612^{ac}	4.35 ± 0.605^{c}	5.97 ± 1.220^{b}
Lateral sepal width	2.27 ± 0.411^{a}	2.28 ± 0.498^{a}	1.80 ± 0.418^{b}	2.15 ± 0.731^{ab}
Lateral petal length	4.34 ± 0.961^{ab}	3.69 ± 0.741^{bc}	3.43 ± 0.614^{c}	5.08 ± 1.240^{a}
Lateral petal width	2.24 ± 0.493^{a}	2.63 ± 0.404^{b}	2.35 ± 0.426^{ab}	2.67 ± 0.621^{b}
Anther apical width	0.94 ± 0.189^{a}	1.16 ± 0.242^{b}	1.04 ± 0.247^{ab}	1.25 ± 0.252^{b}
Anther basal width	1.11 ± 0.112^{a}	1.16 ± 0.136^{a}	1.13 ± 0.162^{a}	1.20 ± 0.248^{a}

were subsequently used to determine which groups differed significantly. Statistical tests were performed using SPSS, version 10 (SPSS, Chicago, IL).

Molecular variation. Genotypes of 99 individuals of *Platanthera dilatata*, representing four populations of eastern var. *dilatata*, five populations of western var. *dilatata*, six populations of var. *albiflora*, and five populations of var. *leucostachys*, were identified using ISSR, RAPD, and chloroplast RFLP markers (Table 1). Not all populations included in the morphological analysis were analyzed with molecular markers, but all of the geographic regions are represented in the molecular data sets. Leaves from five individuals per population were sampled.

Leaf samples were kept on ice in the field and stored at −80°C until DNA was extracted. Total genomic DNA was extracted from approximately 0.06 gm of leaf material using a modification of the CTAB method

Table 3. Primer sequence, annealing temperature, and number of bands scored for primers used in this study. Superscripts following the names of RAPD primers are names assigned by Operon Technologies. Taxonomic designations follow those in Table 1.

			Number of Bands Scored			
Primer Name	Sequence 5′ to 3′	Temp.	E Dil (n = 20)	W Dil (n = 25)	Alb (n = 29)	Leu (n = 25)
ISSR-1	(TC)$_6$RG	46°C	15	19	23	23
ISSR-2	(TC)$_6$RC	45°C	7	13	9	18
ISSR-3	(CA)$_7$YG	47°C	10	16	17	15
ISSR-4	(AC)$_7$RG	47°C	16	18	26	24
ISSR-5	(CTC)$_7$RC	45°C	19	20	25	18
ISSR-6	(CT)$_8$RG	48°C	15	16	26	21
RAPD-1^{BE-19}	AGGCCAACAG	36°C	15	20	24	26
RAPD-2^{C-16}	CACACTCCAG	36°C	6	7	7	5
RAPD-3^{X-03}	TGGCGCAGTG	36°C	10	10	11	10
RAPD-4^{X-13}	ACGGGAGCAA	36°C	15	20	21	21
Total			128	159	189	181
Monomorphic			10	6	6	6
Unique			7	9	17	18

(Doyle and Doyle 1987). Template DNA was quantified by gel, and DNA from at least one individual per population was tested in dilutions to determine an appropriate amount for consistent results. In an initial survey, a subset of individuals of each of the varieties was examined for variation with 22 ISSR primers and 62 RAPD primers. Six ISSR primers and four RAPD primers were chosen for the larger survey because they produced repeatable patterns of variation (Table 3). For ISSR primers, each 25 μl reaction contained 1× PCR buffer (20 mM Tris-HCl and 50 mM KCl; Invitrogen, Carlsbad, CA), 200 μM of each dNTP (Invitrogen), 1 mM MgCl$_2$, 0.4 μM primer (0.8 μM for ISSR-1), 0.5 units of *Taq* DNA polymerase (Invitrogen), and 0.3 μl template DNA. ISSR reactions were subjected to the following thermocycler program: 94°C for 2.5 min. (1 cycle); 94°C for 40 sec., 45°–48°C (depending on the primer; Table 3) for 45 sec., 72°C for 1.5 min. (35 cycles); 94°C for 45 sec., 45°–48°C (depending on the primer; Table 3) for 45 sec., 72°C for 7 min. (1 cycle); soak indefinitely at 4°C. For RAPD primers, each 25 μl reaction contained 1× PCR buffer (20 mM Tris-HCl and 50 mM KCl; Invitrogen), 200 μM of each dNTP (Invitrogen), 2 mM MgCl$_2$, 5 pmoles of primer, 0.5 units of *Taq* DNA polymerase (Invitrogen), and 0.4 μl template DNA. RAPD reactions were amplified according to the following program: 94°C for 2 min. (1 cycle); 94°C for 1 min., 36°C for 1 min., 72°C for 2 min. (35 cycles); 72°C for 7 min. (1 cycle); soak indefinitely at 4°C. A negative control, including all ingredients except template DNA, was included with each set of reactions to detect contamination. The total product was separated on 1.2% TAE agarose gels, stained with ethidium bromide, and visualized with UV light. Images of gels were captured digitally for later analysis. Duplicate reactions and gels were run for all primers and individuals. Non-replicated bands were eliminated from the data set. Band homology was based on similarity of molecular weight and occasionally band intensity. A 1 kb-plus DNA ladder (Invitrogen) was run on each gel as a size standard. Additionally, bands suspected of being similar in size across gels were compared by reamplifying individuals and running them side-by-side on a gel. Bands were scored as present or absent.

Band frequency was determined for each taxonomic group as the number of individuals containing a band relative to the number of individuals surveyed. The data set was examined for the presence of high-frequency, group-specific bands. The data matrix was also examined for fixed genotypes within or between populations. The matrix of bands was subjected to a multivariate analysis using principal coordinates analysis (PCoA) in NTSYS-pc (Rohlf 1998) based on the similarity coefficient of Nei and Li (1979). Mean intravarietal and intervarietal genetic similarity was determined from all inter-individual comparisons using the similarity coefficient of Nei and Li (1979).

Restriction fragment length polymorphisms were also used to elucidate patterns of relatedness and seed dispersal among the varieties. The chloroplast genome is assumed to be passed to offspring maternally as has been demonstrated for other orchids (Chang et al. 2000). Two non-coding regions of the chloroplast genome, the *rpl16* intron and *trn*T-F intergenic region, were amplified by PCR and cut with four restriction enzymes. The *rpl16* intron was amplified using primers F71 (Jordan et al. 1996) and R622 (Les et al. 2002). The *trn*T-F intergenic region was amplified using primers "a" and "f" from Taberlet et al. (1991). Each 25 μl reaction contained 1× PCR buffer (20 mM Tris-HCl and 50 mM KCl; Invitrogen), 200 μM of each dNTP (Invitrogen), 3 mM $MgCl_2$, 0.24 μM of each primer for *rpl16* (0.4 μM of each primer for *trn*T-F), 0.5 units of *Taq* DNA polymerase (Invitrogen), and 1.0 μl template DNA. Amplified products were amplified under the following conditions: 94°C for 5 min. (1 cycle); 94°C for 1 min., 53°C for 1 min., 72°C for 2 min. (35 cycles); a final extension at 72°C for 5 min. (1 cycle). Products were verified on 1% TAE agarose gels and subsequently cleaned by precipitating them with an equal volume of PEG:NaCl (20%:2.5 M). Four μl of the cleaned product were digested with two units of restriction enzyme for 24 hr. according to the manufacturer's instructions. The *rpl16* intron was digested with *Eco*RV (Invitrogen) while *trn*T-F was digested with *Bst*NI, *Dra*I, and *Mse*I (New England BioLabs, Beverly, MA). Separate reactions were set up for each restriction enzyme. Digested products of *Eco*RV were separated on 1.2% agarose TBE gels; the products of *Bst*NI and *Dra*I were separated on 2% agarose TBE gels, and the products of *Mse*I were separated on 2% NuSieve agarose (BioWhittaker Molecular Applications, Rockland, ME) TBE gels. A 1 kb-plus DNA ladder (Invitrogen) was run on each gel as a size standard. Gels were stained with ethidium bromide and visualized under UV light. Individuals suspected of having similar banding patterns were redigested and run side-by-side on a gel. Bands of similar mobility on a gel were assumed to be homologous and to have or lack a restriction site in common. The number of distinct chloroplast haplotypes was determined, and populations were examined for shared haplotypes.

RESULTS

Morphological variation. The varieties of *Platanthera dilatata* are similar in that they have white flowers with strongly dilated lips and pointed stigmas. The three varieties were found to differ, however, in flower size, spur length, and viscidium shape (Table 2). The variety *leucostachys* generally had larger flowers than either of the other two varieties. The spur was approximately one and a half times longer than the lip in var. *leucostachys* (spur:lip length ratio = 1.48), was shorter than the lip in var. *albiflora* (spur:lip length ratio = 0.70), and was approximately the same length as the lip in var. *dilatata* (spur:lip length ratio = 0.99 and 1.05, respectively for eastern and western populations). Although some differences were detected between eastern and western samples of var. *dilatata*, few of these differences were significant. Western samples of var. *dilatata* did have smaller flowers with shorter lips and spurs, more strongly dilated lips, and wider anther apices than eastern samples (Table 2). The viscidia of varieties *dilatata* and *leucostachys* were square-oblong, but differed in size, with var. *dilatata* having shorter viscidia. The viscidia of var. *albiflora* were oblong to lanceolate in shape and generally smaller than those of the other two varieties. Different floral fragrances were also detected among the varieties, but were not consistent within a variety (L. Wallace, pers. obs.). A clove-like scent was characteristic of eastern populations of var. *dilatata* while western populations of this variety exhibited a much sweeter fragrance. A clove-like scent was also

Table 4. Number of bands shared between groups (below the diagonal) and shared exclusively between two groups (above the diagonal). Taxonomic designations follow those in Table 1.

	E Dil	W Dil	Alb	Leu
E Dil	***	4	4	2
W Dil	105	***	7	6
Alb	112	138	***	21
Leu	104	130	152	***

apparent in some populations of var. *leucostachys*. Populations of var. *albiflora* resembled western populations of var. *dilatata* in floral scent.

Molecular variation. From the six ISSR primers and four RAPD primers used, a total of 237 bands was scored among all surveyed individuals. The ISSR primers yielded twice as many bands overall (158) and a greater mean number of usable bands per primer (mean = 26.33 bands) compared to RAPD primers (mean = 19.75 bands). If all bands or just ISSR bands were considered, every individual could be identified by a unique multilocus phenotype. Generally, multilocus phenotypes were more similar within populations than between populations. Most bands were polymorphic and found in fewer than half of the individuals surveyed for each group. A small number of monomorphic bands (i.e., in every individual surveyed) was found in each of the varieties (Table 3), but none of these bands was unique to a single taxonomic group. A total of 51 unique bands was identified, but most occurred infrequently. No unique band occurred with a frequency of greater than 10%. Nearly half of the bands identified were shared by at least two groups, with *Platanthera dilatata* vars. *albiflora* and *leucostachys* having the greatest number of bands in common (152; Table 4). Eastern var. *dilatata* populations shared fewer than 50% of all identified bands with var. *dilatata* in the West or with vars. *albiflora* or *leucostachys*. Several bands were shared exclusively between two groups. The vars. *albiflora* and *leucostachys* shared 21 bands that were absent in var. *dilatata* (Table 4). Interestingly, 10 bands were shared between eastern var. *dilatata* and a taxon from the West.

Indices of genetic similarity were consistently higher within groups than among groups and ranged from 0.494 in *Platanthera dilatata* var. *albiflora* to 0.650 in eastern var. *dilatata* (Table 5). Considering intergroup comparisons, individuals of var. *dilatata* from eastern and western populations exhibited the highest similarity (0.483) while the greatest dissimilarity occurred between eastern var. *dilatata* and var. *albiflora* (0.409) or var. *leucostachys* (0.415).

Table 5. Mean intragroup (on the diagonal) and intergroup (below the diagonal) genetic similarity based on banding patterns at RAPD and ISSR loci. Mean similarities are based on comparisons of Nei and Li's (1979) similarity coefficient among all interindividual comparisons. Taxonomic designations follow those in Table 1.

	E Dil	W Dil	Alb	Leu
E Dil	0.650			
W Dil	0.483	0.570		
Alb	0.409	0.459	0.494	
Leu	0.415	0.432	0.461	0.533

Even though none of the varieties could be identified by a suite of taxon-specific bands, these data collectively suggest a degree of distinction that is also apparent in the morphological data set. The similarity of banding patterns within groups and the different band frequencies among groups are responsible for the patterns depicted in the PCoA of genetic similarities (Figure 1). Samples of *Platanthera dilatata* var. *dilatata* from eastern North America are clearly different from western var. *dilatata*, var. *albiflora*, and var. *leucostachys*, while samples of the three varieties from western North America overlap to a greater degree. Most individuals of var. *albiflora* appear extremely similar to individuals of var. *leucostachys* in the PCoA plot. The first two axes account for 19.24% of the total variation observed in ISSR and RAPD markers.

Variation in chloroplast RFLP patterns was found within varieties and within populations. Digestion of *rpl16* and *trn*T-F allowed the resolution of 12 distinct chloroplast haplotypes. Fragments of two different sizes were identified in amplifications of the *trn*T-F region. Most individuals contained a fragment of approximately 2.2 kb: a smaller fragment of approximately 1.7 kb was found only in *Platanthera dilatata* vars. *dilatata* and *albiflora*. The remaining variation occurred at restriction sites. There was little correspondence between haplotype and varietal status or geographic origin. All of the eastern samples of *P. dilatata* had an identical haplotype which was shared with a population from Alaska as well as with individuals of vars. *albiflora* and *leucostachys* from the western United States. Multiple haplotypes were found in 10 populations of all three varieties.

DISCUSSION

Variation among the varieties. *Platanthera dilatata* is one of the most morphologically variable species in section *Limnorchis*. Unlike

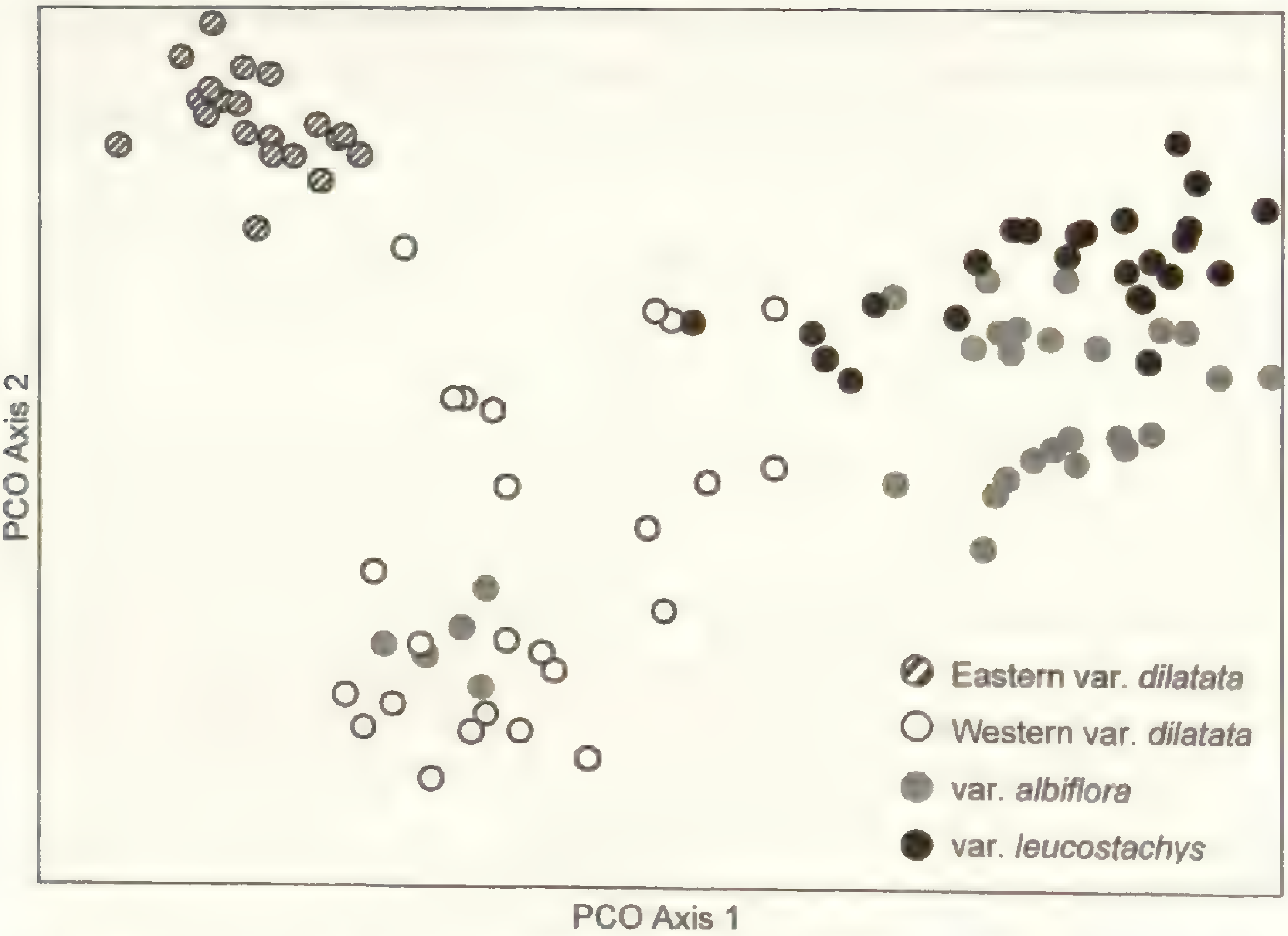

Figure 1. Plot of the first two axes in a principal coordinates analysis based on the similarity coefficient of Nei and Li (1979) derived from ISSR and RAPD banding patterns in each individual of *Platanthera dilatata* surveyed. The first two axes account for 19.24% of the total variation observed.

geographical variants discussed in other species of section *Limnorchis*, many authors agree that variants of *P. dilatata* are generally recognizable in the field. In this study sufficient levels and similar patterns of variation in morphological and molecular ISSR and RAPD markers support Luer's (1975) recognition of three taxa at the rank of variety. Flower size, spur length in relation to lip length, and viscidium shape can be used to distinguish the varieties in most populations. The var. *leucostachys* was found to be the most distinctive, with a spur that was nearly one and a half times longer than the lip (Table 2). Additionally, the flowers of var. *leucostachys* were generally larger, with larger viscidia than in either of the other varieties. Although more similar in overall appearance, vars. *dilatata* and *albiflora* could also be distinguished by spur length and flower size in most populations. The var. *albiflora* displayed very short spurs but slightly larger flowers than var. *dilatata* in the West. Because we found considerable overlap in the sizes of floral features, some individuals with intermediate morphologies will necessarily be difficult to classify. These individuals may be intervarietal hybrids or extremes of one variety or the other; both are earmarks of an actively evolving species.

Variation in floral characters is often an indication of selection by pollinators for traits that increase the chances of successful pollination. Similarly, divergence in floral traits in *Platanthera dilatata* may have been driven by pollinator behavior if the primary suite of pollinators differed across microhabitats. While vars. *dilatata* and *leucostachys* are not specific for a single pollinator species, successful pollination occurs only by lepidopteran insects, and different types of moths and butterflies are confirmed pollinators of these varieties (Boland 1993; Kipping 1971). If primary pollinators differed across microhabitats and populations, divergence in floral traits such as spur length and viscidium shape could occur rather quickly as a result of directional selection by pollinators. Subsequently, new variant populations could spread through long distance seed dispersal (Dodson and Gillespie 1967; Dressler 1993). Although more studies are needed to truly evaluate the strength of selection by pollinators on morphological divergence in *P. dilatata*, there is precedence in other *Platanthera* species. In *P. mandarinorum* (Inoue 1983) and *P. ciliaris* (Robertson and Wyatt 1990), intraspecific variation in floral traits strongly correlates with variation in morphological features of the local pollinator fauna.

Given that at least three morphological variants of *Platanthera dilatata* have been found to be distinct enough to be considered separate taxa, then they are expected to have unique evolutionary histories as well, and patterns of divergence should be traceable with the appropriate molecular markers. However, neither sequence data of nuclear rDNA loci (Wallace 2002) nor the data sets presented in this study indicate with certainty the direction of divergence among the three varieties. No high-frequency variety-specific bands were found, and there is little evidence to suggest that one variety contains a subset of variation found in any other variety. Additionally, many chloroplast haplotypes are shared among the varieties, and no variety exhibits a unique and abundant haplotype. Although principal coordinates analysis suggests a closer relationship between vars. *albiflora* and *leucostachys* than either variety to var. *dilatata*, this result could be interpreted as an indication of derivation from similar genotypes within var. *dilatata* or perhaps that all three varieties evolved independently from a similar ancestral taxon. The low degree of divergence among the varieties, indicated by a lack of fixed or high-frequency molecular markers, suggests that these taxa may have only recently started to diverge. It is expected that geographic isolation and the accompanying effects of genetic drift as well as selection by pollinators were important historical factors promoting divergence in this species.

Geographic variation in var. *dilatata*. The strong differences in ISSR and RAPD banding patterns found between populations of *Platanthera dilatata* var. *dilatata* from eastern and western North America are somewhat surprising, given the lack of significant variation in most morphological traits (Table 2). Because many of the loci amplified by ISSR and RAPD primers are thought to be in non-coding regions, they are expected to evolve rapidly (Wolfe and Liston 1998). It is the differences in the rapidly evolving ISSR and RAPD markers, and a lack of variation in more slowly evolving morphological and chloroplast markers that suggest that divergence of var. *dilatata* populations has also occurred recently. How such a divergence could arise in this taxon is not entirely clear from these data, but several hypotheses are consistent with the data at hand. First, although populations are continuous from the east coast to the west coast, their occurrence may be limited in midwestern North America due to a lack of suitable habitat. Infrequent, widely separated populations may create an effective barrier that prevents substantial gene flow between eastern and western populations. Additionally, differing pollinator faunas across the distribution of plant populations may create a barrier to pollen-mediated gene flow. Alternatively, eastern populations, which exist entirely within the last glacial maximum, may have recolonized the area from different refugia than those from which western populations are derived.

The data presented in this study offer little in the way of differentiating among hypotheses to explain the factors promoting divergence in *Platanthera dilatata*. They have, however, brought to light an interesting example of an actively evolving group and a case of cryptic divergence in var. *dilatata* that was not detectable with morphological or chloroplast markers. Further studies aimed at understanding the distinctness of populations of var. *dilatata* will require sampling populations in the middle part of the range of var. *dilatata*. These populations serve as a bridge, albeit not necessarily functional, between the East and the West. Additional fine-scale molecular markers and their analysis in a genealogical framework may also be helpful for evaluating the taxonomic distinctness of eastern and western var. *dilatata* as well as elucidating factors important for the morphological and molecular distinctness at the varietal level.

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DEVELOPMENTAL MORPHOLOGY OF ROOTS AND SHOOTS OF *PODOSTEMUM CERATOPHYLLUM* (PODOSTEMACEAE – PODOSTEMOIDEAE)

Rolf Rutishauser[1], Evelin Pfeifer, and Philip Moline

Institut für Systematische Botanik, Universität,
Zollikerstr. 107, 8008 Zurich, Switzerland
[1]e-mail rutishau@systbot.unizh.ch

C. Thomas Philbrick

Department of Biological and Environmental Sciences,
Western Connecticut State University, Danbury, CT 06810

ABSTRACT. *Podostemum ceratophyllum* shows peculiar architectural characters that seem to apply to basal members of Podostemoideae. In contrast to more elaborate taxa of this subfamily, *P. ceratophyllum* fits into the classical root-shoot (CRS) model, with clearly distinguishable thread-like roots (with root caps and endogenous lateral roots), as well as stems and leaves. Root-born endogenous shoots initially develop a series of distichous leaves having one stipular sheath each. Shoot modules are terminated by double-sheathed leaves associated with stem branching and/or flower formation. Double-sheathed leaves of *P. ceratophyllum* have two boat-shaped stipular sheaths, each one containing a new leaf (as part of a daughter shoot) or a flower bud. Double-sheathed leaves are an evolutionary novelty of Podostemoideae, leading to branching types not known elsewhere in angiosperms. The vegetative architecture of *P. ceratophyllum* is similar to other American species of *Podostemum*.

Key Words: *Podostemum*, dithecous leaf, vegetative morphology, non-axillary branching, stem bifurcation, stipules

Podostemum ceratophyllum Michx. is the type species of the Podostemaceae (including Tristichoideae and Weddellinoideae), a relatively large aquatic family belonging to the Malpighiales clade in the eurosids I, perhaps related to Hypericaceae (= Clusiaceae; Savolainen et al. 2000; Soltis et al. 1999). The Podostemaceae contains about 46 genera and 280 species (Cook 1996a; Philbrick and Novelo 1993, 1995). Royen (1954) recognized 17 species of *Podostemum* in the Americas, although a monograph by Philbrick and Novelo (in prep.) will recognize only seven. There is growing evidence to support the hypothesis that the genus *Podostemum* is restricted to the New World (e.g., Kita and Kato 2001; Philbrick and Novelo, in prep.); Old World species once placed in *Podostemum* have been moved to other genera (e.g., Cook 1996a,b; Cusset 1992; but see Jäger-Zürn 1999, 2000a,b and Mathew and Satheesh 1997).

Although it is aberrant in terms of its temperate distribution, studies of *Podostemum ceratophyllum* have played an important role in our understanding of the morphology of plants in this intriguing family. Warming's (1881, 1882) accounts of the morphology of *P. ceratophyllum* represent some of the earliest detailed descriptions of the morphology of Podostemaceae. Even so, the developmental morphology of this species, indeed most species in the family, remains incompletely known. The purpose of this contribution is to present an account of the developmental morphology of *P. ceratophyllum* based principally on scanning electron micrographs. These observations will be discussed relative to the published literature (e.g., Graham and Wood 1975; Hammond 1936, 1937; Matthiesen 1908; Royen 1954; Warming 1881, 1882).

Interpretation of the vegetative body in Podostemaceae has been controversial. Consideration of the many aspects of the controversy are beyond the scope of this paper. The reader is referred to Rutishauser (1995, 1997) for a more thorough discussion. In this paper, we will use the structural terms "root," "shoot," "stem," "leaf." The use of these terms, however, does not imply a 1:1 correspondence (complete homology) with the organ categories of more typical angiosperms that show the classical root-shoot model (CRS model; Jäger-Zürn 2000a; Rutishauser and Huber 1991; Rutishauser 1995, 1997). We believe that these descriptive terms are best interpreted as structural categories with fuzzy borderlines that allow the recognition of intermediates or mosaic organs (cf. Rutishauser and Isler 2001). Some workers (e.g., Cusset 1992; Mohan Ram and Sehgal 1992, 1997, 2001; Schnell 1994) have used the neutral term "thallus" for the creeping structures that are called "roots" in the present paper. Herein the podostemaceous "root" is interpreted as a photosynthetic organ that serves an anchorage function, and from which endogenously formed shoots (with leaves) arise.

Plants of the family grow tenaciously attached to rocks or other solid substrata in river rapids and waterfalls. The geographic distribution, biology, and morphology of *Podostemum ceratophyllum* has attracted considerable attention (e.g., Capers and Les 2001; Graham and Wood 1975; Hammond 1936, 1937; Meiger 1976; Philbrick 1981, 1984; Philbrick and Bogle 1988; Philbrick and Crow 1983, 1992). Although few species of Podostemaceae occur in temperate regions, *P. ceratophyllum* has a broad range in eastern North America (as far north as eastern Canada) with disjunct portions of its range in the Dominican Republic and Honduras (Philbrick and Crow 1983; Royen 1954). The species has been shown to be important in the ecology of rivers where it is the dominant macrophyte (Everitt and Burkholder 1991). Some river biota are closely dependent on the plant. The riverweed darter (*Etheostoma podostemone* Jordan, Percidae), a perch-like fish, occurs in habitats closely tied to *P. ceratophyllum* (Connelly et al. 1999). The plant has also been documented as providing important habitat for two fish species (amber darter, *Percina antesella* Williams and Etnier; Conasauga logperch, *P. jenkinsi* Thompson, Percidae) that are listed as federally endangered in the United States (U.S. Fish and Wildlife Service 1985). Human-induced changes in river flow and water quality have likely been factors that have lead to *P. ceratophyllum* being included on rare and endangered species lists for several states in the United States.

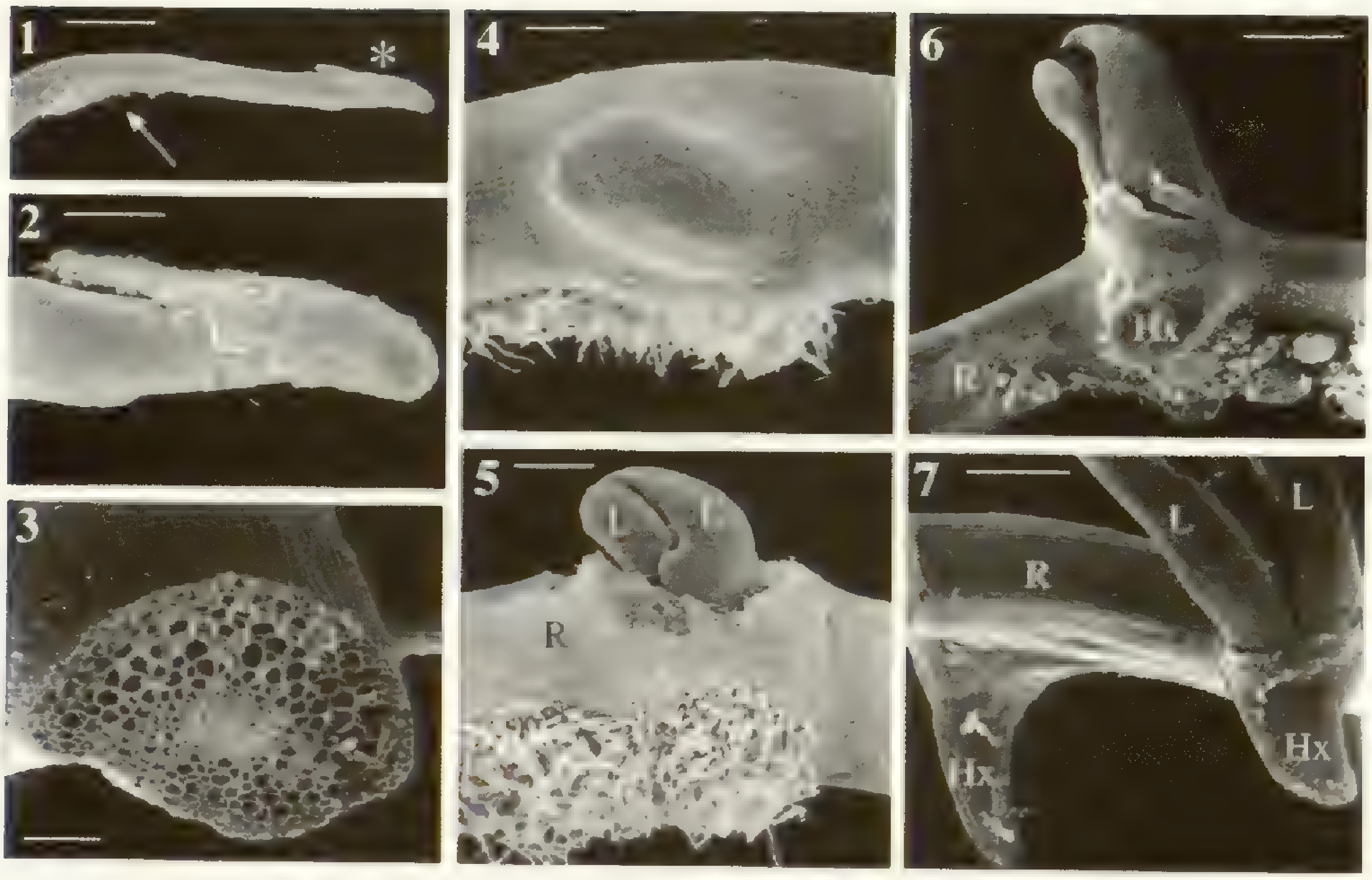
MATERIALS AND METHODS

The data presented in this study were derived from material collected from two populations of *Podostemum ceratophyllum* in the eastern U.S.: (1) Maine. York County, Mousam River, Kennebunk, 30 Aug 1981, *Philbrick 1148* (MEXU, NHA, WCSU, Z); (2) Pennsylvania. Cumberland County, Williams Grove, Yellow Britches Creek, 10 Oct 1981, *Philbrick 1166* (MEXU, NHA, WCSU, Z). Voucher specimens (pressed and/or liquid-fixed) are located in the herbaria listed above. The material used for this study was fixed and preserved in 70% ethyl alcohol. For scanning electron microscopy, the dissected shoot tips were critical-point dried (using acetone/carbon dioxide) and sputter-coated (Au-Pd). The micrographs were taken with scanning electron microscopes (Cambridge S4 and Hitachi S4000) at 20 kV.

RESULTS

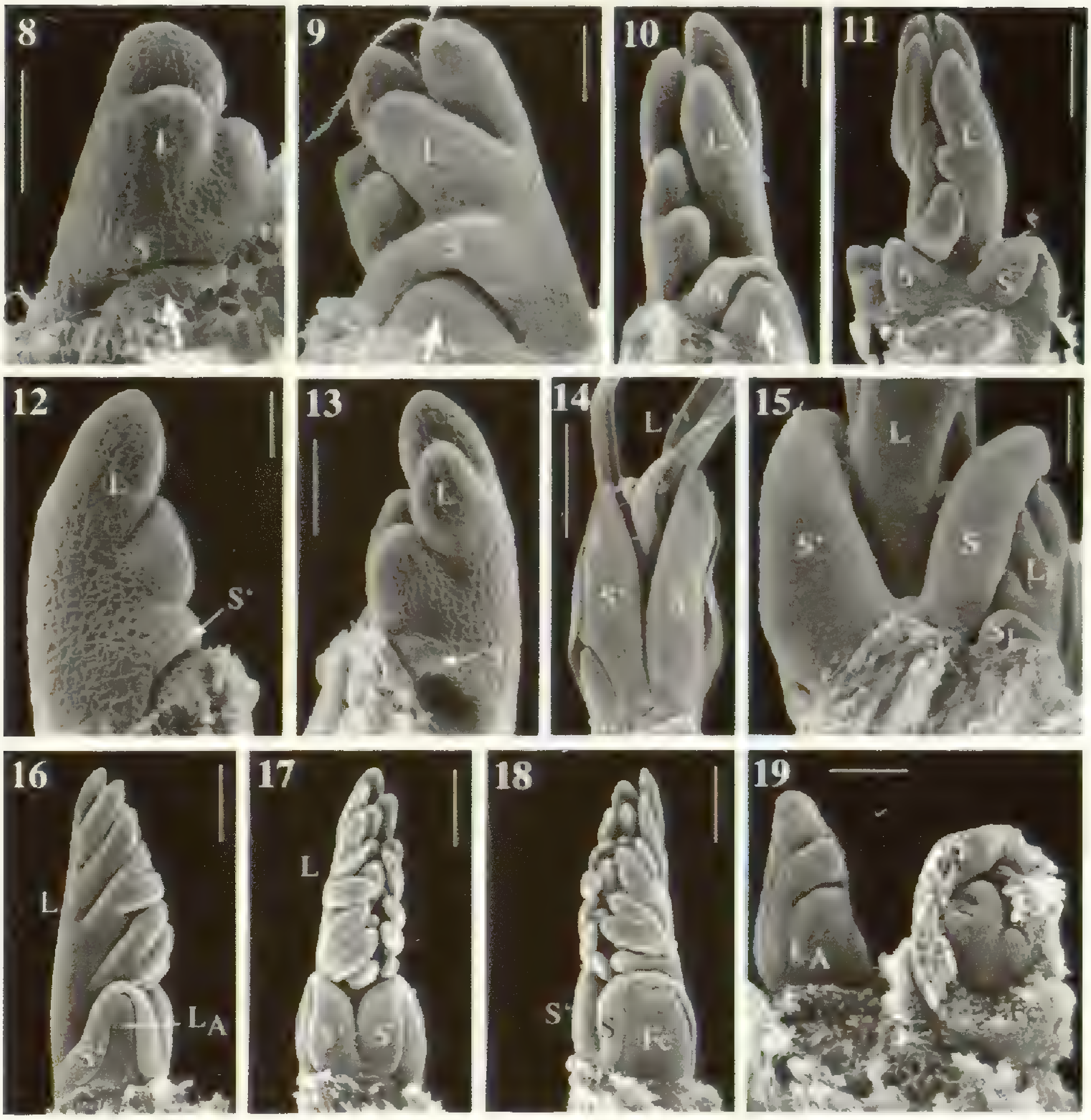
The results will be presented in the following sequence: roots, shoots, leaf morphology and development, stipular sheaths, stem bifurcation, and flower position. These results are illustrated in Figures 1–27.

Dorsiventral roots with endogenous shoot buds and exogenous holdfasts. The roots of *Podostemum ceratophyllum* (Figures 1, 2) are green, thread-like structures that attach to submersed rocks. These slightly dorsiventrally flattened structures are provided with an asymmetric multicellular cap, resembling the calyptra of a typical root (Figure 2; Hammond 1937; Warming 1881). The roots have an oval outline

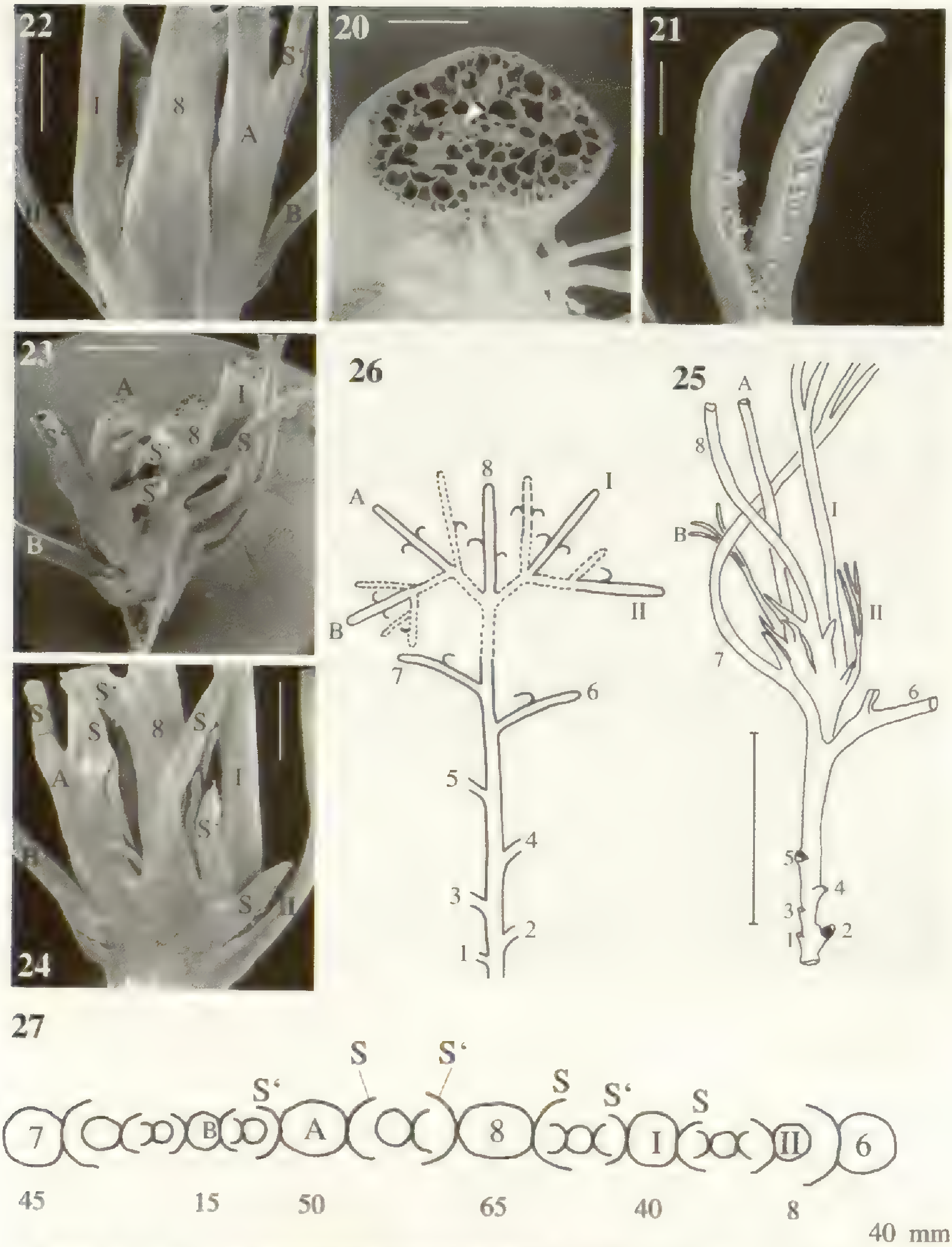


Figures 1–7. *Podostemum ceratophyllum*. Root structure with exogenous holdfasts and endogenous shoots (*Philbrick 1148*). 1–2. Overview and close-up of root tip. Note asymmetric cap (asterisk). Arrow points to zone with adhesive hairs on ventral side. Scale bar = 1 mm and 300 µm, respectively. 3. Transverse section of slightly dorsiventral root. Note central vascular cylinder. Scale bar = 100 µm. 4. Distal portion of root, with protrusion along root flank due to endogenous formation of shoot bud. Note adhesive hairs on ventral surface. Scale bar = 100 µm. 5. Same root portion (R) as Figure 4; peripheral root tissue removed in order to show endogenously formed rosulate shoot with two young leaves (L). Scale bar = 100 µm. 6. Older root portion (R), with rosulate shoot protruding. Note the protruding exogenous holdfast (Hx) associated with the endogenous shoot bud. Scale bar = 200 µm. 7. Portion of a mature root (R), with two finger-like holdfasts (Hx) in alternate positions along the root flank, and endogenously formed rosulate shoot with elongate leaves (L). Scale bar = 200 µm.

when seen in transverse sections (Figure 3). There is a central vascular bundle with inconspicuous xylem elements that are often arranged in two basilateral poles (Hammond 1937, his Figure 3; Warming 1881, his Figure III/11, 15). Just behind the root tip, protrusions arise along the root flanks (Figure 4) that represent early stages of endogenous shoots. The first leaves of the endogenous shoot form while the shoot apex is still within the cortex, and protrude as soon as the cortex and epidermis are ruptured (Figures 5, 6). Finger-like holdfasts arise as multicellular exogenous outgrowths that are directed to the surface of the substratum (Figure 6). Holdfasts of *P. ceratophyllum* roots are opposite or alternate (Figure 7). The holdfasts have also been called haptera (singular hapteron; e.g., Rauh 1937; Warming 1881). They are associated with the endogenously formed shoots that arise in a more dorsal position along



Figures 8–19. *Podostemum ceratophyllum.* Development of single-sheathed and double-sheathed leaves (8–15, *Philbrick 1148*; 16–19, *Philbrick 1166*). 8–10. Three developmental stages of single-sheathed leaves. Each leaf has only one stipular sheath (S) obliquely positioned relative to the orientation of the compound blade. The primary pinnae (L) arise as nearly hemispherical protrusions. Arrows point to initial stages of next younger leaves. Scale bars = 50 µm. 11. Young double-sheathed leaf, seen from upper (dorsal) side. There are two stipular sheaths adjacent to each other (i.e., in oblique lateral positions S, S'). Each sheath contains (covers) a younger leaf primordium (see black arrows). Scale bar = 100 µm. 12–13. Very young double-sheathed leaf seen from opposite sides. S and S' are the two primordial sheaths. Scale bars = 50 µm. 14–15. Proximal portion of two double-sheathed leaves. The two stipular sheaths (S, S') are adjacent to each other, and the base of the blade (L) occurs behind the sheaths. Further dissection has shown that the next younger leaf L_1 is again double-sheathed, with S_1 being its outer visible sheath. Scale bars = 500 µm and 100 µm, respectively. 16–18. Three different views of a half-grown double-sheathed leaf with a pinnate blade (L). Note that sheath S' is covering a daughter leaf (L_A) and sheath S contains a flower bud within a spathella (Fc). Scale bars = 250 µm. 19. Same specimen as Figures 16–18, after removal of the blade and the two sheaths in order to better observe the young leaf (L_A) and the young flower inside the spathella (Fc). Scale bar = 100 µm.



Figures 20–27. *Podostemum ceratophyllum.* Close-ups of blade segments and details of shoot branching associated with double-sheathed leaves (*Philbrick 1148*). 20. Transverse section of nearly mature blade segment with hairs arising from the concave surface. Arrowhead points to vascular bundle. Scale bar = 100 µm. 21. Two distal leaf blade segments of half-grown leaf (length 6 mm). Note hairs on concave surface. Scale bar = 250 µm. 22–24. Vegetative shoot tip after formation of seven leaves (upper portions removed). 22. Seen from "lower" side (toward substratum). Scale bar = 1 mm. 23. Seen from above. Scale bar = 1 mm. 24. Seen from "upper" side (away from substratum). View shown in Figure 24 is same as drawn in Figures 25 and 26. Double-sheathed leaf 8 is in terminal position, and additional ("lateral") leaves occur in both stipular sheaths (S, S') of leaf 8. For further explanation see

the root flanks (Figures 6, 7). Lateral roots are initiated as endogenous buds in the cortex of the mother root (Hammond 1937). Adhesive hairs grow out on the ventral side of the root, thus attaching it to the rock, especially in regions with shoot buds (Figures 4, 5; Warming 1881). The adhesive hairs in Podostemaceae have also been called root hairs or rhizoids (e.g., Hammond 1937; Rutishauser 1997).

Unbranched root-born shoots and their phyllotaxis. After protruding from the root cortex, each shoot bud is first rosulate with two or three leaves (Figures 5–7). As long as the shoot is unbranched the leaves arise along two ranks (i.e., they show distichous phyllotaxis). After the formation of additional leaves and internode elongation the stems may reach a length of over 10 cm, depending on the population (Hammond 1937). Vegetative shoots may produce a flower after the formation of 6–10 leaves (Graham and Wood 1975; Matthiesen 1908; Warming 1881, 1888).

Leaf morphology. The compound leaves of vegetative shoots reach a length of 3–30 cm. The blades are forked once or repeatedly (Figures 10, 16). Each spathulate to filiform subunit (blade segment) is longitudinally grooved, and is provided with a tiny vascular bundle. Short-lived hairs arise along the longitudinal groove or concave surface of the ultimate leaf segments (Figures 20, 21). The leaves along the unbranched stem are subtended by a single stipular sheath that embraces the node and is directed towards the shoot tip (Figures 8–10). Leaves next to branching sites of a stem have two stipular sheaths neighboring each other or obliquely opposite each other (Figures 11, 14, 15).

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Figures 26 and 27 and text. Scale bar = 1 mm. 25. Drawing of the same shoot tip as in Figures 22–24, with seven single-sheathed leaves (1–7) in two ranks along elongated stem, and double-sheathed leaf 8 in terminal position. Additional younger leaves are labeled I and II (right side), A and B (left side). Scale bar = 1 cm. 26–27. Schematic drawings of shoot tip, observed from the side and from above, respectively (same shoot as shown in Figures 22–25). The various double-sheathed and single-sheathed leaves are labeled, including their lengths in mm in Figure 27. Leaves A and B are the first outgrowths in the gap between leaf 7 (single-sheathed) and 8 (double-sheathed); leaves I and II belong to the gap between leaf 6 and 8. Areas drawn with dashed lines are more condensed than shown. The two sheaths of the three double-sheathed leaves (i.e., 8, I and A) are labeled as S and S‘, respectively.

Leaf development. A bulge develops adjacent to the youngest leaf (arrow in Figure 8). This bulge, which may be viewed as a rudimentary shoot apical meristem, increases in size prior to giving rise to the next younger leaf (arrows in Figures 9, 10). In early developmental stages (leaf length ca. 200 μm) only three or four primordial pinnae (blade segments) are observable (Figures 8, 12, 13). A few additional lateral pinnae are subsequently initiated in basipetal order (Figures 9–11). In young leaves (ca. 1 mm long) the first-formed pinnae become subdivided by the formation of lateral pinnae along the rachis (Figures 11, 16). Subsequent differential elongation of the internal (non-terminal) segments of the compound leaf leads to the mature blade being dichotomously or subdichotomously divided. Both sheaths of a double-sheathed leaf are formed at about the same time when the leaf primordium is approximately 200 μm long (Figures 12, 13). Older developmental stages usually show two equal boat-shaped stipular sheaths which cover new leaf primordia or flower buds (Figures 11, 14, 16–18).

Position and development of the stipular sheaths in single-sheathed and double-sheathed leaves. The sheath of a single-sheathed leaf is positioned obliquely relative to the "front" of the folded compound blade (Figures 8–10). In double-sheathed leaves the two stipular sheaths are adjacent to the left and the right set of pinnae, respectively (Figure 11). The two sheaths occupy obliquely lateral positions relative to the orientation of the young pinnae of the blade (Figures 11–18); neither sheath exactly occupies the site "in front" of the compound blade. The two stipular sheaths are adjacent to (i.e., obliquely opposite) each other. Seen from above, the two stipular sheaths of a double-sheathed leaf in *Podostemum ceratophyllum* form the two front corners of a triangle while the primordial leaf blade stands in the third ("rear") corner of this triangle (Figure 11).

Stem bifurcation and modular shoot construction. The root-born shoot shown in Figures 25 and 26 has seven single-sheathed leaves in distichous order and a double-sheathed leaf (i.e., leaf "8") in terminal position. The first double-sheathed leaf is associated with the site of stem bifurcation. New shoot buds (i.e., new leaves) are formed within each of the two stipular sheaths of a double-sheathed leaf (e.g., leaf "8" in Figures 23–27), leading to stem bifurcation. Thus, the stem divides more or less symmetrically into two daughter shoots. Both sheaths of a double-sheathed leaf give rise to a new daughter shoot. Leaves on the daughter shoots are visible in Figures 11, 14, and 15. Similar to the first-order shoot, both daughter shoots (= daughter modules) may again form single-sheathed leaves in distichous arrangement before terminating with another double-sheathed leaf, which initiates the next stem bifurcation. Due to repeated and accelerated stem bifurcation the shoots may appear "bushy" (i.e., with crowded leaves; Matthiesen 1908; Warming 1881). Consecutive branching can be accompanied by the production of a single leaf per branch, in which case the single leaf is double-sheathed. The "bushy" appearance develops when each of the consecutive daughter modules consists of only a single, double-sheathed, terminal leaf. When this occurs the first leaf of a daughter module, which is enclosed by one stipular sheath of a double-sheathed leaf, can itself be double-sheathed, indicating that successive branching has been initiated. Such a scenario is illustrated in Figure 15 where the daughter module on the right side has produced a double-sheathed leaf (L_1), with an outer stipular sheath (S_1) and an inner stipular sheath (not visible in the photograph).

The leaves of these truncated compound shoot systems are more or less arranged in one plane, as illustrated from different perspectives in Figures 22–25. This same compound branching system is illustrated schematically in Figures 26 and 27, as viewed from the side and top, respectively. Subsequent leaves and stem bifurcations are positioned within the plane of the seven distichously arranged leaves of the first order stem (Figures 25, 26). The next younger leaves ("A" on the left and "I" on the right side of Figure 27) are again double-sheathed. One of the next younger leaves ("B" on the left side) is again provided with two sheaths whereas an even younger leaf ("II" on the right side) has only one sheath.

Position of flowers. When flowering occurs, one of the two stipular sheaths of a double-sheathed leaf is occupied by a floral bud instead of a vegetative bud. Only one of the sheaths gives rise to a daughter leaf (L_A in Figures 16, 19) whereas the other sheath is occupied by a flower bud covered by a spathella (Fc in Figures 18, 19). Mature shoots may have up to 12 flowers per shoot, arising from the "proximal" sheaths of double-sheathed leaves in the distal shoot region (Warming 1888, his Figure XIX/16–18).

DISCUSSION

Podostemum ceratophyllum **and the classical root-shoot model (CRS model).** Warming (1881, 1882) gave a careful description of the North American riverweed *P. ceratophyllum. Podostemum ceratophyllum* corresponds closely to the classical root-shoot model (CRS model) typical of most angiosperms (Mohan Ram and Sehgal 2001; Rutishauser 1997; Rutishauser and Huber 1991; Rutishauser and Isler 2001). According to the CRS model the plant body consists of roots and shoots, with leaves and stems as the shoot subunits. In contrast to many other members of the family, *P. ceratophyllum* has thread-like (i.e., only slightly flattened) roots with root caps and endogenous lateral roots.

The presence of stipular sheaths allows for the clear distinction between leaves and stems (Graham and Wood 1975; Hammond 1936, 1937; Rauh 1937; Royen 1954). Axillary branching in *Podostemum ceratophyllum* and most other Podostemoideae is replaced by a type of branching that is associated with double-sheathed leaves (see below).

Roots. As typical for all Podostemaceae, the seedling of *Podostemum ceratophyllum* lacks a long-lasting primary root. During seed germination the "radicle" emerges from the seed coat, bends toward and then flattens onto the substratum. The first structure that emerges from the seed coat may be seen as a short-lived primary root that produces the first adhesive hairs when contacting the substratum (Philbrick 1984). When the endogenously formed secondary root emerges from the base of the hypocotyl, the primary root has stopped growth (Hammond 1937). Mature roots of *P. ceratophyllum* (Figures 1 and 2) are thread-like, but slightly flattened and dorsiventral. Dorsiventrality is expressed by the root cap, which is oblique, and also by the eccentric vascular bundle and by the adhesive hairs that are restricted to the lower (ventral) side of the root. Lateral roots arise from endogenous buds along the root flanks. Similar roots (with caps and endogenous formation of lateral roots) are found in *Indotristicha ramosissima* (Wight) P. Royen, a member of subfamily Tristichoideae (Rutishauser and Huber 1991). In contrast to *P. ceratophyllum* and *I. ramosissima*, more elaborate roots of Podostemaceae (mainly Podostemoideae) lack a permanent cap. These are strongly dorsiventrally flattened and are often described as ribbon-like, crustose, or "foliose." These flattened photosynthetic organs have also been called "thalloid roots" or "thalli," thus avoiding use of the term "root" (Ota et al. 2001; Rutishauser 1997).

Various authors have discussed the apparent role of adhesive hairs ("rhizoids") in the attachment of roots of Podostemaceae to substrata. Jäger-Zürn and Grubert (2000) have reported that a microbial biofilm also plays an important role in attachment of plants of Podostemaceae, and thus question the actual role that the adhesive hairs play.

Holdfasts. As typical for other species of *Podostemum*, *P. ceratophyllum* has exogenous finger-like structures that arise along the root flanks, associated with endogenous shoot buds (Moline 2001, see below). Hammond (1937: 21) compared the holdfasts to root tendrils that are "very sensitive to both gravity and contact, and they soon become firmly attached to the substratum by an adhesive secretion." Branched holdfasts in *P. ceratophyllum* were observed by Warming (1881). The exogenous holdfasts of probably all species of *Podostemum* in the New World stop growing after a few mm. They do not continue their growth and never become lateral roots. Exogenous lobes that develop into lateral roots, however, are found in *Polypleurum* and *Zeylanidium*, including *Z. subulatum* (Gardner) C. Cusset, which has been included in the genus *Podostemum* (as *P. subulatum* Gardner) by some authors (Mathew and Satheesh 1997; Rutishauser 1997; Suzuki et al. 2002).

Leaf initiation and lack of a proper shoot apical meristem. According to Hammond (1937: 27) there is no permanent shoot apical meristem in *Podostemum ceratophyllum*, either between the two cotyledons or at the end of the root-born shoots. While referring to the growth of monopodial stems with single-sheathed leaves Hammond wrote: "The leaves arise each from the base of the second older leaf, i.e., from the next older leaf in its rank." Our observations of the early stages of leaf initiation and the drawings given by Warming (1881, his Figure III/21A+B; Figure IV/1+2) support Hammond's interpretation.

Stipules in Podostemoideae. In many Podostemoideae the leaf sheaths are stipular because they have one or two lobes or teeth that extend beyond the leaf insertion area. Prominent stipular sheaths (two per double-sheathed leaf) are found in various American Podostemoideae such as *Apinagia* and *Marathrum* (Rutishauser et al. 1999). The structural diversity of stipules (including stipular sheaths) is extraordinary in Podostemoideae, especially within the genus *Podostemum* and its sister genus *Crenias* (Ancibor 1990; Cook and Rutishauser 2001; Hammond 1936, 1937; Moline 2001; Novelo and Philbrick 1997; Philbrick and Novelo, in prep.; Tur 1997, 1999). Interpreting exactly what a stipule is in *Podostemum* can be difficult. In some species (e.g., *P. ceratophyllum*) the stipule is an entire boat-like extension of the sheathing leaf base. Sometimes the boat-shaped extension is divided into stipular teeth [e.g., *P. distichum* (Cham.) Wedd., *P. rutifolium* Warm.]. In other species (e.g., *Crenias* spp., *P. muelleri*) the stipule is a single asymmetrically placed lobe on the base of the leaf, which was interpreted by Jäger-Zürn (2002) as a "stipella" rather than a stipule. In still other taxa (e.g., *Cladopus*, *Diamantina*) the digitate segments of the leaf seem to intergrade with "stipules" (i.e., the outer most leaf segments; Philbrick et al. 2004; Rutishauser and Pfeifer 2002). In these latter cases, it is difficult to distinguish morphologically between leaf segments and stipules. *Podostemum irgangii* C. T. Philbrick & Novelo (Philbrick and Novelo 2001) has two types of stipules, one of which is finger-like. The finger-like stipules arise directly from the base of the petiole (in the median area); when mature they seem to arise from the stem, not the petiole itself. A second type of stipule occurs next to the leaf. This latter type is ear-shaped and occurs laterally to the petiole base (Philbrick and Novelo 2001; their Figure 1B, C).

Non-axillary branching and stem bifurcation of *Podostemum ceratophyllum* as compared to other New World Podostemoideae. In most angiosperms, axillary branching entails the production of a lateral shoot bud in the distal axil of a subtending, single-sheathed leaf. Such "typical" axillary branching does not occur in *P. ceratophyllum* and is uncommon in Podostemaceae (Rutishauser 1997). There are only a few documented cases in the family where axillary branching seemingly occurs (Ameka et al. 2002; see below).

In contrast to most other flowering plants, many Podostemoideae are characterized by leaves with two sheaths that are inserted laterally and exactly opposite (many Podostemoideae) or obliquely opposite (i.e., adjacent to) each other (*Podostemum ceratophyllum*). Such leaves have been called double-sheathed or "dithecous" by Warming (1881) and others, whereas the one-sheathed leaves (as typical in angiosperms) have been referred to as single-sheathed or "monothecous" (Jäger-Zürn 2000c, 2002; Rutishauser and Grubert 1999, 2000; Rutishauser et al. 1999). The occurrence of double-sheathed leaves allows the stem to branch by a peculiar process that, due to the absence of a more appropriate term, we refer to as "bifurcation." This phenomenon has also been called dichotomy (Engler 1928) or dichotomous branching (Rutishauser 1997). Bifurcation is a process analogous to typical branching in other angiosperms. Three hypotheses have been proposed to explain bifurcation, non-axillary branching, and the presence of double-sheathed leaves in Podostemoideae:

1. Warming (1881) proposed that stems of *Podostemum ceratophyllum* were monopodial in spite of the presence of double-sheathed leaves. According to Warming the bud in the internal ("notoscopic") sheath is a direct continuation of the main stem (mother shoot) whereas the bud in the external ("basiscopic") sheath gives rise to a lateral shoot.
2. Troll (1941) and Jäger-Zürn (1994, 2002) proposed that the position of the axillary bud relative to the leaf was shifted relative to typical axillary branching. Jäger-Zürn (2002) wrote about the unusual branching in Podostemoideae having double-sheathed leaves: "The branching pattern ... represents a kind of recaulescence that occurs on the 'wrong' (reverse) side of the leaf ... This phenomenon and the evolutionary process of the (deviating) subfoliar branch position remain enigmatic."
3. An alternative explanation is that the bifurcation observable in *Podostemum ceratophyllum* is non-axillary (i.e., not derived from an axillary branching precursor). Rather, this situation is a consequence of the presence of double-sheathed leaves which are unique among flowering plants. Such a view was presented by Engler (1928: 11) who wrote about branching of various podostemoid members: "Depending on the strength of the lateral shoot the whole shoot system expresses a monopodial, dichotomous or sympodial branching pattern. Where dichotomy occurs, the double-sheathed leaf is situated in the middle of the dichotomy, with 1 sheath on each side." [Original German version: "Je nach Stärke des Seitensprosses wird das Sprosssystems monopodial oder dichotomisch oder sympodial. Wo Dichotomie zustande kommt, steht das dithecische Blatt mitten in der Dichotomie, mit 1 Scheide an jeder Seite."]

As a working hypothesis, we prefer the third interpretation. Double-sheathed leaves are interpreted as an evolutionary novelty (key innovation, synapomorphy) of the subfamily Podostemoideae and occur in what seem to be basal genera such as *Apinagia*, *Marathrum*, and *Mourera* (Kita and Kato 2001; Rutishauser and Grubert 1999, 2000; Rutishauser et al. 1999). Jäger-Zürn (2000c) found double-sheathed leaves as parts of branched floral shoots in *Endocaulos*, *Sphaerothylax*, and *Thelethylax* from Africa (including Madagascar). More elaborate podostemoid taxa, including some African and most Asian members, seem to have lost double-sheathed leaves. They show non-axillary shoot branching without the presence of a double-sheathed leaf, or lack shoot branching completely (Rutishauser 1997; Rutishauser and Pfeifer 2002). There are a few podostemoid members [e.g., *Saxicolella submersa* (J. B. Hall) C. D. K. Cook & Rutish., syn. *Polypleurum submersum* J. B. Hall] that seem to have reverted back to the axillary branching that is usual for most angiosperms (Ameka et al. 2002).

Infraspecific variability. The production of truncated shoot systems, and resulting "bushy" growth forms, have been associated with the recognition of subspecific taxa of *Podostemum ceratophyllum*. Four taxonomic varieties have been recognized in *P. ceratophyllum*: var. *ceratophyllum*, var. *circumvallatum* P. Royen, var. *abrotanoides* (Nutt.) Wedd., var. *chondroides* Fassett. Royen (1954, p. 229) did not formally recognize the latter two varieties, stating that they belonged to the typical *P. ceratophyllum* variety "as they are merely extreme variants connected with the ordinary form by a series of intermediate stages." Although Royen (1954) accepted var. *circumvallatum* as distinct, Philbrick and Novelo (in prep.) will not. These later authors interpret plants that have been called var. *circumvallatum* as representing an extreme form of the typical *P. ceratophyllum*. It remains to be seen what factors influence the production of the growth forms of the species.

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FLORA OF NEEDHAM, MASSACHUSETTS—100 YEARS OF FLORISTIC CHANGE

LISA A. STANDLEY

Vanasse Hangen Brustlin, Inc.,
101 Walnut Street, Watertown MA 02471
e-mail: lstandley@vhb.com

ABSTRACT. A floristic survey of Needham, Mass. was undertaken in 2000–2002 to compare the floristic diversity of this suburban community with a checklist of the flora compiled in 1885 by a local naturalist and to identify patterns and potential causes of change in floristic biodiversity. I found a modern flora of 628 species, of which 32% are introduced. Although the total number of species remained fairly constant (691 species were present in 1885), 43.5% of the native species, including 73 genera and 12 families, have been extirpated. The largest changes in the diversity of native species occurred in the Orchidaceae, with the loss of 85% of the species, and the ferns and other cryptogamic groups, with the loss of 50% of the species, including all taxa in the Ophioglossaceae. Of the extant species, 43% are restricted to one or two sites, and are considered at risk of extirpation. The change in biodiversity appears most closely correlated with the loss of open pasture habitats as a result of both development and succession to shrub or tree-dominated communities.

Key Words: Massachusetts, flora, biodiversity, species loss, invasive species, orchids, ferns

This study was undertaken to explore changes in floristic biological diversity in a small suburban Massachusetts town during the 20th century. Rather than a comprehensive flora of Needham, Massachusetts, this study contrasts two snapshots in time: 1880–1885 and 2000–2002. The study is intended to provide data from which to estimate the effects of development and vegetation change on floristic biodiversity. It complements other recent studies (Bertin 2000; Bertin 2003; Drayton and Primack 1996; Holland and Sorrie 1989; Robinson et al. 1994) that have examined floristic change in New England and New York.

The flora of the late 19th century is documented in an unpublished handwritten manuscript found in the New England Botanical Club archives, "A list of the Manual Plants That I have Collected In Needham," December 1885, by T. O. Fuller. Fuller's herbarium (Day 1901) was one of the largest private collections in New England, with more than 2900 sheets representing 1535 species, and was donated to NEBC after his death.

Fuller's only published work (Fuller 1899), appeared in the first volume of Rhodora, and presented an astonishingly modern perspective on biological diversity. The paper begins:

> "Like that of most towns in the vicinity of large cities, the flora of Needham is undergoing slow but continual changes, by the introduction of species foreign to its soil, and the extinction of some endemic ones which are so unfortunate as to grow only in the path of settlement. However desirable the increase of population may be in the view of the political economist, some of its accompaniments cause serious mischief for the lover of wild plants . . . the extermination of a species from his township by the irresistible wave of improvement leaves a sense of keenest regret."

In this study, I have addressed several questions concerning floristic change. I have attempted to determine if there had been changes in the diversity of native species, of introduced species, and of rare or uncommon native species, and whether changes had occurred disproportionately in some plant groups. I have also attempted to determine if change was related to specific habitats or to the abundance of a particular species, and to examine these floristic changes in light of changes in the landscape.

MATERIALS AND METHODS

The flora at the end of the 20th century was documented through field investigations between June, 2000 and September, 2002. During that period, I investigated plant communities and habitats in Needham on numerous occasions throughout the growing season and identified the plant species occuring at each site. This investigation focused on publicly accessible lands owned by the Town of Needham, the Metropolitan District Commission, and the Trustees of Reservations. Some privately owned lands, with owner permission, were also visited. Voucher specimens were collected when necessary for verification of identification, and are deposited at NEBC. I conducted this survey over three field seasons and did not visit all possible sites in Needham. For these reasons, it is likely that a few taxa have been overlooked and may be discovered in subsequent investigations.

The names of plants in Fuller's manuscript were converted to modern species names by verifying Fuller's spelling in the 5th edition of Gray's *Manual* (Gray 1880), and then updating the names using subsequent editions of Gray's *Manual* and Kartesz (1994). All names used in this study are based on Sorrie and Somers (1999), with author citations standardized using the International Plant Names Index (www.ipni.org/index.html; April 27, 2003). Fuller's specimens at NEBC were examined to verify the 1885 data.

An analysis was conducted to determine if species losses were related to losses of particular habitat types. Species were assigned to one of eight habitat types (open water, fen, emergent marsh, red maple swamp, cultural grassland/wet meadow, white pine/oak woods, rich woods, ruderal) based on personal experience and the published literature (Gleason and Cronquist 1991; Magee and Ahles 1999). Plant community types (described below) were combined for analysis, since species occurred in more than one subtype. The open water habitat type included both open water communities and ponds. The fen habitat included acidic graminoid fen and acidic shrub fen communities. The emergent marsh habitat included deep emergent marsh and shallow emergent marsh communities. The red maple swamp habitat category also included shrub swamp communities. The white pine/oak woods habitat category included the acidic rock outcrop, circumneutral rock outcrop, white pine/oak forest, successional white pine forest, oak forest, and hemlock ravine communities. Each species was assigned to the habitat category in which it was most frequent, although some generalist species were found in more than one habitat.

Species abundance was estimated by the number of localities at which I located each species. Species were classified as rare (one locality), at-risk (two localities), or secure (three or more). This classification did not include estimates of abundance.

Description of the study area. Needham is a suburban community located in the southwestern Boston Metropolitan Area, approximately 16 km southwest of downtown Boston (Figure 1). The town was originally settled in the 1640s, and was originally part of the town of Dedham. Needham was incorporated as a separate town in 1711 (with more than 50 families) and included East Needham and West Needham, which separated as the Town of Wellesley in 1881 (Needham Historical Society 1998). The town currently consists of 32.5 km^2 of land, of which 55.5% (1834 ha) is developed. A small amount of land (74 ha, 2.2%) is still in agricultural use, and 90 ha (2.7%) of the town is open water. The remaining 34.8% (1150 ha) is still open and undeveloped (Needham Open Space Plan, unpubl.). The town had a population of 28,911 in 2000 (U.S. Census). Development was concentrated in the northeast portion of the town, in the commercial/industrial area east of Interstate 95 and in the commercial and residential areas close to the Town Center.

Land use and development changed in the mid-1800s. The railroad was extended to Needham in 1853, when large knitting factories were

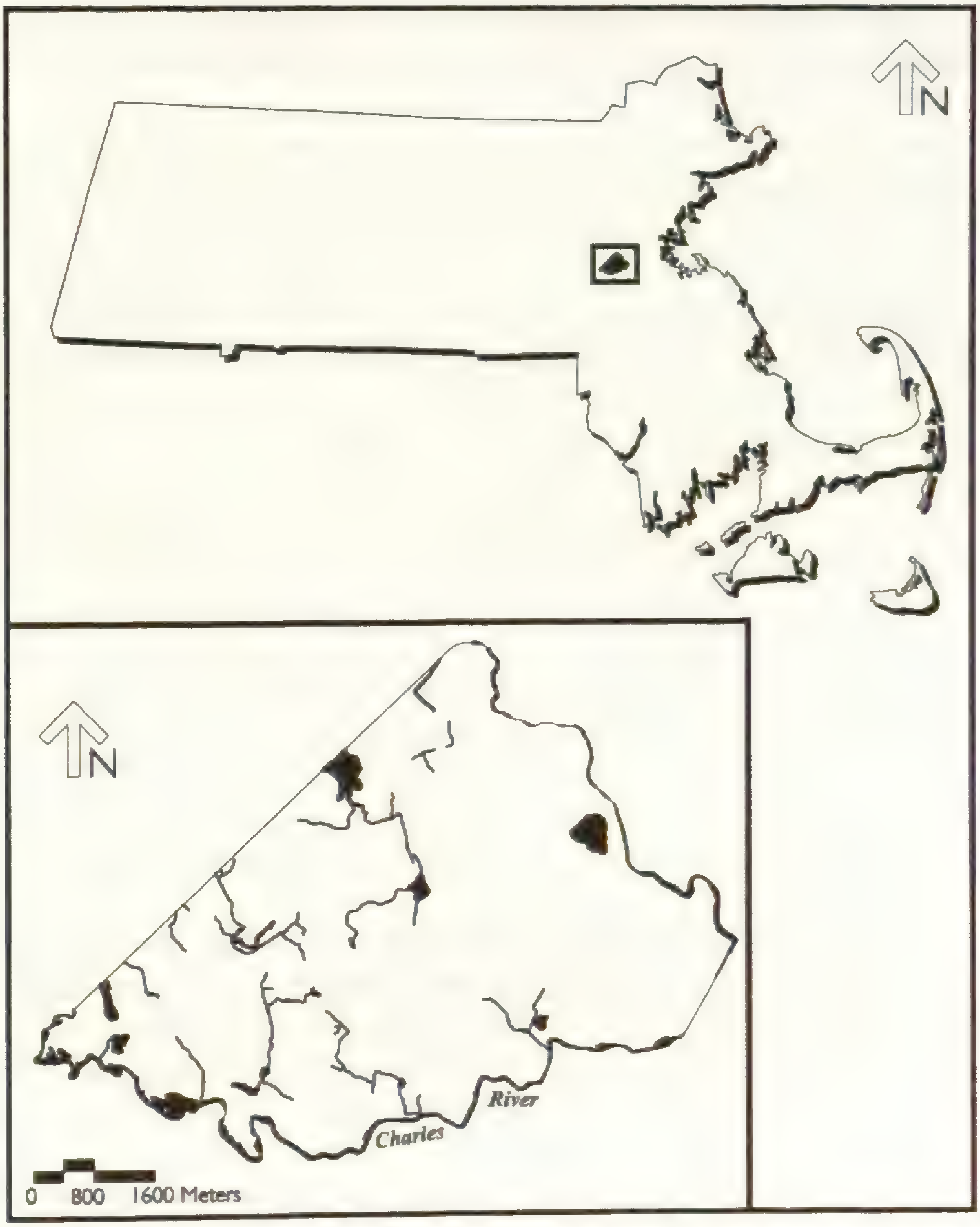

Figure 1. Map of Needham, Massachusetts (adapted from U.S. Geological Survey map).

developed in Highlandville (now Needham Heights). Mills and factories were also located in Charles River Village, Upper Falls, and at the dams of Rosemary Lake and Blacksmith Pond. Farming remained the primary land use in Needham well into the 20th century. Early farmers concentrated on cattle raising and hay. After the establishment of the railroad, Needham also specialized in raising vegetables and flowers. Photographs from the late 1800s show a landscape of rolling pastures and small forested woodlots throughout much of the town. Commercial flower and seedling production was done in large complexes of greenhouses (Needham Historical Society 1998).

Over the past century, forest cover and agricultural land has been lost. Aerial photogrammetry in 1952 showed 1500 ha (44.1% of the town) with a forest vegetation cover. In 1977, forest cover was estimated to have decreased by 20%, to less than 1200 ha. Current (2001) MassGIS mapping shows 39 (1300 ha) of the land in forest (Needham Open Space Plan, unpubl.). The mapping shows that 67% of the agricultural land remaining in 1952 had been lost by 1977. According to the Needham Historical Society (1998), one of the remaining farms has been in cultivation since the early 1700s.

Physical features. Needham has a generally rolling terrain, with elevations from 30 to 100 m msl. The surficial geology of Needham was shaped by regional glaciation, which resulted in the deposition of till. Glacial features of the current landscape include four drumlins and several eskers. Glacial Lake Charles covered approximately 300 ha in the center of Needham (and extended across several other towns), and left behind a flat deposit of sand and fine gravel. A substantial amount of these deposits were excavated and transported to Boston in the 1860s to fill the Back Bay.

Approximately 75 percent of the boundary of Needham is the Charles River, with 20 km of river shoreline (Needham Open Space Plan, unpubl.). The Charles is impounded by several dams, including the Cochrane Dam (1675) at the historic Charles River Village and Upper Falls Dam. The river generally flows through a broad floodplain with oxbows and old channels. Only one reach, immediately south of the Cochrane Dam, passes through a narrow channel and remains free flowing. All of the surface waters in the town are tributary to the Charles River. These include numerous unnamed intermittent streams as well as three major perennial watercourses, Fuller Brook, Hurd Brook, and Rosemary Brook. Ponds occur as a result of artificial impoundment associated with prior mill and agricultural development. Cutler Pond, a 22 ha waterbody, is adjacent to the Charles River and within the Metropolitan District Commission's (MDC's) Charles River Reservation. Rosemary Lake, a 5.7 ha pond, was built in 1830. Other smaller ponds include the Needham Reservoir, Farley Pond, Walker Pond, and Sabrina Lake. These are small man-made impoundments with partially developed watersheds, and are consequently shallow and eutrophic. Several small ponds have been lost since the late 1800s. Blacksmith Pond, a shallow impoundment upstream of Rosemary Lake, was drained and filled in the 1930s.

Needham's bedrock geology is largely formed of relatively old volcanic and sedimentary formations (Needham Open Space Plan, unpubl.). The oldest rock formation is the Dedham granodiorite dated to the Precambrian Era. The Mattapan volcanics, Devonian in age, occur in numerous locations. Outcrops of the Roxbury conglomerate, a massive sedimentation formation locally known as "Roxbury puddingstone," were deposited in the late Carbonifereous, and are overlain and interspersed with a more recent basalt known as the Brighton volcanics. These formations, with the exception of the granodiorite, have a circumneutral pH. Outcrops of these rocks are frequent and spectacular in the steep walls and cliffs of Hemlock Gorge, eroded by the Charles River near the northeast border with Newton.

Soils include Hinkley, Windsor, and Merrimac associations in the eastern half of the town and the extreme western part of town. Paxton and Woodbridge associations occur on the hills and drumlins. Hollis association, characteristically containing many bedrock outcrops, occurs throughout the central part of town, and in the extreme northeast corner.

Vegetation. Needham is in the Northeastern Coastal Zone, Boston Basin subunit, dominated by low rolling topography and suburban land uses (Griffith et al. 1994). Plant community types were identified based on the descriptions in Swain and Kearsley (2000), and include rock outcrops, hemlock ravine, various oak-dominated forests, red maple swamp, and several wetland community types, described below.

None of the rich woods communities (mesic hardwood forests on less-acidic or circumneutral substrates) described by Swain and Kearsley (2000) currently occur in Needham.

Acidic Rock Outcrop Community

This is an open community of exposed acid bedrock dominated by mosses and lichens, with herbaceous and woody vegetation in soil pockets, crevices, or around the margins of the outcrop. Characteristic species include *Pinus strobus* L., *Quercus rubra* L., *Q. ilicifolia* Wangenh., *Gaylussacia baccata* (Wangenh.) K. Koch, *Vaccinium angustifolium* Aiton, *Aronia melanocarpa* (Michx.) Fernald, *Schizachy-*

rium scoparium (Michx.) Nash, *Carex pensylvanica* Lam., and *Corydalis sempervirens* (L.) Pers.

Circumneutral Rock Outcrop Community

Like the Acidic Rock Outcrop, this open community of exposed circumneutral bedrock is often dominated by mosses and lichens, with herbaceous and woody vegetation in crevices. Characteristic species include *Juniperus virginiana* L., *Carya* spp., *Carex pensylvanica*, *Danthonia spicata* (L.) P. Beauv. *ex* Roem. & Schult., *Selaginella rupestris* (L.) Spring, *Corydalis sempervirens*, and *Dichanthelium* spp. Some species more characteristic of calcareous rock cliffs (*Asplenium trichomanes*, *Aquilegia canadensis* L., and *Tilia americana* L.) also occur on these outcrops, which typically support small populations of *C. sempervirens*, *Asplenium platyneuron*, *Dryopteris marginalis*, *Dichanthelium linearifolium* (Scribn.) Gould, *Carex rugosperma* Mack., and *Quercus ilicifolia*. *Krigia virginica* (L.) Willd., which occurs on similar rock outcrops in the adjacent town of Wellesley, has not been located in Needham.

Cultural Grassland Community

Grassland communities occur in former pastures dominated by native graminoids (*Carex pensylvanica*, *Danthonia spicata*, and *Schizachyrium scoparium*) or by introduced graminoids (*Anthoxanthum odoratum* L., *Dactylis glomerata* L., *Festuca* spp., *Phleum pratense* L., *Poa* spp.) depending on moisture regime, soil fertility, and past agricultural practices. Forbs [*Asclepias syriaca* L., *Hieraceum* spp., *Nuttallanthus canadensis* (L.) D. A. Sutton, *Rubus* spp., *Solidago* spp.] also are frequent in this community. A subtype of Cultural Grassland not recognized by Swain and Kearsley (2000) occurs in a few locations in Needham. This is a community of dry, sandy or gravelly disturbed sites that occurs along railroad embankments, old railroad yards, and other disturbed sites. This community is dominated by grasses [*Aristida oligantha* Michx., *A. dichotoma* Michx., *Bromus tectorum* L., *Eragrostis spectabilis* (Pursh) Steud., *E. cilianensis* (All.) Lut. *ex* Janch., *Poa compressa* L.], sedges [*Bulbostylis capillaris* (L.) C. B. Clarke *in* Hook., *C. rugosperma* Mack. var. *tonsa* (Fernald) E. G. Voss, *Cyperus lupulinus* (Spreng.) Marcks] and some characteristic forbs [*Hypericum gentianoides* (L.) Britton, Sterns & Poggenb., *Nuttallanthus canadensis*, *Lechea* spp., and *Plantago aristata* Michx.]. *Comptonia peregrina* (L.) Coult. is the most frequent shrub species.

White Pine-Oak Forest Community

These forests of mixed dominance are found on moderately dry moraine or till deposits and are dominated by *Pinus strobus* and *Quercus* species, also including *Betula lenta* L., *Sassafras albidum* (Nutt.) Nees, *Carya* spp., *Castanea dentata* (Marshall) Borkh., *Vaccinium angustifolium*, *Gaylussacia baccata*, and *Viburnum acerifolium* L. Characteristic herbaceous species include *Maianthemum canadense* Desf., *Cypripedium acaule*, *Melampyrum lineare* Desr., *Lysimachia quadrifolia* L., *Gaultheria procumbens* L., *Dennstaedtia punctilobula*, and *Pteridium aquilinum*.

Successional White Pine Forest Community

This is a transitional community of old fields and pastures, dominated by white pine with scattered oaks and red maples. Exotic or weedy shrub and vine species such as *Rhamnus frangula* L., *Lonicera* spp., *Rosa multiflora* Thunb. *ex* Murray, *Celastrus orbiculata* Thunb., and *Toxicodendron radicans* (L.) Kuntze are common. The herbaceous layer is often dominated by *Maianthemum canadense* and *Lycopodium obscurum*. This is the dominant forest community throughout Needham.

Oak Forest Community

Oak forests occupy a broad ecological continuum across a range of mesic to xeric soils. Depending on slope, soil type, fire frequency, and other disturbance factors, these forests may be classified as mixed oak forest, black oak-scarlet oak forest woodland, or oak-hickory forest. These communities have canopies dominated by *Quercus alba* L., *Q. coccinea* Muenschh., *Q. rubra*, and *Q. velutina* Lam., with *Carya* spp., *Betula lenta*, *Acer rubrum* L., *Sassafras albidum*, and *Fraxinus americana* L. The understory and shrub layers are typically dominated by *Ostrya virginiana* (Mill.) K. Koch, *Castanea dentata*, *Hamamelis virginiana* L., *Cornus florida* L., *Corylus* spp., *Viburnum acerifolium*, *Vaccinium angustifolium*, and *Gaylussacia baccata*. The generally sparse herbaceous layer includes *Dennstaedtia punctilobula*, *Maianthemum canadense*, *Carex pensylvanica*, *C. swanii* (Fernald) Mack., *Danthonia spicata*, *Lycopodium obscurum*, and *Cypripedium acaule*.

Hemlock Ravine Community

A hemlock ravine community occurs in Hemlock Gorge, on the rim and north-facing steep slopes and cliffs of the ravine. The community is dominated by *Tsuga canadensis* (L.) Carr with some patches of *Fagus grandifolia* Ehrh. There is little or no shrub or herbaceous layer, although *Epifagus virginiana* (L.) W. P. C. Barton is common under the beech trees and *Dryopteris marginalis* on rock outcrops.

Red Maple Swamp Community

These forested wetland communities are dominated by *Acer rubrum* in the canopy, with occasional *Nyssa sylvatica* Marshall and *Quercus bicolor* Willd. The dense shrub layer contains *Clethra alnifolia* L., *Vaccinium corymbosum* L., *Rhododendron viscosum* (L.) Torr., *Ilex verticillata* (L.) A. Gray, and *Viburnum dentatum* L. The herbaceous layer characteristically contains *Symplocarpus foetidus* (L.) Salisb. *ex* Nutt., *Osmunda cinnamomea*, *O. regalis*, *Thelypteris palustris*, *Rubus hispidus* L., *Carex stricta* Lam., and *Glyceria striata* (Lam.) Hitchc.

Deep Emergent Marsh Community

This is a community dominated by herbaceous species and occurring in shallow permanent water in broad flat areas adjacent to ponds and the Charles River. Characteristic species include *Typha latifolia* L., *T. angustifolia* L., *Phragmites australis* (Cav.) Trin. *ex* Steud., *Scirpus cyperinus* (L.) Kunth, *Carex stricta*, *Calamagrostis canadensis* (Michx.) Beauv., and *Lythrum salicaria* L., with *Decodon verticillatus* (L.) Ell., *Pontederia cordata* L., *Sparganium* spp., *Sagittaria latifolia* Willd., and *Peltandra virginica* (L.) Schott *ex* Schott & Endl. along the edge of open water.

Shallow Emergent Marsh Community

This community is similar to the deep emergent marsh, but with water depths only seasonally above the surface of the substrate. Dominant species include *Carex stricta*, *Calamagrostis canadensis*, *Phalaris arundinacea* L., and *Lythrum salicaria*. The diverse community often also includes *Carex stipata* Muhl. *ex* Willd., *C. vulpinoidea* Michx., *Carex* spp., *Juncus* spp., and *Thelypteris palustris*. Shallow emergent marshes occur in extensive areas along the Charles River, where they are dominated by *P. arundinacea*. *Cornus amomum* Mill., *Urtica dioica* L., *Acer rubrum*, *Hibiscus moscheutos* L., and *Cephalanthus occidentalis* L. occur in higher hummocks within this marsh system.

Wet Meadow Community

Wet meadow communities are similar to the shallow emergent marsh, but soils are seasonally saturated and rarely inundated. Dominant species include a wide range of *Carex* species [*C. stricta*, *C. lacustris* Willd., *C. stipata*, *C. vulpinoidea*, *C. annectens* (E. P. Bicknell) E. P. Bicknell, *C. vesicaria* L.], *Calamagrostis canadensis*, *Polygonum* spp., *Scirpus cyperinus*, *Juncus effusus* L., *Glyceria canadensis* (Michx.) Trin., *Poa palustris* L., *Thalictrum pubescens* Pursh, *Aster umbellatus* Mill., *Eupatorium dubium* Willd. *ex* Poir., *Onoclea sensibilis*, and *Thelypteris palustris*.

Shrub Swamp Community

This is represented by a group of communities with permanently or seasonally saturated soils, often at the transition between emergent marshes and swamp forests, and likely to be a successional stage in the transition from wet meadow to forested wetland. Shrub swamps are dominated by *Alnus serrulata* (Aiton) Willd., *Cornus amomum*, *Ilex verticillata*, *Salix* spp., *Spiraea alba* Du Roi, *S. tomentosa* L., *Vaccinium corymbosum*, *Viburnum dentatum*, and *Acer rubrum* saplings. Herbaceous species typical of swamps or wet meadows may also occur.

Acidic Graminoid Fen Community

This is an acidic peatland community dominated by sedges and sphagnum, including *Carex comosa* Boott, *C. lupulina* Muhl. *ex* Willd., *Rhynchospora capitellata* (Michx.) Vahl, and *Vaccinium macrocarpon* Aiton. It has a sparse shrub and tree stratum that may include *Acer rubrum*, *Toxicodendron vernix* (L.) Kuntze, *Rhododendron viscosum*, and *V. corymbosum*. *Nuphar variegata* Durand *ex* Clinton, and *Nymphaea odorata* Aiton occur in deeper pools.

Acidic Shrub Fen Community

This community is similar to the graminoid fen, but dominated by shrubs and spagnum. Dominant species include *Decodon verticillatus*, *Chamaedaphne calyculata* (L.) Moench, *Spiraea tomentosa*, *Triadenum virginicum* (L.) Raf., and *Woodwardia virginica*.

Open Water Community

In Needham this community type occurs in the shallow ponds and the Charles River. Characteristic species of the Charles River impoundments include *Nuphar variegata*, *Nymphaea odorata*, *Cabomba caroliniana* A. Gray, *Lemna minor* L., *Wolffia* spp., *Potamogeton epihydrus* Raf., *P. robbinsii* Oakes, *P. spirillus* Tuck., *P. natans* L., *P. crispus* L., *Vallisneria americana* Michx., *Marsilea quadrifolia* L., *Myriophyllum spicatum* L., *Polygonum amphibium* L., and *Ceratophyllum demersum* L. *Utricularia macrorhiza* LeConte occurs in a few locations. *Decodon verticillatus*, *Peltandra virginica*, *Pontederia cordata*, and *Sparganium androcladum* (Engelm.) Morong occur on the river shores. Water levels in these impoundments do not fluctuate greatly, and there are no seasonally exposed mud banks that would provide habitat for annual species.

Pond species include submerged and floating aquatics, typically *Nuphar variegata*, *Nymphaea odorata*, *Egeria densa* Planch., *Elodea*

Table 1. Comparison of 1885 and 2002 floristic composition of Needham, Mass.

	Number of Species		
	Native	Introduced	Total
Year			
1885	563	128	691
2002	427	201	628
Comparison			
Species Common to Both	318	87	405
Species Lost	245	42	287
New Species	107	115	222

canadensis Michx., *Callitriche palustris* L., *Lemna minor*, *Wolffia brasiliensis*., *Potamogeton epihydrus*, and *P. pusillus* L.

RESULTS

In 1885, Fuller recorded 691 species of vascular plants in Needham (Fuller, unpubl. ms.). Of these, 563 were native to New England, and 128 (18.5%) were introduced (Table 1). Species present represented 117 families, 42 species of trees, 36 species of ferns and lycopods, and 12 species of orchids. The largest families were the Asteraceae (75 species), Poaceae (62 species), and Cyperaceae (59 species). In 2000–2002, I recorded 628 species, of which 427 were native and 201 (32%) were introduced. There were 114 families, 57 species of trees, 23 ferns, and 3 species of orchids. The largest families were the Poaceae (70 species), Asteraceae (64), and Cyperaceae (55). Twenty-six species (7 native, 19 exotic) were not previously reported in Norfolk County (Sorrie and Somers 1999; Table 2). In combination, the two surveys included 914 species of vascular plants. The complete lists are available from the NEBC archives, the Harvard University Herbaria library, and the author.

The actual floristic change was determined on a species-by-species comparison of species lost and gained. This analysis demonstrated that 405 species found in 1885 were still present in 2000–2002 (Table 1). Of the native species, 245 (43.5%) found in 1885 have been lost, while 107 native species not found in 1885 have been gained. Of the introduced species, 42 species (primarily agricultural weeds) have been lost, and 115 species have been gained. Only 64.5% of the flora of 1885 was still present at the end of the 20th century.

Table 2. Species new to Norfolk County, 2000–2002.

Family	Species
Asteraceae	*Aster cordifolius* L.
	Aster puniceus L.
	Eupatorium maculatum L.
	Silphium perfoliatum L.
Buxaceae	*Pachysandra terminalis* Siebold & Zucc.
Caprifoliaceae	*Lonicera japonica* Thunb.
Caryophyllaceae	*Cerastium semidecandrum* L.
	Silene japonica (Sw.) Ohwi
Celastraceae	*Euonymus alata* (Thunb.) Siebold
	Euonymus fortunei (Turcz.) Hand.-Mazz.
Cyperaceae	*Carex hirta* L.
Elaeagnaceae	*Elaeagnus umbellata* Thunb.
Fabaceae	*Lotus corniculatus* L.
Hydrangeaceae	*Hydrangea paniculata* Siebold
Lemnaceae	*Wolffia brasiliensis* Wedd.
	Wolffia columbiana H. Karst.
Orchidaceae	*Epipactis helleborine* (L.) Crantz
Papaveraceae	*Macleaya cordata* (Willd.) R. Br.
Poaceae	*Agrostis hyemalis* (Walter) Britton, Sterns & Poggenb.
	Eleusine indica (L.) Gaertn.
Rutaceae	*Phellodendron japonicum* Maxim.
Salicaceae	*Populus deltoides* W. Bartram *ex* Marshall
Scrophulariaceae	*Digitalis purpurea* L.
Solanaceae	*Solanum nigrum* L.
Tiliaceae	*Tilia cordata* Mill.
Vitaceae	*Parthenocissus tricuspidata* (Siebold & Zucc.) Planch.

Taxonomic groups. There has been turnover at the family level as well as at the species level. Twelve families present in 1885 were no longer extant at the time of this study. These include the Ophioglossaceae (5 species), Saxifragaceae (3 species), Isoetaceae, Linaceae, and Menyanthaceae (2 species). The Acoraceae, Adiantaceae, Melastomataceae, Portulacaceae, Sarraceniaceae, Staphyleaceae, and Xyridaceae, each with a single species, were also extirpated. Seventy-three genera have been lost (Table 3). Most of these were represented by a single species, although several genera once present with multiple species have been lost (*Actaea*, *Saxifraga*, *Pycnanthemum*, *Isoetes*, *Myrica*, *Botrychium*, *Platanthera*, *Spiranthes*, *Linum*, *Eriophorum*). Other genera, although persisting, have lost a substantial number of the species present in 1885: *Pyrola*, 2 of 3; *Rynchospora*, 2 of 3; *Thalictrum*, 2 of 3; *Viola*, 5 of 8. Although none of the 5 species of *Desmodium* present in 1885 were extant in 2000–2002, other native *Desmodium* species were found in Needham.

Table 3. Genera of native vascular plants extirpated from Needham, Mass.

Family	Genus	Number of Species Lost
Acoraceae	*Acorus*	1
Adiantaceae	*Adiantum*	1
Apiaceae	*Conioselinum*	1
	Sanicula	1
Araliaceae	*Panax*	1
Asteraceae	*Krigia*	1
	Xanthium	1
Brassicaceae	*Cardamine*	1
Cabombaceae	*Brasenia*	1
Campanulaceae	*Triodanis*	1
Caprifoliaceae	*Triosteum*	1
Caryophyllaceae	*Paronychia*	1
Crassulaceae	*Penthorum*	1
Cupressaceae	*Chamaecyparis*	1
Cyperaceae	*Eriophorum*	3
	Fimbristylis	1
Dryopteridaceae	*Cystopteris*	1
	Deparia	1
	Gymnocarpium	1
	Polystichum	1
	Woodsia	1
Ericaceae	*Andromeda*	1
	Epigaea	1
Fabaceae	*Tephrosia*	1
Gentianaceae	*Gentiana*	1
	Gentianopsis	1
Iridaceae	*Sisyrinchium*	1
Isoetaceae	*Isoetes*	2
Juglandaceae	*Juglans*	1
Lamiaceae	*Hedeoma*	1
	Pycnanthemum	2
	Stachys	1
Liliaceae	*Aletris*	1
	Clintonia	1
Linaceae	*Linum*	1
Lycopodiaceae	*Huperzia*	1
	Lycopodiella	1
Melastomataceae	*Rhexia*	1
Menyanthaceae	*Menyanthes*	1
	Nymphoides	1
Myricaceae	*Myrica*	2
Ophioglossaceae	*Botrychium*	4
	Ophioglossum	1
Orchidaceae	*Arethusa*	1
	Calopogon	1
	Coeloglossum	1

Table 3. Continued.

Family	Genus	Number of Species Lost
	Corallorrhiza	1
	Liparis	1
	Platanthera	3
	Pogonia	1
	Spiranthes	2
Orobanchaceae	*Orobanche*	1
Pinaceae	*Larix*	1
Platanaceae	*Platanus*	1
Poaceae	*Andropogon*	1
	Elymus	1
	Sorghastrum	1
	Zizania	1
Portulacaceae	*Portulaca*	1
Pyrolaceae	*Orthilia*	1
Ranunculaceae	*Actaea*	2
	Hepatica	1
Rutaceae	*Zanthoxylum*	1
Sarraceniaceae	*Sarracenia*	1
Saxifragaceae	*Chrysosplenium*	1
	Saxifraga	2
Scrophulariaceae	*Castilleja*	1
	Lindernia	1
	Pedicularis	1
	Penstemon	1
Staphyleaceae	*Staphylea*	1
Thelypteridaceae	*Phegopteris*	1
Urticaceae	*Pilea*	1
Xyridaceae	*Xyris*	1

Ferns and orchids are the two taxonomic groups that have lost the largest proportion of species. Twenty-one species of ferns and other cryptogamic groups (Isoetaceae, Equisetaceae, Selaginellaceae, Lycopodiacae) were no longer found in Needham, a loss of 50% of the original fern flora (Table 4). Eight genera and 11 of the 13 historical species of orchids—85% of the historical orchid flora—have been lost (Table 5). Only two native species (*Cypripedium acaule* and *Goodyera pubescens*) remained, along with the introduced *Epipactis helleborine*. Oddly, although Brown and Folsom (1997) cited Cutler Park in Needham as a site that often had good orchid populations, I found no orchids there other than the three extant species. Substantial losses (49% of the original 59 species) have also occurred in the Cyperaceae.

Table 4. Status of ferns and fern allies in Needham, Mass. X = present in flora.

Family	Species	Year	
		1885	2002
Adiantaceae	*Adiantum pedatum* L.	X	
Aspleniaceae	*Asplenium platyneuron* (L.) Britton, Sterns & Poggenb.	X	X
	Asplenium rhizophyllum L.	X	
	Asplenium trichomanes L.	X	X
Blechnaceae	*Woodwardia virginica* (L.) Sm.	X	X
Dennstaedtiaceae	*Dennstaedtia punctilobula* (Michx.) T. Moore	X	X
	Pteridium aquilinum (L.) Kuhn	X	X
Dryopteridaceae	*Athyrium filix-femina* (L.) Roth	X	X
	Cystopteris fragilis (L.) Bernh.	X	
	Deparia acrostichoides (Sw.) M. Kato	X	
	Dryopteris carthusiana (Vill.) H. P. Fuchs		X
	Dryopteris cristata (L.) A. Gray	X	X
	Dryopteris marginalis (Linn.) A. Gray	X	X
	Gymnocarpium dryopteris (L.) Newman	X	
	Matteuccia struthiopteris (L.) Tod.		X
	Onoclea sensibilis L.	X	X
	Polystichum acrostichoides (Michx.) Schott	X	
	Woodsia obtusa (Spreng.) Torr.	X	
Equisetaceae	*Equisetum arvense* L.	X	X
	Equisetum fluviatile L.	X	
	Equisetum hyemale L.	X	
	Equisetum sylvaticum L.	X	
Isoetaceae	*Isoetes echinospora* Durieu	X	
	Isoetes engelmannii A. Braun	X	
Lycopodiaceae	*Diphasiastrum digitatum* (Dill. *ex* A. Braun) Holub	X	X
	Huperzia lucidula (Michx.) Trevis.	X	
	Lycopodiella appressa (Chapm.) Cranfill	X	
	Lycopodium clavatum L.	X	X
	Lycopodium obscurum L.	X	X
Ophioglossaceae	*Botrychium dissectum* Spreng.	X	
	Botrychium lanceolatum (Gmelin) Ångstr.	X	
	Botrychium matricariifolium (Döll) A. Braun *ex* W. D. J. Koch	X	
	Botrychium virginianum (L.) Sw.	X	
	Ophioglossum pusillum Raf.	X	
Osmundaceae	*Osmunda cinnamomea* L.	X	X
	Osmunda claytoniana L.	X	X
	Osmunda regalis L.	X	X
Polypodiaceae	*Polypodium virginianum* L.	X	X
Selaginellaceae	*Selaginella apoda* (L.) Spring	X	
	Selaginella rupestris (L.) Spring	X	X
Thelypteridaceae	*Phegopteris hexagonoptera* (Michx.) Fée	X	
	Thelypteris noveboracensis (L.) Nieuwl.	X	X
	Thelypteris palustris Schott	X	X
	Thelypteris simulata (Davenp.) Nieuwl.		X

Table 5. Status of orchids in Needham, Mass. X = present in flora.

Species	Year	
	1885	2002
Arethusa bulbosa L.	X	
Calopogontuberosus(L.)Britton, Sterns & Poggenb.	X	
Coeloglossum viride (L.) Hartm.	X	
Corallorrhiza maculata (Raf.) Raf.	X	
Cypripedium acaule Aiton	X	X
Epipactis helleborine (L.) Crantz		X
Goodyera pubescens (Willd.) R. Br.	X	X
Liparis loeselii (L.) Rich.	X	
Platanthera clavellata (Michx.) Luer	X	
Platanthera lacera (Michx.) G. Don	X	
Platanthera psychodes (L.) Lindl.	X	
Pogonia ophioglossoides (L.) Ker Gawl.	X	
Spiranthes cernua (L.) Rich.	X	
Spiranthes lacera (Raf.) Raf.	X	

The loss of native tree species was relatively small. Tree species lost since 1885 include *Chamaecyparis thyoides* (L.) Britton, Sterns & Poggenb., *Larix laricina* (Du Roi) Koch, *Picea mariana* (Mill.) Britton, Sterns & Poggenb., *Castanea dentata*, *Juglans cinerea* L., and *Platanus occidentalis* L. The tree species found in 2000–2002 but not present in 1885 are primarily introduced, although it is interesting to note that Fuller did not report *Betula populifolia* Marshall, a species now common.

Habitat analysis. Losses of native species were distributed across all habitats (Table 6), with the highest numbers and percentages of lost species occurring in the grassland habitat (58 species, 23.6%) and the rich woods habitat (55 species, 22.4%).

Species of wet and dry fields and pastures have largely disappeared from Needham. These include several *Aster* spp., *Cirsium muticum* Michx., *Carex conoidea* Schkuhr *ex* Willd., *Gentiana andrewsii* Griseb., *Gentianopsis crinita* (Froel.) Ma, *Sisyrinchium angustifolium* Mill., *Pycnanthemum muticum* (Michx.) Pers., *Aletris farinosa* L., *Lilium philadelphicum* L., *Ophioglossum pusillum*, *Platanthera lacera*, *Tridens flavus* (L.) Hitchc., *Polygala cruciata* L., *Rosa caroliniana* L., *Penstemon hirsutus* (L.) Willd., *Selaginella apoda*, *Andropogon gerardii* Vitman, *Sorghastrum nutans* (L.) Nash, and *Xyris torta* Small.

Most of the obligate fen or bog species, including *Chamaecyparis thyoides*, *Larix laricina*, *Picea mariana*, *Myrica gale* L., *Sarracenia*

Table 6. Loss of native plant species by habitat.

Habitat	Number of Native Species	Percent Extirpated (%)
Open Water	17	6.9
Acidic Fen	27	11.0
Emergent Marsh	22	9.1
Red Maple Swamp	22	8.9
Cultural Grassland/Wet Meadow	58	23.6
White Pine/Oak Woods	38	15.5
Rich Woods	55	22.4
Ruderal, disturbed, agricultural	6	2.4
TOTAL	245	100

purpurea L., *Pogonia ophioglossoides Arethusa bulbosa*, *Calopogon tuberosus*, *Menyanthes trifolia* L., *Nymphoides cordata* (Ell.) Fernald, *Eriophorum* spp., *Carex livida* (Wahlenb.) Willd., *C. sterilis* Willd., *Drosera intermedia* Hayne, and *Utricularia inflata* Walter (probably *U. radiata* Small), have been lost, indicating that many fen and bog habitats have disappeared. Some species of other wetland habitats have also been lost, including *Gratiola aurea* Pursh, *Euthamia tenuifolia* (Pursh) Nutt., and *Xyris torta*, all species typical of coastal-plain pondshores or of other pondshores that slope very gradually and are seasonally exposed. *Zizania aquatica* L. has also vanished from the Charles River in Needham.

Most of the rich woods species and species of calcareous rock outcrops [*Staphylea trifolia* L., *Adiantum pedatum*, *Botrychium* spp., *Solidago flexicaulis* L., *Triosteum perfoliatum* L., *Cornus rugosa* Lam., *Carex sparganioides* Muhl. *ex* Willd., *Gymnopcarpium dryopteris*, *Allium canadense* L., *Actaea* spp., *Thalictrum thalictroides* (L.) Eames & B. Boivin, *Geum rivale* L., *Viola pubescens* Aiton, and *Celastrus scandens* L.] also are no longer present.

Invasive exotic species now recognized as significant threats to native communities have been introduced after 1885: *Acer platanoides* L., *A. pseudoplatanus* L., *Ailanthus altissima* (Mill.) Swingle, *Alliaria petiolata* (Bieb.) Cavara & Grande, *Berberis thunbergii* DC., *Cabomba caroliniana*, *Celastrus orbiculata*, *Elaeagnus umbellata*, *Euonymus* spp., *Iris pseudacorus* L., *Lonicera japonica*, *L. morrowii* A. Gray, *Lythrum salicaria*, *Myriophyllum spicatum*, *Phalaris arundinacea*, *Phragmites australis*, *Rhamnus frangula*, and *Rosa multiflora*. *Acer platanoides*, *Lonicera* spp., *C. orbiculata*, *Euonymus alata*, *R. multiflora*, and *Rhamnus frangula* are present at virtually all upland sites regardless of the apparent level of disturbance. *Ailanthus*, *Alliaria*, and

Elaeagnus are characteristic of roadsides and ruderal sites, while the meadows along the Charles River are dominated by *Lythrum salicaria* and *Phalaris arundinacea*. *Wolffia brasiliensis* appears to have replaced *W. columbiana* along the Charles River and in other water bodies. Other exotic species well established in Needham, particularly *Hieraceum sabaudum* L., are not recognized as invasives (Mehrhoff et al. 2003; Randall 1998; Virginia Department of Conservation and Recreation 2003).

Rare species. In 1885, 33 species currently on the Massachusetts List of Endangered and Threatened Species occurred in Needham. None of these species are currently extant. One is now considered Historic [*Castilleja coccinea* (L.) Spreng.]. Seven of these are now listed as Endangered [*Sagittaria subulata* (L.) Buchenau, *Gentiana andrewsii*, *Triosteum perfoliatum*, *Carex livida*, *Galium boreale* L., *Penstemon hirsutus*, and *Viola adunca* Sm.]. Nine are listed as Threatened [*Asclepias purpurascens* L., *Lobelia siphilitica* L., *Carex oligosperma* Michx., *C. sterilis*, *Eriophorum gracile* W. D. J. Koch, *Ophioglossum pusillum*, *Arethusa bulbosa*, *Aristida purpurascens* Poir., and *Sphenopholis pensylvanica* (L.) Hitchc.]. One species is considered of Special Concern [*Conioselinum chinense* (L.) Britton, Sterns & Poggenb.], and 15 are not state-protected but are on the Watch List [*Aster radula* Aiton, *Prenanthes alba* L., *Silene caroliniana* Walter, *Lechea minor* L., *Acalypha virginica* L., *Desmodium cuspidatum* (Muhl. *ex* Willd.) DC. *ex* Loudon, *Lespedeza violacea* (L.) Pers., *Juglans cinerea*, *Utricularia inflata*, *Botrychium lanceolatum*, *B. matricariifolium*, *Coeloglossum viride*, *Polygala verticillata* L., *Ranunculus fascicularis* Muhl. *ex* Bigelow, and *Sparganium angustifolium* Michx.]. Five Watch List species were documented to occur in Needham during this study, one introduced [*Sporobolus compositus* (Poir.) Merr.], and four native (*Carex haydenii* Dewey, *Salix pedicillaris* L., *U. minor* L., and *Wolffia brasiliensis*).

The Massachusetts Natural Heritage and Endangered Species Program (2002) lists 10 state-listed species documented to occur in Needham: *Houstonia longifolia* Gaertn. var. *longifolia*, *Liatris scariosa* (L.) Willd. var. *novae-angliae* Lunell, *Platanthera flava* (L.) Lindl. var. *herbiola* (R. Br.) Luer, *Prenanthes serpentaria* Pursh, *Scirpus longii* Fernald, *Sphenopholis nitida* (Biehler) Scribn., *S. pensylvanica*, *Spiranthes vernalis* Engelm. & A. Gray, *Trisetum spicatum* (L.) Richt., and *Viola brittoniana* Pollard. None of these species were located during the 2000–2002 survey, although *Scirpus longii* and *V. brittoniana* are likely to be present (T. Rawinski, Massachusetts Audubon Society Regional Ecologist, pers. com.).

Fuller (1899) reported that several species, present in 1880, had been lost to development: *Hottonia inflata* Ell., *Polygonella articulata* (L.) Meisn., *Crotalaria sagittalis* L., *Castilleja coccinea*, and *Aletris farinosa*. He listed others that were present in only one site and at risk from extirpation "by what has been termed, not inaptly from our point of view, 'the shabby tide of progress'": *Staphylea trifolia*, *Conioselinum canadense*, *Lonicera villosa* (Michx.) Schult., *Euthamia tenuifolia*, *Andromeda polifolia* L., *Liparis loeselii* (L.) Rich., *Maianthemum trifolium* (L.) Sloboda, *Trisetum spicatum*, *Sphenopholis pensylvanica*, and *Asplenium rhizophyllum*. None of these species were present in 2002.

Species abundance. The native species present in 2002 were categorized by frequency to estimate potential future turnover. Those native species thought to have been planted (*Betula papyrifera*, *Sanguinaria canadensis*) were excluded from the analysis. Over half of the native species (240, or 56.5%) occurred in three or more localities, and are considered to be secure. Some species (58, or 13.7%) occurred in two localities, and 127 native species (29.9%) were found in only a single locality. Species that occurred in one or two localities are considered at risk of loss, and constitute 43.5% of the native flora extant in 2000–2002. Since Fuller did not provide estimates of abundance in his checklist, it is not possible to compare present and historical frequency or abundance.

DISCUSSION

The number of species recorded in Needham (914 taxa in total; 628 extant) is comparable to the results of other studies in New England. Eaton (1974) reported 1151 species in Concord, Massachusetts, a town of comparable size, land use history, and proximity to Boston. Holland and Sorrie (1989) recorded 243 species on a substantially smaller, 17.4 ha area in New Hampshire. Blake (1964) reported 898 species and 113 families in Stoughton, Massachusetts, also comparable to Needham, but Blake's data were collected in 1908–1929, and do not necessarily reflect the current biodiversity. Bertin (2000) recorded 988 species in Worcester, Massachusetts, in an area three times the size of Needham. Weatherbee (1996) reported 1222 taxa of native species and 433 introduced species in Berkshire County, Massachusetts, an area of 2434 square kilometers.

The current percent of introduced species (32%), and the change in the diversity and contribution of alien species over time (118 new species since 1885, when introduced species made up 18.67% of the flora), is also comparable to other studies. Sorrie and Somers (1999) reported that 39% of the Massachusetts flora consists of introduced species, while Bertin (2000) reported 34% in Worcester. Robinson et al. (1994) recorded 33.5% alien species on Long Island, New York, an increase of 100 species from 1930 (26.8%). Weatherbee (1996) reported 27% introduced species in Berkshire County, an increase of 107 species from 1922, when aliens composed 17% of the flora. Drayton and Primack (1996) reported that exotic species increased in abundance from 17% of the flora of the Middlesex Fells to 26% between 1894 and 1993. Eaton (1974) reported that 25% of the species of Concord were exotic.

The pattern of change in native species is similar to other studies, although the percentage of native species lost (44%) is substantially higher than at other locations in New England. In Needham, I documented that 428 of the original native species have been lost, while 109 new native species have been gained. Bertin (2002) found a loss of 18.4% (147 species) of the original flora. Holland and Sorrie (1989) found 27% of native species had been lost since 1911, and documented a turnover of 64 species lost and 57 species gained in what they termed "a continuum of small changes." Drayton and Primack (1996) found that 38% of the flora of the Middlesex Fells, a 400 ha preserve in the suburban Boston area, had been lost in 100 years. This estimate, however, excluded the Cyperaceae, Poaceae, Juncaceae, aquatic families, ferns, and other cryptogams. Weatherbee (1996) documented a loss of only 9.7% (128 species) of the original native flora, with a gain of 35 new species. Robinson et al. (1994) showed the most similar pattern in species change to that of Needham, with a loss of 40.9% of the native flora of Long Island since 1930.

I found some correlation between species loss and habitat loss, with the highest losses (22–24%) of species characteristic of grassland habitats and rich woods. The rich woods community type no longer occurs in Needham. Bertin (2002) did not find higher than average losses for grasslands species, but found the greatest percent of species losses (up to 25%) in bogs, calcareous terrestrial habitats, aquatic habitats, and coniferous forests. Similarly, Drayton and Primack (1996) found the greatest losses of species in open moist habitats. Overlease (1987) described the changes in plant communities in Chester County, Pennsylvania over 150 years, as well as the effects on plant composition. He found similar patterns, particularly in wet meadows and marshes, where invasive species such as *Lythrum salicaria* had become dominant and native species, including *Gentiana andrewsii*, *Gentianopsis crinita*, and *Castilleja coccinea* were extirpated or rare. Robinson et al. (1994) found no correlation between species loss and habitat type, and documented a 40–45% loss of species in all habitat types.

Losses of taxonomic diversity at the generic and family levels in Needham were substantially lower than for Long Island (Robinson et al. 1994) where 46 of the 133 families (35%) and 197 of the 433 native genera (45%) have been lost since 1930. The Long Island study showed that the highest losses were to the group of herbaceous perennials (45%) and the lowest losses to the trees, similar to the results for Needham. Bertin (2002) found the highest losses of species within the same families as in Needham (Menyanthaceae, Ophioglossaceae, Lentibulariaceae, Orchidaceae), although these families still persist in Worcester. Bertin (2002) found also that half of the orchid species in Worcester had been extirpated, and cited numerous studies that have shown the same general pattern that losses of orchids were greater than the overall species loss. Drayton and Primack (1996) documented that 7 of the historical 9 orchid species in the Middlesex Fells had been extirpated. Lamont et al. (1988) found that 40% of the orchids of Long Island (14 of 35 species) had been lost, and that most of the remaining species were known from fewer than 10 populations. *Cypripedium acaule* and *Goodyera pubescens*, the only native orchids remaining in Needham and the Middlesex Fells (Drayton and Primack 1996), were among the most common orchid species remaining on Long Island.

The loss of rare and uncommon taxa in Needham is also similar to patterns observed elsewhere (Bertin 2002). Robinson et al. (1994) showed that uncommon plants and plants of conservation concern had been lost at a higher percentage than common species, and found that overall abundance was the one variable tested that was significantly correlated with the persistence of a species.

Why have so many species vanished? There are likely to have been multiple causes of species loss, which cumulatively have reduced the native flora of Needham by 44%. Habitat loss and habitat change appear to be the two most important factors. Development has undoubtedly resulted in the loss of habitat. As discussed above, agricultural fields, pastures and grasslands, and rich woods have largely disappeared from Needham. This agricultural land may have protected a diversity of habitats, including woodlots, wetlands, and hedgerows as well as pastures (Robinson et al. 1994) and may have made a significant contribution to overall plant species diversity. Although large tracts of oak woods communities remain in Needham, much of this habitat has also been developed, which may have resulted in the loss of some species with small population sizes or limited distributions. Some water bodies, notably Blacksmith Pond, reported by Fuller to have populations of *Isoetes engelmannii* and *Nymphoides cordata* (Ell.) Fernald, were drained and filled in the early 20th century.

Changes in habitat due to succession are also likely to have resulted in floristic change. O'Keefe and Foster (1998) noted that the peak of deforestation in Massachusetts occurred around 1860, when 70% of the land was cleared. With the decline in agriculture in the second half of the 19th century, forests rebounded in most of the state. Fuller (1895 unpubl. ms.) sampled this transitional period between the peak of agriculture and the recovery of forest, although expansion of the Boston suburbs was also beginning to affect land use. When abandoned as pastures, wet meadows and fens develop into shrub swamp and red maple swamp wetlands. Upland fields and pastures develop into successional white pine-oak forest. Both examples of natural community change result in the loss of plant species adapted to open communities.

Other factors may also contribute to the loss of species. Epidemic diseases have resulted in the loss of *Castanea dentata* (as a tree, although it is still present as a shrub or short-lived sapling) and *Juglans cinerea*. Invasive species are also likely to have resulted in floristic change, although this is not well documented in the literature. Many meadows along the Charles River, formerly containing diverse communities of grasses, rushes, sedges and orchids, today are dominated by *Lythrum salicaria* or by dense monodominant stands of *Phalaris arundinacea*. Neither species was present in 1885. The effects of introduction of *Rhamnus frangula*, *Rosa multiflora*, or *Celastrus orbiculata* on native plant communities are not known. Gundale (2002) has suggested that certain exotic earthworms (*Lumbricus rubellus*) reduce the depth of the organic horizon which the mycoheterotrophic gametophytes of *Botrychium mormo* W. H. Wagner and other *Botrychium* species require, and that the removal of the organic horizon has lead to the local extirpation of *B. mormo*. This factor may account for the extirpation of *Botrychium* species in Needham, and may also affect the distribution of mycotrophic orchid species.

The risk of loss of species in the future is due to factors of development (anthropogenic habitat loss), random stochastic events, and habitat change due to succession, invasive species, or management. Species loss due to development is likely to be low, as the majority of remaining undeveloped locations are in conservation ownership (Metropolitan District Commission, Trustees of Reservations, Town of Needham Conservation, or Town Forest lands). However, town-owned lands not dedicated to conservation or parkland could be converted to other uses such as schools or low-income housing. Wetland habitats are protected from development by stringent state and local wetlands protection laws, and by the extensive areas in the Army Corps of Engineers Natural Valley Storage program. Minor changes in management of public lands can affect populations; during this study, the number of populations of *Ceanothus americanus* L. was reduced from two to one as a result of cemetery expansion. Several at-risk species [*Desmodium nudiflorum* (L.) DC., *D. paniculatum* (L.) DC., *Bartonia virginica* (L.) Britton, Sterns & Poggenb., *Carex cumulata* (L. H. Bailey) Mack., and *C. vesicaria*] occur in relatively small populations and are restricted to the grassland community over a natural gas pipeline. If the pipeline needed to be replaced, excavation and construction could result in the loss of these species.

The continued expansion of invasive species and their increasing dominance in many communities could also result in the loss of native species. As demonstrated by numerous researchers, small populations are vulnerable to stochastic change, decrease in size, and localized extinctions. These effects may be offset if there are "source" populations close enough to allow recolonization of suitable habitat, and if habitat fragmentation does not prevent seed dispersal between habitats. However, for many of the at-risk species in Needham, such as *Drosera rotundifolia* L. and *Utricularia minor*, there are not likely to be large source populations within dispersal distance due to their specialized habitat requirements and the degree of development of the surrounding communities. These factors create the potential that, in the next century, researchers may find that the diversity of native vascular plants has declined by a further 43%.

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NEW CYCAD (ZAMIACEAE) REPORTS FROM CHIAPAS, OAXACA, AND TABASCO, MEXICO

Andrew P. Vovides

Instituto de Ecología, A.C., Apdo Postal 63,
Xalapa, Veracruz, 91000 Mexico
e-mail: vovidesa@ecologia.edu.mx

Miguel Angel Pérez-Farrera

Universidad de Ciencias y Artes del Estado de Chiapas,
Calz. Samuel León Brindis 151, A.P. 57, Tuxtla Gutierrez,
Chiapas 29000, México

Carlos Iglesias and Sergio Avendaño Reyes

Instituto de Ecología, A.C., Apdo Postal 63,
Xalapa, Veracruz, 91000 Mexico

Silvia Salas Morales

SERBO, A.C., Porfirio Díaz 211, Oaxaca 68000, Mexico

ABSTRACT. New localities are reported for three cycad species in Mexico. *Ceratozamia miqueliana* was found in montane rainforest in western Chiapas and *C. norstogii* was found in dry tropical oak forest mixed with elements of seasonally dry tropical forest in eastern Oaxaca. *Zamia splendens* was found on karstic topography in lowland tropical rainforest in the hills of southern Tabasco. The additional data are encouraging regarding prospective survival of the species, but small population sizes make them vulnerable to any habitat disturbance.

Key Words: Cycads, *Ceratozamia*, *Zamia*, Zamiaceae, flora, endangered species, Mexico

During the revision of the genus *Ceratozamia* in southern Mexico, we came across a population of *Ceratozamia* with wide and oblanceolate leaflets. The plants were medium-sized to large with epigeal trunks of up to 50 cm long with an open crown of about nine spreading leaves. This was a small population of approximately 200 plants in montane rainforest in Chiapas. Upon comparing this population with the recently described *C. zoquorum* Pérez-Farrera, Vovides & Iglesias from the northern mountains of Chiapas, we found that it differed in leaf, leaflet, and cone morphology. Upon further examination of the plants and herbarium vouchers, we came to the conclusion that the individuals in this population belonged in *C. miqueliana* H. Wendl. (Table 1). The

Table 1. Comparison of *Ceratozamia miqueliana*, *C. norstogii*, and *C. zoquorum*.

Species	Leaflets and Rachis	Megastrobilus Peduncle (at maturity when fresh)
C. miqueliana	Obovate to widely oblanceolate, chartaceous, rachis not spirally twisted	Erect
C. norstogii	Linear, coriaceous, rachis spirally twisted	Erect
C. zoquorum	Oblong to oblanceolate, very coriaceous, rachis not spirally twisted	Divaricate to descending

origin of the specimens of *C. miqueliana* given by Wendland (1854) was *patria ignota*, or country unknown. However, the description by De Candolle (1868) and an illustration of this species in Dyer (1882–1886), as well as a mention of the country of origin, conformed to plants from the neotype locality of Stevenson and Sabato (1986) in Veracruz, Mexico (see also Vovides et al. 1983).

Ceratozamia norstogii D. W. Stev., described from a locality in Chiapas (Stevenson 1982) and commented on by Pérez-Farrera et al. (2001), is a very distinct cycad with an erect, unbranching trunk. Its leaves have narrow, channeled leaflets arranged on a spirally twisted rachis. A small population of less than 100 individuals of this distinct species was found in dry tropical oak forest mixed with elements from tropical deciduous forest in eastern Oaxaca at elevations between 800–1600 m.

During other explorations into Tabasco we came upon a *Zamia* with large shiny leaflets in the southern regions of the state. It had erect to arching red-brownish emergent leaves and large elliptic to oblanceolate, heavily serrulate leaflets with exceptionally shiny adaxial cuticles. This plant differed greatly from *Z. loddigesii* Miq. and *Z. cremnophila* Vovides, Schutzman & Dehgan (Table 2), hitherto the only zamias known from Tabasco. *Zamia loddigesii* has short, erect leaves with linear-lanceolate to lanceolate leaflets not exceeding 2 cm wide, and *Z. cremnophila* has long, decumbent leaves with long-lanceolate to oblong leaflets over 2 cm wide. Upon further examination we concluded that this *Zamia* belonged in *Z. splendens* Schutzman, originally described from Chiapas (Schutzman 1984).

Table 2. Comparison of *Zamia cremnophila*, *Z. loddigesii*, and *Z. splendens*.

Species	Leaflets	Megastrobili (at maturity when fresh)
Z. cremnophila	Narrowly-lanceolate, imbricate, not glossy	Dark brown, tomentulose
Z. loddigesii	Linear-lanceolate to lanceolate, not imbricate, not glossy	Light brown, tomentulose
Z. splendens	Long-elliptic, oblong, oblanceolate, not imbricate, glossy	Dark green, glabrescent

DESCRIPTIONS

Ceratozamia miqueliana H. Wendl., Index Palm. 68. 1854. NEOTYPE: MEXICO. Veracruz: Santiago Tuxtla, 5 Jul 1983, *D. W. Stevenson 542F* (NY!).

Medium-sized plants with epigeal trunks becoming cylindrical with age, 6–15 cm in diameter and up to 40 cm or more long. Leaves 4–21, spirally arranged, forming an open crown, glaucous and pilose when young, 118–224 cm long, 40–70 cm wide; petiole and rachis ascending to spreading, armed with short to long stout prickles. Leaflets 9–20, obovate to widely oblanceolate, more or less chartaceous, with the proximal margin repand and sometimes coarsely unidentate near apex, 23.5–36.4 cm long, 4–6.7 cm wide, apex strongly asymmetrical, number of veins 24–39. Microstrobilus cylindrical to narrowly conical, yellow to light green, 32–45.5 cm long, 3.2–4 cm in diameter, peduncle erect, 0.8–1.5 cm long, 0.5–1.6 cm in diameter, tomentose; microsporophylls cuneiform, 1.1–1.7 cm long, 0.8–1.3 cm wide, distal face hexagonal, bicornate, long axis 0.4–0.6 cm, short axis 0.2–0.4 cm, horns short, ca. 0.2 cm, distance between horns 0.4–0.6 cm. Megastrobilus cylindrical, dark to olive-green, 28.5–30 cm long, 10–12 cm in diameter, peduncle erect at maturity, 4.5–5.2 cm long, 3.4–3.7 cm in diameter; megasporophylls peltate, 5–5.7 cm long, 2.3–2.5 cm wide, distal face hexagonal, bicornate, long axis 3.7–5.5 cm, short axis 2.2–2.6 cm, horns short, ca. 0.2 cm, distance between horns 1.3–2.2 cm. Seeds 2.9–3.3 cm long, 1.4–1.7 cm in diameter.

Coning period is from February to August.

SPECIMENS EXAMINED: MEXICO. Chiapas: Ocozocoautla de Espinosa, 23 Oct 1997, *R. A. Galdámez 04* (UNICACH). Veracruz: Moloacán, 19 Dec 1974, *J. D. Rees 1657, 1658* (XAL, MEXU). Tabasco: Huimanguillo, 22 Feb 1972, *H. Puig 638* (MEXU); 2 Mar 1972, *H. Puig 657* (MEXU); 4 Apr 1972, *H. Puig 751* (MEXU).

Ceratozamia norstogii D. W. Stev., Brittonia 34: 181–184. 1982. TYPE: MEXICO. Chiapas: Rancho Fenix, Mar–Apr 1925, *C. A. Purpus 6* (HOLOTYPE not seen: NY; ISOTYPE: US!).

Medium to large plants with partially subterranean, subglobose, unbranched trunks becoming cylindrical with age, up to 22 cm in diameter and 130 cm long. Leaves 15 or more, forming an erect crown, pinnate, 70–135 cm long, 52–95 cm wide. Petiole and rachis spirally twisted. Leaflets 33–65 pairs, linear, heavily channeled, 22.8–57 cm long, 0.3–0.5 cm wide. Microstrobilus conical, olive-green to light green when immature, creamy yellow to pale yellow when mature, 25–36 cm long, 3.8–6.2 cm in diameter, peduncle tomentose, ca. 4.4–7.2 cm long; microsporophylls cuneiform, 1.6–1.9 cm long, 0.7–1.2 cm wide, distal face hexagonal, bicornate, short axis 0.5–0.6 cm, long axis 0.7–1.2 cm, horns 0.1–0.2 cm long, distance between horns 0.2–0.5 cm. Megastrobilus cylindrical to barrel-shaped, olive-green when immature, dark brown when mature, 14.5–37 cm long, 7.4–13 cm in diameter, peduncle tomentose, 6.1–10 cm long, ca. 1.5 cm in diameter; megasporophylls peltate, 2.8–4 cm long, distal face hexagonal, bicornate, short axis 1.3–1.4 cm, long axis 2.3–2.2 cm, horns 0.3–0.9 cm long, distance between horns 0.6–1.2 cm. Seeds ovoid angular, 2.4–2.9 cm long, 1.5–2.1 cm in diameter, with 6–11 radial lines radiating from the micropile.

Coning period is from March to October.

SPECIMEN EXAMINED: MEXICO. Oaxaca: San Miguel Chimalapa, Mar 1996, *S. Salas-Morales & E. Torres H. 1173* (SERBO).

Zamia splendens Schutzman, Phytologia 55: 299–304. 1984. TYPE: MEXICO. Chiapas: Cultivated, Apr 1984, *J. Watson 1870* (HOLOTYPE: NY!; ISOTYPES: FLAS, MEXU).

Small to medium plants up to 1 m tall (2 m under cultivation) with subterranean stems, sometimes branching. Leaves 2–4 per crown, bright red to salmon pink or green at emergence, up to 80 cm or more long, 18–80 cm wide. Leaflets 4–10 pairs, long-elliptic to oblong or oblanceolate, 9–40 cm long, 3–10 cm wide, margin serrulate-denticulate. Microstrobili two or more per stem apex, conic, light brown tomentulose, up to 5 cm long and 1.3 cm in diameter; peduncles 8–14 cm long, strongly decumbent and pushing the cone into loose surface humus; microsporophylls cuneate, 0.4–0.5 cm long, distal face hexagonal in outline, with smooth dome-shaped surface, long axis 0.3–0.4 cm, short axis 0.15–0.3 cm. Megastrobili subglobose or ellipsoid, with apical projection, up to 8 cm long and 4.5 cm in diameter, dark green, glabrescent; megasporophylls peltate, 1.8–2.2 cm long, distal face hexagonal, with dome-shaped surface, long axis 1.8–2 cm, short axis 1–1.5 cm. Seeds obovoid, sarcotesta pink to red when ripe, ca. 1.5 cm long and 0.6 cm in diameter.

SPECIMENS EXAMINED: MEXICO. Tabasco: Macuspana, 30 May 2000, *A. Vovides, C. Iglesias & V. Luna 1344* (XAL); Teapa, 18 Oct 1993, *C. Hubbuch & T. Walters 171A* (FTG, XAL). Chiapas: Tila, 30 May 2000, *A. Vovides, C. Iglesias & V. Luna 1340* (XAL).

DISCUSSION

Ceratozamia miqueliana was considered endemic to southern Veracruz. It is extremely rare there and known from only three localities. It was reported for the neighboring state of Tabasco in the early 1970s (*H. Puig 638, 657, 751*, MEXU). We returned recently to the Puig locality and other surrounding areas in Tabasco to search for this species; none was found, and we conclude that the species has probably been extirpated in Tabasco. However, the occurrence of *C. miqueliana* in a newly discovered locality in Chiapas, thus increasing its known range of distribution, has increased the probability of the species' survival. *Ceratozamia miqueliana* comprises a complex of species with obovate, oblanceolate to widely oblanceolate leaflets of which *C. euryphyllidia* Vázq. Torres, Sabato & D. W. Stev., *C. zoquorum*, and an undescribed species of *Ceratozamia* are members. All these species appear to be endemic to the region of highest precipitation in lowland Mexico that comprises the "arc refuge" area of Wendt (1987), extending from northern Oaxaca through southern Veracruz and northern Chiapas. Southeastern Mexico is rich in endemics and includes some Pleistocene refuges (González and Vovides 2002; Toledo 1982).

Ceratozamia norstogii and *Zamia splendens*, both thought to be endemic to Chiapas, are known to have wider distributions, extending into Oaxaca and Tabasco respectively. However, the small size of the population in Oaxaca renders it particularly vulnerable to habitat disturbance or commercial collecting. *Zamia splendens* in Tabasco is under great threat owing to limestone exploitation for cement manufacture in one of its more important localities.

Unexpected findings are more common during explorations into the more inaccessible and often rocky zones, especially in areas of rich biodiversity within Veracruz and Chiapas. Owing to the absence of recent explorations, rare endemics have been thought to have become extinct because of their poor representation in herbaria (Sosa et al. 1998). Precise locality information on these cycads has been purposely omitted in order to avoid illegal commercial collecting of these endangered species.

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NEW RECORDS OF VASCULAR PLANTS FOR OHIO AND CUYAHOGA COUNTY, OHIO. PART II

GEORGE J. WILDER

Division of Ecological Studies, Florida Gulf Coast University,
10501 FGCU Boulevard South, Fort Myers, FL 33965-6565
e-mail: gwilder@fgcu.edu

MARTHA R. MCCOMBS

28260 Pine Haven Way, Unit 85, Bonita Springs, FL 34135
e-mail: mccombsmarthar@aol.com

ABSTRACT. Twenty-one species and seven hybrids of vascular plants are listed as new records for Cuyahoga County, Ohio, and fourteen taxa of vascular plants, including two found outside of Cuyahoga County, constitute new Ohio records. One species is first reported for North America. Approximately 37 percent of the 30 taxa are native to the northeastern United States. Five species are designated by the Ohio Division of Natural Areas and Preserves as endangered, threatened, or added, collectively.

Key Words: Ohio, alien species, native species, new records, hybrids

This is the last of a series of papers listing species of vascular plants newly recognized within Ohio and Cuyahoga County, Ohio (Wilder and McCombs 1999, 2002). Cuyahoga County borders the south shore of Lake Erie and ranks among the northernmost of Ohio's 88 counties. Wilder and McCombs (1999) reported two Ohio records: *Hieracium* ×*flagellare* Willd. (a taxon previous workers had collected in Ohio, but had misidentified as *H. pilosella* L.) and *Rhamnus utilis* Decne. Wilder and McCombs (2002) reported 24 additional taxa as new for Ohio, and listed 222 species and 14 hybrids as new to Cuyahoga County. Wilder and McCombs (2002) also cited the recent floristic contributions of other workers and briefly characterized Cuyahoga County. We add to the citations, aforementioned, the accounts of Cooperrider et al. (2001) and Kartesz and Meacham (1999).

MATERIALS AND METHODS

We collected voucher specimens of all species listed herein, between and including 1991 and 2002. Specimens cited belong to the Wilder and McCombs Herbarium, housed at Florida Gulf Coast University (Fort Myers, FL). Species were determined as new to Ohio and/or Cuyahoga

County using Andreas (1989), Braun (1961, 1967), Cooperrider (1982, 1995), Cusick and Silberhorn (1977), Easterly (1964), Fisher (1988), Kartesz and Meacham (1999), Koch (1974), McCance and Burns (1984), Moldenke (1944), Rabeler and Cusick (1994), Raven and Gregory (1972), Schaffner (1932), Vincent and Cusick (1998), Wagner and Beitel (1993), Walters (1995), Weishaupt (1971), and the Ohio Natural Heritage Database. Nomenclature mostly follows Kartesz (1994), but for some taxa synonyms are given that appear in other relevant publications.

Taxa were determined as either native or alien to the northeastern United States based on information from one or more of the following sources: Bailey (1949), Fernald (1950), Gleason and Cronquist (1991), Kartesz and Meacham (1999), Rabeler (1988), Rehder (1940), and Staff of the Liberty Hyde Bailey Hortorium (1976). *Eragrostis tephrosanthos* was difficult to classify as either native or alien. We call it alien, based on Gleason and Cronquist's (1991) characterization of it as "... a weed mainly of trop. N. Amer ..." occurring "... rarely and sporadically with us;" however, Kartesz and Meacham (1999) reported *E. tephrosanthos* in numerous states of the southern U.S.A., fewer states of the northern U.S.A., and in Ontario.

RESULTS

We report 14 new Ohio records of vascular plants: nine species of seven families (*Ageratum houstonianum*, *Calamagrostis epigeios*, *Geum urbanum*, *Hieracium sabaudum*, *Impatiens holstii*, *Juniperus horizontalis*, *Lepidium oblongum*, *Rapistrum rugosum*, *Trifolium fragiferum*) and five hybrids of four families (*Carex debilis* × *C. virescens*, *Chrysanthemum* ×*superbum*, *Lolium* ×*festucaceum*, *Rumex* ×*confusus*, *R. obtusifolius* × *R. patientia*). All taxa were collected within Cuyahoga County except *Calamagrostis epigeios* (Summit Co.) and *Trifolium fragiferum* (Sandusky Co.). *Impatiens holstii* is newly reported for North America (Kartesz and Meacham 1999). Twenty-one species and seven hybrids, representing 15 families of vascular plants, are reported as new to Cuyahoga County (Appendix). Only approximately 37% of the 30 taxa reported here are native to the northeastern United States (Appendix), a result comparable to the approximately 39% of records cited by Wilder and McCombs (2002).

Five newly reported species are cited in the *Rare native Ohio plants 2000–2001 status list* (Ohio Division of Natural Areas and Preserves 2000). These species are listed as endangered (*Carex lucorum*, *Ribes* *missouriense, Solidago puberula*), threatened (*Panicum philadelphicum*), or added (*C. brevior*; "added" is defined in the Appendix).

DISCUSSION

Various records require explanation. Cooperrider et al. (2001) listed *Juniperus horizontalis* as a deletion from the Ohio flora; thus it is surprising to again report this species from Ohio. The species is both native to the northeastern United States and cultivated (Gleason and Cronquist 1991; Rehder 1940). Our collections are from an ample population growing in a wild region of Shaker Median Park (Beachwood, OH).This region, cleared of vegetation years ago, now exhibits native species and escaped plants of numerous non-native cultivated species (e.g., *Pyracantha coccinea*; Wilder and McCombs 2002); thus, we suspect that our *J. horizontalis* is escaped, rather than native. Anton A. Reznicek (MICH) verified the identity of our specimens and those of many other taxa listed in the Appendix.

Solidago puberula is presently known from one locality in Ohio (Highland Heights, Cuyahoga Co.), where it was found by the senior author (Appendix). The species was first located in Ohio, in Pepper Pike (Cuyahoga Co.), by Ann Malmquist in 1994, but her collection locality was subsequently developed and destroyed (James K. Bissel, CLM, pers. comm.). *Solidago puberula* has been formally reported for Ohio (Cooperrider et al. 2001; Ohio Division of Natural Areas and Preserves 2000); however, no published record exists for the species in Cuyahoga County. It is attributed to the County within the Ohio Natural Heritage Database, but this Database is neither online nor otherwise directly accessible to the public.

Ribes missouriense is both native to Ohio and cultivated (Braun 1961; Rehder 1940). Our material is from a clump of this species growing in woods by West Creek (Parma, OH). We cannot determine whether the clump is indigenous or escaped from cultivation. Our new record from Cuyahoga County represents a substantial range extension within Ohio, because previous reports are from the southwestern extremity of the State. Braun (1961) stated that the general range of this species was to the west of Ohio and that it was known in Ohio from two Hamilton County collections. McCance and Burns (1984) subsequently stated for Ohio that "There is a single population extant in Butler County. A pre-1960 specimen exists from Hamilton County." Presently, the species is recorded within the Ohio Natural Heritage Database from Brown, Butler, Clermont, and Hamilton Counties (James McCormac, Ohio

Dept. of Natural Resources – Div. of Natural Areas and Preserves, pers. comm.).

Carex lucorum was discovered in Ohio in 1993. Before the present find in Parma (Cuyahoga Co.) it was known solely from the Oak Openings region of Lucas County, where it grew in areas that are regularly burned (Ohio Natural Heritage Database, James McCormac, pers. comm.). *Carex lucorum* has now been documented from five locations within Lucas County (Timothy Walters, Consultant, The Mannik & Smith Group, Maumee, OH, pers. comm.). The species exhibits considerable similarity to *C. pensylvanica* Lam., and these taxa differ from each other primarily in the length of the perigynium beak (Cusick 1992; Voss 1972). Possibly, some previous workers observed *C. lucorum* in Ohio, but misidentified it as *C. pensylvanica*. Before the initial discovery of 1993, Cusick (1992) remarked presciently that the species "... should be sought in Ohio in the Oak Openings and on the Appalachian Plateau." The Parma locality is within the northern margin of the Plateau (Figure 3 in Andreas 1989).

There have been few previous reports for Ohio for certain other species listed here for Cuyahoga County. Cooperrider (1995) stated that *Gaura longiflora* "was collected once, in 1960, as an adventive weed in Lorain County," and that the species is native from Illinois and Iowa south to Texas. Specimens we collected grew on insolated urban land. Koch (1974) listed *Eragrostis tephrosanthos* for Ohio, but specified no county therein. We located a small population of plants on railroad ballast in urban Cleveland.

It is striking that we acquired three *Rumex* hybrids in Cuyahoga County. All three parental species grow there (*R. crispus*, *R. obtusifolius*, *R. patientia*), but *R. patientia* is essentially confined to urban Cleveland. The hybrids occurred either partly or entirely within urban Cleveland. We found Mitchell and Dean (1978) useful for identifying certain of the hybrids.

The present report of *Carex debilis* × *C. virescens* increases to four the number of *Carex* hybrids known from Ohio. Wilder and McCombs (2002) previously reported *C. albicans* var. *albicans* × *C. umbellata*. Cooperrider et al. (2001) cited *C.* ×*subimpressa* (*C. hyalinolepis* × *C. pellita*) and *C.* ×*sullivantii* (*C. gracillima* × *C. hirtifolia*).

We recognize *Eragrostis tephrosanthos* herein, rather than the more broadly defined *E. pectinacea*. We cite the narrowly defined species to signify the existence in Cuyahoga County of a morphological variant that would remain unspecified solely by citation of the broadly circumscribed taxon. We do not imply that narrow species circumscriptions are more valid. Gleason and Cronquist (1991) and Voss (1972) recognized *E. tephrosanthos*, whereas, Kartesz (1994) recognized *E. pectinacea*.

Certain escaped species require comment. *Ageratum houstonianum* and *Impatiens holstii*, found growing on an exposed portion of creek bed (West Creek in Parma), might not permanently survive the harsh winters of Cuyahoga County. Also, *Cotoneaster divaricatus* grows abundantly in Shaker Median Park (Beachwood), within the same wild, insolated terrain containing *Juniperus horizontalis* and other escaped species. In accordance with these observations, Zika (2002) reported 50–200 individuals of *C. divaricatus* naturalized within a one-mile radius of a point within Cotuit, Massachusetts. He characterized the seeds that produced these individuals as apparently bird-sown.

Certain presently reported taxa probably no longer survive at our original collection localities: *Carex brevior*, *Chenopodium simplex*, *Eragrostis tephrosanthos*, *Lolium ×festucaceum*, *Lepidium oblongum*, and *Rapistrum rugosum*. Habitat destruction is largely to blame, including bulldozing and spraying with herbicide. Some taxa, particularly *L. ×festucaceum* and *R. rugosum*, might therefore be extirpated within Ohio and/or Cuyahoga County. Wilder and McCombs (2002) discussed habitat destruction and the probable loss of additional species within Cuyahoga County.

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APPENDIX

SPECIES AND HYBRIDS THAT REPRESENT NEW RECORDS FOR OHIO AND CUYAHOGA COUNTY, OHIO

Data are presented in the following order after the name of a species or hybrid: relevant synonym(s) (between brackets); designation, if any, in the *Rare native Ohio plants 2000–2001 status list* (Ohio Division of Natural Areas and Preserves 2000); "Added species" signifies "a native Ohio plant species which has recently been added to the Natural Heritage Program rare plant inventory; sufficient information has not yet been obtained to determine the Ohio endangerment status;" habitat(s); the Wilder and McCombs collection number of a representative collection together with the municipality of this collection; any additional municipality(ies) represented by collections in the Wilder and McCombs Herbarium (between parentheses). * = alien to the northeastern United States. SR = state record, species and hybrids newly reported for Ohio; remaining species and hybrids are new solely to Cuyahoga County. Abbreviations represent municipalities: B, Brecksville; Bc, Beachwood; Bk, Brooklyn; BkH, Brooklyn Heights; BP, Brook Park; BV, Bay Village; C, Cleveland; CH, Cuyahoga Heights; Cl, Clyde; ClH, Cleveland Heights; EC, East Cleveland; GM, Gates Mills; HH, Highland Heights; M, Mayfield; MH, Maple Heights; P, Parma; SaH, Sagamore Hills; St, Strongsville; W, Westlake. A dash between abbreviations signifies collection(s) made by the boundary between municipalities.

PTERIDOPHYTES

LYCOPODIACEAE

Lycopodium ×habereri House [*Diphasiastrum ×habereri* (House) Holub; *Lycopodium digitatum* Dill. × *L. tristachyum* Pursh] – Meadow where both parental species occur; *15255*, HH.

GYMNOSPERMS

CUPRESSACEAE

Juniperus horizontalis Moench – SR. Probable escape in wild, insolated portion of Shaker Median Park; *14679*, Bc.

MONOCOTYLEDONS

CYPERACEAE

Carex brevior (Dewey) Mack. *ex* Lunell – Added species; insolated land by railroad tracks; *13760*, MH.

Carex debilis Michx. × *C. virescens* Muhl. *ex* Willd. – SR. Disturbed land near trail extending from Oxbow Lane southward to beaver pond, North Chagrin Reservation; *4284*, GM-M.

Carex lucorum Willd. *ex* Link – Endangered; open woodland within State Road Park; *15981*, P.

POACEAE

**Calamagrostis epigeios* (L.) Roth – SR. Dense population bordering Hike and Bike Trail, Cuyahoga Valley National Recreation Area; *4805*, SaH (Summit Co.).

**Eragrostis tephrosanthos* J. A. Schultes [= *E. pectinacea* (Michx.) Nees *ex* Steud. var. *miserrima* (E. Fourn.) J. Reeder] – Small population along railroad tracks; *2536*, C.

**Lolium ×festucaceum* Link [= ×*Festulolium holmbergii* (Dörfl.) P. Fourn.; *Festuca arundinacea* Schreb. × *Lolium perenne* L.] – SR. Disturbed area within Forest Hill Park; *2639*, ClH-EC.

Panicum philadelphicum Bernh. *ex* Trin. – Threatened; edge of dirt road within Mill Stream Run Reservation (growing together with *Eragrostis frankii* C. A. Mey.); *15169*, St.

DICOTYLEDONS

ACERACEAE

**Acer tataricum* L. – Along railroad tracks; *14828*, C.

ASTERACEAE

*_Ageratum houstonianum_ Mill. – SR. Exposed portion of creek bed within West Creek Preserve; _15120_, P.

*_Chrysanthemum ×superbum_ Bergmans _ex_ J. W. Ingram – SR. Insolated, disturbed area within West Creek Preserve; _15045_, P.

*_Hieracium sabaudum_ L. – SR. Along railroad tracks; meadow within Forest Hill Park; _8469_, Bk (C, C-EC, EC, BV-W, MH).

Solidago puberula Nutt. – Endangered; peripheral portion of meadow; _8919_, HH.

BALSAMINACEAE

*_Impatiens holstii_ Engl. & Warb. – SR. Exposed portion of creek bed within West Creek Preserve; _15119_, P.

BRASSICACEAE

*_Iberis umbellata_ L. – Exposed portion of creek bed within West Creek Preserve; disturbed land at forest edge; second-growth woodland; _15357_, P (C).

*_Lepidium oblongum_ Small – SR. On railroad ballast; _6801_, C.

*_Rapistrum rugosum_ (L.) All. – SR. Railroad ballast; _5276_, C.

CARYOPHYLLACEAE

*_Stellaria pallida_ (Dumort.) Piré – In lawn; _14630_, Bk (C).

CHENOPODIACEAE

Chenopodium berlandieri Moq. – On railroad ballast beneath bridge and away from bridge; disturbed, insolated urban land; insolated land along road; dump; _9044_, C (ClH-EC, EC).

Chenopodium simplex (Torr.) Raf. [= _C. gigantospermum_ Aellen] – Disturbed, insolated land within West Creek Preserve; _15086_, P.

FABACEAE

*_Trifolium fragiferum_ L. – SR. In lawn on west side of Commodore Perry Service Area, south side of I 90; _16226_, Cl (Sandusky Co.).

GROSSULARIACEAE

Ribes missouriense Nutt. – Endangered; open woodland within West Creek Preserve; _15955_, P.

LAMIACEAE

*_Satureja hortensis_ L. – By creek within West Creek Preserve; _15153_, P.

ONAGRACEAE

Gaura longiflora Spach – Insolated urban land; _15203_, BP (C).

POLYGONACEAE

*_Rumex ×acutus_ L. [_R. crispus_ L. × _R. obtusifolius_ L.] – In field; along path and dirt road; on manure pile; _7724_, C (B, CH, HH). A forma with red mature valves also was collected (terminus of a railroad bridge over Cuyahoga River; _13851_, BkH).

*_Rumex ×confusus_ Simonk. [_R. crispus_ L. × _R. patientia_ L.] – SR. Along Riverbed Rd. ("The Flats"); _4359_, C.

*_Rumex obtusifolius_ L. × _R. patientia_ L. – SR. Along Riverbed Rd. ("The Flats"); _4363_, C.

ROSACEAE

**Cotoneaster divaricatus* Rehder & E. H. Wilson – Escape in wild, insolated portion of Shaker Median Park; *14843*, Bc.

**Geum urbanum* L. – SR. Lawn; dry slope along railroad tracks; wooded area of railroad land; *5652*, C (ClH).

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NEW ENGLAND NOTE

ARALIA SPINOSA: AN INTRODUCED WOODY SPECIES WITH INVASIVE POTENTIAL IN MASSACHUSETTS

Tad M. Zebryk
63 Hillside Drive, East Longmeadow, MA 01028

Aralia spinosa L. (common names: Devil's Walking-Stick; Hercules'-Club), a common and easily recognized tall understory shrub found in moist thickets and woodland borders throughout the southeastern and south-central states (Godfrey 1988), has been recorded only sparingly in southern New England (Magee and Ahles 1999; Seymour 1982). In Massachusetts, *Aralia* is known from a few sites in Suffolk and Norfolk counties (eastern coastal Massachusetts), and farther inland from Hampden and Hampshire counties (Ray Angelo, NEBC Herbarium, pers. comm.). Not considered a native species in southern New England, all known collections are apparently derived from naturalized populations originating from introduced plantings. Peattie (1950) observed that *Aralia* was a popular cultivated species during the Victorian period, when it was much favored as a horticultural curiosity because of its unusual growth habit (i.e., the umbrella-like arrangement of large, bi- to tripinnate compound leaves clustered at the top of a prickly, sparingly branched stem).

In early October 1985, while visiting the Metropolitan District Commission's (MDC) Quabbin Reservation in Ware, Hampshire County, Massachusetts, I observed approximately 30 *Aralia spinosa* stems in the vicinity of an old cobblestone home foundation near Gate 24 south of Administration Road. Presumably, *Aralia* was planted by the occupants of the old home site, which was abandoned following the dissolution and incorporation of the former Town of Enfield into the Quabbin Reservation as part of reservoir construction in the late 1930s. Occupying an understory position under a tall canopy of mesic mixed hardwoods including *Quercus rubra* L., *Q. velutina* Lam., *Fraxinus americana* L., and *Prunus serotina* Ehrh., most of the *Aralia* stems were found near open, relatively well-lit portions of the dirt service road passing by the old home site. The *Aralia* stems along the road were observed to be laden with fruits (small drupes), which were being actively consumed by robins on the day of the site visit.

Upon revisiting the site in late August 2002, after the passage of 17 years, it was readily apparent that the *Aralia spinosa* population had proliferated remarkably both in terms of numbers of stems and areal extent, particularly in an area of recently logged, regenerating hardwood forest just west of the dirt road mentioned above. Occurring in a gently sloping, well-drained loamy valley floor measuring approximately 400 ft. long × 150 ft. wide, an estimated 1000–2000 *Aralia* stems formed a near-monoculture over much of the area (*T. M. Zebryk 7878*, NEBC). Stem densities for the *Aralia* population were very high, with most stems being separated by a horizontal distance ranging from 1–3 ft. on center. Stem diameters at breast height (DBH) ranged in size from 0.5–3 in.; DBH for the majority of stems was 2 in. Average height for the *Aralia* stems was about 15 ft. Spot sampling with a 5 basal area factor Cruz-All in the center of the near-monoculture indicated a stocking density of 100 ft.^{2} per acre for *Aralia*. Several of the largest diameter *Aralia* stems were cut down near the ground to determine age; a count of annual growth rings revealed a maximum age of 12 years. Species associated with *Aralia* at the site included sapling to 4 in. diameter hardwoods such as *Betula lenta* L., *Acer rubrum* L., and *Prunus serotina*; common shrubs, herbs, and vines present included *Berberis vulgaris* L., *Spiraea tomentosa* L., *Carex communis* Bailey, *C. laxiflora* Lam., *Rubus flagellaris* Willd., *R. allegheniensis* T. C. Porter, *Dennstaedtia punctilobula* (Michx.) Moore, and *Vitis labrusca* L. In late August 2002, the stand of *Aralia* was in full bloom, suffusing the area with a strong, rich, honey-like odor from the massed terminal compound panicles forming a floral canopy over the stand. Many thousands of pollinators, mostly bees and some flies, were observed on the panicles, and the loud droning sound from their buzzing was audible from many feet away. Upon observing that the *Aralia* had a typically clumped stem distribution at this site, a subsequent excavation of plants indicated that as many as eight subsidiary stems can arise from the crown of a parent stem at or slightly below the soil line; multiple branching of main stems was also found to occur up to a few inches above the soil line. Further excavation of stems seen to arise from the ground in a staggered linear fashion revealed that *A. spinosa* is a clonal species, able to reproduce vegetatively from subterranean root sprouts. This habit seems to explain in large part the tendency towards monocultural growth and the unusually high stem densities at the site. In *Trees of the Southeastern United States*, Duncan and Duncan (1988) noted that when used as an ornamental species, *Aralia* may be "difficult to contain because of sprouting from roots." Godfrey (1988) also observed that while *Aralia* has value as an ornamental, it has the propensity to "spread afar by underground runners," and he warned of this habit being a potential drawback to wider horticultural use.

Numerous, large-diameter softwood stumps were abundant throughout the area where *Aralia spinosa* was prevalent, and provided an indication of former stand history. According to Bruce Spencer, Chief Forester with the Metroplitan District Commission's Division of Watershed Management at the Quabbin Reservation, the area was formerly occupied by a conifer plantation that was severely windthrown in 1988. The timing of this windthrow event coincides with the maximum age of 12 years for the largest *Aralia* stems found at the site. It seems apparent that *Aralia*, released by windthrow and the subsequent salvage cut, spread explosively through the cleared area and quickly achieved dominant status among slower-growing regenerating hardwoods. It is likely that the ability to reproduce vegetatively by root-sprouting enabled *Aralia* to rapidly invade the windthrown area from where it had been previously lingering along the woodland margin. Also, as noted above, *A. spinosa* is capable of ripening fruit in Massachusetts; the fruits are eaten and presumably disseminated by birds and other animals. *Aralia* may thus have colonized the windthrown site via the dispersal of seed originating from mature plants that existed along the margin of the nearby dirt road.

The rapid spread of *Aralia spinosa* at the Quabbin site serves to illustrate that some seemingly innocuous horticultural introductions have the potential to become invasive species in the right circumstances, particularly if left unchecked. At Quabbin, *Aralia* has been determined to be an undesirable introduced species at odds with forest management goals, and the stand has been scheduled for eradication.

ACKNOWLEDGMENTS. Thanks to Bruce Spencer of the MDC for sharing his extensive knowledge of the forests at Quabbin, and to Ray Angelo for providing distribution data for *Aralia*. Special thanks to Marjorie C. Zebryk for her unfailing support and encouragement during this and many other endeavors.

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NOTE

A RANGE EXTENSION FOR *FERNALDIA SPECIOSISSIMA* (APOCYNACEAE, SUBFAMILY APOCYNOIDEAE)

JUSTIN K. WILLIAMS

Department of Biological Sciences, Sam Houston State University,
Huntsville, TX 77341-2116

Lundell (1976) treated *Fernaldia pandurata* (A. DC.) Woodson var. *glabra* Ant. Molina as a species distinct from *F. pandurata* by recognizing the taxon at the species level as *F. glabra* (Ant. Molina) C. L. Lundell. Lundell regarded *F. glabra* as distinct on the basis of its glabrous habit, longer pedicels (18–21 mm vs. 8–12 mm), and longer anthers (9 mm vs. 6 mm). Lundell did not base these observations on the type of var. *glabra*, but rather on two unique specimens collected from Guatemala (*E. Contreras 5925* & *7008*). The type of var. *glabra* differs from *F. pandurata* in only its glabrous habit (the peduncles are moderately pubescent) and not in pedicel or anther dimension. Observations of more than a hundred specimens of *F. pandurata* collected throughout Mexico and Central America reveal that the only specimens that lack pubescence are the type specimen of var. *glabra* and the two specimens Lundell (1976) cited for *F. glabra* (*E. Contreras 5925* & *7008*). Williams (1999) noted that the type of var. *glabra* differs little from *F. pandurata* and treated the variety as a synonym of *F. pandurata*; this decision was further supported by Morales (2002). Williams recognized however, that the specimens *E. Contreras 5925* & *7008* were aberrant and suggested that they might represent an undescribed species. Williams refrained from describing a new species suggesting that "in time, through more vigorous collecting, additional populations of the aberrant individuals may be found."

Recently, Morales (2002) published a revision of *Fernaldia*. In this work, Morales presented evidence that showed a recent aberrant specimen of *Fernaldia*, collected by him in Costa Rica (*Morales 7131*), is a specimen of a nearly unknown species: *F. speciosissima* Woodson. In fact, the specimen collected by Morales is the first recognized collection of *F. speciosissima* since the species was described. The identification by Morales is extremely important because the type specimen consists of only three flowers; no stems, leaves, or

FLORA OF GUATEMALA
Lundell Herbarium

Fernaldia glabra (Molina) Lundell
det. Lundell 1976

Vine, flowers white-yellowish.

DEPARTMENT OF PETEN: San Pedro, km. 150 of
Cadenas Road, in low forest on rocky hill.

Elias Contreras No. 7008 August 12, 1967

Figure 1. Specimen of *Fernaldia speciosissima* (*E. Contreras 7008*, LL).

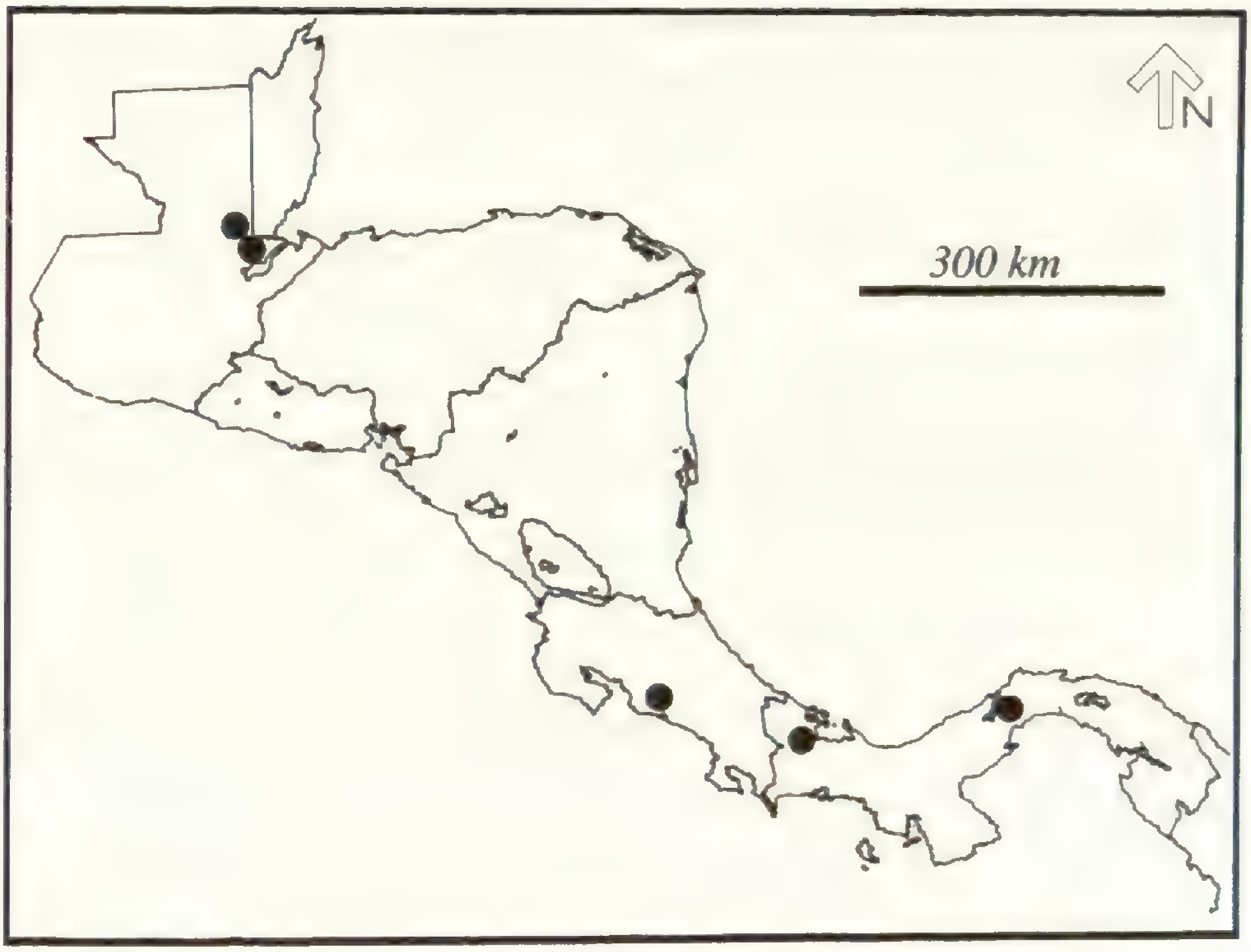

Figure 2. Distribution of *Fernaldia speciosissima*.

vegetative parts of any kind are present on the type. With this fortuitous specimen, Morales was able to expand the description of *F. speciosissima* in his revision. Morales was also able to write a key, based on both floral and vegetative characters, to the three recognized species of *Fernaldia*.

Using the key to the species of *Fernaldia* provided in Morales (2002), I attempted to identify the aberrant specimens (*E. Contreras 5925 & 7008*) discussed in Lundell (1976) and Williams (1999). Examination of the specimens indicates that they have peduncles 15–23 cm long, corolla tubes 19–24 mm long (Figure 1), and anthers 9–11 mm long, just as Morales described for *F. speciosissima*. The enigmatic specimens, *E. Contreras 5925 & 7008*, are consequently treated as *F. speciosissima*. Morales reported the distribution of *F. speciosissima* as Panama and Costa Rica. With the identification of the above specimens, the known range of the species is extended north into Guatemala (Figure 2). Another rare Apocynaceae vine, *Echites turbinata* Woodson, has a similar disjunct distribution (eastern Chiapas, Costa Rica, Honduras, and Panama). In addition, the phenology of the species is extended into August, a month past the previously reported flowering period of July (Morales 2002).

Fernaldia speciosissima Woodson, Ann. Missouri Bot. Gard. 26: 300. 1929. TYPE: PANAMA. Chiriquí: Río Chiriquí to Remedios, 11 Jul 1938, *R. E. Woodson, Jr., P. H. Allen & R. J. Siebert 1179* (HOLOTYPE: MO!).

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

GUATEMALA. Petén: San Padero, km 150 of Cadenas Road, in low forest on rocky hill, 12 Aug 1967, *E. Contreras 7008* (LL); Izabal, Puerto Mendez, in high forest on top of rocky hill, 8 Aug 1966, *E. Contreras 5925* (LL).

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

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BOOK REVIEW

Guide to the Trees, Shrubs, and Woody Vines of Tennessee by B. Eugene Wofford and Edward W. Chester. 2002. x + 190 pp. illus., 380 color plates. ISBN 1-57233-205-0 $29.95 (soft cover). University of Tennessee Press, Knoxville, TN.

The *Guide to the Trees, Shrubs, and Woody Vines of Tennessee* is an important new publication to consult or add to your personal library if you are interested in the flora of the southeastern United States or Tennessee, in particular. Coauthors Eugene Wofford and Wayne Chester have created a major update to previous works dealing with woody plants in the botanically diverse state of Tennessee. For decades students of dendrology in Tennessee have relied on an excellent primer, the *Summer Key to Tennessee Trees* by Shanks and Sharp (1950), now in its 9th unedited printing, and a number of more technical and popular treatments covering broader regions or adjacent states. With this new publication, students of the Tennessee flora will have a handy tool for identifying nearly any woody plant in the state. The only other reference that comes close to filling this niche is *Trees, Shrubs, and Woody Vines of Great Smoky Mountains National Park* by Stupka (1964), another University of Tennessee Press publication which oddly was omitted from an otherwise excellent set of references cited. Although it is not intended to be an exhaustive bibliography, the reference section provides many useful citations for those wanting to dig a little deeper into the flora of the state and region.

Within Tennessee, according to the authors, there are 358 native woody species and infraspecific taxa occurring in one or more of the state's nine major physiographic regions, which stretch from the Unaka Mountains in the east to the Mississippi Valley in the west. Also treated in the book are 45 non-native taxa that have become naturalized. To cover 403 taxa in this compact book, the authors have kept description to a minimum, instead relying on well-written and tested dichotomous keys and plates to help the user get to the correct identification. The 95 plates at the back of the book represent a new approach for books of this type. Instead of using color photographs taken in the field as done by Foote and Jones (1989) or Hunter (1989), or line drawings as done by Viereck and Little (1972), each plate typically presents four separate photographs of herbarium specimens, each depicting a different taxon. While these photographs lack the vitality and brilliance of photographs taken outdoors, the two-dimensional aspect of the pressed material, the authors argue, allows for more diagnostic features to be viewed. In many cases, the carefully chosen specimens, often with diagnostic flowers or fruit material alongside vegetative material, make this work very well. Both sides of flattened leaves are often shown. This presentation does a nice job of illustrating color differences, pubescent surfaces, leaf margin details, and other features not always captured in a single field photo. Occasionally, the authors have added a photomicrograph as an inset to depict a diagnostic feature such as the peltate scales of *Rhododendron minus* or the resin dots of *Gaylussacia baccata*.

Because the images were chosen to show key aspects of each species, they should be useful aids in identification. On occasion, the photo depicting a species will consist of no more than a close-up of a leaf base or margin, but these features were selected to help distinguish the species from related taxa. Drawbacks with the plates include occasional loss of color or details in the specimens, or the omission of a particularly useful characteristic that could have been included. Examples are the poor color on flowers of *Rhododendron periclymenoides*, the lack of flowers or fruit on the specimen of *Berberis thunbergii*, the lack of glandular hairs on the twigs and petioles in the image of *Corylus americana*, or the failure to show the underside of a black cherry (*Prunus serotina*) leaf revealing the diagnostic mustache of rusty hairs along the midrib. The keys and plates will work well in all seasons except winter. Many of the fine details of twigs and fruit characteristics useful in winter are not visible in the plates and are better shown in texts with line drawings or black and white photographs.

A few of the plants treated in this book will surprise some readers; the authors were inclusive when defining a shrub as "a low, woody plant with one to many slender trunks." *Phoradendron leucarpum*, the mistletoe, is described as a "hemiparasitic shrub;" *Opuntia humifusa* is included because of its "evergreen stems;" *Solanum dulcamara* is "suffrutescent;" *Polygonella americana* is called a "subshrub;" and *Chimaphila maculata* is a "nearly herbaceous, evergreen subshrub." More obvious choices for small shrubs, included in the book because of their multiple stems and woody bases, are the diminutive *Conradina verticillata* and *Paxistima canbyi*, both rare species in the state. Conversely, some of the non-native species omitted from the book might surprise readers. An appendix of omitted taxa listing 54 "cultivated and/or persisting taxa represented by collections" includes a few taxa often listed as invasive in other parts of the eastern United States (e.g., *Acer platanoides*, *Lonicera morrowii*, *Rhamnus cathartica*, and *R. frangula*). These examples, and perhaps others, should have been given more consideration for inclusion if they have naturalized in one or more places in the state.

The book serves as more than a woody plant identification tool. The 21-page introduction and the appendices summarize some interesting facts about the state that chose the Tulip Poplar, *Liriodendron tulipifera*, a member of the Magnolia family, as its official state tree. One can learn, for instance, that Tulip Poplar is one of seven members of the Magnolia family that are native to Tennessee. One can also learn that *Vaccinium pallidum* produces what the authors regard as the tastiest of Tennessee's blueberries, whereas *V. stamineum* has berries that are scarcely edible. Using summary tables, it is easy to compare the woody floras of the nine physiographic provinces. One table gives the distribution of each species by province. An interesting fact revealed is that the Cumberland Plateau exceeds the Unaka Mountain province in richness by one genus and 10 species. Analysis of the tabulations in another table shows that there are 12 genera present in the Cumberland Plateau but absent from the Unakas, and conversely there are another 12 genera present in the Unakas that are not represented in the Cumberland Plateau flora. Readers will also appreciate the inclusion of information about which species are considered rare by state and federal authorities (55 taxa), as well as the special discussion of five species considered to be extirpated.

The authors' decades of experience studying the Tennessee flora show in this book. Taxonomy and nomenclature follow closely that provided in a state checklist (Wofford and Kral 1993) and two state atlas volumes (Chester et al. 1993, 1997). In some cases, however, names for certain families have been updated to follow newer treatments (e.g., Flora of North America Editorial Committee 1993, 1997; Luteyn et al. 1996). As a specific example, Box-huckleberry, a Cumberland Plateau endemic, is now called *Buxella brachycera* (Michx.) Small instead of *Gaylussacia brachycera* (Michx.) A. Gray (which, incidentally, is shown in synonymy as *G. brachycera* A. Gray, an error in the text). In defense of the work, however, it is extremely free of such errors and typos. Species are presented alphabetically by scientific name, but are indexed by both common and scientific names, making it very easy to use. A minor flaw to the layout, in my opinion, is that the alphabetic arrangement of the genera is not immediately apparent because the genera appear on the right side of the page opposite the non-alphabetic family names on the left. A nice design feature is that many terms defined in the brief glossary are keyed to particular photographs in the text. Overall it is a thoughtfully put together, up-to-date treatment that will help many people to better understand the diverse woody flora of Tennessee.

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—PAUL SOMERS, Massachusetts Natural Heritage and Endangered Species Program, Route 135, Westborough, MA 01581.

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NEBC MEETING NEWS

September 2003. The September "away" meeting was held at the University of Massachusetts Nantucket Field Station on Polpis Road. The evening speaker was Dr. Ernie Steinauer, Director of the Massachusetts Audubon programs on Nantucket, who spoke on "Restoring and Maintaining Nantucket's Rare Plant Communities."

The particular Nantucket communities of most concern from a botanical perspective are sandplain grassland, which is considered globally endangered, and coastal heathland, which is considered globally threatened. Rare species of these habitats include butterfly-weed (*Asclepias tuberosa*), bushy rockrose (*Helianthemum dumosum*), broom crowberry (*Corema conradii*), silvery aster (*Aster concolor*), New England blazing star (*Liatris borealis* var. *novae-angliae*), and lion's-foot (*Prenanthes serpentaria*). There is a serious debate about the original extent of these habitats. In presettlement times (when there was a large but mostly seasonal population of native Americans) they may have been limited to immediate coastal areas, where salt spray reduced woody plant cover. In any case, it is apparent that they were in large part maintained over a period of more than 200 years by sheep-grazing, which was at times quite intensive (in 1700 there were 17,000 sheep on the island).

With approximately 40 percent of Nantucket's land area in some type of long-term conservation protection, the primary local threat to these habitats is not, as in so many mainland regions, from development. Nor is it from invasion of exotic species. Instead, the encroachment of mostly native, woody species threatens to convert (or, perhaps, reconvert) large areas of these habitats to mere scrub shrub and forest. Scrub oaks (*Quercus ilicifolia, Q. prinoides*), huckleberry (*Gaylussacia baccata*), and bayberry (*Myrica pensylvanica*) are aggressive colonizers and invaders of lands that were kept open by intensive sheep grazing over a long period of time. Pitch pine (*Pinus rigida*), which is said by islanders to have been lacking in presettlement times, and introduced to the island only in 1850, is also a culprit, while Japanese black pine (*P. thunbergii*) is now present on the moors and grasslands as well.

Management is aimed at suspending or retarding the forestation of sandplain grasslands and coastal heathlands. Currently, Massachusetts Audubon is actively managing approximately 2500 acres on Nantucket, primarily through mowing and prescribed burning. Both methods have positive and also negative aspects; neither is inexpensive. One of the major problems, for both methods, is that the woody species are adapted to loss of their crowns or above-ground parts, and very quickly reestablish their dominance in the habitat. Quantitative data show that there is not a significant difference between these two management tools in reducing woody plant cover, at least in the time frame—approximately 15 years—that they have been employed on Nantucket. It is apparent that fire, although it has received good press as a preferred management tool, is an effective maintenance tool but not a restoration tool. Neither fire nor mowing, alone, will be sufficient to restore or enhance these habitats. Ongoing experiments to increase their efficacy include litter removal (i.e., raking off the mowings), and reestablishment of sheep pasturage on a limited scale. It may be necessary to undertake seed supplementation to overcome losses that have already occurred, as there does not seem to be an adequate source of propagula for optimum, or desired, population levels of rare species. In light of this research and his experience on Nantucket, Dr. Steinauer suggests the following conservation priorities:

1. Acquiring and maintaining existing high quality plant communities should be the highest priority.
2. A formula should be developed to rank potential restoration sites that maximize the cost to benefit ratio.
3. Agricultural grasslands should be used as introduction sites for seeds of rare species.
4. The use of other management tools such as herbicides or grazing should be considered.
5. Seed supplementation from on- or off-island populations should be considered.

September 13 Field Trips. Threatening skies held off throughout the day on Saturday while Club members enjoyed a series of outings on Nantucket. Field trips were led by Dr. Ernie Steinauer, speaker the previous evening; Cormac Collier of the Nantucket Land Council; and by Pam Polloni. Beginning at the Middle Moors, a coastal heathland area near Altar Rock, the Club enjoyed an hour of leisurely botanizing that familiarized us with such plants as the locally common, but globally rare golden aster (*Pityopsis falcata*), bearberrry (*Arctostaphylos uva-ursi*), the scrub oaks (*Quercus ilicifolia* and *Q. prinoides*), various asters, narrow-leaved goldenod (*Euthamia tenuifolia*), and goat's-rue (*Tephrosia virginiana*).

Following on to Pout Pond, the high water from a wet summer made aquatic botany difficult. Members found Oakes's pondweed

(*Potamogeton oakesianus*) in full fruit, Robbin's spike-rush (*Eleocharis robbinsii*), and water-willow (*Decodon verticillatus*) in flower. A few members walked north to see one of the smaller bogs on the island, Donut-Hole Bog, tawny with cotton-grass (*Eriophorum* sp.), but also difficult to botanize due to high water.

The next stop was a nearby stand of several acres of broom crowberry (*Corema conradii*), a species of conservation concern on the island. The mounding topography was striking, with taller islands of oaks—rather like a lush alpine garden in aspect. Here, lengthy discussions centered on the Cistaceae: beach-heathers (*Hudsonia ericoides* and *H. tomentosa*), rockroses (*Helianthemum propinquum* and *H. dumosum*), and pinweeds (*Lechea maritima*). Although some of the vehicles bounced uneasily through loose sand and over the bouldery roads on the glacial moraine, everyone was back safely at the University of Massachusetts Field Station for lunch. There, Dr. Rick Kesseli of the University of Massachusetts – Boston explained some of his work on dioecy in groundsel-tree (*Baccharis halimifolia*), which grows abundantly around the field station grounds. Members botanized along the beach and the edge of the salt marsh, where Pam Polloni discovered a population of seabeach knotweed (*Polygonum glaucum*). Matt Hickler pointed out *Parthenocissus vitacea*, perhaps new to the island.

The afternoon was spent at the Smooth Hummocks Coastal Preserve area, where Rachael Freeman described her pollination research on silvery aster (*Aster concolor*), and members studied such attractions as purple gerardia (*Agalinis purpurea*), New England blazing star (*Liatris borealis* var. *novae-angliae*), and showy aster (*Aster spectabilis*). A search for the southern bracken (*Pteridium aquilinum* var. *pseudocaudatum*) was bootless, but members were rewarded with a nice showing of lion's-foot (*Prenanthes serpentaria*), a species of concern on the island. Sandplain flax (*Linum intercursum*) and Nantucket shadbush (*Amelanchier nantucketensis*) rounded out the list of rarities.

Botanizing was not confined to field trips, however. Local botany in Nantucket Village proved interesting for those from colder climes: from the abundantly planted and sparingly escaped sweet autumn clematis (*Clematis ternifolia*) and butterfly bush (*Buddleia davidii*) to the abundance of sycamore maple (*Acer pseudoplatanus*), which might well be christened the Nantucket plane tree, members enjoyed their strolls into and about town.

—ARTHUR V. GILMAN, Recording Secretary *pro tempore*.

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