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Taxonomy of *Eupatorium* section *Verticillata* (Asteraceae)

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TAXONOMY OF *EUPATORIUM* SECTION *VERTICILLATA* (ASTERACEAE)

by

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A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

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Abstract

Taxonomy of Eupatorium section Verticillata (Asteraceae)

by Eric E. Lamont

Advisor: Dr. Arthur Cronquist

Eupatorium section Verticillata, as delimited here, includes five species and three additional infraspecific taxa. The section is usually characterized by the occurrence of verticillate leaves, purplish flowers, and an enlarged style base. The species of section Verticillata are restricted to North America, with the greatest concentration of species in eastern United States. Recognition of species has always been difficult in the section because of variation in such features as shape of the leaves, number of leaves per node, pigmentation of the stems, size and shape of the inflorescence, and number of flowers per head. This variation was studied on the individual, inter- and intra-populational levels. Data collected from extensive field and herbarium studies were combined with the results of phenetic analysis to determine the usefulness of such characters for the determination of species.

A taxonomic treatment of the section is provided. Descriptions, keys, complete synonomy, illustrations, distribution maps, and discussions of all taxa are presented. Supplemental information (taxonomic history, ethnobotany, flavonoid chemistry, cytology, palynology, putative hybridization, and phylogeny) concerning the biology of section Verticillata is also presented.

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Dedication:

To my beloved wife, Mary Laura Lamont

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Introduction

Eupatorium L. is a taxonomically difficult and highly diversified genus. There is marked disagreement over the delimitation of species in the genus. On the basis of the traditional delimitation of classification, the genus has been considered to include nearly 1200 species (Willis, 1966), mostly from North and South America, and a few in Europe, Asia, and Africa. Cronquist (1981) recognized about 600 species in the genus and Whittemore (1987) recognized about 800 species. King and Robinson (1987) proposed a reclassification of the tribe Eupatorieae in which only 45 species of Eupatorium were recognized; all other species previously included in Eupatorium were referred to segregate genera.

The genus as traditionally defined includes several natural groups, the taxonomic ranks of which are much in dispute. Overlapping of major characters makes infrageneric classification difficult and complicated. Eupatorium has been divided into sections by several authors, mostly in the nineteenth century (Loudon, 1830; de Candolle, 1836; Baker, 1876; Hoffmann, 1894). De Candolle (1836) divided Eupatorium into three series, one of which was further divided into four sections. This order is counter to that given in Articles 4.1 and 5 of the International Code

of Botanical Nomenclature (Greuter, 1988), and under Article 33.4 names of taxa of misplaced rank are not validly published. Most taxonomists have treated de Candolle's sections as valid and his series as misplaced; one of de Candolle's valid sections is Verticillata. The sectional nomenclature of Eupatorium has been summarized by Whittemore (1987), who listed 23 sections in the genus.

Section Verticillata DC., a distinct and well defined subunit of Eupatorium, consists of five species and three additional infraspecific taxa. The section is characterized by the combined occurrence of verticillate leaves, purplish flowers, and enlarged style base. Torrey and Gray (1841) first noted the significance of the "bulbous" style base in distinguishing the section. The species of section Verticillata are restricted to North America, with the greatest concentration of species in eastern United States. Three species usually occur in moist habitats and two species usually occur in drier upland habitats.

Historically, 19 species and 17 additional infraspecific taxa of verticillate eupatoriums have been recognized and described (Table 1). Several authors lumped all taxa of verticillate eupatoriums into one species (Torrey & Gray, 1841; Wood, 1845; Gray, 1848; Beck, 1848; Britton, 1881; Watson & Coulter, 1890; Voss, 1894; Robinson & Fernald, 1908;

Bolvin, 1972; Scoggan, 1979). Other authors challenged the generic limits of Eupatorium and established new genera for verticillate eupatoriums (Rafinesque, 1838; Lunell, 1917; King & Robinson, 1970). King and Robinson (1987) reincluded verticillate eupatoriums in Eupatorium.

The species of section Verticillata are outcrossing sexual diploids with a stable chromosome number of $2n = 20$ (Tables 4 & 5). Hybridization within the section does occur but is uncommon; hybridization with species outside the section has never been documented. Many other North American groups of Eupatorium (e.g., the Eupatorium rotundifolium complex) are characterized by polyploidy, pillar complexes, apomixis, and hybridization within and outside the groups (Grant, 1953; Fryar, 1964; Maurushat, 1969; Montgomery & Fairbrothers, 1970; Sullivan, 1972, 1976, 1978).

The most significant contribution to our understanding of Eupatorium sect. Verticillata is that of Wiegand and Weatherby (1937); otherwise the section as a whole has received little taxonomic attention. Although Wiegand and Weatherby's (1937) treatment was widely accepted, it was inconsistent in its treatment of infraspecific taxa and did not note a species endemic to the southern Appalachian Mountains. Additionally, several authors continued to question the

delimitation of species in sect. Verticillata (Bolvin, 1972; Scoggan, 1979; Löve & Löve, 1982).

As in other sections of Eupatorium, the species in section Verticillata show complicated patterns of morphological polymorphism, resulting in taxonomic confusion and difficulty in delimiting specific boundaries. These problems suggested the need for a modern taxonomic study with a focus on the pattern of morphological diversity. The main objective of this study is to provide a taxonomic treatment of Eupatorium sect. Verticillata, based on comparative morphology, cytology, comparative flavonoid chemistry, and phenetic analysis.

Taxonomic History

The verticillate-leaved eupatoriums of North America have had a highly confused taxonomic and nomenclatural history. Linnaeus described two species in the group in 1753, Eupatorium trifoliatum and E. purpureum; in 1755 he added a third, E. maculatum. However, the type specimens of E. trifoliatum and E. purpureum belong to a single species, E. purpureum as we now understand it (E. trifoliatum, which precedes E. purpureum in Species Plantarum, was first united with the latter by Torrey and Gray in 1841 under the name E. purpureum). For almost 200 years Linnaeus' successors struggled unsuccessfully to apply his three names and account for taxonomically significant variation within the group.

Since the publication of Species Plantarum (Linnaeus, 1753), botanists have recognized and described 17 additional species of verticillate-leaved eupatoriums from North America (Table 1). Differences in leaf morphology (e.g., number of leaves per whorl, leaf size, length/width ratio, margin, texture, etc.) were used by many early botanists in differentiating the species. However, leaf morphology is now known to be inter- and intraspecifically variable within this group, and of relatively little taxonomic significance.

Taxonomists eventually began to recognize variation within species and the futility of continually naming new species. Hooker (1833) recognized this taxonomic dilemma when he stated, "I have received nothing under the name of E. maculatum, which was not at once referable to E. purpureum, to which the E. verticillatum and punctatum of Willd. and the E. ternifolium, Ell. (E. trifoliatum, Willd.) may probably be with safety added." Darlington (1837) also noted similar taxonomic problems in his Flora Cestrica (in which he recognized only two species of verticillate eupatoriums, E. purpureum and E. trifoliatum), when he stated, "In its usual appearance it [E. trifoliatum] seems sufficiently distinct from the preceding [E. purpureum]; but it must be confessed, that there are intermediate specimens by which the two are connected, or blended, so as to render it extremely difficult to make a satisfactory discrimination." Barratt (1841) commented: "The confusion in systematic works on this group of North American Eupatoriums is most extraordinary! An attention to the number of leaves of the Verticillate Eupatoria rather than other characters, has led the older botanists into frequent errors, and has occasioned much perplexity and confusion in systematic works." Torrey (1843) recognized only one species of verticillate Eupatorium in New York and stated, "The various forms of this

plant have been regarded as distinct species by many botanists, but they seem to pass insensibly into each other." Wood (1861) recognized three species of verticillate Eupatorium but stated, "Intermediate forms occur, rendering the distinctions of this species and the two preceding numbers a grave question." Wiegand and Weatherby (1937) said of the highly confused nomenclatural status of verticillate eupatoriums: "This was a truly lamentable, indeed an intolerable, condition." Deam (1940) stated, "The Joe-pye-weeds have been misunderstood, and all or most all of the earlier reports should be ignored, because, as far as I know, none of our authors knew of the existance in our area of three species of this group or had keys which would separate them." Boivin (1972) claimed the taxonomy of Eupatorium sect. Verticillata was "too complex an arrangement...there is a general lack of morphological cleavage between the taxa." Smith (1978) stated that the different verticillate eupatoriums "would be better treated as varieties of E. purpureum." Scoggan (1979) lumped six taxa of verticillate eupatoriums into a single species (E. purpureum). Löve and Löve (1982) recognized subspecies of a single species, E. purpureum.

Early botanists working on the group tended to recognize numerous species. However, during the mid-1800's a shift to lumping taxa into one or two

species with numerous infraspecific taxa at various taxonomic levels was initiated. The following account highlights the nomenclatural history of verticillate eupatoriums from Lamarck (1786) to present.

Lamarck (1786) recognized 44 species of Eupatorium, two belonging to section Verticillata: E. trifoliatum and a new species, E. verticillatum. However, in publishing the name E. verticillatum, Lamarck cited as synonyms E. purpureum and E. maculatum. Since, in so doing, he failed to adopt the earliest legitimate epithet available, his name is illegitimate and is rejected. According to Wiegand and Weatherby (1937) there is no specimen labelled E. verticillatum in the herbarium of Lamarck. In 1990, Cronquist (personal communication) also failed to locate a type specimen for E. verticillatum in Lamarck's herbarium; however, a specimen was located in the herbarium of Antoine Laurent de Jussieu, cat. #8398, bearing the handwritten label "Eupatorium verticillatum Lamk."

Walter (1788) and Michaux (1803) did not increase taxonomic understanding of verticillate-leaved eupatoriums. Both described new species in the group (E. fusco-rubrum and E. falcatum, respectively) based primarily upon differences in leaf morphology. Both these names are currently included in synonomy under E. purpureum L. Walter recognized only two species (E.

trifoliatum and E. fusco-rubrum) from southeastern United States, although five distinct species are currently recognized from the same area. Michaux recognized three species (E. purpureum, E. maculatum and E. falcatum) from North America. Many botanists at this time were cataloging morphological variation within taxa (as we now see them) rather than recognizing self-perpetuating natural populations.

Willdenow (1809) described four distinct species of verticillate-leaved eupatoriums from North America. His interpretation of the four taxa somewhat approaches our present understanding of the group. A Willdenow specimen of E. punctatum serves as holotype for the currently accepted species E. dubium Willd. ex Poir., a name substituted by Poiret (1811) for E. punctatum Willd. because of the earlier E. punctatum Lam. In addition, Willdenow first recognized the importance of a fistulose stem as a diagnostic character separating two closely related species of verticillate eupatoriums. Unfortunately, he applied the incorrect name E. purpureum to his hollow stemmed species. Willdenow's remaining two species, E. maculatum and E. verticillatum, were not well defined and embraced a confusing combination of nondistinct characters.

Muhlenberg (1813) listed six verticillate-leaved eupatoriums from North America. It is apparent from the short descriptions that Muhlenberg did not

understand the group's taxonomic complexity. Muhlenberg simply listed different names previously published by Linnaeus (1753, 1755), Lamarck (1786), Michaux (1803), and Willdenow (1809).

Pursh (1814) recognized the same six species recognized by Muhlenberg (1813) and described a new species, E. amoenum. Pursh catagorized his seven species into two distinct groups: three species with 3-5 flowers per head (E. amoenum, E. trifoliatum, and E. falcatum), and four species with more than five flowers per head (E. purpureum, E. maculatum, E. punctatum, and E. verticillatum). All three species in Pursh's first group are now included in synonomy under E. purpureum L. E. amoenum was relegated to varietal status by Gray (1884) and recognized by Wiegand & Weatherby (1937). Gleason and Cronquist (1963) questioned the taxonomic significance of this taxon. E. amoenum is now known to be a depauperate shade form of E. purpureum L.

Eaton (1818, 1836) recognized the same six species previously described by Muhlenberg (1813) and Pursh (1814); however, Eaton (1818) published "a new species by Dr. John Torrey," E. laevigatum. E. laevigatum had a hollow, smooth, sub-glaucous stem with lanceolate leaves in whorls of five and resembled the hollow stemmed Eupatorium previously described by Willdenow (1809). Unfortunately, E. laevigatum was an

illegitimate name because of the earlier E. laevigatum Lam. (1786). Therefore, the distinctive hollow stemmed verticillate-leaved Eupatorium remained to be properly named.

Torrey (1819) recognized six species of verticillate-leaved eupatoriums (including his new hollow stemmed species E. laevigatum) growing within 30 miles of New York City. First mention of the common name, Joe Pye Weed, is found in Torrey's 1819 publication. In 1826, Torrey recognized six species of verticillate eupatoriums from northeastern United States; however, he now recognized a solid stemmed E. punctatum and dismissed the illegitimate name E. laevigatum. By 1843, Torrey drastically changed his taxonomic outlook on verticillate eupatoriums; he now recognized only one species, E. purpureum, with two infraspecific taxa which he simply referred to as "var. 1" and "var. 2." Torrey's description of E. purpureum allowed for wide morphological variation (eg., "stem hollow, or more or less completely filled with pith...leaves sometimes very rugose and of a thick texture, at other times thin and membranaceous"). Torrey's two varieties were largely segregated by number of leaves per whorl (var. 1 = "leaves mostly 4-6 in a whorl;" var. 2 = "leaves mostly 3-4 (sometimes 5) in a whorl"). Torrey ends his description with the statement, "An extremely variable plant."

Elliott (1823) recognized four species of verticillate eupatoriums from South Carolina and Georgia. He recognized a hollow stemmed species but applied the incorrect name E. purpureum, in the tradition of Willdenow (1809). Elliott also described a new species, E. ternifolium, restricted to the coastal plain ("low country") of the Carolinas, having leaves in 3's and 4's, with abaxial leaf surfaces conspicuously dotted with glands. This diagnosis accurately describes E. dubium Willd. ex Poir., published 13 years before Elliott's flora. Elliott's remaining two species, E. maculatum and E. verticillatum, were not well defined and embraced a confusing combination of nondistinct characters.

A. P. de Candolle (1836) largely contributed to the present understanding of Eupatorium by organizing the genus into formal taxonomic sections. Section Verticillata was proposed for verticillate-leaved eupatoriums and included five species (see Table 1). De Candolle recognized a hollow stemmed species but applied the incorrect name E. purpureum; however, he correctly applied the name E. dubium Willd. ex Poir., and correctly listed E. punctatum Willd. as its synonym. De Candolle's remaining species, however, were not well defined, being based largely upon leaf morphology.

Barratt's (1841) major contribution to the taxonomy of Eupatorium sect. Verticillata was the accurate description and legitimate naming of E. fistulosum, the hollow stemmed taxon previously recognized by Willdenow (1809), Torrey (1819), Elliott (1824) and de Candolle (1836). Barratt also clearly described the stem of E. purpureum "with a purple band at the joints about one inch broad." His last two species (E. maculatum and E. ternifolium) were not clearly distinguished from each other and have been interpreted as being misapplied names for E. dubium Willd. (Wiegand and Weatherby, 1937).

Wood (1848) followed Barratt's (1841) treatment of Eupatorium sect. Verticillata: four species and three varieties were recognized (see Table 1). However, in Wood's 1861 edition of Class Book of Botany, only three species were recognized and only one of Barratt's three varieties was recognized.

Gray (1848) was the first and only taxonomist to recognize only one species, with no infraspecific segregates, of verticillate-leaved Eupatorium from North America. Torrey and Gray (1841) first lumped all taxa of verticillate eupatoriums into one species, but recognized two infraspecific taxa. By 1884, Gray still recognized only one species of verticillate Eupatorium from eastern North America but also recognized two varieties, var. maculatum and var. amoenum. In

addition, Gray (1884) recognized a new species from western North America, E. bruneri; this taxon is currently recognized at the rank of subspecies (Douglas, 1986) under E. maculatum. In the 6th edition of Gray's Manual of Botany, Watson and Coulter (1890) once again lumped all taxa into one species (E. purpureum) and recognized only one variety, var. amoenum. In the 7th edition of Gray's Manual of Botany, Robinson and Fernald (1908) also lumped all taxa into one species (E. purpureum) but recognized three varieties, var. maculatum, var. amoenum and a new var. follosum.

Britton (1881) recognized only one species, and no infraspecific taxa, of Eupatorium sect. Verticillata from New Jersey; currently four species are recognized from the state. In 1898, Britton and Brown recognized two species and two varieties of verticillate eupatoriums from North America. In 1901, Britton recognized four species and two varieties of verticillate eupatoriums from North America, including a new species, E. rydbergii, from western United States. In 1913, Britton and Brown revised Britton's (1901) treatment of Eupatorium sect. Verticillata: E. rydbergii was listed in synonomy under E. bruneri and E. trifoliatum was not formally recognized as a distinct species (E. trifoliatum was mentioned in a

note under E. purpureum: "may not be specifically distinct").

Voss (1894) recognized only one species of Eupatorium sect. Verticillata from North America; however, a complex hierarchical classification system of infraspecific taxa was proposed. Eight ultimate taxa were classified into a complex series of varieties and forms. Combinations such as E. purpureum L. var. maculatum L. f. dubium Poir. were proposed. Voss' treatment was a confusing arrangement of names, whereby dissimilar taxa were often grouped together (eg., E. purpureum var. maculatum f. amoenum and E. purpureum var. maculatum f. dubium).

Farwell (1918) was one of the last taxonomic lumpers of Eupatorium sect. Verticillata. Seven infraspecific taxa were lumped under two species, E. trifoliatum and E. purpureum, and four new combinations were proposed under E. trifoliatum. Four of Farwell's seven taxa are currently recognized at different taxonomic ranks; three of his taxa were based upon variable leaf characters of no taxonomic significance.

In the April 1920 issue of Rhodora, Karl M. Wiegand presented a landmark systematic treatment of Eupatorium sect. Verticillata that is still foundational for systematic studies of the group. Briefly stated, Wiegand proposed four species of verticillate-leaved eupatoriums, assigned each species

a number, and listed their most striking characters. He then applied names to the particular species (E. verticillatum, E. maculatum, E. purpureum, and E. falcatum). Wiegand's delimitation of four species met with general acceptance among taxonomists; however, his application of names met with immediate objection.

In the October 1920 issue of Rhodora, Kenneth Mackenzie responded to Wiegand's (1920) treatment of Eupatorium sect. Verticillata. Mackenzie agreed with Wiegand's delimitation of four species, but took issue with Wiegand's nomenclature. Consequently, Mackenzie applied a different epithet to each of Wiegand's four species; no agreement in the application of epithets existed between the treatments of Mackenzie (1920) and Wiegand (1920).

In 1927, Mackenzie shed "further light on the purple-flowered Eupatoriums." He defended his earlier application of names, stating, "the names should be applied in accordance with descriptions given and not according to specimens...that these old species should be identified by specimens in the old herbaria is most incorrect and mischievous."

In 1937, Wiegand and Weatherby proposed a completely new arrangement of names for verticillate-leaved eupatoriums, based exclusively upon "actual, existent herbarium material (the object and peculiar virtue of the "type method")." The result of

this study was relative taxonomic and nomenclatural stability of the group; the proposed arrangement found its way into major regional manuals (Deam, 1940; Fernald, 1950; Cronquist, 1952a, 1980; Steyermark, 1963; Gleason & Cronquist, 1963; Radford et al., 1964; Mohlenbrock, 1975; and Barkley, 1986).

Agreement with Wiegand and Weatherby's (1937) taxonomy was not unanimous. Boivin (1972), following the taxonomy of Torrey and Gray (1841), recognized only one species and two varieties of Eupatorium sect. Verticillata (E. dubium and E. fistulosum were listed in synonomy under E. purpureum var. maculatum). In Scoggan's (1979) Flora of Canada, one species, two varieties and four forms of Eupatorium sect. Verticillata were recognized (E. dubium was listed in synonomy under E. purpureum var. purpureum; E. fistulosum and E. maculatum were listed in synonomy under E. purpureum var. maculatum f. maculatum).

After general acceptance of Wiegand and Weatherby's (1937) treatment of Eupatorium sect. Verticillata, two further taxonomic developments occurred. Eupatorium species were dissected into numerous taxonomic formae, and several botanists removed sect. Verticillata from the genus Eupatorium.

Jennings (1942) conducted extensive research on verticillate eupatoriums in western Pennsylvania. He brought attention to the possibility that hybridization

was more prevalent in the group than previously suggested. Two of Jennings' taxonomic forms were possibly the result of hybridization: E. fistulosum x E. maculatum = E. fistulosum f. truncatum, and E. purpureum x E. maculatum = E. purpureum f. depressum. Another of Jennings' segregates was an albino flower form (E. fistulosum f. albidum) and his last segregate was an unusual leaf form (E. purpureum f. laciniatum).

Several other botanists at this time also cataloged morphological variation within taxa; however, proposed segregates did not represent self-perpetuating natural populations and therefore had no taxonomic significance. Marie-Victorin (1944) described E. maculatum f. anomalum, Fernald (1945) described E. dubium f. elutum and E. maculatum f. faxonii, Lepage (1952) described E. maculatum f. eresinatun, Boivin (1959) described E. maculatum f. tegulosum, and Seymour (1969) described E. purpureum f. decolor.

The generic limits of Eupatorium have been recently (as well as historically) questioned and challenged. Rafinesque (1838) established a new genus, Eutrochium, for verticillate eupatoriums and stated, "as to Eutrochium I have prepared a monograph of it with many new species." This monograph was never published. Conversely, Greene (1903) considered verticillate eupatoriums to be the only representatives of Eupatorium in America. Lunell (1917) transferred

verticillate eupatoriums from Eupatorium to Cunigunda Bubani. Lunell's treatment was not taken seriously until King and Robinson (1970) claimed the traditional classification system of Eupatorium was a "highly artificial concept." Consequently, King and Robinson split Eupatorium into over 100 genera, Eupatoriadelphus being the new genus established for verticillate eupatoriums. Several botanists readily accepted King and Robinson's (1970) treatment of Eupatoriadelphus (Earll, 1971; Johnson, 1972; Jones, 1974; Wunderlin, 1982; Soil Conservation Service, 1982; Clewell, 1985; Reed, 1986; Harvill et al., 1986).

Earll (1971) found many of King and Robinson's (1970) microcharacters to be inconsistant in separating Eupatoriadelphus from Eupatorium. Earll (1971) concluded: "It is true that the verticillate species [Eupatoriadelphus] have a tendency for distinct carpopodia; however this same tendency is also present in Eupatorium...The more pointed pappus setae is an inconsistent character to use in separating the verticillate species [Eupatoriadelphus] from others [Eupatorium]...The corollas of all species studied of both genera are glabrous...Exothecial cells with their thickened walls are the same in both genera...The bases of the anthers were likewise the same for all species [in both genera]...The pappus and achenes showed no

noticeable differences...Other characters were studied which appear to be similar in both genera."

Subsequently, in their most recent treatment of the tribe Eupatorieae, King and Robinson (1987) restored the verticillate eupatoriums (*Eupatoriadelphus*) to *Eupatorium*.

The most recent contribution to the taxonomy of *Eupatorium* sect. *Verticillata* has been the discovery of a new species from the southern Appalachian Mountains of eastern U.S.A. (Lamont, 1990a).

Table 1

Summary of the taxonomic history of Eupatorium section Verticillata. An upper case "X" indicates the use of a specific name by each corresponding author; a lower case "x" indicates the use of a specific name at the infraspecific level by each corresponding author. Species are designated by the first three letters of their epithets: AME = americanum, AMO = amoenum, ATR = atromontanum, BRU = bruneri, DUB = dublum, FAL = falcatum, FIS = fistulosum, FUS = fusco-rubrum, HAR = harnedii, HOL = holzingeri, LAE = laevigatum, MAC = maculatum, PUN = punctatum, PUR = purpureum, RYD = rydbergii, STE = steelei, TER = ternifolium, TRI = trifoliatum, VER = verticillatum.

	AME	AMO	ATR	BRU	DUB	FAL	FIS	FUS	HAR	HOL	LAE	MAC	PUN	PUR	RYD	STE	TER	TRI	VER
Linnaeus (1753, 1755)											X		X						X
Lamarck (1786)											x		x						X
Walter (1788)								X											X
Michaux (1803)							X				X		X						
Willdenow (1809, 1811)							X				X		X						X
Muhlenberg (1813)							X				X		X						X
Pursh (1814)						X		X			X		X						X
Eaton (1818, 1836)						X		X			X		X						X
Torrey (1819, 1826)						X					X		X						X
Elliott (1829)											X		X						X
Hooker (1833)											X		X						
DeCandolle (1836)							X				X		X						X
Darlington (1837)											x		X						X
Barratt (1841)									X		X		X						
Torrey & Gray (1841)											x		X						
Wood (1848)									X		X		X						
Gray (1848)						x		X			x		X						
Voss (1894)						x		x			x		X						x
Britton (1901)						x		x			X		X						X
Small (1903)								x			X		X						X
Farwell (1918)						x		x			x		X						X
Mackenzie (1920)								X			X		X						X
House (1924)								X			X		X						X
Harned (1931)						x				X			X						
Rydberg (1932)							X		X			X							
Wiegand & Weatherby (1937)					x			X		X			X						
Fernald (1950)							X		X				X						
Radford et al. (1968)							X		X				X						
Scoggan (1979)											x								
Kartesz & Kartesz (1980)					x		x		X				X						
Gleason & Cronquist (1991)					x				X				X						
Lamont (1991)					x				X				x						

Morphology

Descriptions of the morphological structures in the following pages are based primarily on dried herbarium specimens. In addition to my own collections, Eupatorium section Verticillata collections from the following herbaria were examined: ARIZ, BH, BKL, BYU, CANA, CM, COLO, DAO, FLAS, GA, GH, ILL, IND, ISC, KANU, KSC, MICH, MIN, MO, MT, NDA, NEB, NLU, NMC, NY, NYS, OBPF, OKL, OS, PH, RM, TEX, UARK, UNA, UNC, US, VPI, and WIS. In all, over 4800 voucher specimens besides my own were studied. In addition to studies of dried specimens, field work from 1987-1990 not only resulted in the collection of large enough samples to study morphological variation, but also allowed observation of forms, putative hybridization, flowering behavior, stem height, colors, microhabitat preferences, and other features best studied on living plants.

HABIT

The species of section Verticillata are stout perennial herbs, rhizomatous and fibrous-rooted. Stems are erect, unbranched below the inflorescence, and vary in height from 0.3 m to 3.5+ m at maturity. E. fistulosum, frequently 2 to 3.5+ m tall when growing in very wet soil, is the largest species. Populations of

E. purpureum may only average 0.3 m in height when growing in shade and depauperate soil. E. fistulosum and E. maculatum usually form large clones, sometimes producing hundreds of individual stems. E. purpureum and E. steelei usually have only 1 to 3 stems from each rhizome. E. dubium usually grows in loose clonal aggregates or as separate individuals.

ROOTS

The fibrous roots of section Verticillata may arise either at the base of the stem or more commonly from the nodes of rhizomes. They are relatively uniform and are of little diagnostic importance.

STEMS

Stem morphology of section Verticillata shows intraspecific, infraspecific, and age-related variation, but is useful in recognizing species. In E. fistulosum stems are hollow with a large central cavity. All other species have stems containing pith that usually remains intact. A slender central cavity rarely develops in mature stems of E. maculatum and E. purpureum, and insects sometimes bore through lower stems in other species making them secondarily hollow.

Stems of E. steelei are conspicuously glandular pubescent with long, spreading, persistent hairs. In E. maculatum subsp. bruneri, stems are densely puberulent throughout; in subsp. maculatum, lower stems are rarely sparingly puberulent, becoming glabrous with age. In the remaining taxa, stems are glabrous, and in E. fistulosum they are strongly glaucous when fresh.

Anthocyanic pigments are usually present in varying concentrations in stems of section Verticillata. In E. purpureum stems are dark purple only at the nodes, otherwise greenish. Stems of E. fistulosum are uniformly purple throughout. In E. steelei stems are usually greenish to greenish-purple throughout or rarely purplish only at the nodes. In E. maculatum and E. dubium stems are usually purple-speckled throughout, sometimes uniformly purple or greenish-purple with dark purple spots scattered throughout. When interspecific hybridization occurs, offspring usually express complicated patterns of stem pigmentation. Stem characteristics of section Verticillata are summarized in Table 2.

LEAVES

Leaves of section Verticillata are whorled and simple with serrate margins, usually with a large gland at the tip of each marginal tooth. Leaf blades are

mostly lance-elliptic or lance-ovate to deltate-ovate, acuminate at the tip, and gradually or sometimes abruptly tapered to the short-petiolate base. E. fistulosum usually has the narrowest leaves (leaf length/width ratio averages 4.59), E. dubium and E. steelei usually have the broadest leaves (leaf length/width ratios averaging 2.43 and 2.35, respectively). Leaf shapes characteristic of the section are illustrated in Figure 1. The leaf length/width ratio for each taxon is provided in Table 3. Leaf characters of section Verticillata show intraspecific and infraspecific variation, but are relatively useful in recognizing some species.

The number of leaves per node is fairly useful in delimiting some species (Fig. 2). E. fistulosum commonly has 5 or 6 leaves per node, rarely only 3. E. dubium, E. purpureum, and E. steelei commonly have 3 or 4 leaves per node, rarely 5. The number of leaves per node on a single plant does not usually vary, but the number does usually vary within a single population. The importance of this leaf character in identifying species is limited and must be evaluated in the context of multiple correlations of characters.

Leaf blades usually have glabrous to glabrescent adaxial surfaces; abaxial surfaces are minutely atomiferous-glandular and pilose on the midrib and main veins. In E. steelei abaxial surfaces are

conspicuously glandular pubescent, and in E. maculatum subsp. bruneri abaxial surfaces are densely covered with short spreading hairs. Leaf blades usually have coarsely serrate margins, but in E. fistulosum leaf margins are finely serrate with more rounded, blunter teeth. Several taxonomic formae have been proposed on the basis of leaf margin variability in individuals, but the variability does not represent self-perpetuating natural populations. Leaves are usually triplinerved in E. dubium; the remaining species are pinnately veined.

INFLORESCENCES

In section Verticillata discoid flower heads are arranged in a compound corymbiform inflorescence. As in most Asteraceae the sequence of flowering within a head is indeterminate, but the flowering sequence among heads is determinate. Foliaceous bracts are alternately scattered throughout the inflorescence. Branchlets and peduncles are conspicuously pubescent to glandular pubescent. Each inflorescence is subtended by a whorl of leaves much reduced in size; however, in E. maculatum var. follosum the subtending whorl of leaves equals or exceeds the height of the inflorescence.

Inflorescence size and shape are useful characters in recognizing some species. In E. maculatum the inflorescence is dense, flat-topped, and rarely exceeds 20 cm in diameter. In E. fistulosum the inflorescence is dense, convexly domed, and commonly exceeds 20 cm in diameter. In E. purpureum and E. steelei the inflorescence is loosely domed and rarely exceeds 20 cm in diameter. The inflorescence of E. dubium is variable in size and shape: sometimes relatively flat-topped with numerous heads, other times relatively loosely domed and depauperate in size.

INVOLUCRE

Traditional infrageneric classifications of Eupatorium have been largely based upon differences in the involucre (Robinson, 1918). In section Verticillata involucral bracts are tightly appressed and imbricate in several lengths, the outer ones obtuse, the inner acutish. Bracts are usually purplish, prominently midveined, and range from 6.5 to 9 mm in length. The receptacle is naked and flat or weakly convex. Features of the involucre are not important in the delimitation of species of section Verticillata .

FLOWERS

Flowers of section Verticillata are tubular and perfect, sessile or borne on pedicels less than 1.0 mm long. Corollas are regular and 5-toothed, usually purplish or very pale pinkish to rarely white, and range from 3.0 to 7.5 mm in length. The outer surface of the corolla tube is usually minutely atomiferous-glandular, sometimes with a few scattered hairs. The pappus consists of a single series of 25 to 40 slender, capillary, scabrous, persistent bristles, usually slightly longer than the expanded corolla.

The number of flowers per head is a relatively useful character in recognizing some species (Fig. 3). In E. purpureum and E. fistulosum, heads usually have 5 to 7 flowers; heads of E. maculatum usually have 9 to 20 flowers; heads of E. dubium and E. steelei usually have 5 to 9 flowers. The number of flowers per head on an individual plant varies slightly from head to head; the number of flowers per head on different individuals within a single population varies more than within a single individual (Fig. 4).

Features of the androecium and gynoecium are not important in the delimitation of subgeneric taxa. They reflect familial and tribal relationships. Thus as in other composites the androecium is composed of filaments attached to the corolla tube, alternate with the lobes, with elongated anthers united into a tube;

pollen is released into the interior of the anther tube and pushed out by growth of the style. Style branches are slightly broadened or flattened distally, papillate, with paired stigmatic lines located only below the middle, a character of the tribe Eupatorieae.

ACHENES

Achenes of section Verticillata are prismatic and 5-ribbed, ranging from 3.0 to 5.5 mm in length. The surface is atomiferous-glandular, sometimes with a few setulae along the nerves. The color of the achenes is usually dark brown to black, but is sometimes yellowish-brown. Features of the achene are not important in the delimitation of species in the section.

Table 2. Summary of selected stem characteristics of *Eupatorium* section *Verticillata*.

	E. dubium	*E. maculatum*	*E. steelei*	*E. purpureum*	*E. fistulosum*
height (m)	0.4-1.2 (1.7)	0.6-2.0	0.6-2.0	0.3-2.0	0.6-3.0
pith	solid	solid or sometimes hollow near the base at maturity	solid	solid or rarely developing a slender central cavity	hollow with large central cavity
pigmentation	purple-spotted or sometimes uniformly purple throughout	purple-spotted or sometimes uniformly purple throughout	greenish-purple or sometimes evenly purplish	distinctly dark purple only at nodes, otherwise greenish	evenly purple throughout
glaucosity	scarcely or not at all glaucous	scarcely or not at all glaucous	not at all glaucous	scarcely or not at all glaucous	strongly glaucous when fresh
vesture	glandular-puberulent near summit, glabrous below	glandular-puberulent near summit, glabrous below to densely puberulent throughout	conspicuously glandular-pubescent throughout	glandular-puberulent near summit, glabrous below	glandular-puberulent near summit, glabrous below

Fig. 1. Representative leaves of *Eupatorium* section *Verticillata*. a. *E. purpureum*; b. *E. fistulosum*; c. *E. steelei*; d. *E. maculatum*; e. *E. dubium*.

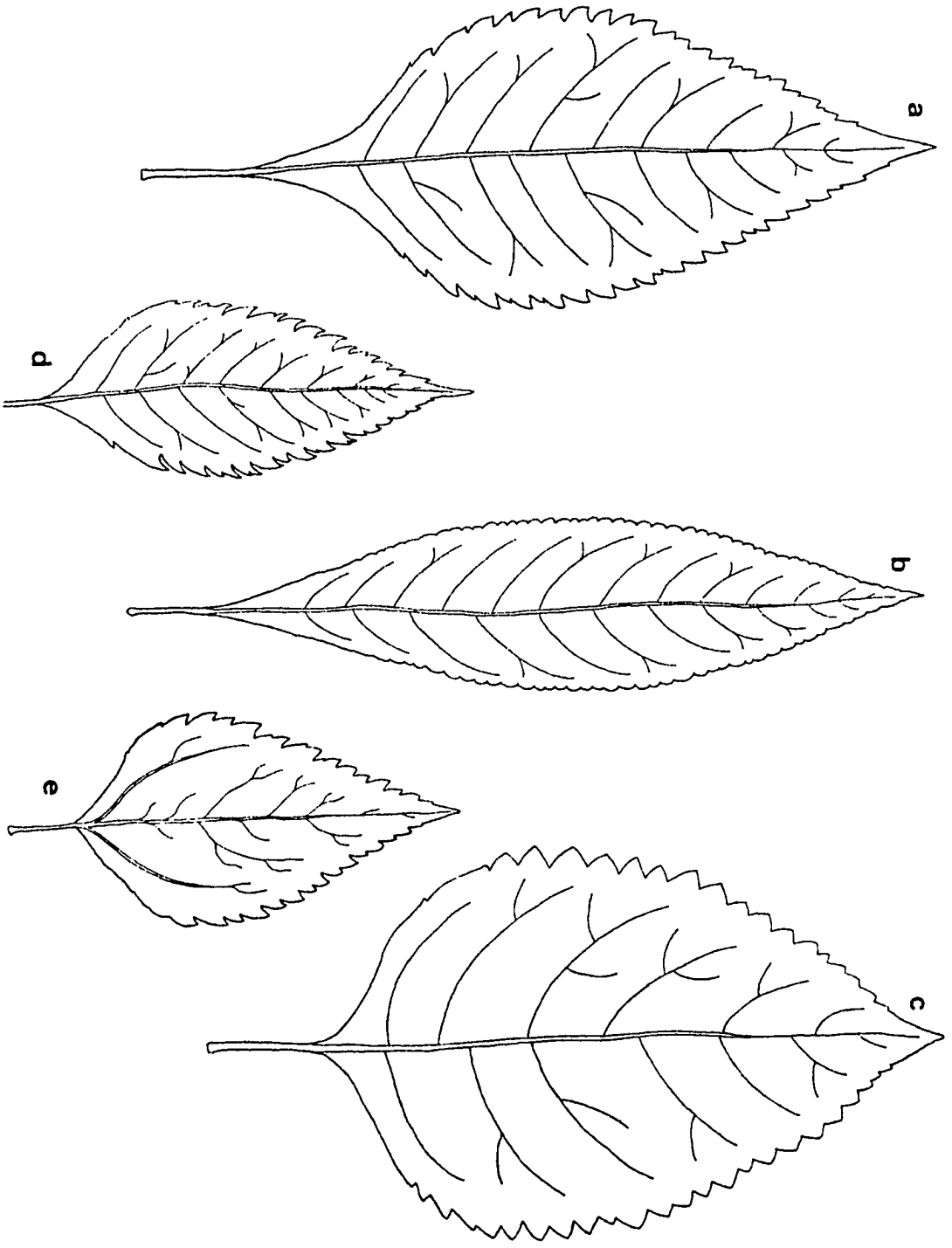


Table 3

Leaf length/width ratios of *Eupatorium* section *Verticillata* species. Numbers given are mean ± standard deviation. Measurements were taken from herbarium specimens (number of specimens examined of each species = 30).

Taxa	Leaf length/width
E. dubium	2.43 ± 0.37
E. maculatum	
subsp. *maculatum*	
var. *maculatum*	3.61 ± 1.15
var. *follosum*	3.15 ± 0.68
subsp. *bruneri*	3.36 ± 0.59
E. steelei	2.35 ± 0.23
E. purpureum	
var. *purpureum*	3.29 ± 0.51
var. *holzingeri*	3.11 ± 0.29
E. fistulosum	4.59 ± 1.10

Fig. 2. Summary of number of leaves per node (measured at first node below inflorescence) of species of *Eupatorium* section *Verticillata*, based upon herbarium specimens from throughout the geographic range of each species. Frequency is expressed as a percent (number of specimens examined of each species = 30 to 300).

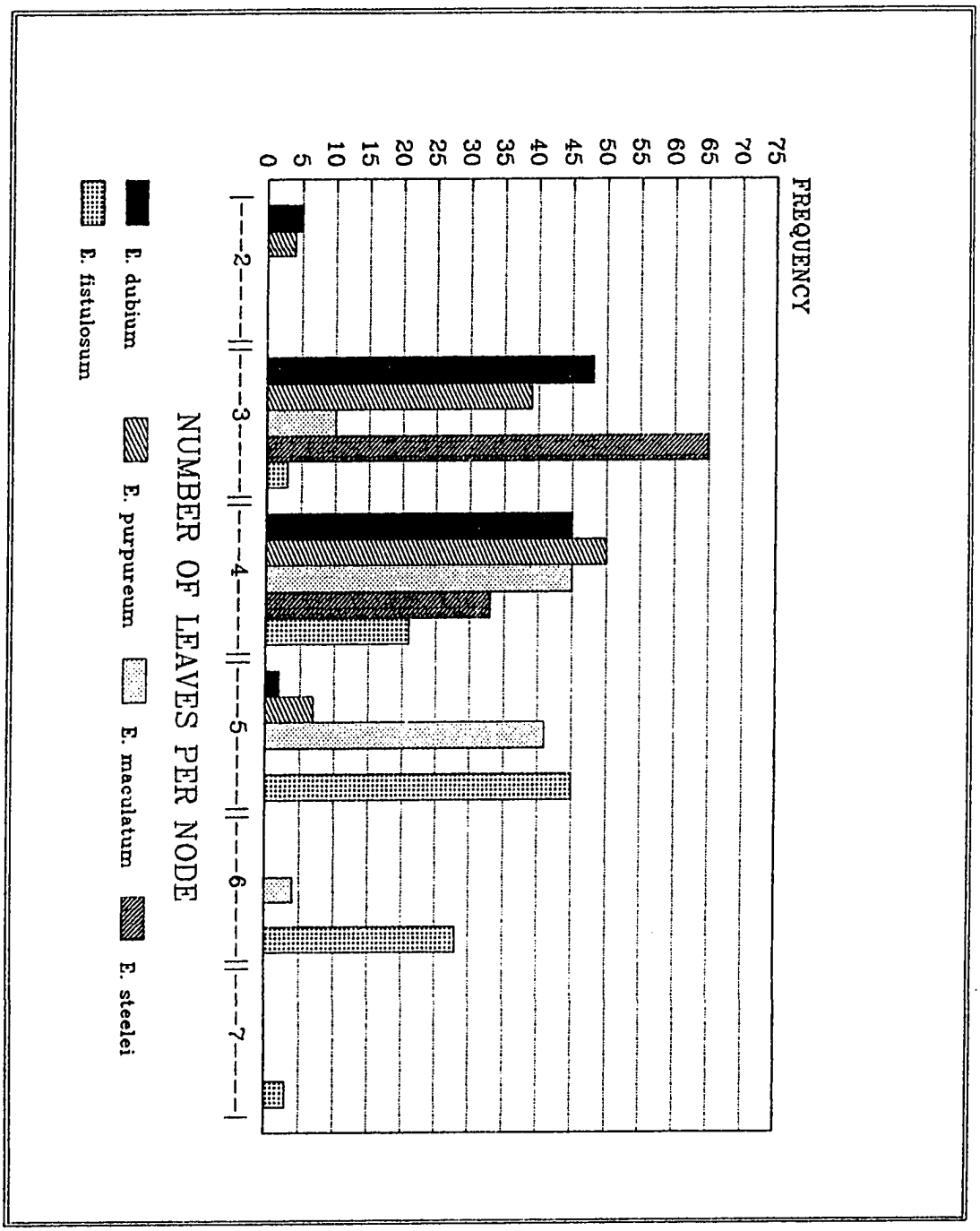


Fig. 3. Summary of number of flowers per head of species of Eupatorium section Verticillata, based upon herbarium specimens from throughout the geographic range of each species. Frequency is expressed as a percent (number of specimens examined of each species = 30 to 300).

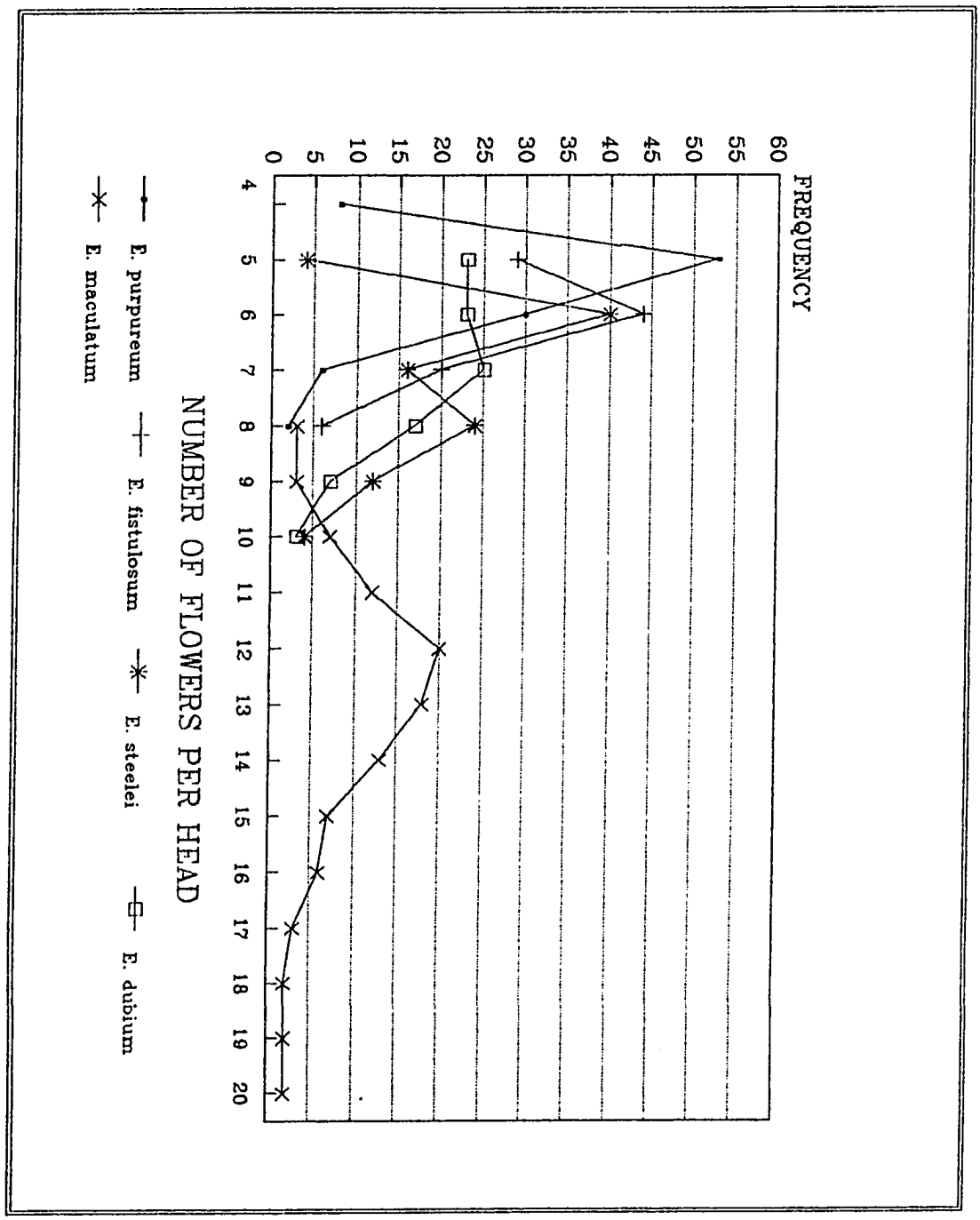


Fig. 4. Summary of variation in number of flowers per head between allopatric populations (A, B, C) of each species of Eupatorium section Verticillata, based upon natural populations. A single flower head was randomly selected from each individual within each population. Frequency is expressed as a percent (number of specimens examined in each population = 20 to 230).

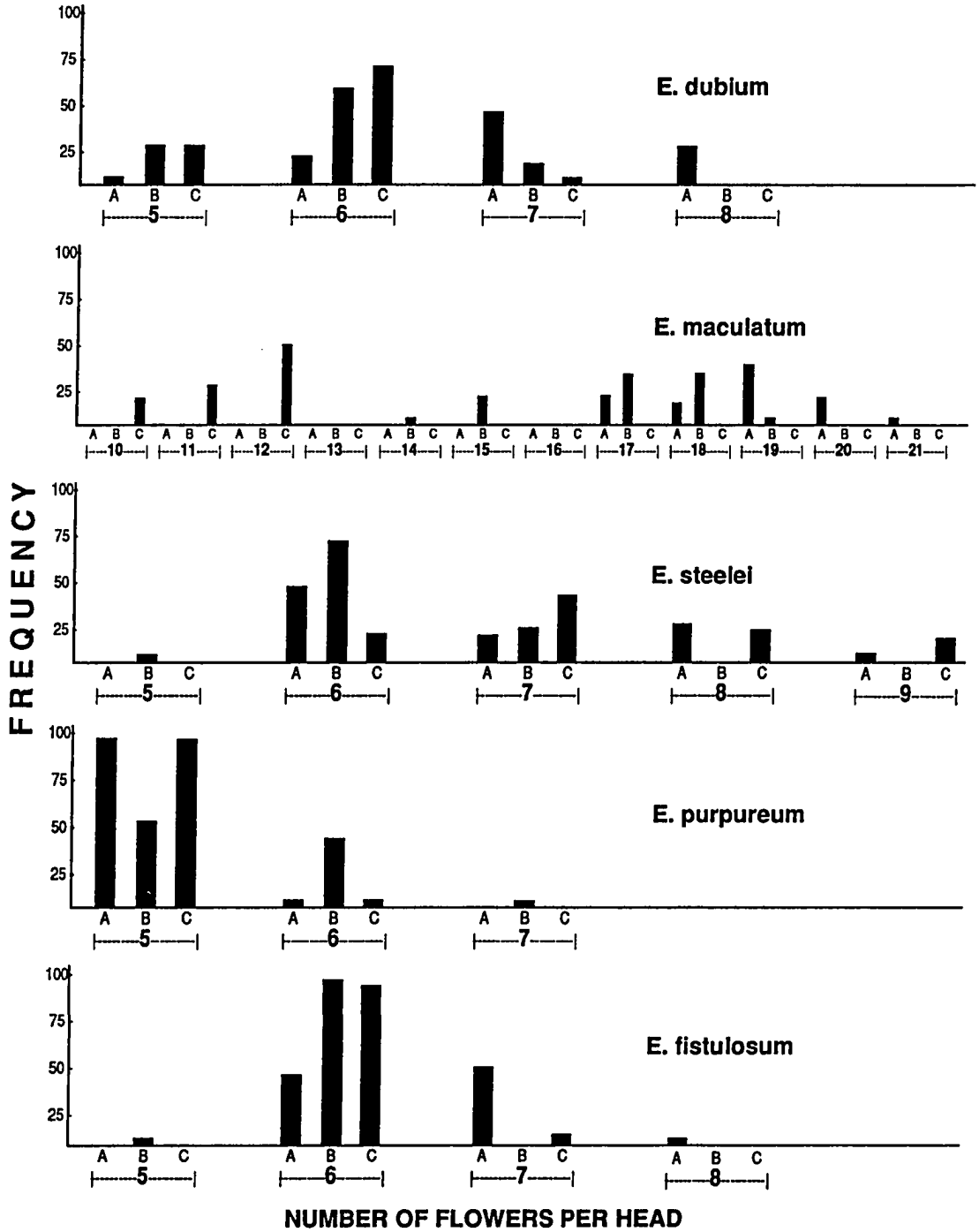
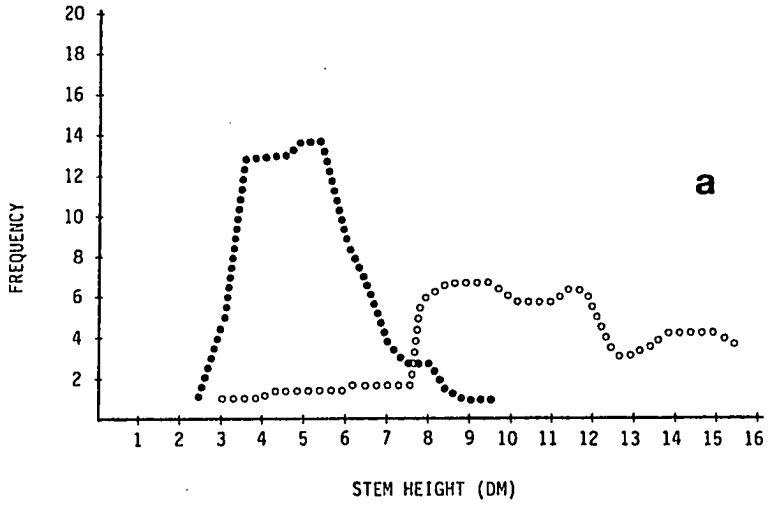
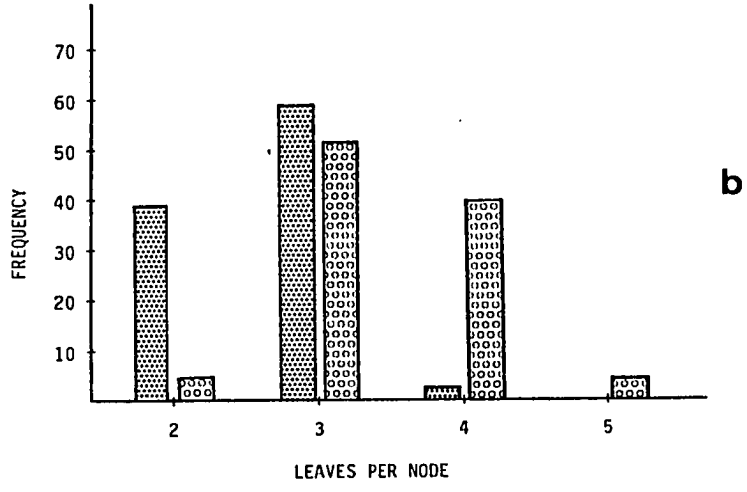
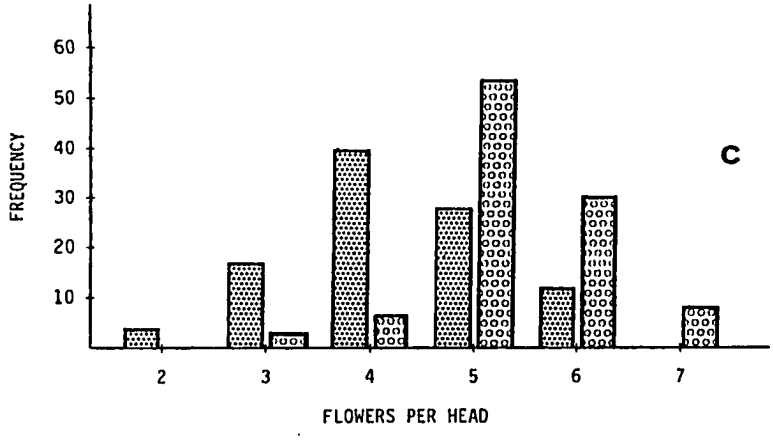


Fig. 5. Comparison of selected morphological characters (a. stem height; b. number of leaves per node; c. number of flowers per head) between one natural population (number of individuals = 98) of E. purpureum and one natural population (number of individuals = 112) of E. "amoenum". Both populations were located in Sussex Co., New Jersey, approximately 15 km from each other. Frequency is expressed as a percent. (Key: solid circle = E. "amoenum"; open circle = E. purpureum.)







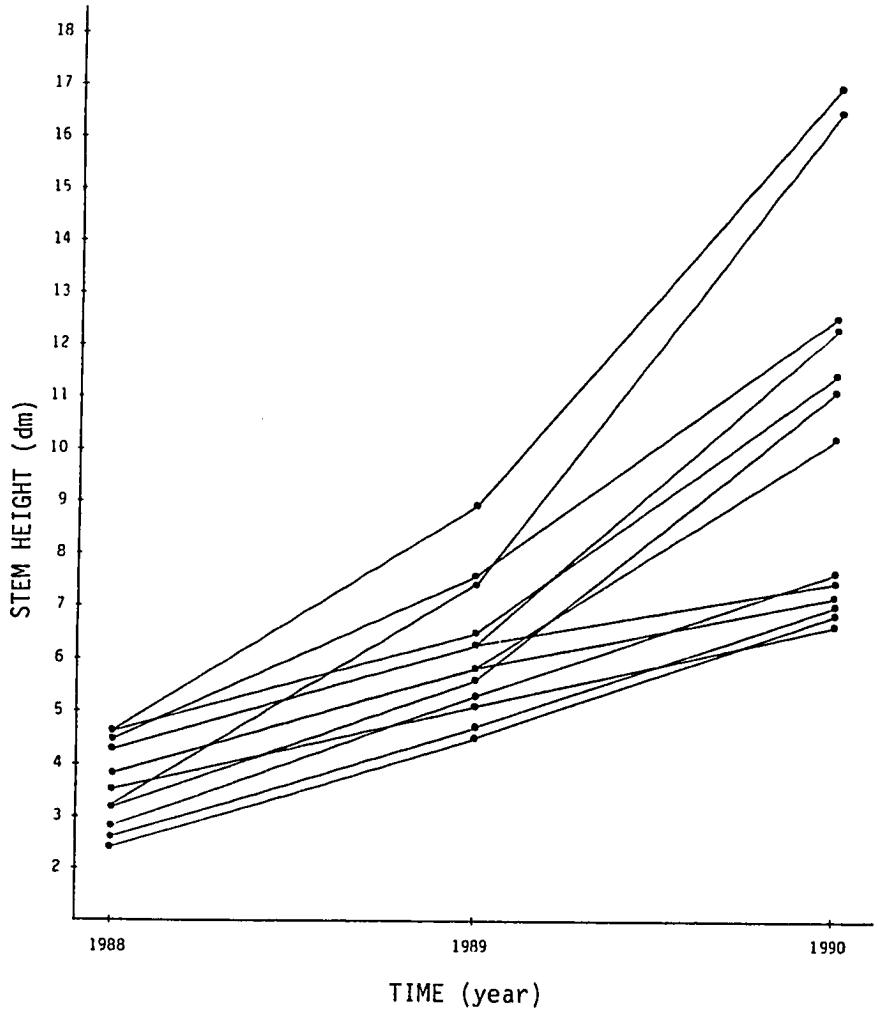


Fig. 6. Stem height (measured at time of flowering) of 9 plants of Eupatorium "amoenum" at the time of collection in their natural habitat (1988) and one and two years subsequently in uniform cultivation.

Distribution

The species of section Verticillata are restricted to North America, from Newfoundland to northern Florida, west to Saskatchewan, Idaho, Utah, and Arizona, with outlying populations in southwestern British Columbia, and adjacent Washington (Fig. 7). The section occurs in greatest abundance and diversity in eastern United States. Only one species, E. maculatum, is common west of the Mississippi River, where it occurs in wet or moist habitats usually in association with calcareous soils.

Species diversity maps of section Verticillata are shown in Figures 8 to 14. The size of the distributional range varies greatly from species to species. E. steelei, endemic to the southern Appalachian Mountains, is restricted to the Blue Ridge Province of western North Carolina and eastern Tennessee, the Ridge and Valley Province of southwestern Virginia, and the Appalachian Plateaus Province of eastern Kentucky (see Fenneman, 1938, for discussion and delimitation of physiographic boundaries). E. dubium is restricted to the Atlantic coastal plain from South Carolina to Massachusetts, with outlying populations in coastal New Hampshire, southern Maine, and southern Nova Scotia. The occurrence of disjunct coastal plain species in southern Nova Scotia is well documented (Keddy &

Wisheu, 1989). E. maculatum has the widest geographic distribution of all species in the section. Subspecies maculatum occurs mostly east of the Mississippi River and is the most common species in Canada; subsp. bruneri occurs mostly west of the Mississippi River. The E. maculatum complex in the northern part of its range exists as small, localized, and widely separated populations. E. purpureum is strongly sympatric with E. fistulosum. Both species are widely distributed throughout eastern United States, but each species occupies its own ecological niche. E. purpureum usually occurs in dry upland habitats, E. fistulosum usually occurs in wet or moist habitats.

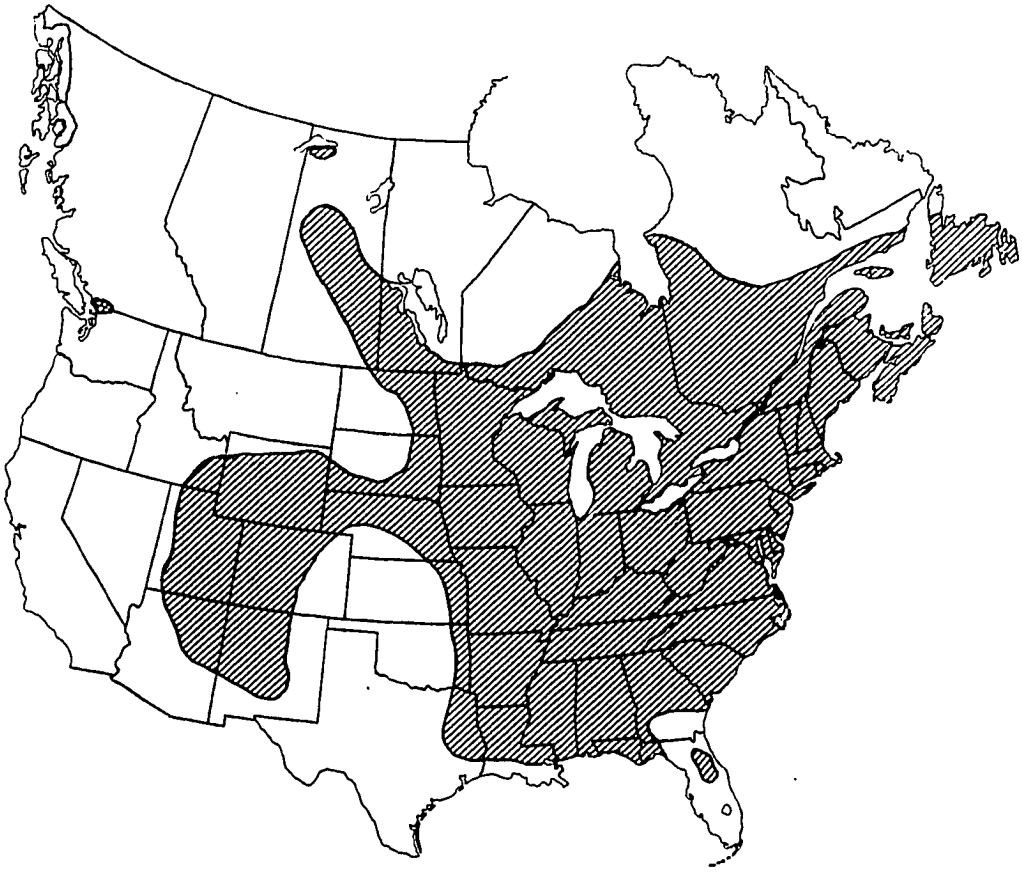


Fig. 7. Worldwide distribution of Eupatorium sect. Verticillata.

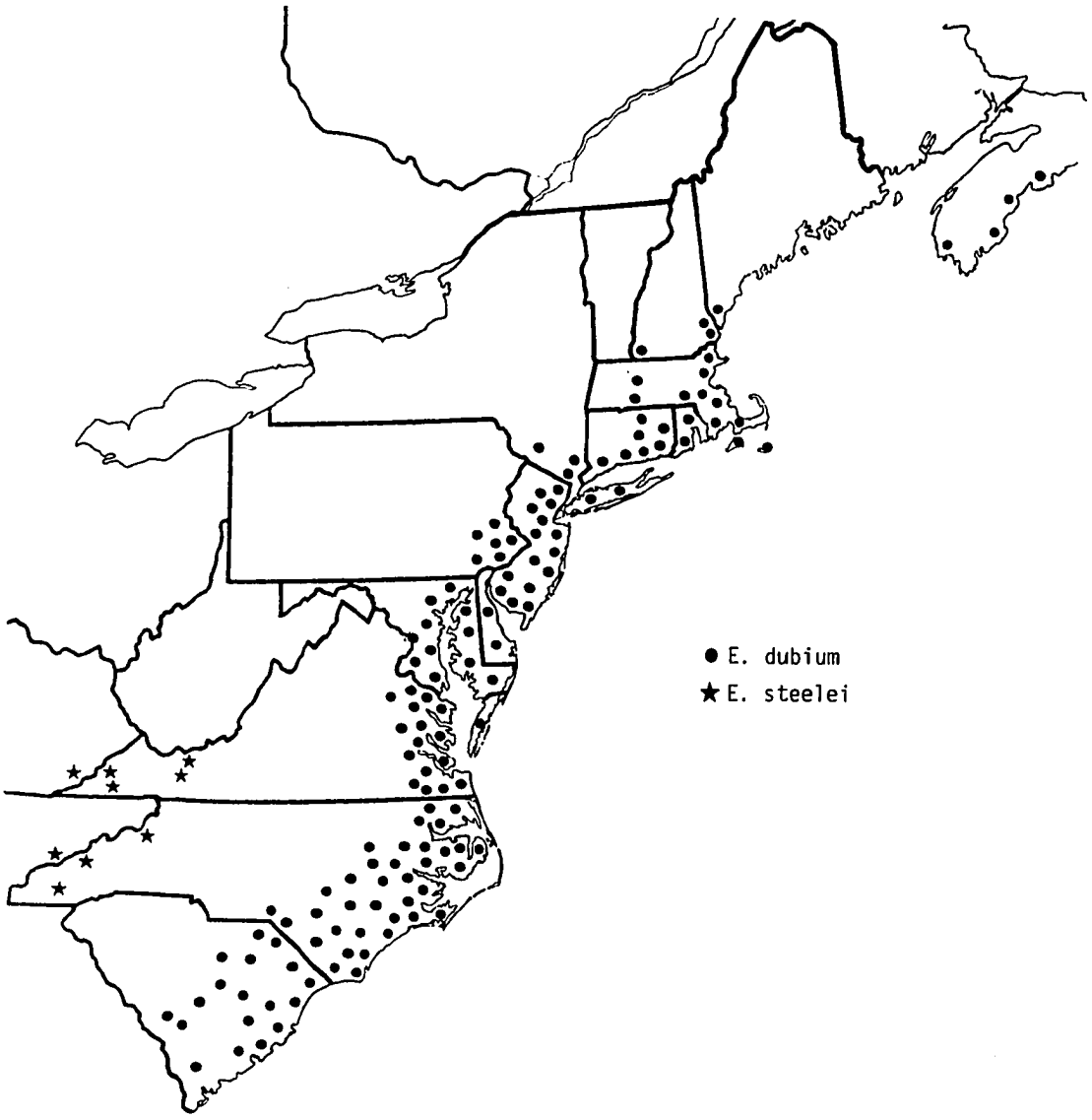


Fig. 8. Distributions of Eupatorium dubium and E. steelei.

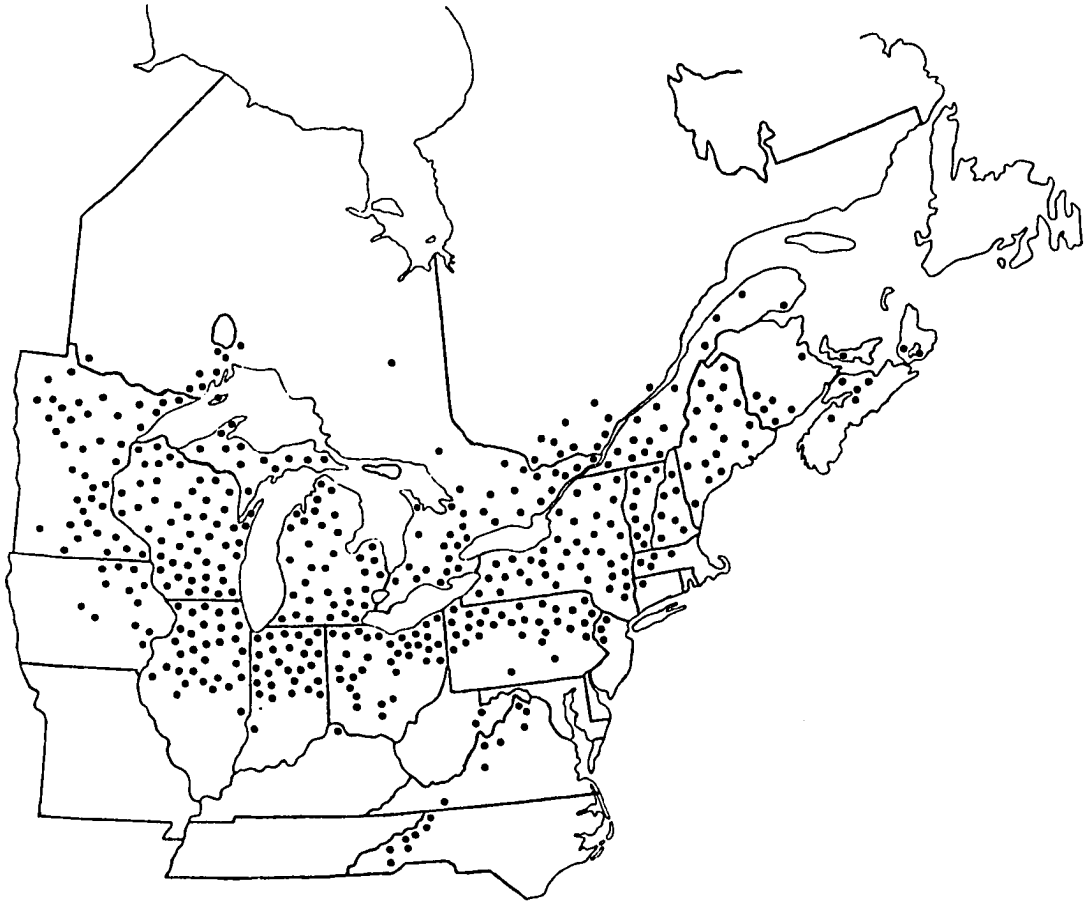


Fig. 9. Distribution of Eupatorium maculatum var. maculatum.

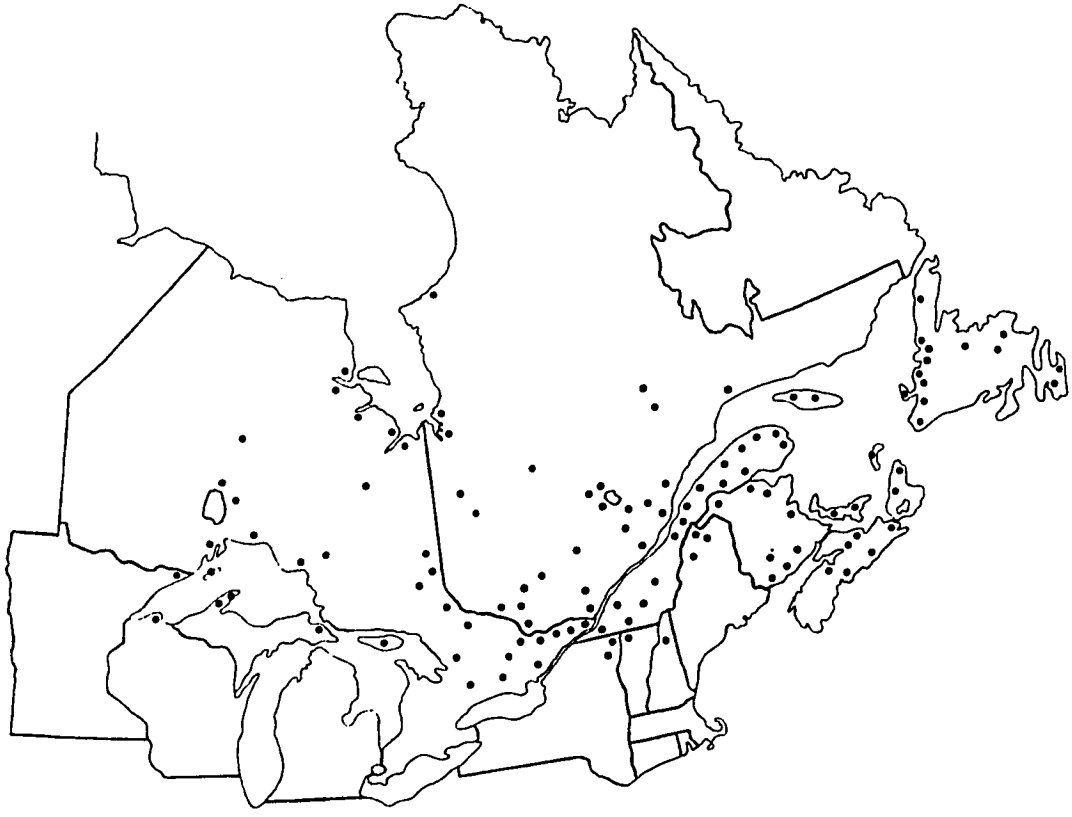


Fig. 10. Distribution of Eupatorium maculatum var. foliosum.

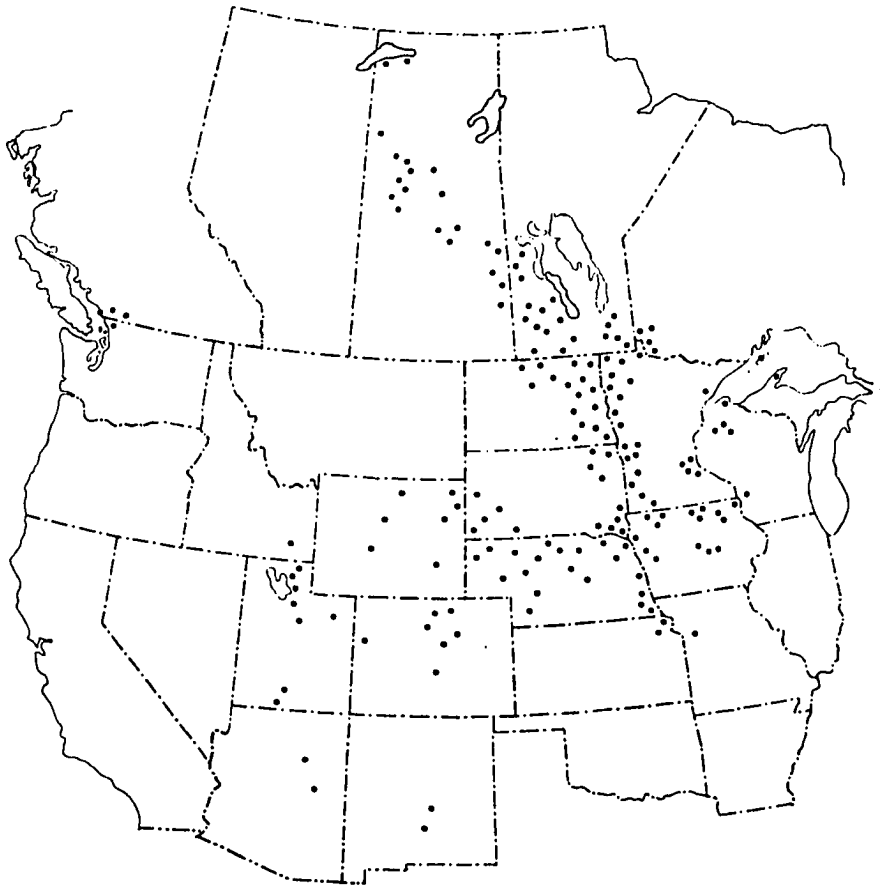


Fig. 11. Distribution of Eupatorium maculatum subsp. bruneri.

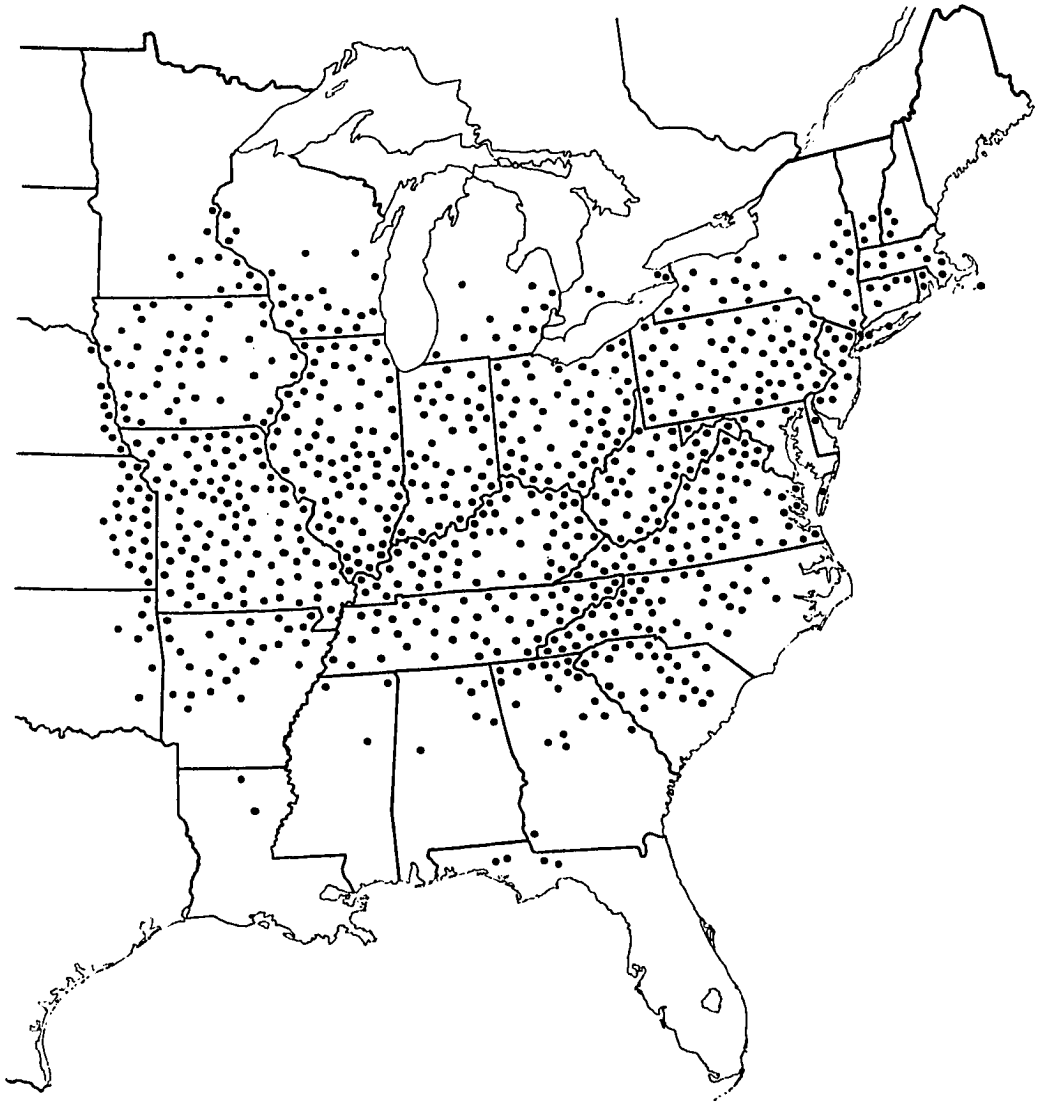


Fig. 12. Distribution of Eupatorium purpureum var. purpureum.

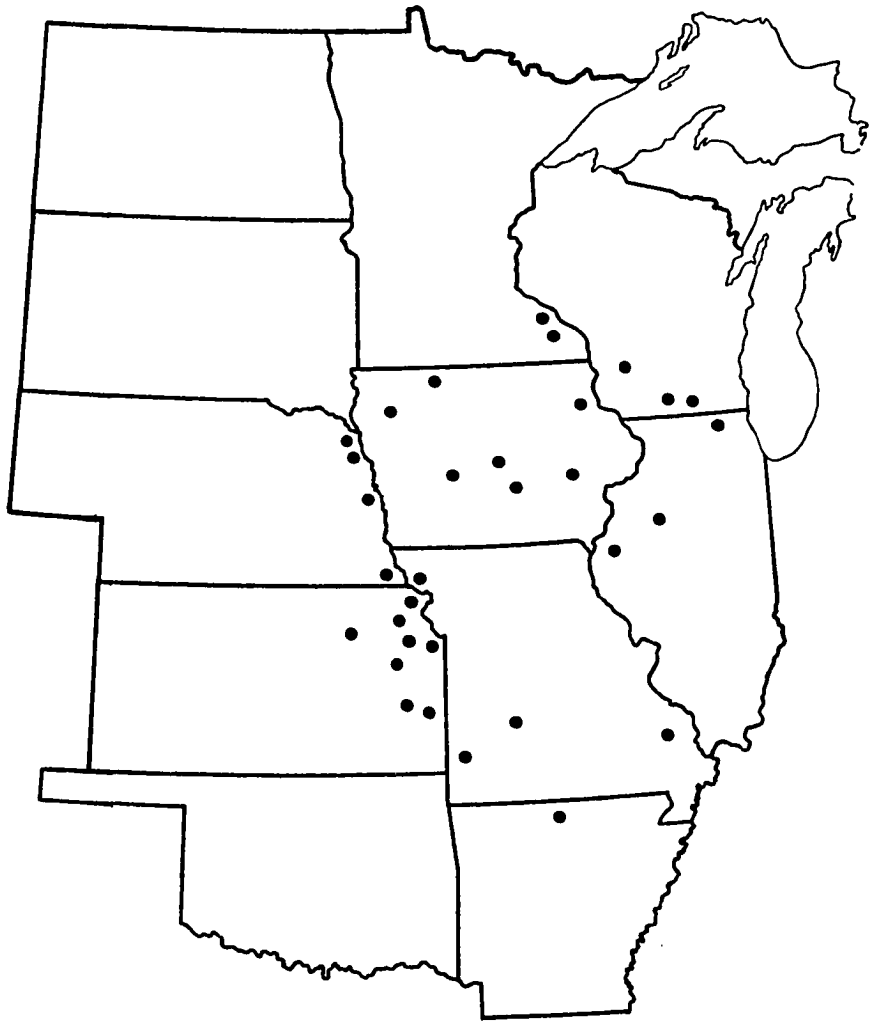


Fig. 13. Distribution of Eupatorium purpureum var. holzingeri.

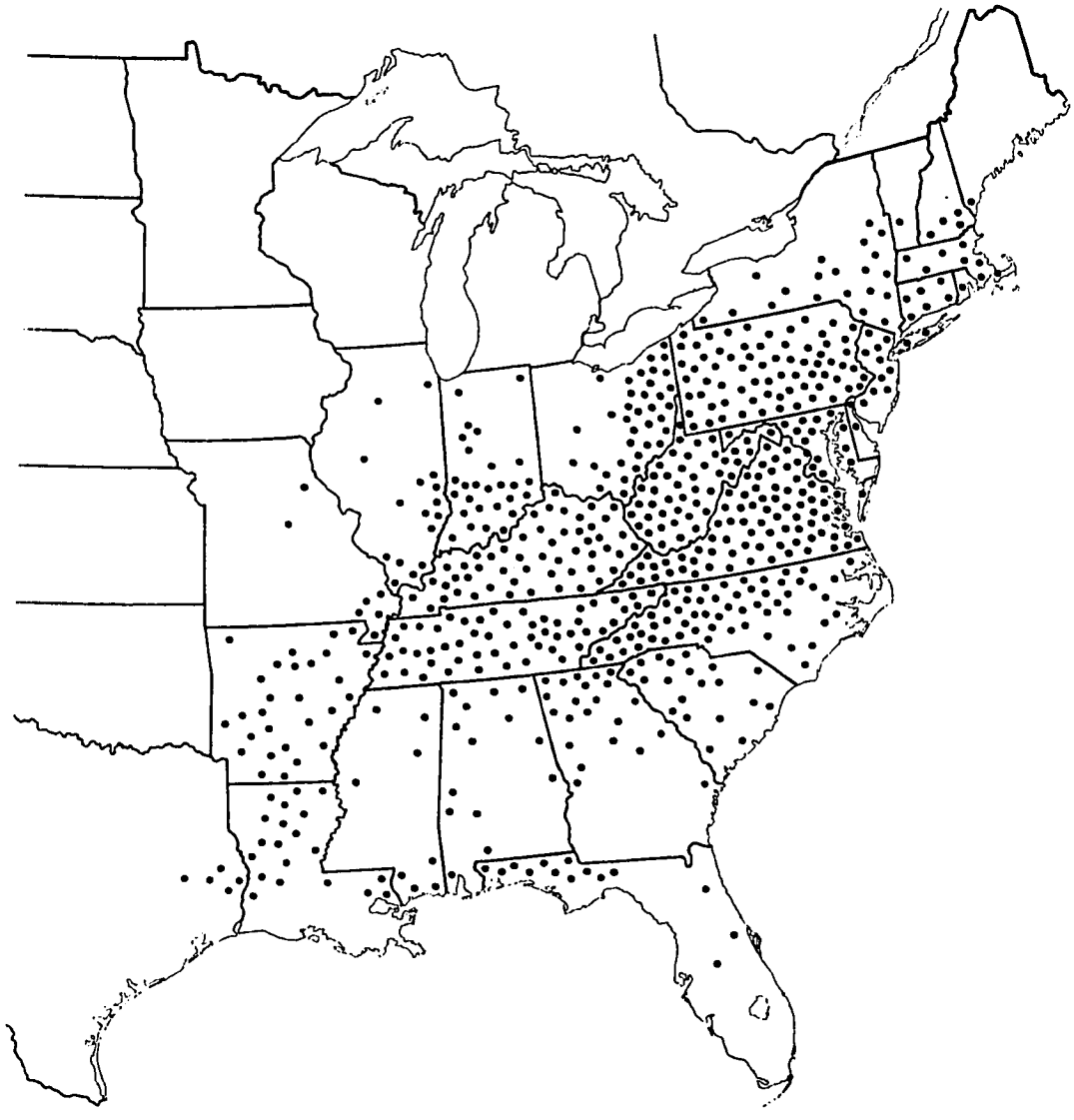


Fig. 14. Distribution of Eupatorium fistulosum.

Etymology

The genus Eupatorium was dedicated to Mithridates Eupator VI (132-63 BC), King of Pontus, who is said to have used a species of the genus in medicine. Linnaeus (1753) took up the name originally proposed by Tournefort (1700).

Legend has it that Mithridates lived in constant fear of being poisoned by his enemies (Dwyer & Rattray, 1986). He reputedly concocted an antidote from many poisonous ingredients, and then took small but increasingly larger doses of the mixture in an effort to make himself immune to poisons. An antidote, mithridate, bore his name in medieval pharmacology. His name lives on in the term mithridatism, "acquired tolerance of a poison."

The kingdom of Pontus was located on the shores of the Black Sea and was conquered by the Roman general Pompey in 66 BC. Facing capture by Roman enemies, Mithridates reputedly tried in vain to poison himself and had to get a slave to stab him to death (Dwyer & Rattray, 1986).

Accounts written after his death portray Mithridates as a diligent biological investigator who knew 22 languages (Dwyer & Rattray, 1986). He is said to have been skilled in medicine. Mithridates' physician Crateuas was famous for his lifelike botanical paintings, now thought to have been the basis

for some illustrations in Dioscorides' De Materia Medica.

Common names. The following colloquial names for taxa of Eupatorium sect. Verticillata are listed chronologically according to publication dates, with author citations in parentheses: Hemp-Agrimony (Hill, 1756); Joe Pye Weed, (Torrey, 1819); Purple Eupatorium, Three-Leaved Eupatorium (Darlington, 1837); Purple Hempweed (Beck, 1848); Trumpet-Weed (Gray, 1848); Spotted Eupatorium (Wood, 1848); Queen of the Meadow, Purple Boneset, Gravel-root, Jopi Weed (Millspaugh, 1887); Tall Boneset, Spotted Boneset, Kidney-root (Britton & Brown, 1898); King-of-the-meadow, Indian gravel-root, Marsh-milk weed, Nigger-weed, Skunk-weed, Quill-wort, Motherwort (Britton & Brown, 1913); Smokeweed (Uphof, 1968); Ague-weed, Indian Sage (Durant, 1976).

Ethnobotany

The rhizome, leaves, and flowers of several species of Eupatorium section Verticillata have been used for medicinal purposes. Darlington (1837) noted, "Dr. Barton speaks highly of it [E. purpureum] as a tonic" and Torrey (1843) claimed, "A decoction of the root [rhizome] is used as a remedy for gravel. The popular name [Joe Pye weed] is said to be that of an Indian who recommended it to the whites."

The northeastern Algonquian Indians used the rhizome of several species (probably E. fistulosum, E. maculatum, and E. purpureum) to clear gravel stone from the urinary bladder and to dissolve kidney stones (Speck, 1917). Early names of this plant given by colonial settlers were gravel-root, kidney-root, and Indian sage. The rhizome was also used as a stimulant, diuretic, and nervine tonic (Uphof, 1968).

Harned (1931) stated, "This plant [Eupatorium purpureum] derived its common name, Joe-Pye Weed, from a New England Indian doctor who gained notoriety in the application of the plant in cases of typhus fever." Durant (1976) stated, "Joe Pye was an Indian known for his special skill as a medicine man who made the rounds of rural New England in the late 1700's. He apparently was specially skilled at reducing fevers. One of the few records of him show that he bought "1 qt rum, 1 s[hilling] 6 p[ence]" at a tavern in Stockbridge,

Mass., in 1775, so perhaps he made an elixir as well as an herb infusion." Although Joe Pye weed was of obvious medicinal use it is likely that its relative Eupatorium perfoliatum L. was more frequently used by the North American Indians for treatment of fevers.

The Chippewa Indians had several uses for E. maculatum (Densmore, 1928). Rhizomes collected in autumn were dried, pulverized, boiled, and prepared in the form of a decoction. Sick children would be bathed in the decoction: "if a child is fretful this will make it go to sleep" (Densmore, 1928). Decoctions from the rhizome were also used as a wash for inflamation of the joints and skin. Dried leaves and flowering tops were used to prepare a diaphoretic tea.

Barratt (1841) commented on the economic use of E. fistulosum: "The hollow stems of this species have been used extensively for blasting rocks at the Middletown Feldspar Quarry [Connecticut]." By filling the hollow stems with gun powder they could be used as fuses in the quarries (Earll, 1971).

Most species of Joe Pye weed have been cultivated in Europe and deserve greater recognition in North America. Their conspicuous purple flowers and commanding height offer the gardener unique material suitable for different displays. Plants can be propagated from seed and, more commonly, by division of the root stock. Eupatorium maculatum was first

cultivated in Europe in 1656 (Alton, 1810), and Lamarck (1786) wrote that Eupatorium purpureum was "used in the king's garden." Three species are currently offered for sale by native plant dealers in the United States: E. fistulosum, E. maculatum, and E. purpureum.

Flavonoid Chemistry

No systematic phytochemical study of Eupatorium section Verticillata has been previously made. The present investigation was a simple chemical survey of leaf tissues for their flavonoid patterns by two-dimensional paper chromatography. Primary constituents were not identified in this study.

Leaf samples of four species of section Verticillata and four other closely related (see King and Robinson, 1987) species of Eupatorium were collected. Leaves were used from dried herbarium specimens or were collected from plants in the field and dried in a plant drier. One gram of each sample was extracted with 10 ml of 80% methanol at room temperature for 20-24 hours. Chromatograms of each sample were spotted on 3 MM Whatman paper and run at 24°C in a descending manner in butanol:acetic acid:water (6:1:2) for the first dimension and in 15% acetic acid for the second dimension. The chromatograms were exposed to concentrated NH_3, and the color changes after exposure in visible light and UV light were noted.

It is clear from the chromatograms (Fig. 15) that the four surveyed species of section Verticillata show nearly identical spot patterns. The length and shape of spots may vary in exact size but their position on

the chromatogram remains approximately the same. Fairly clear-cut differences in chromatographic patterns exist in the four other species of Eupatorium studied (Fig. 16).

Color key of spots (Figs. 15 and 16) after chromatograms were fumed with ammonia and examined under UV light:


blue


dull brown


yellow

faint brown (tan)

bright orange

blue/green

pink

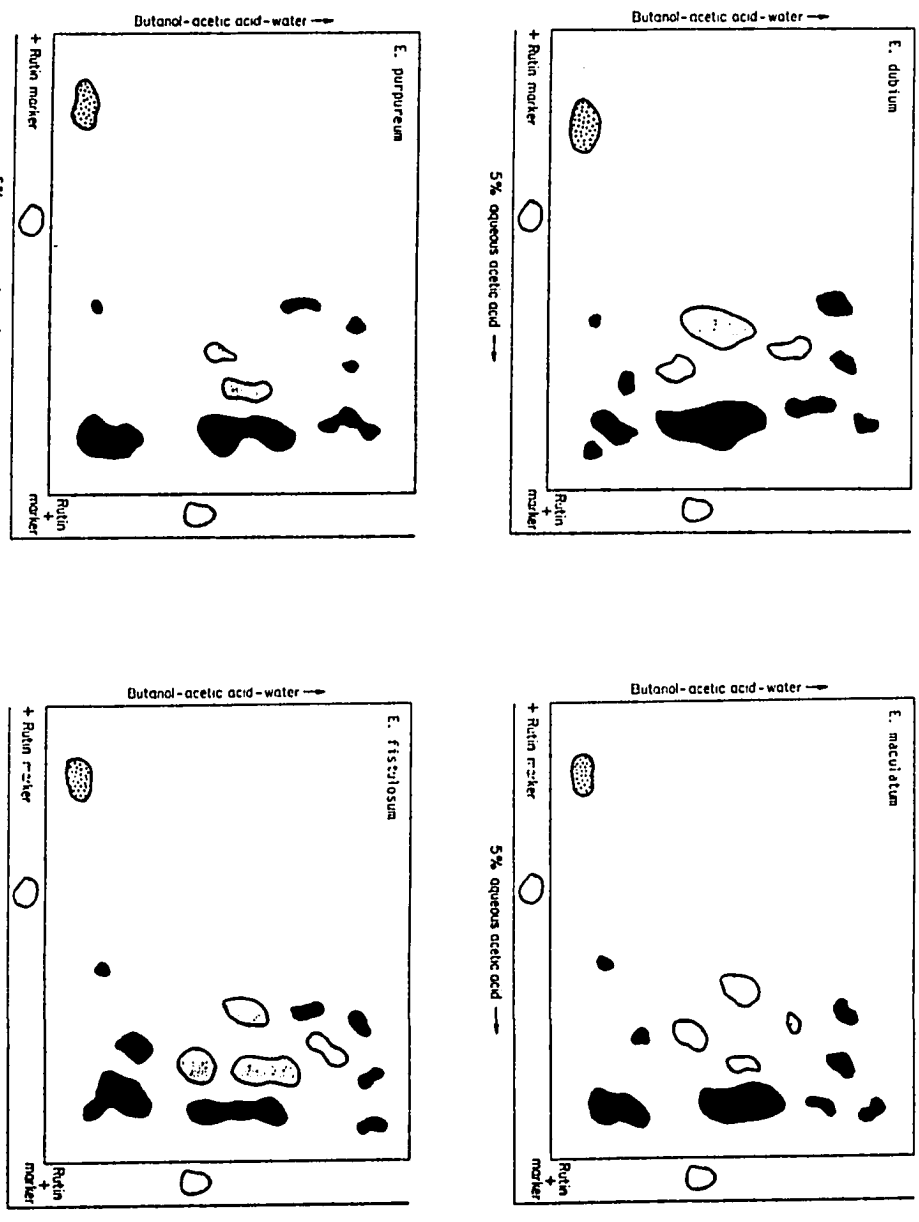


Fig. 15. Two-dimensional chromatograms of flavonoids of four species of Eupatorium sect. Verticillata.

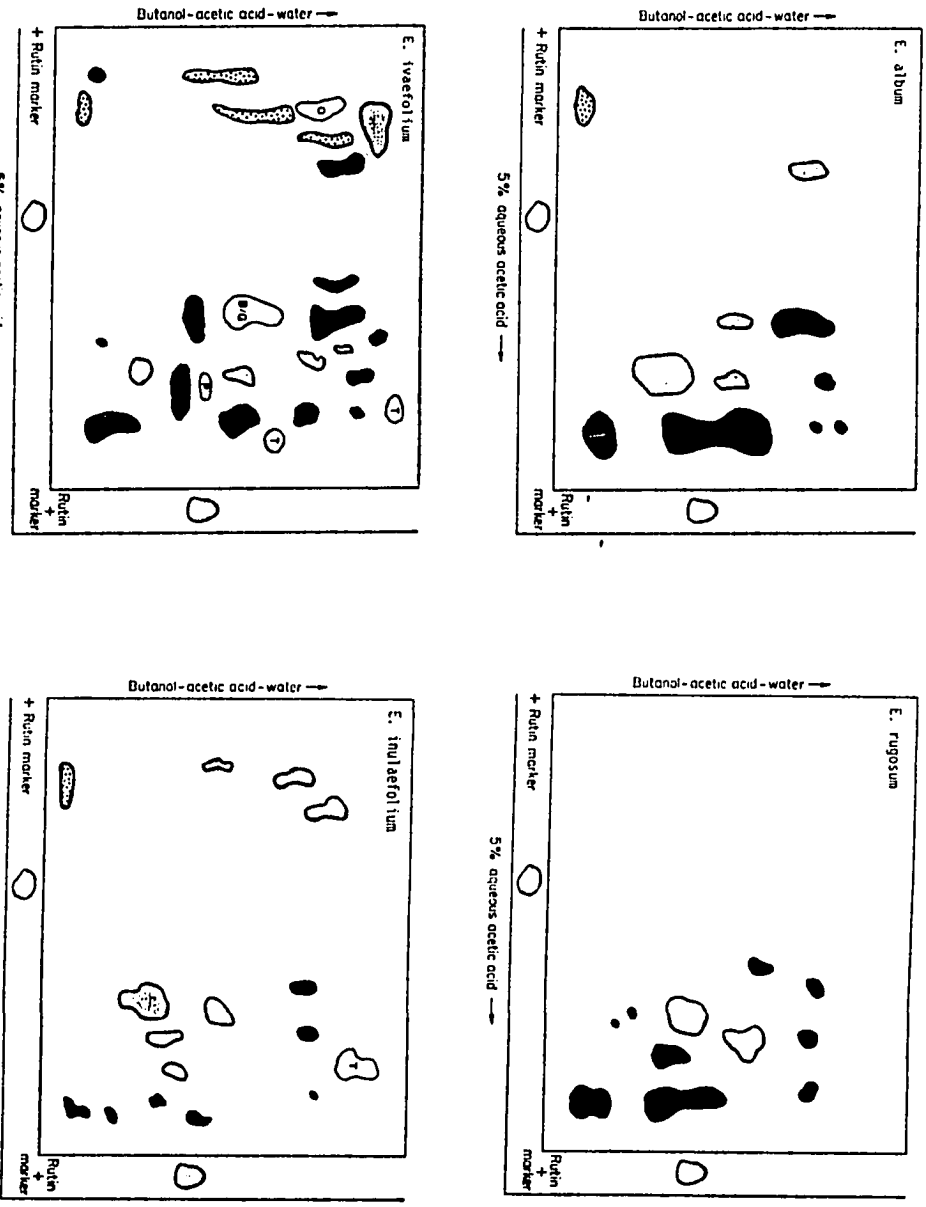


Fig. 16. Two-dimensional chromatograms of flavonoids of four species of Eupatorium closely related to section Verticillata.

Cytology

Floral buds of taxa of Eupatorium section Verticillata were collected from natural populations. The buds were fixed in Carnoy's solution (2:3:1, chloroform: 95% ethanol: glacial acetic acid) for 24 hr, washed in three changes of 70% ethanol, and stored in 70% ethanol at 10°C. The floral tissue was incubated in alcoholic-carmine stain (Snow, 1963) for 48 hr at 50°C, prior to dissecting the anthers in 45% acetic acid. The anther tissue was then squashed and mounted in Hoyer's mounting medium. Chromosome counts were made at diakinesis of Meiosis I and in the first postmeiotic division of microsporogenesis, and suitable figures were drawn with aid of a camera lucida. Cytovouchers have been deposited in the herbarium at NY.

In general, the results presented here (Table 4) and elsewhere (Table 5) confirm that species of section Verticillata are sexual diploids with a stable chromosome number of $2n = 20$ (Fig. 17). In the present investigation, meiosis appeared to be normal in all of the taxa, and all pairing at metaphase was bivalent. There were no obvious differences among the taxa in the size and shape of chromosomes, but no detailed study of chromosome shape and size was made. Grant (1953) reported chromosome numbers from 32 different

populations of section Verticillata. In all cases a number of 2n = 20 was confirmed or reported for the first time, with the exception of one tetraploid report (2n = 40) for E. purpureum from the northern limit of its range (Welland Co., Ontario, Canada).

Yahara et al. (1989) has suggested that Eupatorium species with a chromosome number of 2n = 20 are of polyploid origin. Conversely, some chromosome counts of E. maculatum showed several B chromosomes (Kapoor et al., 1987). This could indicate a reduction from a higher chromosome number, but even if this were so, there is no way to determine whether a higher number is the primitive number for the genus.

Table 4

Chromosome counts of *Eupatorium* section *Verticillata* made for the present study

Taxa	Number	Collection
E. dubium	2n = 20	*Lamont 373*
E. fistulosum	2n = 20	*Lamont 366*
E. maculatum		
subsp. *maculatum*		
var. *maculatum*	2n = 20	*Lamont 359*
var. *follosum*	2n = 20	*Lamont 240*
subsp. *bruneri*	2n = 20	*Lamont & Cronquist 349*
E. purpureum	2n = 20	*Lamont 379*
E. steelei	2n = 20	*Lamont & Wieboldt 357*

Table 5

Previously published chromosome counts of *Eupatorium* section *Verticillata*

Species	Number	Source
E. dubium	2n = 20	Grant, 1953
	2n = 20	Kell, 1979
E. fistulosum	2n = 20	Grant, 1953
	2n = 20	Watanabe, 1986
E. maculatum	2n = 20	Grant, 1953
	2n = 20	King *et al.*, 1976
	2n = 20	Gervais, 1979
	2n = 20	Löve & Löve, 1980
	2n = 20	Parfitt, 1981
	2n = 20	Kapoor & Ramcharitar, 1982
	2n = 20	Löve & Löve, 1982
	2n = 20	Watanabe, 1986
	n = 10	Kapoor *et al.*, 1987
	2n = 20	Kapoor *et al.*, 1987
	2n = 20+6B	Kapoor *et al.*, 1987
E. purpureum	n = 10	Cooper & Mahony, 1935
	2n = 20, 40	Grant, 1953
	2n = 20	King *et al.*, 1976
	2n = 20	Watanabe, 1986
E. steelei	2n = 20	Lamont, 1990a

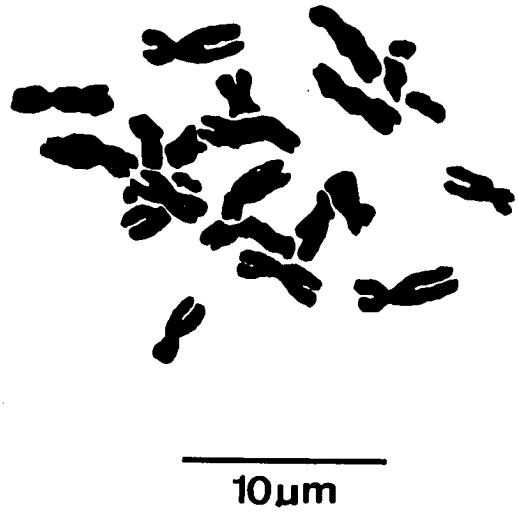


Fig. 17. Camera lucida drawing of meiotic chromosomes of Eupatorium steelei, Lamont & Wieboldt 357 (NY), 2n = 20.

Palynology

An SEM survey showed that pollen of all species of Eupatorium section Verticillata is echinate and tricolporate (Fig. 18). This was not unexpected, as the pollen of the Eupatorieae is known to be very uniform (King and Robinson, 1987). Pollen viability, measured by using Lactophenol Cotton Blue (Hauser and Morrison, 1964), showed almost 100% stainability for all species.

The pollen is approximately 22-25 μm in diameter, with sharp-pointed or occasionally blunt spines that range in length from 1.8-2.4 μm. Interspinal distances range from 1.2-3.0 μm. Perforations, which appear at the base of many spines in all taxa, vary in number and are of unknown significance. (The pores may have bearing on the efficiency of insect transport whereby the body hairs of insects could enter these pores and more efficiently retain the pollen (Whitehead, 1969). No evidence is available to support this hypothesis.) The internal structure of the exine is caveate, a condition that is most common in the subfamily Asteroideae (Skvarla, et al., 1977).

Spiny pollen has been shown to be characteristic of entomophilous Compositae (Faegri and Pijl, 1966). Plants of section Verticillata have rather showy flowers and stiffly upright inflorescences. The stiff

upright inflorescence would provide a stable landing platform for insect pollinators, while the showy purple flowers and nectaries provide attraction and reward, respectively (Faegri and Pijl, 1966).

Pollen morphology of section Verticillata is neither a taxonomically useful character in the delimitation of species, nor useful in distinguishing the different sections of eastern North American Eupatorium from each other (Sullivan, 1975).

Fig. 18. Scanning electron micrographs of pollen of *Eupatorium purpureum* (*Lamont 185*, NY).

Putative Hybridization

Evidence for hybridization among eastern North American species of Eupatorium is well documented (Fryar, 1964; Maurushat, 1969; Montgomery & Fairbrothers, 1970; Sullivan, 1972, 1976, 1978; Tucker & Dill, 1989). Hybridization in the genus has also been reported by others (Fernald, 1950; Grant, 1953; Gleason & Cronquist, 1963; Radford, et al., 1964; Cronquist, 1977, 1980, 1985; King & Robinson, 1987; Lamont, 1990a, 1990b). Previously published results of hybridization studies show that diploids of the species examined are uniformly sexual and outcrossing, whereas polyploids are uniformly apomictic and do not produce good pollen.

Current field work and herbarium searches indicate that hybridization within section Verticillata does occur but is not common (Fig. 19); hybridization with species outside the section has never been documented. In the course of field work mixed populations of E. purpureum and E. fistulosum, E. purpureum and E. steelei, and E. maculatum and E. fistulosum, with intermediate appearing plants were found. The putative hybrids produced normal looking pollen that stained positive with Lactophenol Cotton Blue (stainability was equated with fertility; Hauser and Morrison, 1964), and set normal amounts of seed. However, the putative

hybrids usually consisted of only a few individuals and did not form large populations. Herbarium searches revealed additional putative hybrids between E. maculatum and E. purpureum, and between E. dubium and E. purpureum. Herbarium studies indicate that hybridization in section Verticillata occurs more frequently at the periphery of the range of one or both of the parent species. For example, numerous voucher specimens from Florida appear intermediate between E. fistulosum and E. purpureum, and several specimens from South Carolina appear intermediate between E. dubium and E. purpureum.

In 1935 W. H. Camp selectively collected a series of voucher specimens (deposited at NY) from Stark Co., Ohio that obviously represented a hybrid swarm among E. maculatum, E. fistulosum, and E. purpureum. Voucher specimens of each parent species were morphologically distinct, but a confusing series of intermediate appearing plants strongly indicated introgressive hybridization. The putative hybrids produced normal looking pollen that stained positive with Lactophenol Cotton Blue, and set normal amounts of seed.

Jennings (1942) selectively collected and studied morphological variation in verticillate eupatoriums from western Pennsylvania (voucher specimens deposited at CM), and suggested the occurrence of hybridization. The "intermediate between E. fistulosum Barratt and E.

maculatum L., suggesting the possibility of it being a hybrid," was taxonomically recognized as E. fistulosum f. truncatum. Plants of "typical E. purpureum L. with a flattened or even concave inflorescence," suggesting hybridization with E. maculatum, were taxonomically recognized as E. purpureum f. depressum. Holotypes of Jennings' putative hybrids were borrowed from CM; plants had pollen of normal appearance that stained positive with Lactophenol Cotton Blue, and set normal amounts of seed.

Grant (1953) reported the first and only tetraploid ($2n = 40$) chromosome count for a species (E. purpureum) of section Verticillata. Grant speculated that the tetraploid may have been of hybrid origin: "The tetraploid race is on the periphery of the range of the species and represents the most northern extension for a polyploid species in the genus...It is most likely they have arisen by means of allopolyploidy, possibly as a result of the recession of the Pleistocene glaciation which allowed the intermingling of the diploid Verticillate species...Polyploidy in nature has been most often found to be associated with hybridization between species or subspecific races."

The cytovoucher of Grant's tetraploid specimen was borrowed from BH. The specimen was not strikingly different morphologically from the diploid specimens of

E. purpureum, although the inflorescence was somewhat depauperate in overall size (not an unusual feature for the species). Flowers had pollen of normal appearance that stained positive with Lactophenol Cotton Blue. Two additional specimens of E. purpureum (borrowed from DAO), collected near Grant's tetraploid specimen, also had pollen of normal appearance that stained positive with Lactophenol Cotton Blue.

Artificial crosses were not attempted in the present investigation; however, self-compatibility tests were performed in the field. Putative diploid plants of E. fistulosum failed to produce seeds when isolated with nylon bags, although the plants produced abundant pollen. These results indicate that diploids are self-incompatible since they produce seeds under field conditions where cross pollination presumably occurred.

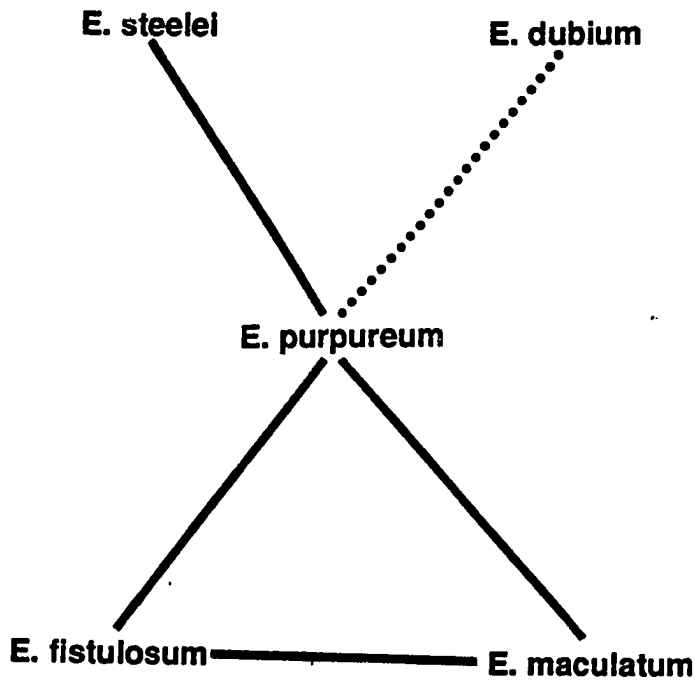


Fig. 19. Putative hybridization in Eupatorium section Verticillata. Solid lines indicate putative hybridization between species based upon field observations and herbarium searches; dotted lines indicate putative hybridization between species based only upon herbarium searches.

Phenetic Analysis

Overall phenotypic similarity of all species of section Verticillata was assessed using clustering and ordination techniques. One hundred thirty five individual herbarium specimens were selected as operational taxonomic units (OTUs) (30 from each species except E. steelei which included only 15; specimens selected are indicated in the Taxonomic Treatment). To insure adequate sampling the OTUs were chosen from across the geographic ranges of all species.

A list of nineteen characters known to vary among the taxa was prepared on the basis of published descriptions of the taxa, study of herbarium specimens, and study of the taxa in natural populations (Table 6). This list included all characters known to vary among the taxa that could be scored reliably in the specimens available. Leaf ratios were used, rather than direct leaf measurements, to eliminate size differences that might result from environmental modification. Only those specimens that could be scored for every character were included in the analysis.

After scoring the characters on each individual (Appendix), the data set was analyzed with the numerical taxonomy system programs (NT-SYS; Rohlf et al. 1979). To give characters approximately equal

weight, the 19 characters were standardized by transformation of means to zero and standard deviations to unity (Sneath and Sokal, 1973). An OTU by OTU similarity matrix was generated based on average taxonomic distances.

Two complementary methods were used to assess phenetic similarity. Cluster analysis was performed with the unweighted pair group method using arithmetic averages (UPGMA). This produced a hierarchical phenogram representing the associations among the OTU's. Additionally, a character by character correlation matrix was computed and analyzed by principal component analysis (PCA) for ordination of the OTUs.

The phenogram in figure 20 depicts a measure of similarities among the species of section Verticillata. It indicates a strong similarity between the OTUs purpureum and steelei. At a lower similarity level, dublum clusters with maculatum. The most phenetically distinct OTU is fistulosum. The cophenetic correlation coefficient is 0.84.

Phenetic similarities among species are also presented in figures 21 and 22, the results of principal component analyses. The three groups of OTUs in the plot of the first two principal components (Fig. 21) correspond to the primary clusters of the phenogram (Fig. 20). The first three principle component axes

account for 58.8% of the total character variation; 24.7%, 20.6%, and 13.5%, respectively (Table 7). In the first principal component characters 1, 2, and 7 are the most important in determining an individual's component score. Thus, the first component is primarily a weighed measure of stem and leaf serration characters. These characters provide clear separation of E. fistulosum from the other species. In the second principal component characters 12 and 17 are the most important in determining an individual's component score. The second principal component is primarily a measure of the number of leaves per node and corolla length. The third principal component is primarily a measure of leaf venation, and provides separation of E. dubium from the other species.

The results just presented indicate that the taxa in this study are distinguishable by a suite of correlated qualitative and quantitative morphological characters. On a phenetic basis E. steelei is more closely related to E. purpureum, E. dubium is more closely related to E. maculatum, and E. fistulosum is the most phenetically distinct species of the section.

Table 6. Characters and character states used in phenetic analyses of Eupatorium sect. Verticillata.

Qualitative characters

1. Stem (0 = hollow, 1 = solid). 2. Stem (0 = glaucous, 2 = non-glaucous). 3. Stem vestiture (0 = absent, 1 = present). 4. Node pigmentation (0 = purple, 1 = non-purple). 5. Internode pigmentation (0 = green, 1 = purple, 2 = spotted). 6. Leaf venation (0 = pinnate, 1 = triplinerved). 7. Leaf serration (0 = coarsely serrate (less than 20 teeth/10 cm), 1 = finely serrate (more than 20 teeth/10 cm)). 8. Leaf base (0 = abruptly contracted, 1 = gradually tapered). 9. Abaxial leaf surface (0 = atomiferous, 1 = glandular). 10. Inflorescence bracts (0 = reduced (uppermost whorl of leaves not as long as height of inflorescence), 1 = foliaceous (uppermost whorl of leaves equaling or surpassing height of inflorescence)). 11. Inflorescence (0 = convex, 1 = flat).

Quantitative characters

12. Number of leaves per node (measured at first node below inflorescence). 13. Leaf length/width ratio (measured at middle of leaf blade). 14. Leaf length/width ratio (measured at base of leaf blade). 15. Petiole length (cm). 16. Number of flowers per

Table 6 (continued).

head (measured from one randomly selected head). 17. Corolla length (mm). 18. Achene length (mm). 19. Inflorescence width (cm).

Table 7. Principal components for Eupatorium sect. Verticillata.

Character number	Component number 1	2	3
1	0.807	0.486	0.183
2	0.807	0.486	0.183
3	0.242	0.227	0.203
4	0.224	-0.522	-0.343
5	0.602	-0.539	-0.300
6	0.251	0.179	-0.822
7	-0.726	-0.407	-0.225
8	-0.375	-0.237	0.564
9	-0.120	0.556	0.128
10	0.397	-0.304	0.335
11	0.703	-0.466	0.418
12	-0.205	-0.683	0.168
13	-0.507	0.255	0.547
14	-0.368	-0.551	0.328
15	-0.355	0.114	0.025
16	0.700	-0.439	0.343
17	-0.359	0.608	0.245
18	-0.308	-0.093	-0.048
19	-0.675	-0.017	-0.045
Percent of variance	24.7	20.6	13.5

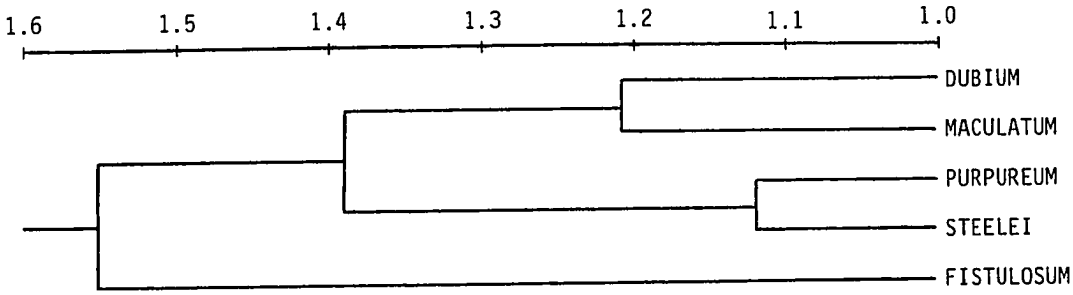


Fig. 20. UPGMA phenogram of Eupatorium section Verticillata based upon average taxonomic distances.

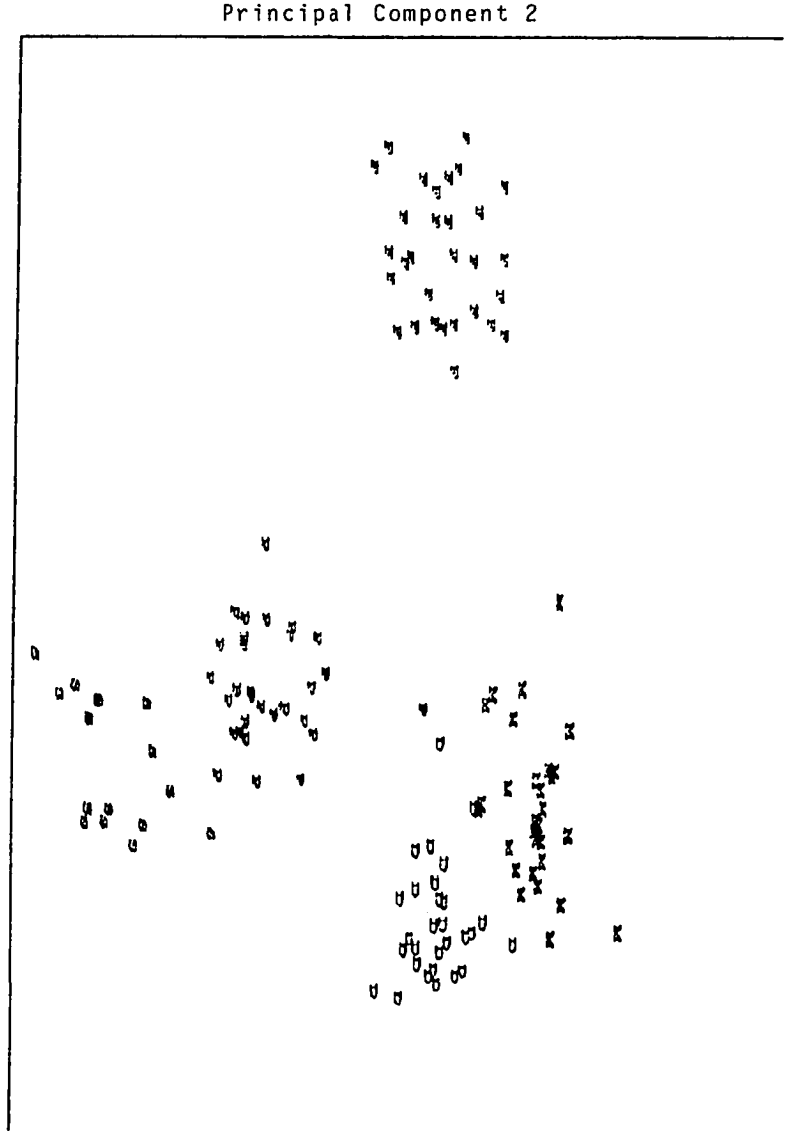


Fig. 21. Bivariate plot of first two principal components in PCA of Eupatorium sect. Verticillata. D = E. dubium, F = E. fistulosum, M = E. maculatum, P = E. purpureum, S = E. steelei.

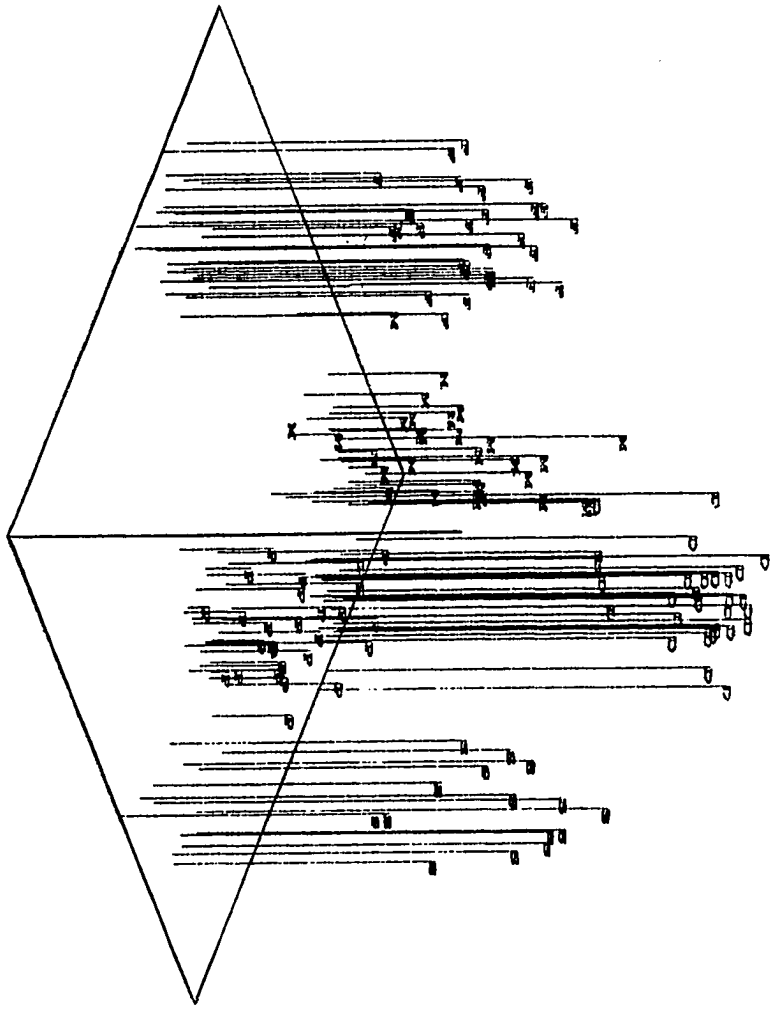


Fig. 22. Projections of 135 OTUs in Eupatorium sect. Verticillata onto first three principal components. First component explains 24.7% of total character variance, second component 20.6%, and third component 13.5%. D = E. dubium, F = E. fistulosum, M = E. maculatum, P = E. purpureum, S = E. steelei.

Phylogeny

While I do not propose to present a cladistic analysis of Eupatorium section Verticillata, a few general statements about probable evolution in the group can be made. Section Verticillata has long been considered a distinct but highly variable group; the distinctiveness of the group has rendered its phylogenetic affinities doubtful. No formal efforts to elucidate the group's phylogeny have ever been made.

The verticillate eupatoriums share many similar trends in morphology and chromosome number with the European Eupatorium cannabinum L. (sect. Eupatorium). A notable observation was that of E. L. Greene (1903): "respecting the genus which has Eupatorium cannabinum for its type, I have for some years past felt convinced that our verticillate-leaved, purple-flowered plants, a group headed by E. purpureum, are its only representatives in America." Fernald (1950) also included the verticillate eupatoriums in section Eupatorium. Eupatorium cannabinum, the only species of the genus occurring naturally in Europe, is usually regarded as reflecting a comparatively recent range extension of the genus (King & Robinson, 1987). As such, the species is not useful in the out-group comparison method (Brooks & Wiley, 1985) for polarizing character states.

The polarity of certain contrasting character states in section Verticillata can be presumed based on similar trends in morphology in the tribe Eupatorieae and the family Asteraceae. Also, both the frequency and association of character states in section Verticillata can be useful in presuming the polarity of some contrasting character states.

The vast majority of the Eupatorieae (and Asteraceae) have uniformly green stems with a solid pith, and non-glandular leaves and stems; in the absence of any reason to suppose to the contrary, it seems likely that these three characters are plesiomorphic in the tribe (and family). Most Eupatorieae have pinnate leaf venation, but many have triplinerved leaf venation. In section Verticillata only one species has triplinerved venation; again, in the absence of any reason to suppose otherwise, pinnate venation appears to be plesiomorphic in the section. In Asteraceae, many-flowered heads are usually considered to be plesiomorphic and few-flowered heads are considered to be apomorphic (Cronquist, 1955b). A domed inflorescence is common in the Eupatorieae (and Asteraceae), but a flat inflorescence is not uncommon in the genus Eupatorium. Only one species in section Verticillata has an evidently flat inflorescence; a domed inflorescence may be considered plesiomorphic in the section, but the polarity is questionable. A

summary of presumed polarity of several contrasting character states in section Verticillata is presented in Table 8.

Based on the polarities in Table 8, it is apparent that E. fistulosum and E. steelei are the two most advanced species in the section. Eupatorium maculatum is relatively archaic; E. purpureum and E. dubium are intermediate, the former is more archaic than the latter.

Table 8

Presumed polarity of several contrasting character states in Eupatorium section Verticillata.

Character	Plesiomorphic	Apomorphic
Stem pith	solid	hollow
Leaf & stem vestiture	not glandular	glandular
Stem pigmentation	uniformly green	purple nodes
Leaf venation	pinnate	triplinerved
Flower heads	many-flowered	few-flowered
Inflorescence	domed	flat

Taxonomic Treatment

Eupatorium L. sect. Verticillata A. P. de Candolle, Prodr. 5: 151. 1836. Type species: E. verticillatum Muhl. ex Willd. (=Eupatorium purpureum L.).

Eutrochium Raf., New Fl. 4: 78. 1838. Type species: none.

Eupatoriadelphus R. King & H. Robinson, Phytologia 19: 431. 1970. Type species: Eupatorium purpureum L.

Stout perennial herbs, erect, rhizomatous, fibrous-rooted, often forming clonal colonies. Stems 0.3-3.5+ m, unbranched, terete, fistulose or solid, purple-speckled or dark purple only at nodes to uniformly purple or greenish purple throughout, sometimes glaucous, viscid-puberulent near summit, glabrous to densely puberulent or glandular pubescent below. Leaves verticillate in 3's to 7's, rarely merely opposite; blade simple, mostly 6-30 cm long, 1.5-18 cm wide, lance-elliptic or lance-ovate to deltate-ovate, pinnately veined or triplinerved, acuminate at apex, gradually or sometimes abruptly tapered to the short-petiolate base, margins serrate with a large gland at apex of each marginal tooth, adaxial surface glabrescent to scabrous-hirsute, abaxial surface atomiferous or conspicuously glandular pubescent to loosely hirsute on the midrib and main

veins or densely pubescent throughout; petiole 0.5-2 (7) cm long, sometimes obscured by decurrent blade, glabrescent to ciliate. Inflorescence a flat-topped to convex compound corymbiform cyme of many dense heads with foliaceous bracts alternately scattered throughout; subtending whorl of leaves reduced to size of bracts or large and foliaceous; peduncles 1-8 mm long, glandular pubescent to glabrescent; flowering sequence within heads indeterminate (when numerous flowers present) but flowering sequence among heads determinate. Involucre cylindrical, 5.5-9 mm high, 2.5-7 mm wide, pale pink to purple, rarely white; bracts 10-22 in 5 or 6 series (outer 2 or 3 series glabrescent to densely pubescent and often resinous-glandular, the innermost ones glabrous to glabrescent), lanceolate, imbricate, tightly appressed in several lengths (the outermost series half or less than half as long as the innermost series), the outer ones obtuse, the inner acutish, few-striate or at least with prominent midvein; receptacle naked, flat or weakly convex. Flowers tubular, perfect, 4-22 in a head, scarcely exserted at anthesis; pedicels less than 1 mm long; corollas regular, 5-toothed, purplish or very pale pinkish to rarely white, 3-7.5 mm long, outer surface of tube usually minutely atomiferous-glandular, sometimes with a few scattered hairs, lobes ovate to deltate, less than 1.0 mm long, usually slightly longer

than wide; pappus a single series of 25-40 slender, capillary, antrorsely barbed, persistent bristles, 4-7 mm long, cream colored to pinkish purple; stamens as many as the corolla lobes, anthers with a small, hyaline, apical appendage, minutely rounded-auriculate at the base; style to 12.5 mm long, style branches about 2-6 mm long, equalling or exceeding the undivided part, slightly broadened or flattened distally, papillate; stigmatic lines obscure (only below middle of style branch), style base puberulous, bulbous. Fruit a prismatic, 5-ribbed achene, 3-5.5 mm long, atomiferous-glandular, sometimes with a few setulae along the nerves, usually dark brown to black, sometimes yellowish-brown. Pollen grains echinate, tricolporate, 22-25 μm in diam. $2n = 20$.

A section of five species restricted to North America, from Newfoundland to northern Florida, west to Saskatchewan, Wyoming, Utah, and Arizona, with outlying populations in southwestern British Columbia, and adjacent Washington (Fig. 7).

Key to the species of Section Verticillata

1 Leaves triplinerved, with lowest pair of lateral veins more prominent and more prolonged than the others; leaf blade abruptly contracted to petiole, thick and firm; flowers mostly 5-9 per head; near the coast from S Carolina to New Hampshire and Nova Scotia..... 1. E. dubium.

1 Leaves otherwise, either pinnately veined, or gradually narrowed to petiole, or commonly with both these differences.

2 Flowers mostly 9-22 per head; inflorescence or its divisions flat-topped or nearly so..... ..... 2. E. maculatum.

2 Flowers mostly 4-8 per head; inflorescence with rounded or strongly convex summit.

3 Stem persistently glandular-hairy throughout; abaxial leaf surface glandular-hairy; endemic to the southern Appalachian Mountains of SW Virginia, E Kentucky, E Tennessee, and W North Carolina..... 3. E. steelei.

3 Stem glabrous below inflorescence; abaxial leaf surface sparingly and minutely atomiferous; relatively widespread throughout eastern U.S.A.

4 Stem dark purple at nodes only, solid or rarely developing a slender central cavity toward the base..... 4. E. purpureum.

4 Stem purplish throughout, strongly glaucous (unique among our species), hollow with a large central cavity..... 5. E. fistulosum.

1. Eupatorium dubium Willd. ex Poir. in Lam., Encycl. Suppl. 2: 606. 1811 (not Eupatorium dubium Sesse & Moc. Fl. Mex. Ed. 2: 182. 1894). Eupatorium punctatum Willd., Enum. Pl. Berol. 853. 1809 (not Eupatorium punctatum Mill., Gard. dict. Ed. 8. 1768; not Eupatorium punctatum Lam., Encycl. Meth. 2: 408. 1786). Eupatorium purpureum var. maculatum f. dubium (Willd. ex Poir.) Voss, Vilm. Blumengartn. Ed. 3. 1: 447. 1894. Eupatoriadelphus dubius (Willd. ex Poir.) R. King & H. Robinson, Phytologia 19: 432. 1970. Type (of Eupatorium punctatum Willd.). Protologue: "North America." Without specific locality, date, and collector's name (holotype, B Crong.!; microfiche, NY!).

Eupatorium purpureum L. var. β, Sp. pl. 838. 1753. Type. Not cited in protologue. [holotype, not seen; by description = E. dubium (there is no specimen of E. purpureum var. β in the herbarium of Linnaeus according to Savage, 1945, page 143)].

Eupatorium americanum Hill, Brit. Herb. 453. 1756. Type. Not cited in protologue [holotype, not seen; by description = E. dubium. Inquiry to BM and K failed

to locate the type. (Hill (1756) did not consistently employ the Linnaean system of binary nomenclature for species; according to Article 23.6(c) (see Ex. 9) of the International Code of Botanical Nomenclature (Greuter, 1988) Eupatorium americanum is a descriptive phrase reduced to two words, not a binary name in accordance with the Linnaean system, and is to be rejected as not validly published)].

Eupatorium ternifolium Ell., Sketch bot. S. Carolina 2: 306. 1823. Eupatorium purpureum var. ternifolium (Ell.) Wood, Classbook. Ed. 1861. 416. 1861. Eupatorium purpureum var. maculatum f. ternifolium (Ell.) Voss, Vilm. Blumengartn. Ed. 3. 1: 447. 1894. Type. Protologue: "The low country of Carolina, in damp soils." Without specific locality, date, and collector's name [holotype, not seen; by description = E. dubium (inquiry to CHARL and other major herbaria failed to locate the type; Weatherby (1942) did not include E. ternifolium Ell. in the list of type specimens in Elliott's herbarium)].

Eupatorium ternifolium var. β vesiculosum Barratt, Eupatoria verticillata no. 3 (see Fig. 31). 1841. Type. Protologue: "Connecticut. Straddle Hill, west part of Middletown" [holotype, not seen; by description = E. dubium (search at NY and inquiry to

other major herbaria failed to locate the type; Grimes & Keller (1982) did not include E. ternifolium var. vesiculosum Barratt in the list of type specimens in Barratt's herbarium)].

Eupatorium dubium f. elutum Fern., Rhodora 47: 195. 1945. Type. United States. Connecticut. [Middlesex Co.]: Saybrook Junction, low ground near Long Island Sound, 14 Sep 1914, Woodward s. n. (holotype, GH!).

Erect herb, 0.4-1.2 (1.7) m tall; stems solid, usually purple-spotted or sometimes uniformly purple throughout, viscid-puberulent near summit, glabrous below, scarcely or not at all glaucous. Leaves mostly in 3's or 4's; blades thick and firm, often rugose, deltate-ovate or ovate to lance-ovate, usually abruptly contracted to the short petiole, 5-16 cm long, 2-8 cm wide, coarsely serrate, usually with a large gland at apex of each marginal tooth, strongly triplinerved (especially prominent on abaxial surface), rarely pinnately veined, adaxial surface scabrous and sparingly glabrescent, abaxial surface densely atomiferous and sparingly hirsute on the midrib and main veins; petioles usually 0.7-2.5 cm long, glabrous. Inflorescence slightly to strongly convex, sometimes flat-topped in life, less than 20 cm wide in life, heads short pedunculate, peduncles conspicuously glandular pubescent. Involucre 6.5-9 mm high, 2.5-5 mm

wide, often purplish, bracts 10-22, lanceolate, obtuse at apex, well imbricate, few-striate or at least with prominent midvein; receptacle naked, flat or weakly convex. Flowers (4) 5-9 (10) in a head; corollas usually dark purple, rarely pinkish or white, 4.5-7.5 mm long, 5-toothed, outer surface usually minutely atomiferous-glandular, lobes ovate to deltate; style base puberulous, enlarged. Achenes prismatic, 3.0-4.5 mm long, 5-ribbed, atomiferous-glandular, sometimes with a few setulae along the nerves; pappus a single series of 25-40 slender, capillary, scrabrous, persistent bristles. $2n = 20$.

Habitat and distribution. Predominantly in moist habitats, especially in sandy or gravelly, acid soil, commonly in open sun or partial shade. Occurring naturally in wet lowlands, especially in margins of tidal marshes, swamps, ponds, and occasionally in shaded thickets along streams. Common as a weed along wet roadside ditches and depressions, and in moist abandoned fields. Restricted to the coastal plain (and inland along major river systems) of eastern North America from South Carolina to Massachusetts, with disjunct populations in coastal New Hampshire, southern Maine (York Co.), and southern Nova Scotia (Fig. 8).

The taxonomic status of Eupatorium dubium has been less understood than any other species in section Verticillata. In the 120 years following Willdenow's

(1809) original description of E. dubium, only de Candolle (1836) recognized the species as it is presently understood. Identification of E. dubium still remains difficult for many field botanists, as evidenced by many misidentified herbarium specimens.

The most prominent character distinguishing E. dubium from its relatives is the triplinerved leaf venation: the lowest pair of lateral veins are more prominent and more prolonged than the others. This character is best observed on abaxial leaf surfaces. However, all leaves on an individual plant are not always conspicuously triplinerved and sometimes several leaves must be inspected before the venation character is seen. Rarely the triplinerved leaf character is not present on a specimen; when absent, identification in the field can be accomplished by locating the character on other individuals in the same population. Identification of herbarium specimens can be difficult when the triplinerved leaf character is absent.

Eupatorium dubium differs from E. fistulosum, E. purpureum, and E. steelei in stem and leaf characteristics. E. dubium has solid stems that are usually purple-speckled and non-glaucous; leaves are often deltate-ovate and usually in whorls of three or four. E. fistulosum has hollow stems that are usually purple throughout and strongly glaucous; leaves are often lance-ovate and usually in whorls of five or six.

In addition, E. dubium rarely exceeds 1.5 m in height; E. fistulosum commonly exceeds 1.5 m in height. E. purpureum usually has stems with anthocyanic pigment concentrated in 1-2 cm bands at leaf nodes, internodes are usually green. E. dubium usually occurs in moist habitats, E. purpureum usually occurs in drier upland habitats. E. steelei has green, glandular-hairy stems, glandular-hairy abaxial leaf surfaces, and occurs in dry upland habitats. E. dubium has glabrous stems below the inflorescence and atomiferous abaxial leaf surfaces. E. dubium is not sympatric with E. steelei.

Eupatorium dubium and E. maculatum are morphologically rather similar. Both species have solid, purple-speckled stems that are glabrous below the inflorescence, pubescent above. The inflorescence of E. maculatum is usually flat-topped; E. dubium has a convex inflorescence but sometimes it is somewhat flat-topped (especially in some pressed herbarium specimens). Both species commonly have four leaves at a node, coarsely toothed leaf blade margins, atomiferous abaxial leaf blade surfaces, and similar leaf length/width ratios.

The two species are strongly allopatric (Figs. 8 and 9); however, ranges overlap along the upper Connecticut River and throughout southern Nova Scotia. E. dubium is local and rare in southern Nova Scotia, where it grows in isolated clumps on rocky lake shores in the

Tusket Valley, Yarmouth Co., scattered east to Halifax and Lunenburg Cos. E. maculatum is common and conspicuous in wet habitats throughout northern Nova Scotia from Digby Neck to northern Cape Breton, but is rare southward.

Triplinerved leaf venation readily distinguishes E. dubium from E. maculatum. When this character is obscure or absent the two species sort out by correlation of multiple characters. E. dubium has (4) 5-9 (10) flowers in a head, rugose, deltate-ovate leaf blades often less than 15 cm long and abruptly contracted to the petiole, and usually grows in acid soils. E. maculatum has (8) 9-18 (22) flowers in a head, relatively thin, lance-ovate leaf blades often over 15 cm long and gradually narrowed to the short petiole, and usually grows in calcareous soils.

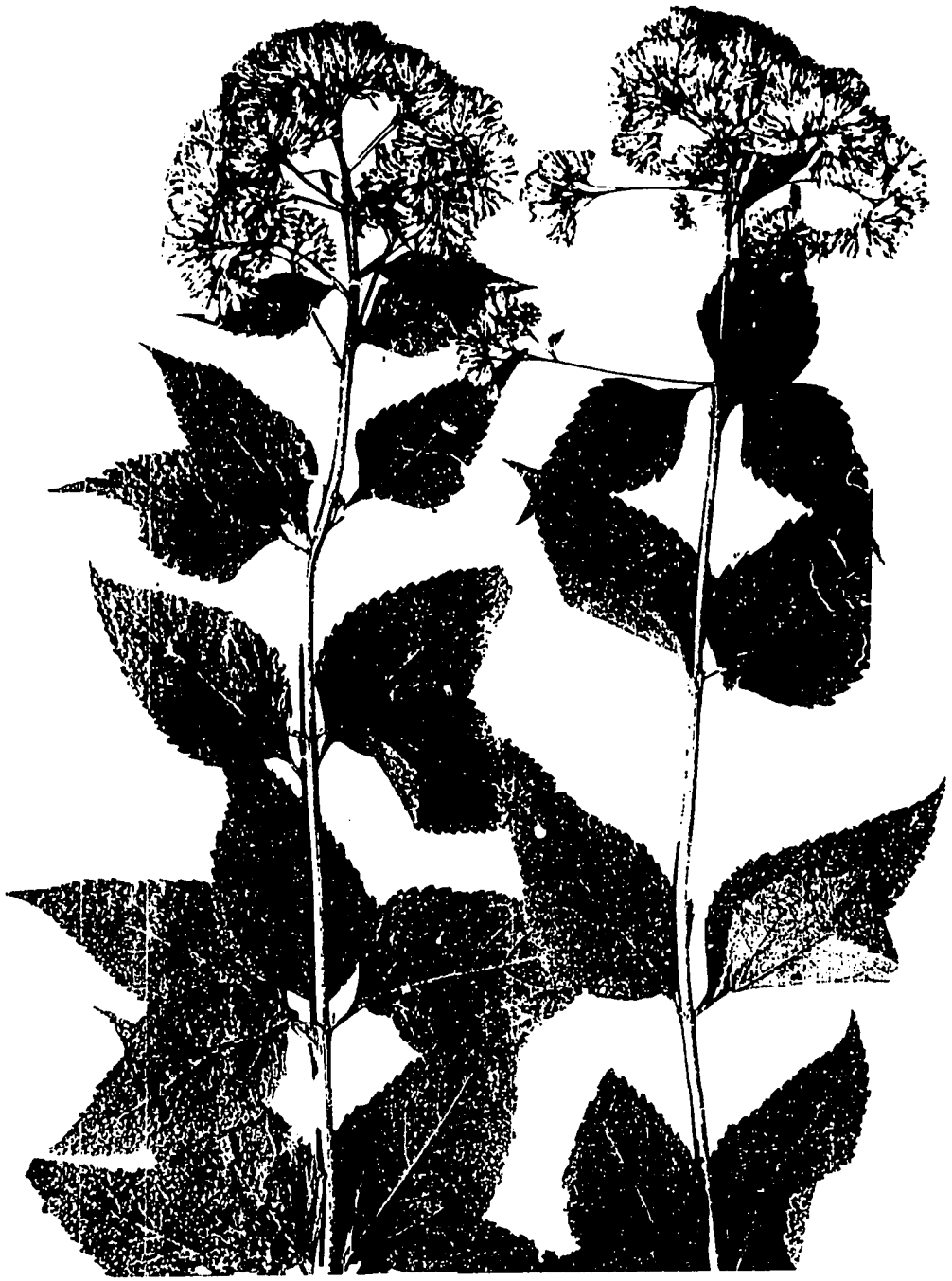


Fig. 23. Holotype of Eupatorium dubium at Willdenow Herbarium (B).

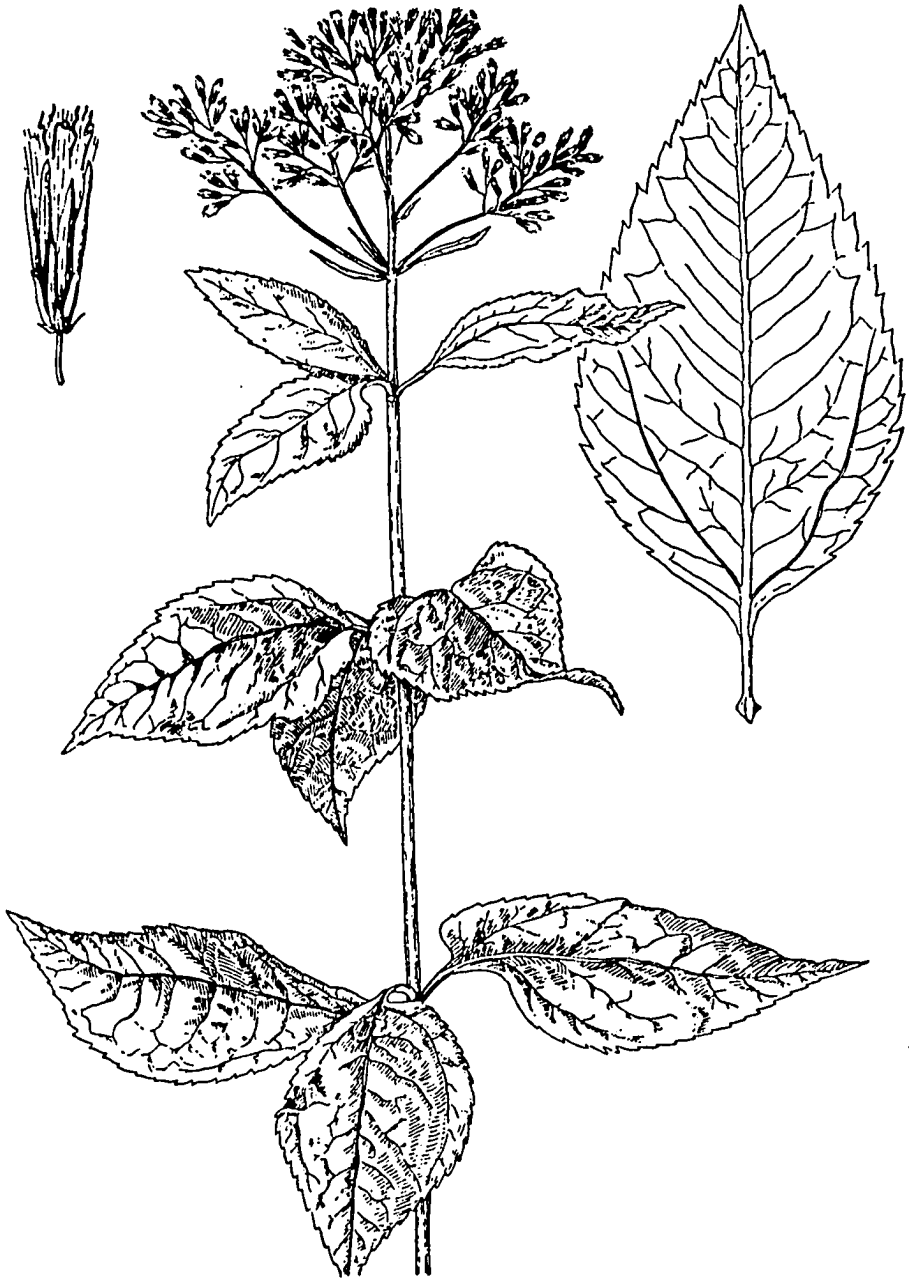


Fig. 24. Eupatorium dubium. Photographed from illustration in Gleason (1952).

Selected specimens examined (an asterisk indicates a specimen used in the phenetic analysis; see Appendix). CANADA. **NOVA SCOTIA**. Yarmouth Co.: Thickets at gravelly margin of Salmon (Greenville) Lake, 31 Jul 1920, Fernald & White 22649* (NY); upper border of cobble-beach, Salmon (Greenville) Lake, 13 Aug 1920, Fernald et al. 22652 (NY).

UNITED STATES. **CONNECTICUT**. Hartford Co.: Floodplain of Connecticut River, The Meadows, NE area near Putnam office development, Meadow Road, Wethersfield, 14 Aug 1986, Hill 17011* (UNC); without specific locality, Hartford, 13 Aug 1871, Day s.n. (NY). Middlesex Co.: Veranda lawn, Grove Beach, 6 Sep 1919, Enequist 188 (NY). New London Co.: Latimer's Point, marsh and oak woods at int. Rte. 1, Latimer's Point Rd., and RR, Stonington (near Mystic), 13 Aug 1987, Lamont 197* (NY). **DELAWARE**. New Castle Co.: Meadow, Holly Oak, 10 Sep 1918, Pennell 9893 (NY); tidal marsh along Duck Creek, near Smyrna, 7 Aug 1987, Lamont et al. 188 (NY). **MAINE**. York Co.: Low ground, York Harbor, 13 Aug 1901, Hubbard s.n. (UNC). **MARYLAND**. Worcester Co.: In sandy field, Snow Hill, 30 Sep 1931, Moldenke 6597* (NY). **MASSACHUSETTS**. Barnstable Co.: Boggy swales at head of Allen's Harbor Creek, Harwich, 15 Aug 1987, Lamont 208* (NY). Dukes Co.: Meadow region of Mill Pond, West Tisbury, 7 Sep 1917, Seymour 1354* (NY). Essex Co.: Without specific locality, Ipswich, 7 Sep 1868, Morong

s.n. (NY). Hampden Co.: Sparsely wooded sand plains, "The Plains," Chicopee, 29 Jul 1925, Seymour 530 (NY). Middlesex Co.: Swampy woods, Winchester, 10 Sep 1930, Smith 1153* (NY). Nantucket Co.: Marsh, head of "Creeks Area," Nantucket, Nantucket Island, 2 Sep 1964, Mackeever 866* (NY). **NEW HAMPSHIRE.** Cheshire Co.: Moist roadside, Richmond, 21 Aug 1919, Batchelder s.n. (NY). Strafford Co.: Low cut-over woods, Madbury, Schreibers, 20 Aug 1966, Hodgdon 15355* (UNC). **NEW JERSEY.** Bergen Co.: Brackish marsh, west of Leonia, 28 Sep 1916, Pennell 9274 (NY). Camden Co.: Shores of Newton Creek, S of Collings Road, Fairview, Camden, 8 Aug 1987, Lamont 192 (NY). Morris Co.: Edge of drainage ditch, wet roadside, elev. 300 ft., Woodland Road, Morris Twp., 11 Sep 1962, Zuck 15 (NY). Ocean Co.: Pine barren swamp, Forked River, 6 Sep 1908, Mackenzie 3854* (NY). Salem Co.: Roadside 1 mile west of Fedricktown, 23 Aug 1935, Fogg s.n. (NY). Somerset Co.: In meadow, Watchung, 12 Aug 1932, Moldenke 7397* (NY). **NEW YORK.** Bronx Co.: Moist sandy soil, swale, Jerome Park, 26 Sep 1916, Pennell 9250 (NY). Nassau Co.: White cedar swamp, Merrick, 30 Aug 1908, Bicknell 8929* (NY). New York Co.: Bedford Park, N.Y. City, 28 Sep 1899, Wilson s.n. (NY). Queens Co.: SE of Jamaica, Long Island, 1 Sep 1906, Bicknell 8957 (NY). Richmond Co.: Without specific locality, New Dorp, Staten Island, 7 Aug 1892, Britton s.n.* (NY). Rockland Co.: Dirt road going east

of Wanamaker Road, Suffern, Ramapo Township, 5 Sep 1961, Lehr 545 (NY). Suffolk Co.: Blydenburgh Co. Park, Smithtown, N. shore of Mill Pond, 1 Aug 1987, Lamont 177* (NY); Bow Drive marsh, edge of creek, Smithtown, 1 Aug 1987, Lamont 178 (NY); Carman's River, 6 Sep 1940, Murphy s.n.* (NY); Cathedral Pines Co. Park, Middle Island, where Carmans River passes under Bartlett Rd., 2 Aug 1987, Lamont 179 (NY); Cranberry Bog Co. Park, Sweezy Pond, 2 mi. S of Riverhead, 2 Aug 1987, Lamont 180 (NY); Napeague State Park, wet roadside swale along Montauk Hwy., 1.5 mi. E of Cranberry Hole Rd., 3 Aug 1987, Lamont 181 (NY). Sullivan Co.: Vicinity of Lake Shandelu, 20 Aug 1918, Wilson s.n. (NY). Westchester Co.: Without specific locality, Mt. Vernon, 31 Aug 1901, Rydberg s.n.* (NY). **NORTH CAROLINA.** Harnett Co.: Swampy woodland, 8 miles south of Lillington along NC Rt. 210, 15 Sep 1950, Godfrey & Fox 50508* (NY). Pasquotank Co.: Flat pine-oak woods border, 8.1 miles SE of Pasquotank-Camden County line on U.S. 17-158, 15 Oct 1958, Ahles & Duke 51295 (UNC). Pender Co.: Old field, SE portion of Moores Creek National Military Park, 25 Aug 1981, Sleren 3100 (UNC). Richmond Co.: Peat-sedge bog, 2.5 miles N of Hoffman near Drowning Creek, 6 Oct 1956, Radford 19361* (UNC). Robeson Co.: Low woods, 5 miles NW of St. Pauls, 1 Aug 1957, Ahles & Leisner 33024 (UNC). Sampson Co.: Creek bottom, 0.9 mile E of Hulls Store, vicinity of Little Coharie

Creek, 8 Aug 1957, Ahles & Leisner 33627* (UNC). Scotland Co.: Sandhill, 2.2 miles S of Hoke-Scotland Co. line on US 15, then 2.7 miles E on road to Wagram, 16 Oct 1957, Ahles 36889* (UNC). Tyrrell Co.: Savannah, 1.5 miles SE of Cross Landing, 18 Oct 1958, Radford 42529 (UNC). Washington Co.: Fresh water marsh, near US 64 and Welch Creek, 3.2 miles SW of Plymouth, 17 Oct 1958, Radford 42417 (UNC). Wayne Co.: Bog, Sleepy Creek, 5 miles east of Dudley, 28 Aug 1957, Radford 28773* (UNC). Wilson Co.: Bog, near US 264, 0.5 mile NW of Sims, 28 July 1958, Radford 38013 (UNC). **PENNSYLVANIA.** Chester Co.: Meadow E of Nantmeal Village, 2 Aug 1924, Pennell 12260* (NY). Philadelphia Co.: Vacant lot E of P.R.R. Lie yard, Delaware Ave, Phila., 7 Sep 1921, Meredith s.n. (NY). **RHODE ISLAND.** Newport Co.: Jamestown, Narragensett Bay, 13 Aug 1987, Lamont 201 (NY). Providence Co.: Without specific locality, s.d., Olney s.n. (NY). Washington Co.: Without specific locality, N. Kingstown, Sep 1871, Phoenix s.n. (NY). **SOUTH CAROLINA.** Aiken Co.: Marshy border of Little Horse Creek on US I-76 (ESE of North Augusta), 27 Oct 1961, Ahles & Crutchfield 55401* (UNC). Beaufort Co.: Border of low woodland, 5.1 miles N of Beaufort on US Hwy. 21, 6 Sep 1956, Bell 4751* (UNC). Berkeley Co.: Upland roadside, just S of Oakley on US. 52, 27 May 1957, Ahles & Haesloop 26539 (UNC). Chesterfield Co.: Wet shrubby thicket, in the Sandhills

1 mile west of McBee, 7 Sep 1939, Godfrey 8040* (NY). Clarendon Co.: North bank of Santee River, 14 mi. S of Manning, 31 July 1939, Godfrey & Tryon 1001 (NY). Georgetown Co.: Freshwater marsh, Winyah Bay near US 17, N of Georgetown, 22 Aug 1957, Radford 28445* (UNC). Hampton Co.: Swamp along railroad, 1.8 mi. NW of Yemassee on SC 28, 10 Sep 1956, Ahles & Bell 18344 (UNC). Kershaw Co.: Moist sandy soil along small stream, 14 miles NE of Camden, 16 Sep 1947, Cronquist 4727* (NY). VIRGINIA. Henrico Co.: Edge of marsh W of Elko Station, 3 Sep 1967, Harville 17611 (UNC). James City Co.: Low swampy soil border of woods and marsh; Capitol Landing NE of Williamsburg, 22 Aug 1921, Grimes 4298* (NY). Nansemond Co.: Railroad right-of-way, 3.5 mi. ENE of Suffolk on US 13-58-460, 1 Sep 1962, Ahles & Baird 57523 (UNC). New Kent Co.: In shallow water in open, marshy thicket, edge of stream flowing into south end of Davis Pond, Barhamsville, 5 Aug 1989, Lamont 349* (NY). Northumberland Co.: Low, wet area in pasture 3 mi. SW of Callao on Rt. 360, 29 Sep 1971, Johnson 4127 (UNC). Princess Anne Co.: Wet woods, Munderm, 3-19 Sep 1905, Mackenzie 1803* (NY). Richmond Co.: Wet roadside ditch 1 mi. W of Warsaw on Rt. 360, 29 Sep 1971, Johnson 4114 (UNC). Southampton Co.: Marsh, 1 mi. W of Blackwater River on VA 189, 1 Sep 1962, Ahles & Baird 57490 (UNC).

2. **Eupatorium maculatum** L., Cent. plant. I: 27. 1755. Eupatorium purpureum var. maculatum (L.) Darl., Fl. Cestrica 453. 1837. Eupatorium trifoliatum var. maculatum (L.) Farwell, Rep. Michigan Acad. Sci. 20: 191. 1918. Eupatoriadelphus maculatus (L.) R. King & H. Robinson, Phytologia 19: 432. 1970. Eupatorium purpureum subsp. maculatum (L.) Löve & Löve, Taxon 31: 357. 1982. Type. Without locality and date, K[alm] s.n. (there is only one specimen of E. maculatum in the herbarium of Linnaeus according to Savage, 1945, page 143) [holotype, LINN (microfiche, NY!; photo, GH!)].

Eupatorium verticillatum Lam. var. β, Encycl. 2: 405. 1786 (not Eupatorium verticillatum Muhl. ex Willd., Sp. Pl. 3: 1760. 1804). Type. No specimens were directly cited in the protologue, which evidently applies to what we would now call E. maculatum L. It seems clear that Lamarck intended to include E. maculatum L. in his E. verticillatum var. β, although the citation is indirect. Lamarck's name is therefore nomenclaturally superfluous under Article 63.1 of the Code (Greuter, 1988), and ought to be typified on E. maculatum L. (see Article 7.13 of the Code). (See additional discussion under E. verticillatum var. α, listed in synonomy under E. purpureum L.).

Eupatorium maculatum var. β urticifolium Barratt, Eupatoria verticillata no. 2. 1841 (see Fig. 31). Type. United States. Connecticut. In the Middletown meadows, near the banks of the Connecticut [River], s.d. Barratt s.n. (holotype, NY!).

Eupatorium maculatum f. faxoni Fern., Rhodora 47: 195. 1945. Eupatorium purpureum f. faxoni (Fern.) Bolvin, Phytologia 23: 11. 1972. Type. United States. New Hampshire. [Carroll Co.]: Gate of Crawford Notch, 2 Sep 1884, Faxon s.n. (holotype, GH!).

Erect herb, 0.6-2 m tall; stems solid or sometimes hollow near the base at maturity, purple-spotted or sometimes uniformly purple throughout, viscid-puberulent near summit to densely puberulent throughout, scarcely or not at all glaucous. Leaves mostly in (3's) 4's or 5's (rarely 6's); blades lance-elliptic to lanceolate or lance-ovate, mostly (6) 8-23 (30) cm long, (1.5) 2-7 (9) cm wide, gradually or sometimes abruptly tapering to the short-petiolate base, acuminate at the apex, pinnately veined, sharply serrate or doubly-serrate, adaxial surface glabrous to sparingly glabrescent, abaxial surface atomiferous and glabrate to densely pubescent; petioles usually 0.5-2 cm long, glabrous to pubescent. Inflorescence flat-topped, usually less than 20 cm wide in life, heads short pedunculate. Involucre 6.5-9 mm high,

3.5-7 mm wide, often purplish; bracts 10-22, glabrous to densely pubescent, lanceolate, obtuse at apex, well imbricate, few-striate or at least with prominent midvein; receptacle naked, flat or weakly convex. Flowers (8) 9-20 (22) in a head; corolla 4.5-7.5 mm long, 5-toothed, purplish, funnelform, outer surface usually minutely atomiferous-glandular, lobes ovate to deltate, usually slightly longer than wide; style base puberulous, enlarged. Achene prismatic, 3.0-4.5 mm long, 5-ribbed, atomiferous-glandular, sometimes with a few setulae along the nerves; pappus a single series of 25-40 slender, capillary, scabrous, persistent bristles. $2n = 20$.

Eupatorium maculatum L. has the widest geographic distribution and greatest morphological variability of all species in section Verticillata. Three infraspecific taxa have been proposed for Eupatorium maculatum, but recognition of these taxa has varied among botanists. For example, the western variety bruneri (A. Gray) Breitung was recognized by Cronquist (1952b, 1955), Gleason and Cronquist (1963), King and Robinson (1980), Barkley (1986), Looman and Best (1987), and Welsh (1987); however, no taxonomic recognition of this taxon was given by Wiegand and Weatherby (1937), Fernald (1950), Rousseau (1974), and Scoggan (1979). Conversely, the variety foliosum (Fern.) Wiegand was recognized by Wiegand and Weatherby

(1937), Scoggan (1950), Fernald (1950), Erskine (1960), Roland and Smith (1969), Gardner (1973), and Seymour (1982); however, this taxon was not recognized by Gleason and Cronquist (1963), Scoggan (1979), King and Robinson (1980), Hinds (1986), and Mitchell (1986).

Herbarium studies indicate that distinct phenetic differentiation exists within Eupatorium maculatum, and these recognizable differences are correlated with geography (Figs. 9, 10, and 11). Field observations confirm this; however, geographic and morphological lines of demarcation separating these infraspecific taxa are not precise.

A revised taxonomic interpretation of the group better reflects the totality of similarities and differences among infraspecific taxa. The wide-ranging western taxon, subsp. bruneri (A. Gray) G. Douglas, could almost stand as a distinct taxonomic species, as proposed by Gray (1884), until the eastern limit of its range is studied and a "sloppy," imprecise transition into Eupatorium maculatum sens. strict. is observed. Conversely, the northeastern taxon of the Canadian maritimes, variety follosum, does not warrant equal taxonomic recognition with its western counterpart, due to its more restricted range, limited phenetic differentiation and even more "sloppy," imprecise transition into E. maculatum sens. strict. The southern range of var. follosum has been described as

extending into southern Maine (Bean et al., 1966), central New Hampshire (Seymour, 1982), central Vermont (Dole, 1937), and central New York (Smith, 1968). However, field studies indicate the southernmost part of this distribution pattern is the result of misrepresentation in herbaria. Within some populations of E. maculatum sens. strict. are individuals that approach var. foliosum; however, these populations as a whole do not reflect affinity with var. foliosum. Based on herbarium specimens and field observation I find the southern limit of var. foliosum to be in northernmost New York, northern New Hampshire, northern Vermont, and northern Maine. In the area where their distributions overlap (Figs. 9 and 10), var. foliosum usually occurs at higher elevations than does var. maculatum.

To recapitulate, Eupatorium maculatum is a morphologically complex species with attributes that warrant a hierarchal infraspecific organization of taxa. A comparison between the two subspecies of E. maculatum is summarized in Table 9.

TABLE 9

Selected characteristics of the subspecies of *Eupatorium maculatum*

characteristic	subsp. *bruneri*	subsp. *maculatum*
stem height	6-15 dm	6-20 dm
stem pubescence	densely puberulent throughout	puberulent only near summit; glabrous below
leaf dimension	6-17 cm long, 1.5-5 (7) cm wide	8-25 cm long, 2.5-9 cm wide
ventral leaf pubescence	densely covered with short, spreading hairs	± glabrescent; ± puberulent on veins
leaf texture	firm	relatively thin
leaf blade base	abruptly or sometimes gradually narrowed to the short petiole	gradually narrowed to the short petiole
leaves subtending inflorescence	reduced in size, not surpassing height of inflorescence	either reduced in size, or surpassing height of inflorescence
distribution	mostly west of the Mississippi River and Great Lakes	mostly east of the Mississippi River and Great Lakes

Key to the infraspecific taxa of Eupatorium maculatum

1 Leaves glabrate (seldom very strongly puberulent) on lower surfaces, relatively thin; stems puberulent about inflorescence, glabrous below; mostly east of Mississippi River.....subsp. maculatum

2 Uppermost whorl of leaves subtending inflorescence equaling or surpassing height of inflorescence; from maritime Canada and adjacent N New England to NE Minnesota, N Michigan and S Ontario.....
.....var. follosum

2 Uppermost whorl of leaves subtending inflorescence reduced, not as long as height of inflorescence; from Newfoundland to SW Ontario, S to N and W New England, Pennsylvania, mountains to North Carolina, Ohio, Indiana, Illinois, and Iowa.....
.....var. maculatum

1 Leaves densely pubescent on lower surface, relatively firm; stems densely puberulent throughout; mostly west of Mississippi River.....subsp. bruneri

Eupatorium maculatum L. subsp. maculatum

Stems 6-20 dm tall, purple-speckled or sometimes evenly purplish, solid or rarely hollow with slender central cavity, puberulent only near the summit, rarely to the base. Leaves relatively thin, mostly in 4's or

5's, blades lance-elliptic to lanceolate or lance-ovate, 8-25 cm long, 2.5-9 cm wide, gradually narrowed to the short, glabrous petiole; abaxial surface seldom very strongly puberulent; uppermost whorl of leaves directly subtending inflorescence either reduced in size and not as long as height of inflorescence, or large and foliose, and equaling or surpassing height of inflorescence. Involucral bracts essentially glabrous, or the outer often inconspicuously short-hairy.

2a. Eupatorium maculatum L. subsp. maculatum var. maculatum

Uppermost whorl of leaves directly subtending the inflorescence reduced in size, usually 4-8 (10) cm long, 1.5-2.5 cm wide, lance-elliptic to lanceolate, not as long as the height of the inflorescence; sometimes the upper leaves reduced to the size of bracts, 1.5-2.5 cm long, 0.2-0.5 cm wide.

Habitat and distribution. Predominantly in moist habitats, usually in association with calcareous soils, commonly in open sun or partial shade. Occurring naturally in wet lowlands, especially in moist meadows that have permanently saturated and seasonally flooded organic soils with little peat accumulation in the substrate; also abundant along streams and near the inlets and outlets of lakes and ponds; also common in

lake basins at the zone near the upland edge of shallow emergent marshes. Common as a weed along wet roadside ditches and depressions, and in moist abandoned fields. From Newfoundland to SW Ontario, S to N and W New England, Pennsylvania, mountains to North Carolina, Ohio, Indiana, Illinois, and Iowa (Fig. 9).

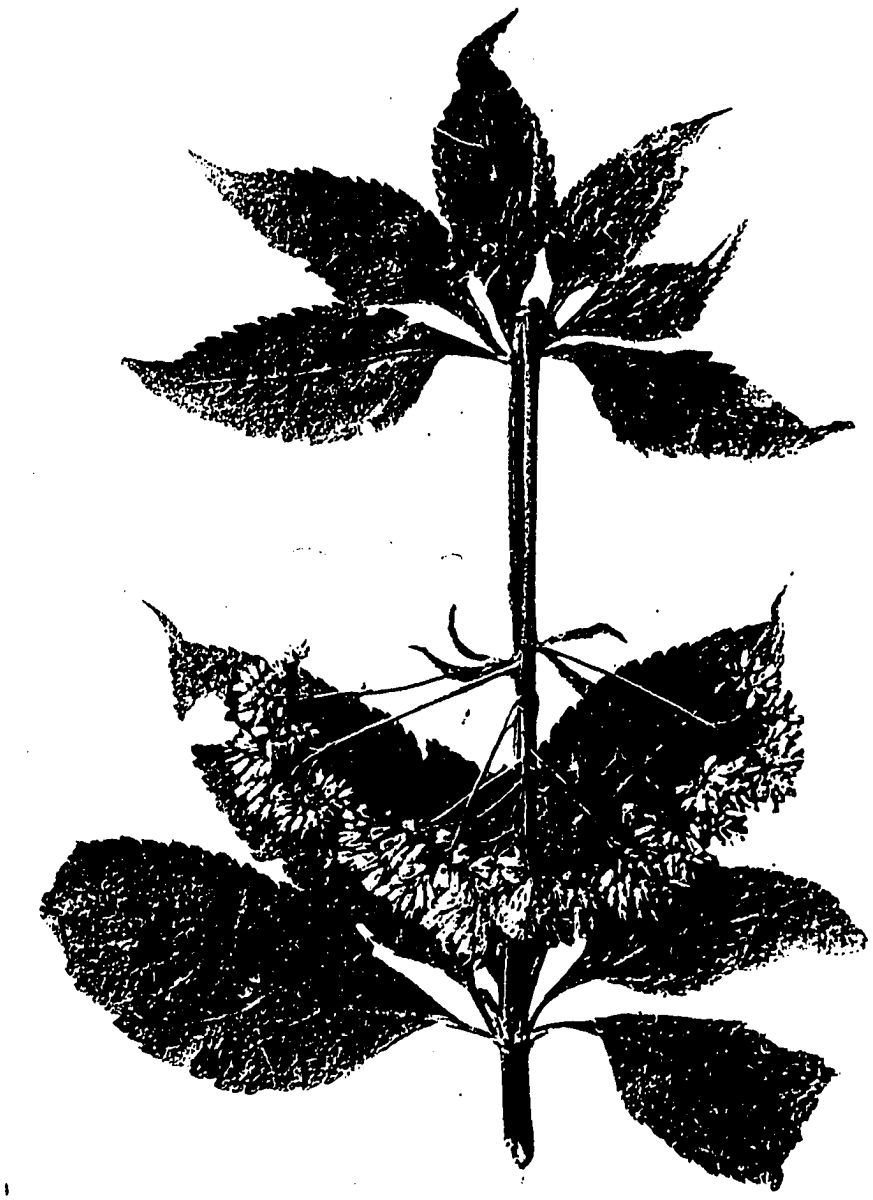


Fig. 25. Holotype of Eupatorium maculatum in herbarium of Linnaeus (LINN).

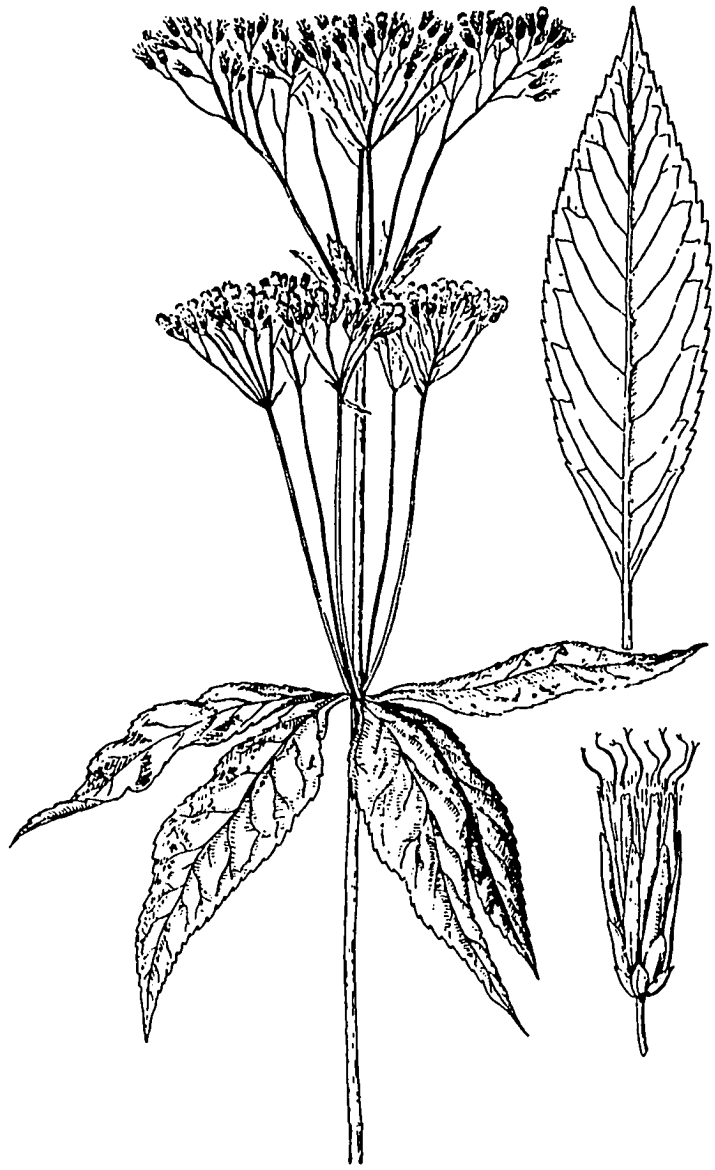


Fig. 26. Eupatorium maculatum. Photographed from illustration in Gleason (1952).

Selected specimens examined. CANADA. **NEW BRUNSWICK.** Kent Co.: Without specific locality, 1 Sep 1871, Fowler s.n. (NY). Kings Co.: Roadside ditch 5.5 mi. NE of Nothesay, 27 Jul 1953, Bassett & Mulligan 2928 (DAO). Madawaska Co.: N side of St. John River, 3 mi. E of Edmundston along Hwy. 120, 10 Aug 1988, Lamont 221 (NY). York Co.: Roadside 0.5 mi. from Graham Corner on road to Kirkland, 14 Aug 1963, Robert & Drury 64-1414 (DAO). **NOVA SCOTIA.** Cape Breton Co.: Swampy area, Grand Narrows, 21 Aug 1951, Smith et al. 5504 (DAO). Cumberland Co.: Margin of brook, Leak Lake, 31 Jul 1953, Schofield 3484 (DAO). Pictou Co.: Bailey's Brook, 13 Aug 1963, Smith et al. 21533 (DAO). **ONTARIO.** Halton Co.: Low ground along shore of Lake Medad, 2.5 mi. E of Nelson, 21 Sep 1960, Cody & Spicer 11273 (DAO). Norfolk Co.: Marshy area between road and sandy shore of Lake Erie, Turkey Point, Charlotteville Twp., 17 Aug 1965, Bowden 2967* (DAO). Russell Co.: Open grassy area in old bog, Moose Creek Bog, Cambridge Twp., 27 Aug 1981, Darbyshire 1653 (DAO). **PRINCE EDWARD ISLAND.** Prince Co.: Damp ditches, Wellington, 29 Jul 1952, Erskine 1423 (DAO). **QUEBEC.** Gatineau Co.: Along shore margin, E side of Lake Philippe, Gatineau Park, Eardley Twp., 6 Aug 1941, Minshall & Zinck 263* (DAO). Papineau Co.: Edge of swamp, Templeton Parish, Conc. XI, Lot 15, 9 Aug 1946, Calder M-141 (DAO). Portneuf Co.: Flat limestone shore, St. Lawrence River, Grondines, 22-23

Aug 1955, Gillett & Van Rens 9657 (DAO). Temiscouata Co.: Shore of Lake Temiscouata, 1.5 mi. N of Cabano off Hwy. 232, 10 Aug 1988, Lamont 222 (NY).

UNITED STATES. **CONNECTICUT.** Litchfield Co.: Edge of brook leading from Bantam Lake at bottom of Apple Hill, Litchfield-Morris Wildlife Sanctuary, Litchfield, 15 Jul 1941, Dwyer 2279 (NY). **ILLINOIS.** Kankakee Co.: Along ditch near St. Anne, 9 Sep 1944, Jones 16663 (ILL). Lee Co.: Franklin Creek Swamp, 2 mi. E of Kingdom, 28 Jul 1946, Keithley s.n. (ILL). Tazewell Co.: Spring Mill Bog near East Peoria, 2 Sep 1947, Chase 9045* (ILL). **INDIANA.** Grant Co.: Low border of the lake located ca. 5 mi. NE of Fairmont, 4 Sep 1914, Deam 15276 (IND). Henry Co.: Boggy place a few rods NE of Springport, 18 Sep 1919, Deam 30048 (IND). Knox Co.: Low ground which before draining was a cypress swamp, about 2 mi. N of Decker, 20 Sep 1918, Deam 26577* (IND). **IOWA.** Buchanan Co.: Peaty marsh, Iowa drift sheet, Hazelton, 24 Aug 1925, Pammel 770 (ISC). Clayton Co.: Swampy meadows and islands of the Mississippi River, McGregor, 15 Aug 1925, Pammel 598 (ISC). Muscatine Co.: Low ground W of Skunk Cabbage Bog, NW of Bayfield, 21 Aug 1915, Shimck s.n. (ISC). **KENTUCKY.** Campbell Co.: Seep on bank of Ohio River between mouth of Twelvepole Creek & BM 502, St. Rt. 8, S of Oneonta, New Richmond Quad., 31 Jul 1984, Cusick 23746 (UNC). **MAINE.** Aroostook Co.: Wet meadow along Fish River off

Hwy. 11, 1.7 mi. N of Fort Kent Mills, 12 Aug 1988, Lamont 223 (NY). Hancock Co.: Mt. Desert Is., stream bank where Duck Brook flows out of Eagle Lake near Hwy. 233, 9 Aug 1988, Lamont 220 (NY). Knox Co.: Boggy soil along Rd. 137 between Warren and West Rockport, 18 Aug 1939, Friesner 14077 (NY). Oxford Co.: In marsh, Denmark, 3 Sep 1902, Bailey s.n.* (NY). Waldo Co.: Wet meadow just N of Mesery Brook, E of Lincolnville Center, 26 Jul 1958, Rossback 4588 (UNC). York Co.: In moist grassy meadow, Ocean Park, 28 Aug 1931, Moldenke 6269* (NY); moist meadow where Mousam River flows under Hwy. 109, 1.5 mi. E of Emery Mills, 9 Aug 1988, Lamont 219 (NY). **MASSACHUSETTS.** Berkshire Co.: Along the margin of Hoosic River off Hwy. 8, 3.2 mi. N of Cheshire, 16 Aug 1987, Lamont 209 (NY). Hampshire Co.: Stream bank along Resevoir Road, Roberts Meadow Brook, Leeds (Northampton), 7 Aug 1977, Ahles 84592 (VPI). **MICHIGAN.** Berrien Co.: Open marshy ground near Blue Creek, ca. 1 mi. W of Millburg, Benton Twp., 14 Sep 1958, Voss 8098 (MICH). Chippewa Co.: Open marsh along Lake George, 27 Aug 1947, McVaugh 8723* (MICH). Oceana Co.: Sandy mucky N shore of Gilbert Lake, ca. 2.5 mi. NE of Walkerville, Colfax Twp., 14 Sep 1959, Voss 9204 (MICH). **MINNESOTA.** Becker Co.: Tamarack bog, Green Water Lake Natural Area, 5 mi. W of Ponsford, T141N, R38W, S33, 3 Sep 1980, Petron 443 (MIN). Beltrami Co.: In a partially dried-up patterned fen, ca. 14.5 mi. N

of Waskish Airport on Rt. 72, T156N, R31W, S1, 5 Jul 1978, Wheeler & Glaser 3172 (MIN). Clearwater Co.: Ash swamp, Itasca Lake, the headwaters of the Mississippi River, T144, R36, S35, 23 Aug 1929, Grant 3136* (MIN). **NEW HAMPSHIRE.** Cheshire Co.: Roadside, sandy spot where water runs off road into woods, opposite entrance to Toll Road up Mt. Monadnock, 3.5 mi. W of Jaffrey Center, 17 Aug 1987, Lamont 212* (NY). Grafton Co.: In grass sward by edge of woods, Rt. 115, 1 mi. SW of Meadows, 18 Jul 1976, Uttal 12159 (VPI). Merrimack Co.: Edge of Smith River along Rt. 104, ca. 5 mi. SW of Bristol, 23 Jul 1970, Uttal 7591* (VPI). **NEW JERSEY.** Sussex Co.: Swampy woodlands, Andover Junction, 14 Sep 1919, Mackenzie s.n. (NY); wet limestone meadow along Delaware River 0.5 mi. S of Dingmans Ferry Bridge, 9 Aug 1987, Lamont 193 (NY). **NEW YORK.** Dutchess Co.: Wet meadow where Appalachian Trail crosses Swamp River, ca. 2 mi. N of Pawling, 9 Aug 1987, Lamont 195 (NY). Essex Co.: Wet soil, Newcomb, 1600 ft. alt., 1 Aug 1921, House 8427 (NY). Greene Co.: Catskill Mountains, near Hunter, 30 Jul-1 Aug 1898, Britton s.n. (NY). Oneida Co.: Moist thicket, Sylvan Beach, 14 Sep 1921, House 8704* (NY). Sullivan Co.: Marshy margin of Basher Kill Lake, ca. 3 mi. S of Wurtsboro off Hwy. 209, 9 Aug 1987, Lamont 194 (NY). **NORTH CAROLINA.** Avery Co.: Elk Creek, vicinity of Banners Elk toward Hanging Rock, alt. 1050 m., 21 Aug 1915, Steele 7* (NY). Mitchell

Co.: Grass bald, Roan High Knob, S slope near road, 7 Aug 1956, Ramseur 1167 (UNC). Yancey Co.: Roadside and border of parking area at camp ground, Mt. Mitchell, 21 Aug 1957, Ramseur 4200 (UNC). OHIO. Champaign Co.: Marshy area on SE side of Brush Lake, ca. 3 mi. due W of Woodstock, Rush Twp., 8 Aug 1971, Roberts 1597 (OS). Huron Co.: On silt over shale in bottom of E Branch of Huron River at crossing of Lovers Lane Rd. No. 48, ca. 2 mi. NW of Norwalk, Norwalk Twp., 20 Sep 1968, Stuckey 7897 (OS). Lorain Co.: Low ground near river, Cooper's Hollow, Brownhelm Twp., 2 Sep 1965, Jones s.n. (OS). **PENNSYLVANIA.** Butler Co.: Along Wolf Creek 2 mi. N of Slippery Rock, 20 Aug 1922, Jennings s.n.* (UNC). Carbon Co.: Hughs Swamp, ca. 2 mi. N of Jim Thorpe off Hwy. 93, 7 Aug 1987, Lamont 190 (NY). Lancaster Co.: Dillerville Swamp in limestone, 10 Sep 1901, Heller s.n. (NDA). Lawrence Co.: East of Castle, W of railroad, 1 Sep 1924, Bright s.n. (NDA). **VERMONT.** Bennington Co.: Wet meadow on margin of Hoosic River, off Hwy. 346 ca. 1.5 mi. N of Pownal, 16 Aug 1987, Lamont 210 (NY). Windham Co.: In meadow, Londonderry, 29 Aug 1935, Moldenke 8800 (NY); swamp and wood, 0.7 mi. W of Saxton's River, Rt. 121, 19 Jul 1976, Uttal 12187* (VPI). **VIRGINIA.** Frederick Co.: Calcareous wet meadow along railroad grade 0.25 mi. E of White's Pond along Abrams Creek E of St. Rt. 621 along the western city limits of Winchester, elev. 775 feet, 16 Aug 1980,

Wieboldt 3866 (VPI). Grayson Co.: On slope of Mt. Rogers, in 1954, Shields s.n. (VPI). **WISCONSIN.** Kenosha Co.: Wet sandy swamp along Lake Michigan Shore, T1N, R22E, S26, 21 Sep 1938, Cook C312 (WIS). Pierce Co.: Along the Rush River 8 mi. ESE of Ellsworth, 14 Sep 1976, Hansen et al. 4193* (WIS). Wood Co.: On sandy dike on cranberry marsh, T21N, R4E, S4, 1 Aug 1961, Skroch 196 (WIS). **WEST VIRGINIA.** Randolph Co.: Stone Coal Road off US 250 on top of Cheat Mt., 29 Jul 1955, Clarkson 590 (UNC).

2b. Eupatorium maculatum L. subsp. maculatum var. foliosum (Fern.) Wieg., Rhodora 22: 66. 1920. Eupatorium purpureum var. foliosum Fern., Rhodora 10: 86. 1908. Eupatorium trifoliatum var. foliosum (Fern.) Farwell, Rep. Michigan Acad. Sci. 20: 191. 1918. Eupatorium bruneri var. foliosum (Fern.) House, New York State Mus. Bull. 254: 679. 1924. Type. United States. Maine. Aroostook Co.: River thicket at Van Buren, valley of St. John River, 18 Sep 1900, Fernald s.n. (holotype, GH!).

Eupatorium maculatum f. anomalum Vict., Nat. Canad. 71: 208. 1944. Eupatorium maculatum var. foliosum f. anomalum (Vict.) Lepage, Nat. Canad. 79: 180. 1952. Eupatorium purpureum var. maculatum f. anomalum (Vict.) Bolvin, Nat. Canad. 94: 646. 1967. Type. Canada. Quebec. New Quebec, Rupert's House, James Bay, at the edge of a damp woods, 20 Jul 1943, Dutilly & Lepage 11080 (holotype, MT!; photo, DAO!).

Eupatorium maculatum var. foliosum f. eresinatum Lepage, Nat. Canad. 79: 181. 1952. Type. Canada. Quebec. "Estuair de la riviere Broadback, Baie James," 4 Sep 1946, Dutilly & Lepage 16978 (holotype, CANA!).

Uppermost whorl of leaves directly subtending the inflorescence large and foliose, usually 8-17 (20) cm long, 2-4 cm wide, lance-elliptic to lanceolate or

commonly lance-ovate, equaling or surpassing the height of the inflorescence.

Habitat and distribution. Predominantly in moist habitats, usually in association with calcareous soils, commonly in open sun or partial shade. Occurring naturally in wet lowlands, especially in moist meadows that have permanently saturated and seasonally flooded organic soils. Abundant near the upland edge of spruce-fir swamps where there is some nutrient input from groundwater discharge or subsurface flow. Also abundant along streams and near the inlets and outlets of lakes and ponds. Common as a weed along wet roadside ditches and depressions, and in moist abandoned fields. From Newfoundland to NE Ontario, S to Nova Scotia, N New England, N New York, N Michigan, and NE Minnesota (Fig. 10).

Selected specimens examined. CANADA. NEW BRUNSWICK. Charlotte Co.: Borders of thickets in moist ground, Grand Mann, 20 Aug 1934, Weatherby 691 (NY); wet area, Chocolate Cove, Deer Island, 8 Aug 1966, Squires s.n. (DAO). Gloucester Co.: Roadside, 19 mi. NNW of Bathurst, 6 Aug 1953, Mulligan & Bassett 1428 (DAO). Kent Co.: Carleton Parish, Kouchibouguac National Park, 0.5 mi. NW of Hwy. 11 from junction of Hwy. 480, 5 Aug 1977, Munro 1404 (DAO). Madawaska Co.: Wet roadside ditch off Hwy. 120, ca. 2.3 mi. N of Caron Brook, 11 Sep 1988, Lamont & Cronquist 239 (NY). Sunbury Co.:

Stream bank N of bridge, Burpea Stream, near Fredericton, 1 Aug 1939, McKenney 5615 (DAO). **NEWFOUNDLAND.** In moist clay soil along roadside to Corner Brook, 15 mi. W of Deer Lake, 5 Aug 1949, Bassett 688 (DAO). Along river shore near Little Codroy River, 1.5 mi. SW of Tompkins, Codroy Valley, 18 Aug 1949, Bassett 824 (DAO). Swampy area, 0.5 mi. E of Cartyville, west coast, 7 Aug 1949, Bassett 708 (DAO). Low damp clearings, valley of Exploits River, Grand Mann, 11 Aug 1911, Fernald & Wiegand 6276* (NY). On rocky beach, Gander Lake, Gander District, 8 Sep 1941, Gillett 330 (DAO). Without specific locality, Bay St. George, 5-7 Aug 1901, Howe & Lang 997 (NY). Without specific locality: Port-au-Port, 30 Jul 1921, Mackenzie s.n. (NY). Without specific locality, Salmonier River, 27 Aug 1894, Robinson & Schrenk 40 (NY). Shaded alder thickets near the shores of the Humber River, Steady Brook, Humber District, 22 Aug 1948, Rouleau 492 (DAO). Shore of Gander River, Joe Batt's Brook, island facing the mouth of Gov't. Cabin, 11 Aug 1960, Rouleau 6190 (DAO). **NOVA SCOTIA.** Guysborough Co.: Swamp, South River Lake, 11 Aug 1958, Smith et al. 18025 (DAO); edge of Goshen Lake, 11 Aug 1958, Smith et al. 18088 (DAO). Inverness Co.: River beach, Red River, 11 Aug 1949, Smith et al. 2882 (DAO); swampy areas, Red River, 27 Jul 1951, Smith et al. 4674 (DAO); swamp, Presqu'ile, 10 Sep 1959, Smith et al. 19405 (DAO). **ONTARIO.** Algoma

District: Bank of Dore River, vicinity of Michipicoten Harbor, 27 Aug 1938, Hosie et al. 448 (DAO). Chapleau District: Without specific locality, Montreal River, 10 Aug 1966, Ropke 171 (DAO). Cochrane District: In lush sloping meadow at Lands & Forest Check Point ca. 10 mi. NE of Moosonee on NW bank of Moose River on Point 5 and opposite Shipsand's Island N of Nicholson's Creek, Moose Twp., 3 Aug 1968, Dickinson & Haber 562 (DAO); rivage de la riviere, Attawapiskat, James Bay, 52°56'N Lat., 28 Aug 1946, Dutilly & Lepage 16548* (DAO); platiere argileuse, Fort Albany, James Bay, 12 Aug 1946, Dutilly & Lepage 16210 (DAO); rivage graveleux, Attawapiskat, James Bay, 23 Aug 1946, Dutilly & Lepage 16476 (DAO). Manitoulin District: Manitoulin Island, West Bay, 21 Jul 1952, Senn 6118 (DAO). Thunder Bay District: Steep low cliff along shore, N end of Lake Nipigon, 19 Aug 1914, Jennings 7130 (DAO); in overflow from beaver pond along thicketed stream, logging road to Postagoni Lake, 2 mi. E of Hwy. 11, 27 Jul 1960, Garton 7857 (DAO). PRINCE EDWARD ISLAND. Prince Co.: Damp ditches, Wellington, 29 Jul 1952, Erskine 1423* (NY). Queens Co.: Moist soil, National Park, 4 mi. S of Dalvay House along No. 16 Hwy., 5 Aug 1950, Bassett 1589 (DAO). QUEBEC. Bonaventure Co.: Riviere Escuminac, canton Flauvel, 11 Aug 1963, Gerardin et al. 5347 (DAO). Chicoutimi Co.: Lake Simoncouche, Laurentides Provincial Park, 31 Jul 1952, Desmarais 1543 (DAO).

Kamouraska Co.: Without specific locality, St. Andre, 28 Jul 1948, Paquin 343X (DAO). Labelle Co.: Without specific locality, Nominingue, 6 Aug 1931, Roy 2083 (DAO). L'Islet Co.: Without specific locality, swamps, low ground, 1 Sep 1942, Jackson 102 (DAO). Magdalen Island Co.: Wet ditch, South Cape, Amherst Island, 27 Jul 1955, Webster & Bentley 368 (DAO). Matapedia Co.: Sainte Irene, canton Nemtaye, rang V, 18 Jul 1938, Boivin 188 (DAO). Megantic Co.: Eclaircie dans une foret mixte, sol humide, A louest de la colline Martin, Thetford Mines est, rang 6, canton Thetford, 4 Aug 1965, Blais et al. 10666 (DAO). Montreal Co.: Ile Sainte Helene, 20 Sep 1936, Boivin 440* (DAO). Pontiac Co.: By a brook near Wharf Road, Norway Bay, Bristol Twp., 13 Jul 1941, Zinck 949 (DAO). Rimouski Co.: Bord d'un fosse, St. Fabien, 31 Aug 1945, Lepage 9854 (DAO). Riviere du Loup Co.: Riviere-Trois-Pistoles, 25 Aug 1964, Blouin et al. 7842 (DAO). St. John's Co.: Bords du Richelieu, St. John, 2 Aug 1953, Cinq-Mars & Raymond s.n. (DAO). Temiscouata Co.: Wet roadside ditch off Hwy. 185, 1.7 mi. S of Notre Dame du Lac, 11 Sep 1988, Lamont & Cronquist 237 (NY).

UNITED STATES. MAINE. Aroostook Co.: River thicket, valley of Aroostook River, Fort Fairfield, 15 Aug 1901, Fernald s.n. (NY); wet roadside meadow off Gilmore Brook Road, 0.7 mi W of Plaisted (NW Eagle Lake), 12 Sep 1988, Lamont & Cronquist 240 (NY). Piscataquis Co.:

Gravelly thicket, valley of Piscataquis River, Dover, 19 Jul 1895, Fernald 307 (NY). **MICHIGAN.** Chippewa Co.: Wet ground along St. Mary's River, Sault Ste. Marie, 27 Jul 1940, Gleason 9773 (NY). Houghton Co.: Moist roadside ca. 3 mi. S of Houghton along US Hwy. 41, 18 Aug 1950, Richards 4224 (MICH). Keweenaw Co.: Muck ground, Chickenbone Lake, Isle Royale, 7 Aug 1930, Brown 3556 (MICH); in swamp along stream, head of Tobin Harbor, Isle Royale, 23 Jul 1930, Brown 3434 (MICH); without specific locality, moist thickets, Aug 1883, Wood 1205 (MICH); without specific locality, cedar thickets, 25 Jul 1890, Farwell 441 (MICH). **MINNNESOTA.** Cook Co.: Shore of Lake Superior, around the village of Grand Portage, 11 & 12 Aug 1929, Rydberg 9686 (NY); 2 mi. N of Grand Portage, near old trail, 29 Jul 1929, Beuner 524 (MIN). **NEW HAMPSHIRE.** Coos Co.: Riverbank, Stratford, 31 Jul 1946, Pease 32284 (UNC). **NEW YORK.** Clinton Co.: In bottomlands along a small stream ca. 5 km NW of Sciota, elev. ca. 100 m, mixed hardwood and coniferous second growth woods on Ordovician limestone substrate, 23 Aug 1975, Cronquist 11332* (NY). Essex Co.: Near Keene Valley, Adirondacks, 3 Sep 1894, Britton s.n. (NY). **VERMONT.** Franklin Co.: Moist roadside depression in coniferous woodland, ca. 1.0 mi. E of East Highgate off Hwy. 78, 11 Sep 1988, Lamont & Cronquist 236 (NY). **WISCONSIN.** Iron Co.: Very moist

soil, Kimball Road, 200 yards N of Rt. 77, 11 Jul 1977, Uttal 12525 (VPI).

2c. **Eupatorium maculatum** L. subsp. **bruneri** (A. Gray) G. Douglas, Can. J. Bot. 64: 2726. 1986. Eupatorium bruneri A. Gray, Syn. Fl. Vol. 1, part 2: 96. 1884. Eupatorium purpureum var. bruneri (A. Gray) B. L. Robinson, Proc. Amer. Acad. Arts 42: 44. 1906. Eupatorium trifoliatum var. bruneri (A. Gray) Farwell, Rep. Michigan Acad. Sci. 20: 191. 1918. Eupatorium maculatum var. bruneri (A. Gray) Breitung, Canad. Field-Naturalist 61: 98. 1947. Eupatoriadelphus maculatus var. bruneri (A. Gray) R. King & H. Robinson, Phytologia 45: 465. 1980. Type. United States. Colorado. Damp ground, in the Rocky Mountains at Fort Collins, 21 Aug 1881, Bruner s.n. (holotype, GH!).

Eupatorium atromontanum A. Nels., Bot. Gaz. 31: 400. 1901. Type. United States. Wyoming. Beaver Creek, Black Hills, 30 Jul 1896, Nelson 2553 (holotype, RM!; isotype, GH!).

Eupatorium rydbergii Britton, Man. fl. n. states. 921. 1901. Type. United States. Nebraska. The sand hills of central Nebraska, south fork of Dismal River in wet meadow, 12 Aug 1873, Rydberg 1682 (holotype, NY!; isotypes, GH!, US!).

Eupatorium maculatum f. tegulosum Bolvin ex Löve & Bernard, Sv. Bot. Tidskr. 53: 431. 1959. Eupatorium purpureum f. tegulosum (Bolvin) Bolvin, Phytologia 23: 11. 1972. Type. Canada. Manitoba. Provencher District: In the parish of St. Genevieve near the borders of Otterburne, at the edge of the road junction to Kleefeld, 4 mi. E of the House of St. Joseph and 1 mi. from the road to Winnipeg, 16 Aug 1954, Bernard 559 (holotype, DAO!).

Stems 6-15 dm tall, purple-speckled or sometimes evenly purplish, densely puberulent throughout (losing pubescence at base with age). Leaves firm, mostly in 4's or 5's, lance-elliptic to lanceolate or lance-ovate, seldom very large, usually 6-17 cm long, 1.5-5 (7) cm wide; gradually or often abruptly narrowed to the short, glabrescent to pubescent petiole; densely covered beneath with short, spreading hairs; uppermost whorl of leaves directly subtending the inflorescence reduced in size, not as long as height of the inflorescence. Involucral bracts glabrescent, or the outer series conspicuously densely pubescent.

Habitat and distribution. Predominantly along river and canal banks, wet meadows, bogs, and seeps, usually in calcareous soils. From Minnesota, Iowa, and NE Kansas to Manitoba, Saskatchewan, Wyoming, Utah, Arizona, and New Mexico, with outlying populations in SW British Columbia, and adjacent Washington (Fig. 11).

A single herbarium specimen from Pickaway Co., Ohio (Bartley & Pontius 41 [NY]) keys out to E. maculatum subsp. bruneri. It is uncertain whether this single specimen represents an anomaly or an established self-perpetuating natural population. Prairie remnants have been documented from central Ohio (Transeau, 1935).

Selected specimens examined. CANADA. BRITISH COLUMBIA. Yale District: Without specific locality, Chilliwack Valley, 16 Aug 1901, Macoun 26486 (NY). New Westminister District: Along roadside 6.5 mi. E of Chilliwack, 29 Jul 1955, Mulligan & Woodbury 1857 (DAO); Lulu Island, 17 Aug 1935, Henson s.n. (DAO). MANITOBA. Beautiful District: In dried out ditch along wild hedges along fence, loam soil, Riding Mountain (town), along Hwy. 5, 29 Jul 1960, Tkachyk 98 (DAO). Carillon District: Wet meadow 1 mi. E of Marchand, 15 Jul 1949, Breitung 8047* (DAO). Gilbert Plains District: Wet ditch near Sarah Lake, Duck Mountain Provincial Forest, 20 Aug 1975, Keleher & Daulishyn 246 (DAO). Lansdowne District: Moist soil along ravine, Brandon, Experimental Farm, 18 Aug 1958, Stevenson 1543 (DAO). Morden and Rhineland District: Pembina Valley, SW of Morden, 5 Aug 1929, Neatby s.n. (DAO). Neepawa District: 10 mi. N of Austin, 28 Aug 1946, Gorden s.n. (DAO). Swan River District: Damp place, fire range station, 5 mi. SW of Minatonas, 18 Aug 1929, Taylor

s.n. (DAO); moist roadside ditch, Swan River Region, Mafeking, SW13-43-26W, 23 Aug 1955, Hudson 1746 (DAO). Turtle Mountain District: Marsh, Dead Lake, near Max Lake, Turtle Mountain Provincial Park, 26 Jul 1978, Keleher 485 (DAO). **ONTARIO.** Kenora District: Clearwater Bay, Lake of the Woods, 25 Aug 1946, Gordon s.n. (DAO); on floor of ash swale S of BL 1800, Kakagi Lake S shore, at E end of Blacky Bay, 16 Aug 1957, Bentley 57557* (DAO); without specific locatily, Ingolf, 20 Jul 1939, Denike 674 (DAO). Rainy River District: In grassy watercourse through silty meadow, now forested, Rainy River, 1.5 mi. SE of Pinewood, Dilke Twp., 9 Aug 1961, Garton 9315* (DAO). **SASKATCHAWAN.** Ile a la Crosse District: 45 mi. NE of Meadow Lake, near junction of the Beaver River crossing the Waterhen River, s.d., Breitung 8436 (DAO); crossing of creek near rapids of the Beaver River, 35 mi. S of Beauvel, 18 Aug 1949, Breitung 8438 (DAO); S side of Lake Athabasca, W side of MacFarlane River, ca. 6.5 km above mouth, near head of "inland delta" area, 59°07.5′N, 107°54′W, shoreline of river rapids main channel, ca. 1.5 km S of Lake, [Annotation Label: "Northernmost record in Saskstchewan for this sporadic species! V.L. Harms."], 10 Aug 1979, Harms & Wright 27349 (DAO). Melfort District: Along the Saskatchewan River, Nipawin, 29 Jul 1941, Breitung 1395* (DAO), in springy places along the Saskatchewan River, Nipawin, 6 Sep 1947, Breitung 5977 (DAO).

Tisdale District: Shore of Red Deer River, 3 mi. S of Hudson Bay Junction, 24 Jul 1940, Breitung 776 (DAO). Yorkton District: Wet springy black poplar woods at foot of Slope, Cote, SW34-29-31W, 18 Aug 1957, Hudson 2008 (DAO).

UNITED STATES. **ARIZONA**. Apache Co.: At E end of small pond, Rock Creek, E of White River, Fort Apache Indian Reservation, elev. 1975 m, T5N, R24E, S22, 6 Aug 1981, Windham et al. 81-300 (ARIZ); in moist meadows, Bog Creek, near McNary, 6 Aug 1935, Bolles s.n.* (ARIZ). Navajo Co: Without specific locality, Fort Apache, Sep 1893, Hoyt s.n. (NY); in wet soil at edge of stream, along Showlow Creek, 0.5 mi. NW of Lakeside Ranger Station, elev. 6600′, 4 Aug 1945, Pultz 1705 (ARIZ). **COLORADO**. Adams Co.: Without specific locality, Monument, Jul 1883, Eastwood s.n. (COLO). Arapahoe Co.: Platte, near Wolhurst, 31 Jul 1916, Heustis s.n. (COLO). Boulder Co.: Along the margin of Shadow Canyon Creek, N of Colo. 170, near Eldorado Springs, T1S, R70W, S30, 23 Jul 1984, Wittmann 2446 (COLO); roadside ditch just E of Lyons, 22 Aug 1953, Weber 8635* (COLO). Fremont Co.: Without specific locality, Canon City, Sep 1873, Brandegee 778 (NY). Larimer Co.: Fort Collins, alt. 5000 ft., 5 Aug 1891, Cowen s.n. (NY). Mesa Co.: On seepy slope of West Creek, Unaweap Canyon, 6000 ft. alt., 8 Jul 1985, Young 252 (COLO). Weld Co.: Without specific locality, Windsor, 5 Sep 1912, Osterhout s.n.

(COLO). IDAHO. Bannock Co.: Without specific locality, Pocatello, 20 Sep 1956, Allen s.n. (GA). IOWA. Bremer Co.: Wet boggy prairie in an upland drainageway, Brayton Prairie 2 mi. S of Sumner, T92N, R11W, S2, 25 Jul 1981, Lammers 4352 (ISC). Emmet Co.: In a hanging bog 1 mi. N of Wallingford, Center Twp., Sec. 6, 13 Aug 1934, Hayden 10591 (ISC). Jasper Co.: Hillside bog along gravel road, 4 mi. NW of Colfax, T80, R21, S29, 13 Aug 1956, Monson 3061 (ISC). Palo Alto Co.: In the sedge zone of a hillside spring, "hanging bog," W side of Des Moines River 2.5 mi. W of Osgood, Walnut Twp., Sec. 34, 9 Sep 1940, Hayden 8887 (NY). Winnebago Co.: Without specific locality, Lake Mills, 17 Aug 1922, Pammel s.n. (ISC). Worth Co.: Without specific locality, Hanlantown, 20-23 Sep 1902, Pammel s.n. (ISC). KANSAS. Atchison Co.: Muscotah Marsh, 0.25 mi. E, 1.25 mi. S of Muscotah, 22 Sep 1976, Brooks 12676* (NY); in the Muscoutah Marsh, 14 Aug 1961, Richards 3577 (NY). Doniphan Co.: On raised marsh area on N facing slope of marshy valley, Bottiger Marsh, 1.75 mi. W, 0.25 mi. S of Denton, 18 Sep 1981, Brooks 15764 (GA). MICHIGAN. Keweenaw Co.: In swamp, Isle Royale, Rainbow Cove, 8 Jul 1930, Brown 3244 (MICH); rocky ground along shore of Lake Superior just W of Cat Harbor, 2 mi. W from Eagle Harbor, 28 Jul 1958, Bennett 6628 (NY); without specific locality, wet places, Aug 1898, E.A.T. 777 (NY). MINNESOTA. Anoka Co.: Moon Lake,

5 Sep 1926, Rydberg 9656 (NY). Big Stone Co.: In springy ground at edge of hardwood patch 6 mi. N of Ortonville, 13 Sep 1950, Moore 20832 (MIN). Clearwater Co.: In moist soil, almost full shade, ca. 2 mi. N of Clearbrook on Rt. 5, T149N, R37W, S8, 11 Aug 1982, Wheeler 6492 (MIN). Jackson Co.: Sloping calcareous fen, on a NE facing bluff in the Des Moines River Valley, T103N, R35W, S7, 6 Aug 1981, Smith 5310 (MIN). Stevens Co.: Meadow at upper end of Lower Pomme de Terre Lake, 14 Sep 1950, Moore 20851 (MIN). Winona Co.: Around Lake, Winona, Aug 1905, Holzinger s.n. (NY). **NEBRASKA.** Cuming Co.: Prairie lowland marsh creek, 5 mi. S of West Point and 0.5 mi. E, T21N, R6E, S26, 23 Aug 1974, Churchill 4124* (NY). Knox Co.: Without specific locality, Fort Niobrara, 25 Jun 1888, Wilcox s.n. (NY). Thomas/Hooker Co.: Wet meadow on South Fork of Dismal River, 12 Aug 1893, Rydberg 1682 (NY). **NEW MEXICO.** Without specific locality, 2 Sep 1904, Shimek s.n. (UNC). Colfax Co.: Vicinity of Ute Park, alt. 2200 to 2900 meters, 24 Aug 1916, Standley 13716 (NY). Lincoln Co.: Tularosa Creek, alt. 6700′, 7 Aug 1901, Wooton s.n. (NMC). Otero Co.: Along Tularosa Creek, 18 Aug 1899, Wooton s.n. (NY). **NORTH DAKOTA.** Bottineau Co.: Low wet wooded valley, margin of pothole, 12 mi. N, 5 E of Bottineau, 7 Sep 1968, Stephens 28853 (NDA). Eddy Co.: Boggy margin of spring fed creek, Warwick Spring Game Management Area, 3 mi. S of Warwick, 9 Aug

1973, Larson 3716 (NDA). Kidder Co.: Wet, clayey soils with shallow standing water, Tappen Slough N of old Hwy. 10, 1.5 mi. W of Tappen, 23 Jul 1973, Williams 1800 (NDA). Pembina Co.: Marshy lowland, 1 mi. SW of Walhalla, 14 Aug 1969, Willenbring 543 (NDA). Richland Co.: Open hillside, 3 mi. W of 4-H camp, 3 Aug 1972, Seiler 4600 (NDA). Strutsman Co.: 2 mi. S, 5 mi. E of Jamestown Spring, 31 Jul 1971, Godfread 2061 (NDA). **SOUTH DAKOTA.** Bennett Co.: Sandhills near La Creek P.O., Pine Ridge Reservation, Aug 1911, Visher 2072 (NY). Lawrence Co.: Spearfish Canyon, streamside, 31 Jul 1926, Hayward 87 (NY); Iron Creek, along creek 12 mi. S of Spearfish, 5 Aug 1919, Petersen s.n. (NY). **UTAH.** Box Elder Co.: Along freeway I-15, opposite Willard Bay Recreational Area, 5 Aug 1986, Shaw 4204 (NY); near Willard Bay, 6 mi. from Brigham City, 4220 ft. elev., 28 Aug 1982, Goodrich 17817* (NY). Cache Co.: Logan, 300 yards NW of railroad depot, E edge of swamp, 28 Aug 1938, Cronquist 11098 (NY); 1 mi. W of old railway depot on W side of Logan city, ditches bordering cultivated field, T12N, R1E, S6, elev. 4600 ft., 1 Sep 1978, Shultz 3042 (NY). Kane Co.: In wet roadside swale in Long Valley ca. 2 km N of Glendale, elev. about 1300 m, T40S, R7W, S14, 26 Aug 1982, Cronquist et al. 11797 (NY); moist roadside depression ca. 1.4 mi. N of Glendale, W side of Hwy. 89, 30 Jul 1989, Lamont & Cronquist 349 (NY); SC Vermillion, 3 mi.

N of Sand Dune Park, 6100 ft. elev., T42S, R7W, S8, 19 Aug 1977, Foster & Foster 5382 (NY). Salt Lake Co.: Without specific locality, Salt Lake City, alt. 4300 ft., 26 Aug 1879, Jones 1338 (NY). Utah Co.: Moist roadside depression near Utah Lake, Provo, 28 Jul 1989, Lamont et al. 348 (NY). **WASHINGTON.** Whatcom Co.: In swamp W of Sumas, 21 Aug 1937, Muenscher 8492 (GH, MO). **WISCONSIN.** Baxfield Co.: Ditch along Hwy. 2 along Fish Creek Slough, T47N, R5W, S2, 22 Aug 1968, Hill 1270 (WIS). Price Co.: Sedge meadow 0.5 mi. W of Kennan at R.R. crossing, T35N, R2W, S10, 14 Aug 1972, Iltis 26431 (WIS). Richland Co.: Sedge meadow along Bear Creek, 7 mi. N of Lone Rock, T9N, R2E, S1, 19 Jul 1973, Nee 6213 (WIS). Sawyer Co.: Marshy area along Snoose Creek, 1.5 mi. E of Fishtrap Lake, T40N, R4W, S18, 25 Jul 1971, Hansen 330 (WIS). Washburn Co.: Boggy roadside 9 mi. SE of Spooner, T38N, R11W, S16, 13 Aug 1947, Stevens 163 (WIS). **WYOMING.** Crook Co.: Riverbank, Belle Fourche River near Mona, ca. 14.5 air mi. NNE of Hulett, Black Hills, elev. 3500 ft., T56N, R63W, S15, 29 Aug 1983, Marriot 5887 (RM); streambanks, Black Hills, Miller Creek, ca. 9.5 air mi. SSE of Devils Tower, elev. 4300 ft., T52N, R65W, S23, 14 Jul 1983, Marriott 4533* (RM). Platte Co.: Shaded stream bank, Palmer Canyon road W of Wheatland on Laramie River, 4600 ft., 6 Aug 1959, Porter & Porter 7998 (RM). Sheridan Co.: In the copses, Sheridan, 24 Jul 1901, Nelson 8478 (RM). Washakie Co.:

Wooded canyon bottom, Big Horn Mountains, near the mouth of Tensleep Canyon, ca. 5 air mi. NE of Ten Sleep, elev. 4800 ft., T47N, R87W, S6, 14 Aug 1980, Nelson & Fonken 7141 (RM). Weston Co.: Without specific locality, Beaver Creek, 30 Jul 1896, Nelson 2553 (RM).

3. **Eupatorium steelei** E. Lamont, Brittonia 42: 279-282. 1990. Type. United States. Virginia. Wise Co.: Stone Mt., 0.8 km N of High Knob Lookout Tower, 3.6 km S of Norton, 3800 ft (1160 m), 7 Aug 1989, Lamont & Wieboldt 357 (holotype, NY!; isotypes, GH!, NY!, US!, VPI!).

Erect herb, 0.6-2 m tall. Stems solid, greenish-purple or sometimes evenly purplish, conspicuously glandular pubescent nearly or quite to the base with long, spreading, persistent hairs, occasionally merely densely puberulent and sparingly glandular. Leaves firm, mostly in 3's or 4's; blades lance-ovate or ovate to deltate-ovate, mostly 7-30 cm long, 2.5-18 cm wide, relatively abruptly or sometimes gradually tapering to the short-petiolate base, acuminate at the apex, pinnately veined, sharply serrate, adaxial surface glabrescent to more often scabrous-hirsute, abaxial surface conspicuously to sparsely glandular pubescent and loosely hirsute on the midrib and main veins, usually rather sparsely so over the surface as well; petioles usually (0.7) 1.3-2.8 (3.6) mm long, glabrate to densely ciliate. Inflorescence a loosely convex compound cyme, usually less than 20 cm wide in life, heads short pedunculate, peduncles conspicuously glandular pubescent. Involucre 6.5-9 mm high, 3.5-5 mm wide, often purplish; bracts

10-22, lanceolate, obtuse at apex, well imbricate, few-striate or at least with prominent midvein; receptacle naked, flat or weakly convex. Flowers (5) 6-9 (10) in a head; corolla 4.5-7.5 mm long, 5-toothed, generally very pale pinkish or purplish, funnelform, outer surface usually minutely atomiferous-glandular, lobes ovate to deltate, usually slightly longer than wide; style base puberulous, enlarged. Achenes prismatic, 3.0-4.5 mm long, 5-ribbed, atomiferous-glandular, sometimes with a few setulae along the nerves; pappus a single series of 25-40 slender, capillary, scabrous, persistent bristles. 2n = 20.

Habitat and distribution. Usually on gentle slopes of degraded sandstone and shale, in openings of Acer rubrum, Liriodendron tulipifera, Quercus velutina, Q. borealis, and Q. alba, above 700 m (2300 ft). The species is particularly common on hilltops, from which it colonizes roadbanks below. Eupatorium steelei is known from the Blue Ridge Province of western North Carolina (Avery, Haywood, and Macon Cos.) and eastern Tennessee (Sevier Co.), the Ridge and Valley Province of southwestern Virginia (Bland, Scott, Smythe-Wythe, and Wise Cos.), and the Appalachian Plateaus Province of eastern Kentucky (Harlan Co.). (See Fenneman, 1938, for discussion and delimitation of physiographic boundaries).

Eupatorium steelei is closely related to E. purpureum L., a species of wide distribution throughout eastern North America. The former can be readily distinguished by its persistently glandular-hairy stems, glandular-hairy abaxial leaf surface, and lack of concentrated anthocyanic pigment at leaf nodes. In addition, E. steelei is a coarser plant with firmer leaves that are broader in shape and are more abruptly contracted to the petiole than in E. purpureum.

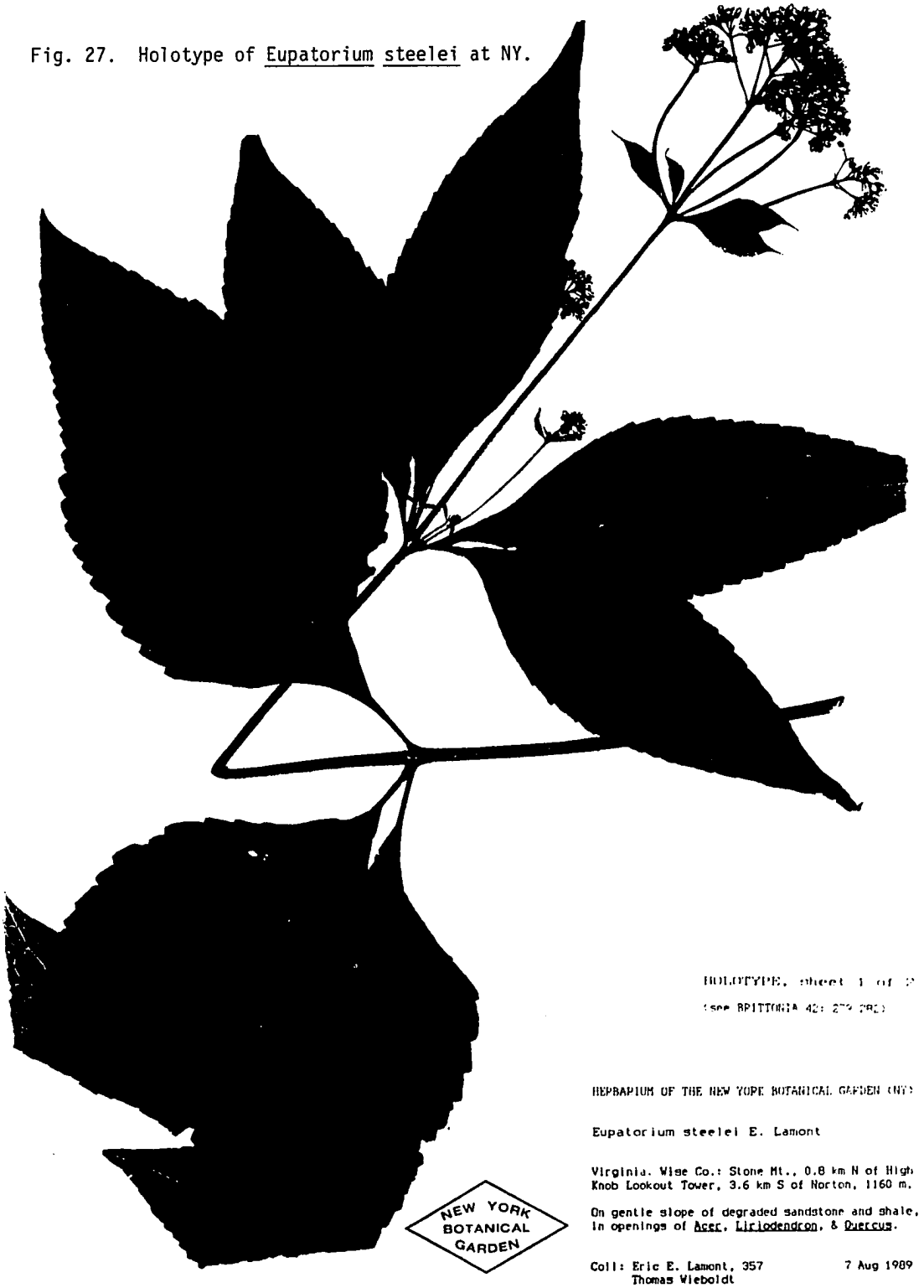
Eupatorium steelei has been collected in close proximity to E. purpureum and E. fistulosum. At one station in Wise Co., Virginia (near the type locality), E. steelei was found growing with E. purpureum. Both species maintained their morphological identity but there were a few putative hybrids. Introgressive hybridization within Eupatorium is not uncommon and has been well documented in North American species (Sullivan, 1972). It would appear that E. steelei is more closely related to E. purpureum than to E. fistulosum, but all three stand as a closely related and apparently monophyletic group.

Additional specimens examined. UNITED STATES. **KENTUCKY.** Harlan Co.: Black Mt., dry ridge in oak-chestnut summit forest, 27 Aug 1931, Braun 278* (US). **NORTH CAROLINA.** Avery Co.: Vicinity of Banners Elk, including Beech and Grandfather Mts., 1200 m (3940 ft), 21 Aug 1915, Steele 1* (GH, NY, US); Rocky Peak,

foot of Hanging Rock, vicinity of Banners Elk, 1200 m (3940 ft), 21 Aug 1915, Steele 5* (GH, NY, US); Sugar Mt., McCandles Gap, 1200 m (3940 ft), 1 Sep 1915, Steele 69* (US); Beech Mt., above Klonteska, 1250 m (4100 ft), 7 Sep 1915, Steele 142* (NY, US). Haywood Co.: Along trail on S slope of Big Catalochee, fire cherry, yellow birch community, 20 Aug 1956, Ramseur 1775* (UNC); vicinity of Eagles Nest, in thin woods, near Waynesville, 900-1500 m (2950-4920 ft), 8 Sep 1910, Standley 5671* (US), 5672* (US). Macon Co.: Summit of Wayah Bald Mt., 18 Aug 1949, Godfrey & Fox 49973* (NY). **TENNESSEE.** Sevier Co.: In clearing on Blanket Mt., 3800 ft (1160 m), 19 Aug 1919, Ainslie s.n.* (GH). **VIRGINIA.** Bland Co.: Garden Mt., 2.3 mi (3.7 km) S of Tazewell Co. line, 10 Sep 1970, Uttal 7708* (VPI). Scott Co.: Open roadside along route 664, 0.5 km S of Wise Co. line, 920 m (3150 ft), 7 Aug 1989, Lamont & Wieboldt 363* (NY); Little Stony Creek, in woods bordering roadside, 5.5 km (3.5 mi) N of Dungannon, 710 m (2340 ft), 1 Oct 1989, Lamont & Cronquist 390 (NY); NW of jct. of Corder Branch and Little Stony Creek, open roadside, 3.4 mi (5.5 km) N of Dungannon, 2340 ft (710 m), 23 Aug 1978, Peake 399* (FLAS). Smythe-Wythe Co.: Without specific locality, 29 Aug 1944, Massey 22717* (VPI). Wise Co.: Open roadside along route 619 within Norton city limits, 750 m (2550 ft), 1 Oct 1989, Lamont & Cronquist 391 (NY); Powell

Mt., frequent in open hardwood clearcut, 4 mi (6.5 km) SSW of Norton, 3250 ft (990 m), 9 Sep 1987, Wieboldt 6538* (NY, VPI).

Fig. 27. Holotype of Eupatorium steelei at NY.



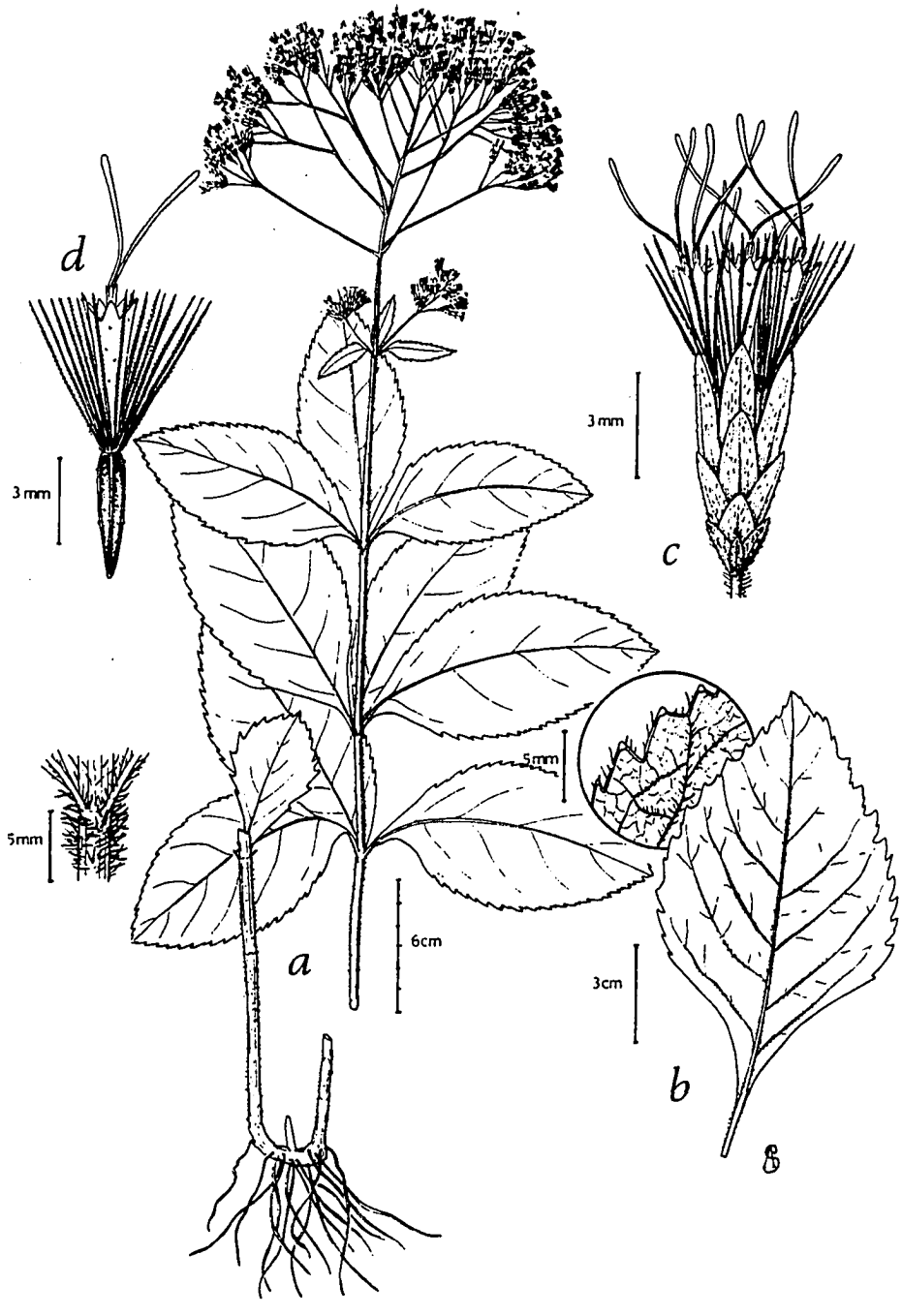


Fig. 28. Eupatorium steelei. A. Habit. B. Leaf. C. Head. D. Flower.

4. **Eupatorium purpureum** L., Sp. pl. 838. 1753. Cunigunda purpurea (L.) Lunell, Am. Midland Nat. 5: 35. 1917. Eupatoriadelphus purpureus (L.) R. King & H. Robinson, Phytologia 19: 432. 1970. Type. Protologue: "North America." Without specific locality, date, and collector's name (there is only one specimen of E. purpureum in the herbarium of Linnaeus according to Savage, 1945, page 143) [holotype, LINN (microfiche, NY!; photo, GH!)].

Eupatorium trifoliatum L., Sp. Pl. 837. 1753. Eupatorium purpureum var. maculatum f. trifoliatum (L.) Voss, Vilm. Blumengartn. Ed. 3. 1: 447. 1894. Type. Protologue: "Virginia." Without specific locality, date, and collector's name (there is only one specimen of E. trifoliatum in the herbarium of Linnaeus according to Savage, 1945, page 143) [holotype, LINN (microfiche, NY!; photo, GH!)].

Eupatorium verticillatum Lam. var. α, Encycl. 2: 405. 1786 (not Eupatorium verticillatum Muhl. ex Willd. Sp. Pl. 3: 1760. 1804). Eupatorium purpureum var. verticillatum (Lam.) Wood, Class-book Bot., Ed. 1. 184. 1845. Type. No specimens were directly cited in the protologue, which evidently applies to what we would now call E. purpureum L. It seems clear that Lamarck intended to include E. purpureum L. in his E. verticillatum var. α, although the citation is

indirect. Lamarck's name is therefore nomenclaturally superfluous under Article 63.1 of the Code (Greuter, 1988), and ought to be typified on E. purpureum L. (see Article 7.13 of the Code). (Wiegand & Weatherby (1937) were unable to locate a specimen in Lamarck's herbarium at P; Cronquist (1990, personal communication) was also unable to find a specimen at P, but a specimen was located in the herbarium of Antione Laurent de Jussieu, cat. no. 8398, bearing the handwritten label "Eupatorium verticillatum Lamk." In any case, Lamarck's name falls into synonymy under E. purpureum L.).

Eupatorium fusco-rubrum Walt., Fl. Car. 199. 1788. Type. Without locality, date, and collector's name. Wiegand & Weatherby (1937) identified the type specimen in Walter's herbarium at BM as E. purpureum L.; Fernald & Schubert (1948) also concluded that Walter's "E. fusco-rubrum, no. 733 on p. 46 of the collection, is small E. purpureum L.;" Cronquist (personal communication) concluded that Walter's type specimen at BM is ambiguous and had been severely shriveled before being pressed thus making identification difficult; my examination of the type photo at GH was also inconclusive, but I herewith follow traditional determinations of the type specimen (holotype, BM Cronq.!; photo, GH!).

Eupatorium falcatum Michx., Fl. Bor.-Am. 2: 99. 1803. Eupatorium purpureum var. falcatum (Michx.) Britt., Mem. Torr. Bot. Club 5: 312. 1894. Eupatorium purpureum var. angustifolium f. falcatum (Michx.) Voss, Vilm. Blumengartn. Ed. 3. 1: 447. 1894. Type. Ohio. "ad ripas fluviorum Ohio et Scioto," s.d. Michaux (bearing the handwritten label "Eupatorium No. 16") (holotype, P Cronq.!).

Eupatorium verticillatum Muhl. ex Willd., Sp. Pl. 3: 1760. 1804 (not Eupatorium verticillatum Lam., Encycl. 2: 405. 1786). Type. Protologue: "North America." Without specific locality, date, and collector's name. There are two sheets (cat. no. 15127) of Eupatorium verticillatum Muhl. ex Willd. at the Willdenow herbarium in Berlin; both sheets were seen at B by Cronquist in 1991, and I have examined corresponding microfiche at NY. Sheet 1 bears an unsigned handwritten notation "lectotype," and is here formally accepted as such (lectotype, B Cronq.!; microfiche, NY!).

Eupatorium amoenum Pursh, Fl. Am. Sept. 2: 514. 1814. Eupatorium purpureum var. amoenum (Pursh) A. Gray, Syn. Fl. Vol. 1, part 2: 96. 1884. Eupatorium maculatum var. amoenum (Pursh) Britt., Mem. Torr. Bot. Club 5: 312. 1894. Eupatorium purpureum var. maculatum f. amoenum (Pursh) Voss, Vilm. Blumengartn.

Ed. 3. 1: 447. 1894. Eupatorium trifoliatum var. amoenum (Pursh) Farwell, Rep. Michigan Acad. Sci. 20: 191. 1918 [1919]. Type. Protologue: "On the New Jersey mountains." Without specific locality, date, and collector's name [holotype, not seen; by description = E. purpureum (search at PH and inquiry to other major herbaria failed to locate the type; Wiegand & Weatherby (1937) were also unable to locate the type)].

Eupatorium purpureum var. β album Barratt, Eupatoria verticillata no. 3 (see Fig. 31). 1841. Type. Protologue: "In dry woods and hillsides, in rocky places." Without specific locality, date, and collector's name [holotype, not seen; by description = E. purpureum (search at NY and inquiry to other major herbaria failed to locate the type; Grimes & Keller (1982) did not include E. purpureum var. album Barratt in the list of type specimens in Barratt's herbarium)].

Eupatorium purpureum var. γ ovatum A. Wood, Class-book Bot., Ed. 1. 184. 1845. Type. Not cited in protologue. [holotype, not seen; by description = E. purpureum (search at NY and inquiry to other major herbaria failed to locate the type)].

Eupatorium harnedii Steele ex Harned, Wildflowers Alleghanies 501. 1931. Type. United States. Maryland.

Without specific locality, Oakland, Sep 1909, Harned s.n. (holotype, US!).

Eupatorium purpureum f. depressum Jennings, Castanea 7: 47. 1942. Type. United States. Pennsylvania. Allegheny Co.: Partly shaded lower slope near mouth of Falls Run, Glenshaw, 15 Aug 1918, Jennings s.n. (holotype, CM!).

Eupatorium purpureum f. laciniatum Jennings, Castanea 7: 47. 1942. Type. United States. Pennsylvania. Allegheny Co.: Shaded floodplain, rocky soil, upper part of Falls Run Ravine, Glenshaw, 15 Aug 1918, Jennings s.n. (holotype CM!).

Eupatorium purpureum f. decolor Seymour, Fl. Vermont Ed. 4. 344. 1969. Type. United States. Massachusetts. Worcester Co.: Without specific locality, Worcester, 9 Aug 1925, Bemis s.n. (holotype, GH).

Erect herb, 0.3-2 m tall; stems solid or rarely developing a slender central cavity toward the base, usually dark purple only at nodes otherwise greenish or rarely purplish-green, viscid-puberulent near summit, glabrous below inflorescence, scarcely or not at all glaucous. Leaves mostly in 3's or 4's (rarely 5's); blades lance-ovate or ovate to deltate-ovate, mostly (7) 9-26 (30) cm long, (2.5) 3-15 (18) cm wide, relatively abruptly or sometimes gradually tapering to

the short-petiolate base, acuminate at the apex, pinnately veined, coarsely serrate with a large gland at apex of each marginal tooth, adaxial surface glabrous to sparingly glabrescent, abaxial surface atomiferous and glabrate to densely pubescent; petioles usually 0.5-1.5 (2) cm long, glabrous to sparingly puberulent or rarely ciliate. Inflorescence a loosely convex compound cyme, rather sparse, usually less than 20 cm wide in life, the branches ascending from widely diverging bases, heads short pedunculate, peduncles conspicuously glandular pubescent. Involucre 6.5-9 mm high, 2.5-5 mm wide, often purplish; bracts 10-22, lanceolate, obtuse at apex, well imbricate, few-striate or at least with prominent midvein; receptacle naked, flat or weakly convex. Flowers (4) 5-7 (8) in a head; corolla 4.5-7.5 mm long, 5-toothed, generally very pale pinkish or purplish, funnelform, outer surface usually minutely atomiferous-glandular, lobes ovate to deltate, usually slightly longer than wide; style base puberulous, enlarged. Achene prismatic, 3.0-4.5 mm long, 5-ribbed, atomiferous-glandular, sometimes with a few setulae along the nerves; pappus a single series of 25-40 slender, capillary, scabrous, persistent bristles. $2n = 20$.

Eupatorium purpureum L. is a morphologically variable species. Historically, over a dozen infraspecific taxa have been proposed, based largely upon differences in

leaf shape. One such taxon, E. purpureum var. amoenum, has been widely accepted by taxonomists and was recognized by Wiegand and Weatherby (1937) in their landmark treatment of section Verticillata. Subsequently var. amoenum has received little taxonomic attention.

Eupatorium amoenum was based on extremely depauperate plants and described by Pursh (1814) as a small, attenuate plant with chiefly opposite leaves and a small inflorescence with few heads. Each head contained only 3-5 flowers. No geographic isolation separated var. amoenum from var. purpureum.

Eupatorium amoenum appears distinctive in the field (see Fig. 5), but living plants transplanted by the author (from near the type locality in northwestern New Jersey to a garden in New York) grew into ordinary small plants of the widespread and variable species E. purpureum. After two growing seasons in the garden the small attenuate plants grew into robust plants, well within the morphological limits of E. purpureum (Fig. 6). It was concluded that E. amoenum represented a depauperate shade form of E. purpureum and did not warrent taxonomic recognition. There may have been some ecotypic selection in the wild, but the morphologic expression is increased by the direct effect of the environment. Similar cases have been documented for Erigeron provancheri (Cronquist, 1947;

1988) and Calopogon tuberosus var. latifolius (Catling & Lucas, 1987).

In north central United States, plants with densely and persistently pubescent abaxial leaf surfaces occur sporadically and have been formally recognized as a distinct species (Rydberg, 1931). These plants, however, are not consistently distinguishable from E. purpureum by any characters other than leaf pubescence. Both taxa occur in similar habitats and are only weakly differentiated geographically. In view of the overall similarities to E. purpureum, Rydberg's species was recognized as a taxonomic variety by Lamont (1990b). The two varieties may be distinguished as follows:

1. Abaxial leaf surface glabrous or nearly so, sometimes sparsely pubescent along the major veins; S New Hampshire to N Florida, west to SE Minnesota, Iowa, and E. Oaklahoma.. var. purpureum

1. Abaxial leaf surface densely and persistently puberulent to villose throughout; S Minnesota, Iowa, and NE Kansas to S Wisconsin, N Illinois, and N Missouri..... var. holzingeri

4a. E. purpureum L. var. purpureum.

Leaves usually glabrous on abaxial surface or sometimes sparsely to densely pubescent with fine

simple unicellular hairs along the major veins; petioles glabrous.

East of the Mississippi River abaxial leaf surfaces tend to be glabrous and rarely densely pubescent along the major veins. West of the Mississippi River (and in the high xeric sand-hills of South Carolina) abaxial leaf surfaces are commonly densely pubescent along the major veins.

Habitat and distribution. Predominantly in drier habitats than other species (except E. steelei) of section Verticillata. Occurring naturally in rich, open deciduous woodlands, woodland borders, and thickets; usually in wooded ravines and near the bases of slopes bordering wet grounds, and in at least partial shade or commonly in deep shade. Frequent as a weed along well drained roadsides and slopes. From southern New Hampshire and southeast Minnesota to Iowa, south to Virginia, North Carolina and South Carolina (in the mountains and piedmont province), Georgia (mountain province), with outlying populations in the coastal plain province of southwest Georgia and the Apalachicola region of Florida, in the west to southeast Nebraska, eastern Kansas, northeastern Oaklahoma, and the Ozarks and northern Mississippi embayment province of Arkansas (Fig. 12).

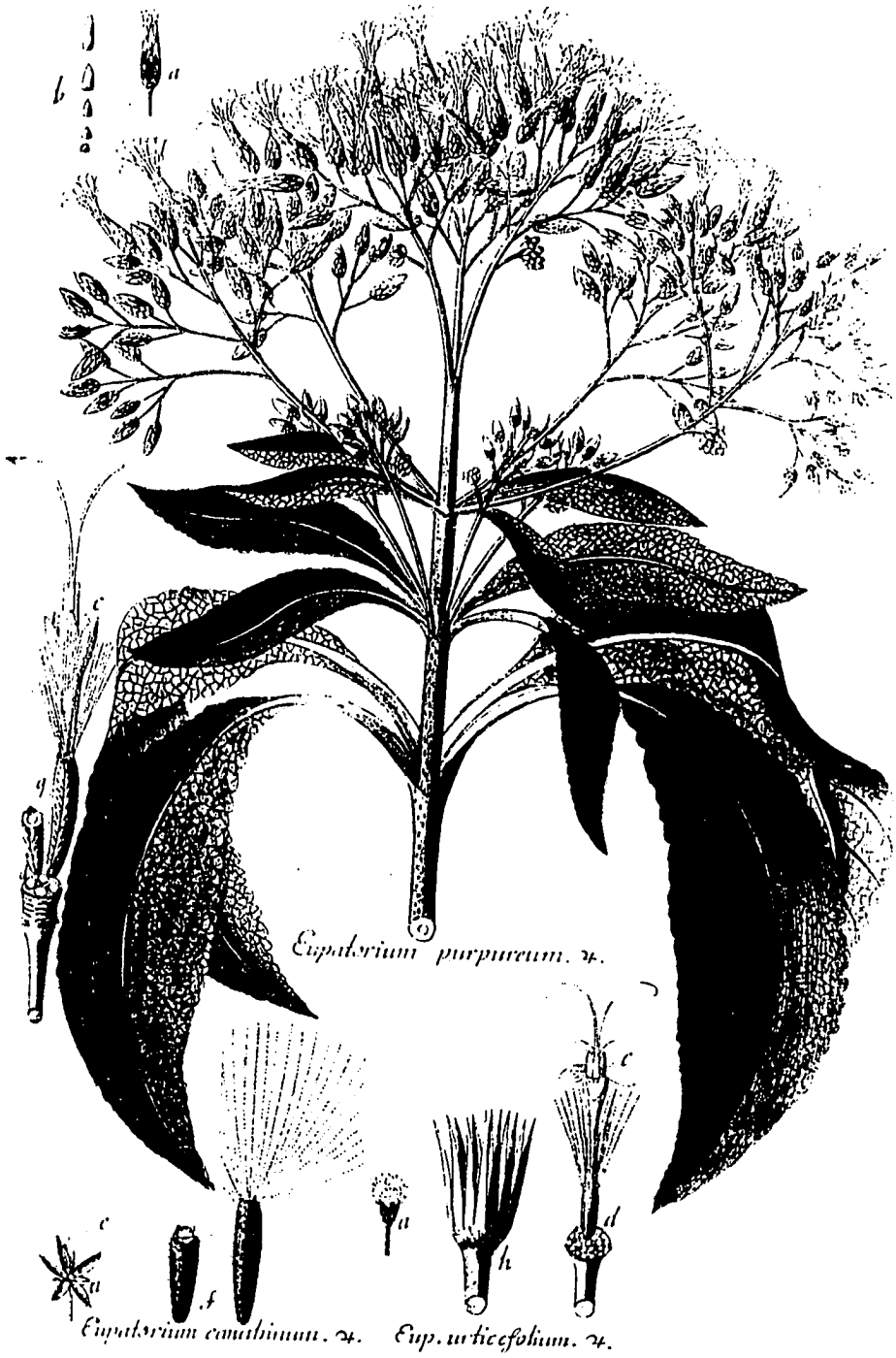


Fig. 30. Eupatorium purpureum. Photographed from tabula 237 in Schkuhr (1808).

Selected specimens examined. CANADA. **ONTARIO.** Lincoln Co.: Without specific locality, St. Davids, 3 Sep 1906, Scott s.n. (DAO); without specific locality, Queenston, 23 Aug 1902, Scott s.n. (DAO). Middlesex Co.: Peter's Bank, along Thames River, near London, 6 Aug 1890, Dearness s.n.* (DAO); shady woods on banks of the Thames River, 2 mi. W of London, Aug 1879, Saunders s.n. (DAO). Welland Co.: Stamford Township, 200 feet north of Welland-Lincoln Co. line on Niagara River Road, 7 Oct 1948, Miller & Grant s.n. (BH).

UNITED STATES. **ALABAMA.** De Kalb Co.: Mountainous woods, flanks of Lookout Mt. near Mentone on the road to Valley Head, elev. 1800 ft., 7 Sep 1898, Mohr s.n. (UNA). Madison Co.: In oak-hickory forest on the NW slope of Monte Sano Mt., Monte Sano State Park, Huntsville, T3S, R1E, S29, 10 Jul 1980, Meigs 983 (UNA). **ARKANSAS.** Franklin Co.: Along Mountain Creek ca. 2 mi. E of Cass, alt. ca. 1000 ft., T12N, R26W, S19-20, 6 Jul 1965, Redfearn 17295 (UNC). Madison Co.: Moist wooded hillside near jct. in National Forest, going S from Hwy. 16 near the Madison-Newton Co. line, 24 Jul 1988, Stewart 196 (UARK). Sharp Co.: Spring River bottoms, Williford, 20 Jul 1947, Demaree 26244* (UNC). **CONNECTICUT.** Fairfield Co.: In woods off Hwy 25 roadside clearing, ca. 4.3 mi. S of Newtown, 13 Aug 1987, Lamont 198 (NY). New Haven Co.: Without specific locality, New Haven, 21 Sep 1875, Hatcher s.n.* (NY).

DELAWARE. New Castle Co.: In rich woods off dirt trail, Brandywine Creek State Park, 7 Aug 1987, Lamont 187 (NY). **DISTRICT OF COLUMBIA.** Woodley Park, 1 Sep 1914, Steele s.n.* (VPI). **FLORIDA.** Gadsden Co.: Old uncultivated field, exp. sta., Quincy, 30 Jul 1936, Foster 85 (FLAS). Leon Co.: Without specific locality, mixed climax woods, 15 Aug 1942, Kurz s.n. (FLAS). Walton Co.: Ravine near Eucheanna Church, 2 Jun 1954, West & Arnold s.n. (FLAS). Washington Co.: Slope of ravine in hardwoods area, ca. 2 mi. S of jct. FL 277, along FL 79, SW of Vernon, 9 Jun 1962, Ford & White 6355* (FLAS). **GEORGIA.** Rabun Co.: In oak-hickory woods near Dick's Creek Gap, 10 mi. E of Hiawassee, 24 Jul 1948, Cronquist 5541 (GA). Walker Co.: South end of Pigeon Mt. at Doughtery Gap, Pigeon Mountain Wildlife Management Area, SW of Lafayette, 11 Jul 1984, Jones & Colle 24245 (GA). **ILLINOIS.** Adams Co.: Along the wooded bluff of Burton Creek, Burton, T2S, R8W, S19, 13 Aug 1941, Evers 736* (ILL). Macon Co.: Wooded area near the S shore of Lake Decatur, 23 Aug 1947, Winterringer 183 (ILL). **INDIANA.** Jefferson Co.: Wooded beech slope in Clifty Falls State Park, 7 Aug 1932, Deam 52528* (IND). Vermillion Co.: Wooded ravine about 12 mi. W of Montezuma, 15 Aug 1932, Deam 52800 (IND). **IOWA.** Boone Co.: Along stone wall at intersection of canyon road and Des Moines River Road, 11 Aug 1982, Johnson-Groh 758 (ISC). Hardin Co.: Unpastured upland woods, 4 mi. E

of Hubbard, T87, R20, S30 & 31, 16 Jul 1956, Monson 2741 (ISC). **KANSAS.** Cherokee Co.: In wooded area along Shoal Creek, 1.5 mi. S of Galena, 19 Jul 1961, Richards 3106 (KANU). Linn Co.: In woods, lowlands, 3 mi. W of Mound City, Dingus National Area, T22S, R23E, S10 & 15, 19 Sep 1976, Hulbert 4667* (KSC). **KENTUCKY.** Fayette Co.: Rich woods on steep bank above Raven Run creek, 4 Aug 1955, Wharton 9289* (UNC). Pendleton Co.: In woods along Rt. 8, near Black River Lime mine ca. 3 mi. NE of Foster, Buddell 1314* (UNC). **LOUISIANA.** Caldwell Co.: Gorges NE of Copenhagen, NE corner of Sec. 14, T12N, R4E, clay soil and mixed hardwoods forest, 2 Jun 1973, Marx et al. 1179 (NLU); prairie and gorges in hills E of Copenhagen and La. 849 S of Columbia and W of Ouachita River, T12N, R4E, S47, 28 Mar 1987, Thomas 99196 (NLU). **MARYLAND.** Frederick Co.: Along trail in moist woods, Catoctin Mountain Park, elev. 1450 ft., 7 Aug 1987, Lamont 189 (NY). Washington Co.: Alluvial woods along Potomic River on varicolored shales and sandstones at Bearre, 29 Sep 1969, Downs 9829* (UNC). **MASSACHUSETTS.** Berkshire Co.: In dry woods, Stockbridge, 28-31 July 1901, Britton s.n.* (NY). Hampden Co.: In rich woods along Hwy. 57, ca. 2.2 mi. W of Tolland, 15 Aug 1987, Lamont 207 (NY). Nantucket Co.: Shawkemmo, Nantucket Island, 7 Jun 1908, Bicknell 8972* (NY). **MICHIGAN.** Lapeer Co.: Open thickets near South Branch Flint River, Oregon Twp., ca. 3 mi. SE of

Columbiaville, 18 Sep 1958, Voss 8248 (MI). Lenawee Co.: Edge of woods, upper edge of slope between Oakwood Cemetary and Island Park, Adrian, 23 Jul 1985, Smith 969 (MI). **MINNESOTA**. Mower Co.: Alluvial woods on the N bank of the Iowa River, Lake Louise State Park, about 1.5 mi. NW of LeRoy, T101N, R14W, S28, 16 Aug 1983, Smith 8674 (MIN). Winona Co.: In shade, Jackson Park woods, Aug 1906, Holzinger s.n. (MIN). **MISSISSIPPI**. Desoto Co.: Deciduous woods along main road below swimming pool area at Camp Currier, 4 Jul 1970, Ferrari 565* (UNC). Oktibbeha Co.: Northern slope facing Trim Cane Creek flood plain, secondary mixed hardwood cover, calcareous soil, 6 mi. N of Starkville, 9 Jul 1956, Ray 6727 (UNC). **MISSOURI**. Hickory Co.: Roadside near Stark's Creek just E of Jordan, 24 Jul 1963, Bradley 1267 (UNC). Shannon Co.: Base of E facing bluff along Jacks Fork River, T28N, R5W, S9, 12 Jul 1969, Redfearn 26337* (UNC). **NEBRASKA**. Douglas Co.: Riverview Park, Omaha, 17 Jul 1898, Cleburne s.n. (NEB). Nemaha Co.: In low woods along N side of the road near Spring Hollow picnic area, oak-linden bluff forest at Indian Cave State Park, 17 Aug 1989, Rolfsmeier & Kaul (NEB). **NEW HAMPSHIRE**. Cheshire Co.: In rich woods off dirt trail, Pisgah Mtn. State Park, W of Winchester, 17 Aug 1987, Lamont 213* (NY). Grafton Co.: Without specific locality, Hanover, 1846, Rickard C-B314 (NY). **NEW JERSEY**. Bergen Co.: Wooded slope above Dyckman St.

Ferry Landing, 31 Aug 1916, Pennell 8359 (NY). Somerset Co.: In open woods, Watchung, 20 Aug 1933, Moldenke 7860* (NY). Sussex Co.: In dry woods on slope above Delaware River, ca. 1.2 mi. S of Dingmans Ferry Bridge, 8 Aug 1987, Lamont 191 (NY). **NEW YORK.** Rockland Co.: Base of TMI trail, Ladentown, Ramapo Twp., 30 Jul 1957, Lehr 534* (NY). Suffolk Co.: Rich deciduous woods and edge of roadsides, Caumsett State Park, Lloyd Harbor, 28 July 1987, Lamont 176 (NY); along edge of rich woods and roadside, Moriches Road N of Rt. 25A, Nissequogue, 2 Aug 1987, Lamont 182 (NY); rich woods along Sound View Ave., S of Great Pond, 3 Aug 1987, Lamont 185 (NY). Warren Co.: Shaded roadside, 2 mi. S of Brayton, Lake George, 27 Aug 1901, Burnham s.n.* (NY). **NORTH CAROLINA.** Union Co.: Wooded slope, Rocky River on NC. 742, 14 Jul 1957, Ahles & Haesloop 31492 (UNC). Wilkes Co.: Edge of dry woods, S slope, on dirt road up Pores Knob Mt., 3 mi. from NC. #16, 21 Jul 1940, Radford & Stewart 1763 (UNC). **OHIO.** Harrison Co.: Beech woods along Route 22 W of Cadiz, 1 Sep 1955, Welshaupt s.n. (OS). Holmes Co.: On dry wooded roadbank off Rt. 404, 1 mi. SW of Jct. with St. Rt. 520, NE 1/4 Sec. 9, Richland Twp., 4 Sep 1971, Wilson 2564* (OS). **OKLAHOMA.** Cherokee Co.: In woods of Ill. R. valley, Ozarks, 7 mi. NE of Tahlequahnon State 10, 13 Jul 1958, Wallis 7562 (OKL). Delaware Co.: Wooded calcareous slopes, 3 mi. W and 2.5 mi. N of state line, W of Siloam Springs, 27

Jul 1949, Waterfall 9192 (OKL). **PENNSYLVANIA.** Northampton Co.: Top of Chestnut Hill, Easton, 2 Sep 1898, Porter s.n.* (NY). Wayne Co.: In grassy swale under maple-chokeberry copse, Scott Center Road at entrance to Scott Gun Club, Scott Twp., 22 Aug 1984, Uttal 13429 (VPI). **RHODE ISLAND.** Kent Co.: Without specific locality, Warwick, 23 Aug 1874, Phoenix s.n.* (NY). **SOUTH CAROLINA.** Oronee Co.: Brasstown Creek E of Boatwright Mtn., N to NW facing slopes and floodplain, elev. ca. 270 m, 1 Jul 1975, Boufford & Wood 16879* (UNC). Pickens Co.: Mixed deciduous forest, 1 mi. N of Rocky Bottom near US 178, 22 Aug 1956, Radford 16806 (VPI). **TENNESSEE.** Cocke Co.: Mixed deciduous forest along Brush Creek near Cocke-Greene county line S of Hwy 107, Cherokee Natl. Forest, 22 Aug 1967, Winstead & Mahler 4459* (UNC). Grundy Co.: Rocky woods, top of bluff, Fiery Gizzard Creek, Tracy City, 31 Jul 1962, Magee 90 (UNC). **VERMONT.** Bennington Co.: Without specific locality, Pownal, 8-11 Sep 1899, Eggleston 1351* (NY). Windham Co.: In rich deciduous woods and edge of roadside, along Hwy. 9, S of Richardson Mt., 16 Aug 1987, Lamont 211 (NY). **VIRGINIA.** Nelson Co.: In rocky oak woods along the Appalachian Trail, on the N side of the summit of Three Ridges Mt., ca. 3600-3700 ft. elev., 30 Jul 1976, Watson 560 (VPI). Wise Co.: Open mixed hardwoods along old logging trail just N of Beaverdam Gap, Powell Mountain, about 3.75 mi. SSW of

Norton, elev. ca. 3350 ft., 9 Sep 1987, Wiebolt 6537* (VPI); Stone Mt., 0.8 km N of High Knob Lookout Tower, 3.6 km S of Norton, 3800 ft (1160 m), 7 Aug 1989, Lamont & Wieboldt 358 (NY). **WEST VIRGINIA.** McDowell Co.: On moist loam, shade of mature hardwoods, Indian Ridge, 2 Sep 1956, Kral 3378 (VPI). Monongalia Co.: Davis Farm, Dellslow, 13 Jul 1964, Allamong s.n.* (VPI). **WISCONSIN.** Grant Co.: Oak-hickory-ash-maple woods on uppermost 1/4 of steep, rocky (limestone) NE facing slope of ridge along Mississippi River, Nelson Dewey Memorial Park, T3N, R6W, S13, 22 Jul 1956, Iltis & Neess 6477 (WIS). Outagamie Co.: In shade in a ravine, Appleton, T21N, R17E, S25, 21 Aug 1949, Seymour 10868* (WIS).

4b. Eupatorium purpureum L. var. holzingeri (Rydberg) E. Lamont, Phytologia 69: 467-468. 1990. Eupatorium holzingeri Rydberg, Brittonia 1: 97. 1931. Type. United States. Minnesota. Winona Co.: Without specific locality, Aug 1906, Holzinger s.n. (holotype, NY!).

Leaves densely and persistently puberulent to villose throughout abaxial surface; petioles glabrous to sparingly puberulent or ciliate.

Habitat and distribution. Predominantly occurring on steep slopes of rocky, deciduous woodlands and woodland borders, commonly in shade. Frequent as a weed along well drained roadsides. From southern Wisconsin to southeastern Minnesota and Iowa, south to northeastern Illinois and central Missouri, west to southeastern Nebraska and northeastern Kansas (Fig. 13).

Additional specimens examined. UNITED STATES. ARKANSAS. Baxter Co.: Creek bottoms above Norfork Dam, elev 600 ft., Ellis, 14 Jul 1942, Demaree 23589 (NY). ILLINOIS. Hancock Co.: Without specific locality, Nauvoo, 3 Aug 1958, Jones 22324 (ILL). McHenry Co.: Without specific locality, Algonquin, 23 Aug 1879, Nason s.n. (ILL). Peoria Co.: Open wooded hills, Peoria Heights, 1 Aug 1946, Chase 8358 (ILL); in low grounds, Peoria, Sep 1889, McDonald s.n. (ILL). IOWA. Cherokee Co.: Shaded slope on woods of N.L. Stiles farm near the

Big Sioux River, Pilot Twp., 14 Aug 1938, Hayden 10765 (ISC, NY). Clayton Co.: Wooded bluff, N of Marquette, 13 Aug 1927, Shimek s.n. (NY). Emmet Co.: Estherville woods, 1 Aug 1922, Wolden 578 (ISC). Guthrie Co.: Unpastured woodlot, 5 mi. NE of Guthrie Center, T80, R31, S14, 16 Aug 1956, Monson 3332 (ISC). Jasper Co.: Without specific locality, Colfax, Jul 1922, Sipe s.n. (ISC). Johnson Co.: Open woods, Lake MacBride, Aug 1938, Loufek s.n. (NY). Story Co.: Low ground, Ames, without specific date, 1927, Loleusberry s.n. (ISC). **KANSAS.** Anderson Co.: Rocky wooded hillside, Garnett City Park, 18 Jul 1957, McGregor 13203 (KANU). Atchison Co.: Woods near lake, moist limestone soil, Atchison Co. State Lake, 4 mi. N, 2 W of Atchison, 30 Jul 1972, Stephens 57975 (KANU). Doniphan Co.: Wooded bluff of Missouri River, moist rich limestone soil, 4.5 mi. SE of White Cloud, 31 Jul 1972, Stephens 58058 (KANU). Douglas Co.: Wooded hillside, 3 mi. N of Baldwin City, 22 Jul 1959, McGregor 14568 (NY). Leavenworth Co.: Quercus-Carya woods above and along Pony Creek, ca. 7.5 km SW of Tonganoxie, 22 Jul 1979, Churchill 10903 (NY); on steep rocky wooded bank just SE of lake dam, Leavenworth County State Lake, 8 Aug 1979, Brooks 14411 (NY). Linn Co.: Roadside, Marais des Cygnes Waterfowl Refuge, Area B, 29 Jul 1965, Richardson & Robertson 943 (KANU, NY). Pottawatoane Co.: Without specific locality, St. George, 1 Aug 1893, Norton s.n. (KSC).

Wyandotte Co.: Wyandotte Co. State Park, 27 Jul 1961, Richards 3291 (KANU). **MINNESOTA.** Wabasha Co.: Ditch and bank adjacent to roadway, U.S. Rte. 61, 1.9 mi. W of Camp Lacupolis, T111N, R11W, S17, 10 Aug 1979, Ownbey 6337 (MIN). **MISSOURI.** Cape Girardeau Co.: Along K, E. of Gordonville, 6 Jul 1972, Brooks 6597 (GA). **NEBRASKA.** Dakota Co.: On low E facing slope at base of oak-linden forest bluff near sandstone outcrop, S of parking area at Basswood Ridge W.M.A., 10 Aug 1989, Rolfsmeier 5555 (NEB). Douglas Co.: Hanscom Park, Omaha, 29 Jul 1885, Cleburne s.n. (NEB); near Riverview Park, S of Omaha, 6 Aug 1897, Cleburne s.n. (NEB); without specific locality, Omaha, 31 Jul 1916, Bates 428 (NEB). Richardson Co.: In woods on slope by W shoulder of road in NE corner of S16, R17E, T3N, 8 Aug 1974, Shildneck C-6958 (NEB). Thurston Co.: On low slopes of oak-linden bluff forest at Big Elk Park, 1 mi. E, 3 mi. N of Macy, T25N, R10E, S7, 10 Aug 1989, Rolfsmeier 5554 (NEB). **WISCONSIN.** Green Co.: Mesic woods, "Spring Grove," Ecolog. Sta. #1032, T1N, R9E, S29, 1 Jul 1957, Struik s.n. (WIS). Richland Co.: Opening on wooded slope, town of Akan, T10N, R2W, S13, 14 Jul 1985, Clark s.n. (WIS). Rock Co.: Mesic deep soil prairie remnant on roadside opposite entrance to "Forty Acres" camp, S side Cleophas Rd., T1N, R11E, S15, 30 Jul 1964, Cochrane 196 (WIS).

5. Eupatorium fistulosum Barratt, Eupatoria verticillata no. 1 (see Fig. 31). 1841 (not Eupatorium fistulosum B. L. Robinson, Proc. Bost. Soc. Nat. Hist. 31: 249. 1904). Eupatoriadelphus fistulosus (Barratt) R. King & H. Robinson, Phytologia 19: 432. 1970. Type. Without locality, date, and collector's name (there is only one specimen of E. fistulosum in the herbarium of Barratt according to Grimes & Keller, 1982) (holotype, NY!).

Eupatorium laevigatum Torr. in Eaton, Man. Bot. Ed. 2. 245. 1818 (not Eupatorium laevigatum Lam., Encycl. Meth. 408. 1786). Type. Not cited in protologue [holotype, not seen; by description = E. fistulosum (search at NY, NYS, and inquiry to other major herbaria failed to locate the type)].

Eupatorium purpureum var. γ angustifolium T. & G., Fl. N. Am. 2: 82. 1841. Type. United States. Tennessee. Without specific locality, s.d., Currey s.n. (there is only one specimen of E. purpureum var. angustifolium from the Torrey Herbarium at NY) (holotype, NY!).

Eupatorium fistulosum f. albidum Jennings, Castanea 7: 45. 1942. Type. United States. Pennsylvania. Allegheny Co.: Middle plateau above Wildwood Station, Butler Short Line, 15 Aug 1919, Millward s.n. (holotype, CM!).

Eupatorium fistulosum f. truncatum Jennings, Castanea 7: 45. 1942. Type. United States. Pennsylvania. Clarion Co.: Open floodplain field, three miles north of New Bethlehem, 11 Sep 1940, Jennings s.n. (holotype CM!).

Erect herb, 0.6-3.5+ m tall; stems hollow below inflorescence with a large central cavity, solid above, usually evenly purple throughout, sometimes greenish when growing in dense shade, sometimes purple-spotted when young, viscid-puberulent near summit, glabrous below inflorescence (rarely pubescent toward base when young), strongly glaucous throughout (when fresh). Leaves mostly in 4's-6's (7's); blades narrowly to broadly lanceolate, mostly (8) 12-25 (28) cm long, (1.5) 2-6 (9) cm wide, gradually tapering to the short-petiolate base, acuminate at the apex, pinnately veined, finely serrate with rounded blunt teeth, usually with a large gland at apex of each marginal tooth, adaxial surface glabrous to sparingly glabrescent, abaxial surface atomiferous and glabrous to sparingly fine-pubescent; petioles usually (0.5) 1-3 (5) cm long, glabrous. Inflorescence a strongly convex, dome-shaped, compound corymbiform cyme (broadly cylindrical when fully developed), its branches diverging abruptly from the stem and then turning upward, usually 10-30 (50) cm high and 10-30 cm wide in

life, heads short pedunculate, peduncles conspicuously glandular pubescent. Involucre 6.5-9 mm high, 2.5-5 mm wide, often purplish; bracts 10-22, lanceolate, obtuse at apex, well imbricate, few-striate or at least with prominent midvein; receptacle naked, flat or weakly convex. Flowers (4) 5-7 in a head; corolla generally very pale pinkish or purplish, but variable, 4.5-7.5 mm long, funnelform, outer surface usually minutely atomiferous-glandular, 5-toothed, lobes ovate to deltate, usually slightly longer than wide; style base puberulous, enlarged. Achene prismatic, 3.0-4.5 mm long, 5-ribbed, atomiferous-glandular, sometimes with a few setulae along the nerves; pappus a single series of 25-40 slender, capillary, scabrous, persistent bristles. $2n = 20$.

Habitat and distribution. Predominantly in moist habitats, commonly in open sun or partial shade. Occurring naturally in wet lowlands, especially in alluvial woods, along streams, and in moist meadows, bogs, and marshes that have permanently saturated and seasonally flooded organic soils. Common as a weed along wet roadside ditches and depressions, and in moist abandoned fields. From southwestern Maine to Illinois and Missouri, south to northern Florida, and in the west to eastern Texas and Arkansas (Fig. 14).

In the field Eupatorium fistulosum is the most strikingly distinct species of section Verticillata.

Because of the tall robust nature of the plants, herbarium voucher specimens do not always document the distinguishing characteristics of this species: height commonly surpassing 2 m, lower stem diameter usually 2 cm or greater, strongly glaucous stem, large inflorescence size (commonly 30 cm high, 22 cm wide), commonly 6 or 7 leaves per node. In addition, the upper stem of E. fistulosum is often all that is collected for voucher specimens; although E. fistulosum has a distinctly hollow stem, the uppermost stem directly below the inflorescence is sometimes solid.

There has been some confusion concerning the correct authority for E. fistulosum. For example, Jones and Fuller (1955) attributed the name E. fistulosum to Barratt ex Wood, and Soil Conservation Service (1982) attributed the epithet to Barratt ex Hooker. Barratt described E. fistulosum in a single folio page publication (Fig. 31), titled Eupatoria verticillata, which was distributed among "botanical friends and correspondents" (see Gandhi and Fryxell, 1990). According to Articles 29.1 and 32.1 of the International Code of Botanical Nomenclature (Greuter, 1988) it is evident that Barratt effectively and validly published a new species, and the correct authority for E. fistulosum is Barratt.

EUPATORIA VERTICILLATA.

SPECIMENS TO ILLUSTRATE THE NORTH AMERICAN VERTICILLATE SPECIES AND VARIETIES

OF THE

GENUS EUPATORIUM:

With Synonymes and References.

By JOSEPH BARRATT, M. D.
MIDDLETOWN, CONNECTICUT.

MAY, 1841.

*** A number of uniform sets of Specimens have been preserved for distribution among Botanical friends and correspondents.

No. 1. EUPATORIUM FISTULOSUM* *Barratt*; — E. purpureum *Willd. sp. pl.* 3, *p.* 1759; (partly; excl. ref. et Syn. except Cornuti (q. v.) *Pursh, fl.* 2, *p.* 515; *Ell. fl.* 2, *p.* 307 !; *Bigelow, fl. 2d Ed, p.* 297!; *Decand. Prodr.* 5, *p.* 151, *n.* 68. (in part); — E. maculatum. *Linn. sp. pl.* 1174, (in part,) *et Herb.* fide Dr. Gray. — E. purpureum *γ angustifolium. Torr. & Gray Flor.* 2, *p.* 82.

(Eupatoria) foliis Enulæ, *Cornuti Canad. p.* 191. "Caules rubescentes cinereo tamen colore suffusi rotundi inanes intus." *Cornuti, (l.c.)*

The specific character given by Willdenow of E. purpureum, applies to our E. fistulosum. The full description there taken from L. sp. pl n 13 is = E. verticillatum W.! so that Willdenow has here confounded two different species. These and other descrepancies detected several years ago, induced me to study the plants in the *growing state*; nor was I able to settle the synonyms satisfactorily, till I had made a full collection of Specimens.

Stem hollow from the corymb to the base; height 6-9 or 10 feet; smooth bluish purple and glaucous; reddish purple upwards; petioles and midrib purple. This is one of the most stately herbaceous plants in New-England, and truly distinct from the next species, no. 2. In some rare instances I have found 2 or 3 upper joints or whorls solid. The small varieties which grow on uplands, retain the hollow stem, and other characteristics. The hollow stems of this species have been used extensively for blowing corks at the Middletown [illegible]. E. fistulosum does not appear to possess the acrid properties of E. maculatum. The original E. purpureum, *Linn.* is shown, (no 3,) to be a different plant, presenting also several interesting varieties, but all retaining the characteristics of that species, and not passing by gradations into other species. The name here given by me, (since a new name was required,) is sufficiently expressive to remove all ambiguity. The confusion in systematic works on this group of North American Eupatoriums, is most extraordinary! It is hoped that these specimens, with the notes and references, will render the study of this groupe easy and perfectly satisfactory to the Botanist. Should our European correspondents detect [illegible] after comparison with the original Herbaria cited, any errors, it will give us pleasure to receive their communications and corrections.

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1. EUPATORIUM FISTULOSUM.* *Barratt.*
A small variety.

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2. EUPATORIUM MACULATUM *Linn. Amœn. Ac.* 4, *p.* 288; *Linn. sp. pl.* 1174; *Willd. sp. pl.* 3 1760; *Michaux. Flor.* 2, *p.* 99; *Pursh fl.* 2, *p.* 515; *Decand. Prodr.* 5, *p.* 152, *n.* 69.

Stem 6 feet high, solid striate hispid or pubescent, greenish and purple, with numerous glands and purple lines. The glands on the stem and leaves give out an acrid effluvium in flowering time. There are several varieties in the number of its leaves.

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2. EUPATORIUM MACULATUM *L.*
With 4 leaves in a whorl.

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2. EUPATORIUM MACULATUM. *L.*
With 3 leaves in a whorl.

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2. EUPATORIUM MACULATUM.
Var. β urticifolium.* *Barratt.*

Height 4-5 feet, stem solid, slender; the leaves are thin and much longer than the usual form of E. maculatum. It is found in the Middletown meadows, near the banks of the Connecticut; and to this river we are perhaps indebted for many of our Eupatoriums, and other interesting plants.

3. EUPATORIUM PURPUREUM *Linn. sp. pl.* 1173, et Herb. ejus.!; (spec. char. bad, excl. syn.;) not *E. purpureum of Decandolle, Willdenow or Pursh.* — E verticillatum, *Willd. sp. pl.* 3 1760, (et Herb. fol. 1 and 2!) *fide Gray; Bigelow fl.* 2d *ed. p.* 298, excl. Syn. Michx. 2, p. 99.

Stem solid, 6 feet high, glaucous green, sometimes purplish, with a purple band, at the joints about 1 inch broad—leaves in whorls of 3, 4 and 5—smooth above, with a soft pubescence beneath and along the midrib and nerves; length from 9-12 inches, wedge-shaped at the base, including a petiole of 1 or two inches, 4 inches wide, with large serratures. The leaves are thin, soft, and of greater size than any species of Eupatorium known to me. Corymbs lax, flowers mostly pale purple, varying to whitish.

HAB. Grows in dry woods or meadows. The Linnean name has not been happily applied to this species, and that great Botanist, (l. c.) has mixed up the characters of two distinct species.

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3. EUPATORIUM PURPUREUM.
Var. β album.* *Barratt.*

Flowers dull white; with 5 leaves in a whorl, large and distant. Grows in dry woods, and [illegible] places. Stem solid.

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3. EUPATORIUM PURPUREUM.
Var. β album* *Barratt.*

With 4 leaves in a whorl—a tall variety, upper leaves sub-falcate—flowers dull white. an *E. falcatum Mich!* Grows in dry woods. Stem solid.

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3. EUPATORIUM PURPUREUM.
Var. β album* *Barratt.*

With 3 leaves in a whorl; stem tall and slender, upper leaves sub-falcate; *Elliott Flor.* 2, *p.* 307; note! sub *E. ternifolium*, the last 4 lines! — E. trifoliatum. Darlington Flor. Cœstrica 2d ed. p. 453!

Stem solid, variable in size; leaves with a soft pubescence beneath, deeply serrate, flowers white or sometimes faint purple. An attention to the number of leaves of the Verticillate Eupatoria rather than other characters, has led the older botanists into frequent errors, and has occasioned much perplexity and confusion in systematic works, which requires to be cleared away.

4. EUPATORIUM TERNIFOLIUM. *Elliott Flor.* 2, *p.* 306! (in part.) *Decandolle Prodr.* 5, *p.* 151, *n.* 67.

Stem solid, somewhat hispid and glandular; greenish, with purple dots and lines. Height from 3-5 feet, a rather slender species; the upper and last whorls of leaves small and finely serrate. There is a variety of *E. ternifolium*, with smooth purple stems, which is sometimes irregularly branched upwards. It has mostly 4 leaves in a whorl.

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4. EUPATORIUM TERNIFOLIUM.
Var, β. vesiculosum.* *Barratt.*

Height 2-3 feet; stem solid, striate purplish; in meadows and pastures abundant—Saddle Hill west part of Middletown. This handsome variety bears a profusion of purple flowers with a large branched and spreading corymb, (in the finest plants.) The *E. dubium Poir. D. C. Pr.* 5, *p.* 152, (excl. Syn.) may perhaps prove a small variety of our plant? The leaves are strongly reticulated. The upper surface presents a vesicular appearance, in a remarkable degree, but which is mostly effaced in the hard pressed dried specimens.

Fig. 31. Joseph Barratt's 1841 single folio page publication, titled Eupatoria verticillata.

Fig. 32. Holotype of Eupatorium fistulosum at NY.

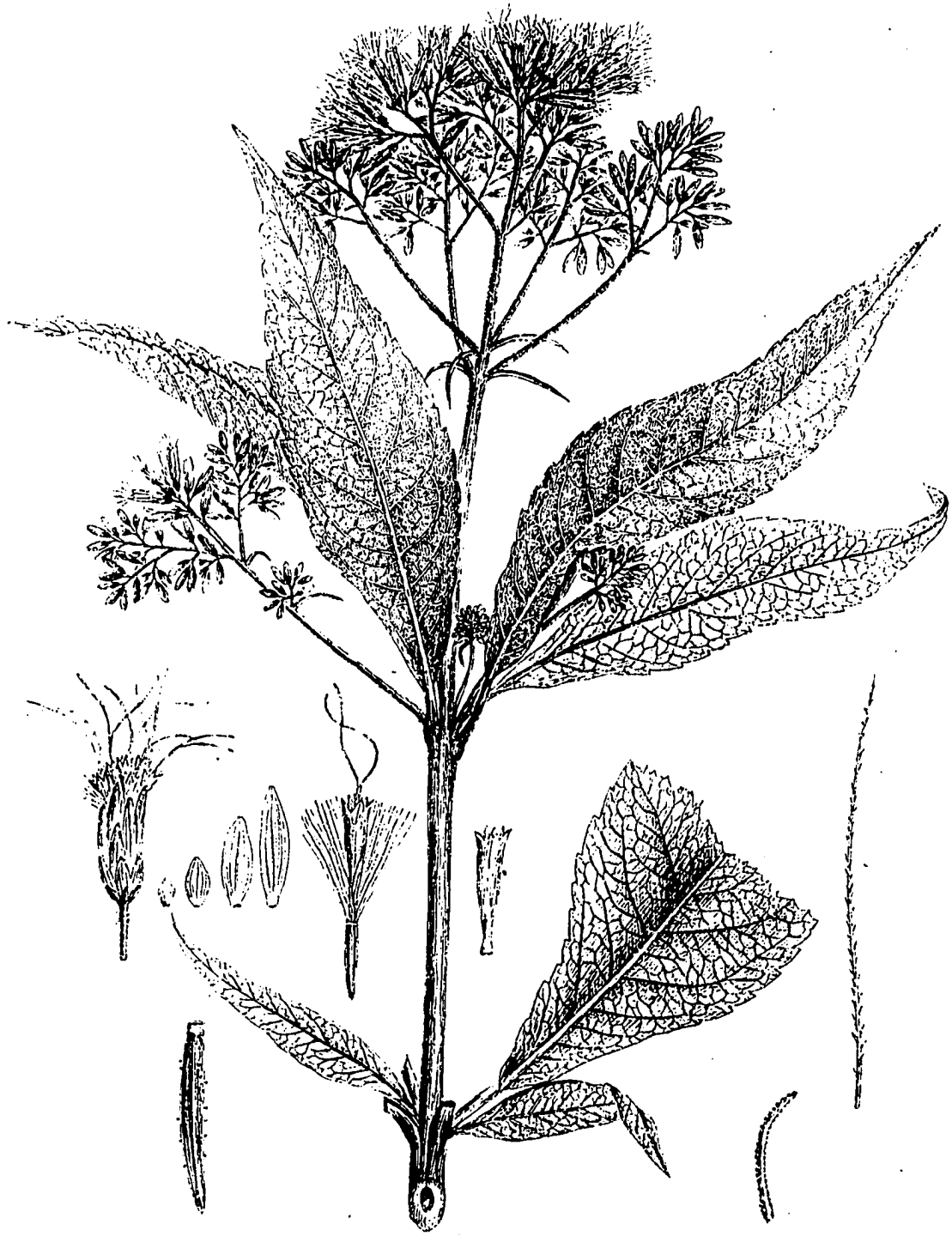

Fig. 33. Eupatorium fistulosum. Photographed from unpublished illustration by Koehler; courtesy of The New York Botanical Garden.

Selected specimens examined. UNITED STATES. **ALABAMA.** Escambia Co.: On US 31 at small creek crossing, 1.7 mi. W of Flomaton (jct hwys 29 & 113), T1N, R8E, S29 & 30, 7 Aug 1979, Davenport 1481 (UNA). Lee Co.: In woods of native growth, 7.5 mi. N of Auburn and 1 mi. S of Gold Hill, 20 Jul 1972, Nelson 074 (UNA). Wilcox Co.: On W shore of Alabama River, overhanging river from moist, partly sunny sandy clay on bluff face, Coal Bluff, ca. 7.5 mi. SW Camden, T11N, R14E, S17, 17 Jul 1982, Gunn 996* (UNA). **ARKANSAS.** Bradley Co.: Limestone bank, 1.5 mi. S of border of Cleveland Co.-Bradley Co. on Hwy. 8, 16 Jul 1969, Wright J697K (UARK). Garland Co.: Rich moist banks of mountain stream, along Wildcat Hollow Road just W of Mt. Pine Road, 2.5 mi. NW of Hot Springs, 16 Jul 1934, Gregg 262* (UARK). Polk Co.: Moist shady roadside, Big Fork Creek, alt. 1275′, 1 Aug 1951, Moore & McWilson s.n. (UARK). **CONNECTICUT.** New Haven Co.: Streambank along Eight Mile Brook, ca. 2.4 mi. E of Stevenson, 13 Aug 1987, Lamont 196 (NY). Litchfield Co.: Along margin of W Aspetuck River, off Hwy. 7, ca. 1.7 mi. W of New Milford, 13 Aug 1987, Lamont 199* (NY). **DELAWARE.** New Castle Co.: Marsh near Pigeon Point, on river shore SE of Wilmington, 7 Aug 1987, Lamont 186 (NY). **DISTRICT OF COLUMBIA.** Without specific locality, 18 Sep 1902, Steele s.n. (NY); Cheseapeake Junction, 18 Aug 1904, House 256* (NY). **FLORIDA.** Escambia Co.: In grassy roadside ditch near

Morgan Branch Creek, ca. 5 mi. S of Bogia, along US 29, T3N, R31W, S5, 31 Jul 1967, Smith 1736 (FLAS). Santa Rosa Co.: Along Juniper Creek, clay slope in mixed pine & hardwood, 4 mi. SW of Munson, 6 Aug 1954, Ford 14180 (FLAS). Seminole Co.: Swamp along Wekiwa River, ca. 5 mi. N of Sanlando Springs, 28 Aug 1962, Laessle 280* (FLAS). GEORGIA. Bartow Co.: Edge of "springy place" in open deciduous woods on hillside on W side of Allatoona Creek 1.25 mi. SE of Allatoona Dam, elev. ca. 760′, 18 Sep 1948, Duncan 8878 (GA). Lumpkin Co.: West side of Chestatee River near New Bridge over river, high sandy terrace, open area in deciduous woods, S tip of county, 2 Oct 1955, Duncan & Adams 19765 (GA). Pickens Co.: Tributary to Swamp Creek, just off GA Hwy. 53 along RR around pond 2 mi. SW of Marble Hill, elev. ca. 1030′, 8 Sep 1988, Jones et al. 25046 (GA). ILLINOIS. Lawrence Co.: Edge of moist wood, 3 mi. N of Sumner, 2 Sep 1946, Sivert s.n. (ILL). Richland Co.: Edge of the Embarrass River, 5 mi. NE of Olney, 20 Jul 1947, Scherer 374* (ILL); open woods 8 mi. SW of Olney, T12N, R9E, S2, 29 Aug 1974, Ebinger 015094 (ILL, NLU). INDIANA. Decatur Co.: On the boggy wooded bank of Flat Rock Creek about a mile above St. Paul, 12 Sep 1911, Deam 10024 (IND). Jennings Co.: Wooded creek bottom near Graham Creek ca. 3 mi. SE of Butlerville, 19 Aug 1918, Deam 26289* (IND). Monroe Co.: Wet places along road near Station C., Salt Creek Twp., 8 Sep 1931, Potzger 2159* (IND).

KENTUCKY. Bracken Co.: In weedy field at Meldahl Dam, ca. 2.5 mi. E of Foster on Rt. 8, 27 Jul 1983, Buddell 2273* (NY). Campbell Co.: In Silver Grove RR yard, 7 Aug 1982, Buddell 623 (NY). Madison Co.: Bank of Silver Creek, 2.25 mi. SE of Berea, 5 Sep 1939, Gleason & Griffitts 287* (NY). **LOUISIANA.** Claiborne Co.: Tributary of Dry Creek, intermittent stream ca. 1 mi. W of LA 9, W of Junction City, T23N, R4W, S10, 22 Jul 1980, Lewis & Dixon 2852 (NLU). St. Tammmany Co.: Wet area beside LA 1081 at Little Bogue Falaya River E of LA 437 E of Blond, T5S, R11E, S26, 24 May 1979, Thomas 64876* (NLU). Washington Co.: Swampy woods beside Lawrence Creek N of LA 10, 2 mi. E of Franklinton, T2S, R11E, S29, 27 Jul 1974, Thomas et al. 40408 (NLU). **MARYLAND.** Allegany Co.: Alluvial thicket along Potomac River ca. 1 mi. E of Westernport on Rt. 135, 28 Jul 1967, Downs 1432* (UNC). Garrett Co.: Along stream 1 mi. N of Grantsville on River Road, W side of Casselman River, 20 Sep 1980, Hill 9520* (NY). Washington Co.: Alluvial woods on granite along Potomac River within 1 mi. W of Frederick Co. line, 6 Aug 1968, Downs 4485 (UNC). **MASSACHUSETTS.** Franklin Co.: In wet meadow at jct. of Rts. 2 & 2A, Greenfield, 15 Aug 1987, Lamont 206* (NY). Hampshire Co.: Meadow near junction of Ryan Road and Spring Street, (Florence) Northampton, 7 Aug 1977, Ahles 84583 (UNC). **MISSISSIPPI.** Marshall Co.: In and along edge of Coldwater River swamp, 5.6 mi. NE of

Holly Springs, St. Hwy. 7, 31 Jul 1967, Temple 6126* (UNC). Neshoba Co.: Along small stream on St. Hwy. 19, 4.1 mi. SE of Winston-Neshoba Co. line, 3 Aug 1968, Temple 10371* (UNC). Pearl River Co.: Wet grassy roadside, Hwy. 11 ca. 2 mi. N of Picayune, 15 Jul 1978, Darwin & Sundell 607 (UNC). **MISSOURI.** Butler Co.: Rich hillside woods, Poplar Bluff, 15 Sep 1919, Palmer 16442 (MO). Marion Co.: Without specific locality, Hannibal, 23 Aug 1919, Davis s.n. (MO). **NEW JERSEY.** Morris Co.: Along US 206, 0.5 mi. S of I-80, ca. 1.5 mi. S of Netcong, 21 Aug 1988, Lamont 230 (NY). Somerset Co.: In moist woods along roadside, Watchung, 8 Aug 1930, Moldenke 1352* (NY). Sussex Co.: Swampy thickets, Andover, 5 Sep 1920, Mackenzie s.n. (NY). **NEW YORK.** Nassau Co.: Along spring-fed braided streams, Shu Swamp Nature Preserve, Mill Neck, 28 Jul 1987, Lamont 175 (NY). Orange Co.: Along road near Upper Res., Black Rock Forest, 8 Aug 1936, Raup 7822* (NY). Saratoga Co.: Low ground along stream near Malta, 3 Sep 1933, House 20893* (NY). Suffolk Co.: Wet roadside depression, along Rt. 25A at Twin Ponds Nature Preserve, Centerport, 2 Aug 1987 Lamont 183 (NY); along banks of creek running through Moores Woods Nature Preserve, Greenport, 3 August 1987, Lamont 184 (NY); moist ground, North Fork Preserve, Northville, 20 Aug 1987, Lamont 214* (NY). Westchester Co.: Wet open fields, Yonkers, 8 Aug 1934, Gleason 1521 (NY). **NORTH CAROLINA.**

Cleveland Co.: Wooded creek bottom, 3.5 mi. NE of point where N.C. 150 crosses Broad River on tributary of Broad River, 18 Sep 1956, Ahles & Leisner 19096* (UNC). Macon Co.: Maple-birch-magnolia (cove) association, Corundum Hill Olivine Deposit, 1.5 mi. NW of Gneiss, 24 Aug 1946, Radford s.n. (UNC). Mitchell Co.: Roadside ditch, 0.5 mi. N of Penland, then 3.3 mi. W on road to Boonford, 25 Sep 1958, Ahles & Duke 49798 (UNC). **OHIO.** Jefferson Co.: Thickets along Cross Creek, 2 mi. NE of Unionport, Wayne Twp., 16 Aug 1964, Cusick s.n. (OS). Scioto Co.: Turkey Creek bottoms, Camp Gordon, C.C.C., Shawnee State Forest, 5 Aug 1934, Demaree 10807* (OS). Tuscarawas Co.: Wet Ditch, Co. Rt. 14, 0.5 mi. E Co. Rt. 16, Salem Twp., 30 Aug 1967, Cusick 6451 (OS). **PENNSYLVANIA.** Chester Co.: Along stream on serpentine, below Lees Mills, 21 Sep 1920, Pennell 10958* (NY). Fayette Co.: Along roadside of PA Hwy. 381-711 ca. 2 km WSW of Melcroft and the sandy banks of Indian Creek, 15 Sep 1980, Utech 152 (VPI). Lycoming Co.: Streambank, 1.5 mi. NE of Maple Hill, 22 Aug 1955, Westerfeld 17925 (UNC). **RHODE ISLAND.** Providence Co.: Wet roadside depression, Hwy. 102, ca. 2.2 mi. S of Clayville, 13 Aug 1987, Lamont 200 (NY). **SOUTH CAROLINA.** Aiken Co.: Marsh 1.3 mi. W of junction US I-76 and SC 254 on US I-76, 27 Oct 1961, Ahles & Crutchfield 55486* (UNC). Cherokee Co.: Wooded stream bank, 0.5 mi. WSW of junction US 29 and Co. 52 then 0.4 mi NW on dirt road

(N of Blacksburg), 18 Sep 1957, Ahles 34172* (UNC). Lancaster Co.: Wooded stream, Forty Acre Rock, S of Taxahaw, 13 Jul 1957, Ahles & Haesloop 31344 (UNC). **TENNESSEE.** Cheatham Co.: Creek bottoms, Big Maribone, Ashland, 19 Aug 1964, Demaree 51104 (UNC). Greene Co.: Mixed deciduous forest along bank of Paint Creek, ca. 0.2 mi. from S entrance to Paint Creek Recreation Area near Paint Rock, Cherokee Nat'l. Forest, Bald Mtns., 16 Aug 1967, Winstead & Mahler 4451* (UNC). Montgomery Co.: East side of Cumberland River across from old Lock B between Muddy Branch and Midnight Hollow along RR tracks, 10 Aug 1967, Wofford & Chester 1783* (UNC). **TEXAS.** Angelina Co.: Hillside seepage bog, N of tributary to Big Creek, ca. 10 mi. SE of Zavalla, Angelina National Forest, ca. 0.6 air mi. N of Jasper Co. line, 26 Aug 1988, Orzell & Bridges 8333 (TEX). Jasper Co.: Along stream on edge of forest, 2 mi. SW of Magnolia Springs, 1 Jul 1963, Correll et al. 28131 (TEX, UNC). San Augustine Co.: Sandy creek bank, 5.2 mi. NNW of San Augustine, 29 Jul 1956, Shinners 24251 (TEX, UNC). **VERMONT.** Rutland Co.: Streambank, Emerald Lake State Forest, 16 Aug 1987, Lamont 205* (NY). **VIRGINIA.** Augusta Co.: Roadside ditch, Rt 814 (Back Creek Road), 1.5-2 mi. down from Blue Ridge Pkwy., 21 Aug 1968, Freer 12206 (VPI). Chesterfield Co.: Moist soil along railroad, A.C.L., Hopkins Road and Petersburg Pike, Richmond, 19 Aug 1945, Hopkins 78

(VPI). Montgomery Co.: Banks of stream at Slusser Bridge, VA 624, 30 Sep 1969, Uttal 6834 (VPI). **WEST VIRGINIA.** Grant Co.: In a wet swampy area within a dense woods along Allegheny Front, 5 mi. SE of Mt. Storm, 5 Sep 1963, Clarke 364* (UNC). Preston Co.: Vicinity of Terra Alta, on the Allegheny Plateau, 5 Sep 1920, Steele 505* (NY). Wirt Co.: Standingstone Creek near Oil Rock Run, 27 Aug 1952, Bartholomew W3218 (FLAS).

APPENDIX

Data matrix of 135 OTUs and the 19 characters listed in Table 6.

OTUs	CHARACTER NO.																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1	1	1	0	1	2	1	0	0	0	0	0	3	3.2	2.6	1.1	6	4.5	3.6	12.0
2	1	1	0	1	2	1	0	1	0	0	0	3	4.3	3.0	.6	5	4.9	3.9	7.5
3	1	1	0	1	2	1	0	0	0	0	0	4	3.4	2.6	1.1	7	5.0	3.0	14.2
4	1	1	0	1	2	1	0	0	0	0	0	4	3.1	2.4	1.2	10	5.0	4.0	13.7
5	1	1	0	1	2	1	1	0	0	0	0	4	2.9	2.1	1.3	7	4.5	4.0	19.0
6	1	1	0	1	2	1	0	0	0	0	0	3	3.3	2.5	1.1	6	4.8	3.5	9.3
7	1	1	0	1	2	1	1	0	0	0	0	2	4.2	2.2	1.2	8	5.0	3.7	18.9
8	1	1	0	1	1	1	0	0	0	0	0	3	3.7	2.2	1.1	5	4.8	3.0	7.8
9	1	1	0	1	2	1	0	1	0	0	0	3	3.3	2.7	.4	5	4.9	3.0	7.2
10	1	1	0	1	2	1	0	0	0	0	0	3	4.4	2.4	1.1	7	4.7	3.3	10.6
11	1	1	0	1	2	1	0	0	0	0	0	4	3.7	2.0	1.3	7	4.5	3.0	9.9
12	1	1	0	1	1	1	0	0	0	0	0	4	3.2	2.5	1.1	9	4.8	3.8	11.7
13	1	1	0	1	2	1	0	1	0	0	1	3	4.1	2.7	.9	6	5.0	3.6	14.1
14	1	1	0	1	2	1	0	0	0	0	0	4	3.9	3.2	.7	5	4.8	4.0	6.0
15	1	1	0	1	2	1	0	1	0	0	0	4	3.8	3.4	.8	7	4.2	3.6	15.0
16	1	1	0	1	2	1	0	0	0	0	0	4	4.3	2.4	1.1	8	5.0	3.0	18.4
17	1	1	0	1	2	1	0	0	0	0	0	3	3.5	2.3	1.0	5	5.0	3.7	13.5
18	1	1	0	1	2	1	0	0	0	0	0	3	3.6	2.6	1.1	7	4.4	4.0	9.1
19	1	1	0	1	1	1	0	0	0	0	0	4	4.1	2.3	1.2	6	5.0	3.7	11.6
20	1	1	0	1	2	1	0	0	0	0	0	4	3.2	2.3	1.2	6	4.9	3.9	8.3
21	1	1	0	1	1	1	0	0	0	0	0	3	3.4	2.4	1.0	8	5.0	4.0	9.6
22	1	1	0	1	2	1	0	0	0	0	0	4	3.1	2.2	1.0	5	4.4	3.6	16.0
23	1	1	0	1	2	1	0	0	0	0	1	4	3.9	2.5	1.1	8	4.3	3.8	13.5
24	1	1	0	1	2	1	0	0	0	0	0	2	4.4	1.8	1.8	6	5.0	3.6	10.0
25	1	1	0	1	2	1	1	0	0	0	0	4	3.6	1.8	1.8	7	5.1	3.4	9.3
26	1	1	0	1	2	1	0	0	0	0	0	3	3.2	1.9	1.6	9	4.7	3.4	14.6
27	1	1	0	1	2	1	0	0	0	0	0	3	3.7	2.0	1.3	8	5.1	3.8	14.3
28	1	1	0	1	2	1	0	1	0	0	0	3	3.8	2.9	.6	5	4.8	3.9	14.8
29	1	1	0	1	2	1	0	0	0	0	0	4	3.8	2.7	1.0	6	4.6	3.8	10.8
30	1	1	0	1	2	1	0	0	0	0	0	3	3.3	2.3	1.2	7	5.0	3.6	10.9

OTUs 1-30 = DUBIUM

APPENDIX

Continued

OTUs	CHARACTER NO.																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
31	1	1	0	0	0	0	0	1	0	0	0	3	3.7	11.5	1.2	5	5.5	3.7	13.6
32	1	1	0	0	0	0	0	1	0	0	0	3	4.2	9.7	1.2	6	6.0	3.2	17.1
33	1	1	0	0	0	0	0	1	0	0	0	4	4.3	10.2	.5	6	5.2	3.8	16.9
34	1	1	0	0	0	0	0	1	0	0	0	3	2.9	12.1	1.4	5	5.7	3.0	10.5
35	1	1	0	0	0	0	0	1	0	0	1	4	2.8	11.7	2.1	5	5.1	3.6	10.2
36	1	1	0	0	0	0	1	1	0	0	0	4	3.1	10.8	1.2	6	6.0	3.0	12.4
37	1	1	0	0	0	0	0	1	0	0	0	3	4.3	10.1	.7	5	5.6	3.0	15.0
38	1	1	0	0	1	0	0	1	0	0	0	3	2.9	9.9	1.1	4	5.2	3.7	8.5
39	1	1	0	0	0	0	0	1	0	0	0	4	3.3	11.2	1.1	6	5.1	4.3	16.8
40	1	1	0	1	0	0	0	1	0	0	0	5	3.4	11.9	1.3	7	4.1	3.6	9.9
41	1	1	0	0	0	0	0	1	0	0	0	4	4.6	10.6	.4	5	7.0	4.1	17.7
42	1	1	0	0	0	0	0	1	0	0	0	4	3.2	11.3	1.5	6	4.8	3.6	8.4
43	1	1	0	0	0	0	0	1	0	0	0	2	3.1	10.8	1.2	5	6.1	3.8	8.8
44	1	1	0	0	0	0	0	1	0	0	0	3	3.5	11.7	1.4	5	5.0	3.1	9.5
45	1	1	0	0	0	0	0	1	0	0	0	4	3.4	11.7	1.0	5	6.3	3.6	12.0
46	1	1	0	0	2	0	0	1	0	0	0	4	2.5	12.1	2.3	6	5.8	3.6	12.9
47	1	1	0	0	0	0	0	1	0	0	0	3	3.0	10.7	1.0	8	6.2	3.7	13.5
48	1	1	0	0	0	0	0	1	0	0	0	3	3.2	11.6	1.4	5	5.1	3.9	20.0
49	1	1	0	0	0	0	1	1	0	0	0	4	3.4	11.1	1.0	5	5.4	3.7	14.0
50	1	1	0	0	0	0	0	1	0	0	0	4	2.8	12.3	1.7	4	5.8	3.6	10.6
51	1	1	0	0	0	0	0	1	0	0	1	3	3.0	11.1	1.2	5	7.0	4.0	14.9
52	1	1	0	0	0	0	0	1	0	0	0	4	2.8	12.2	1.1	5	6.6	3.1	16.5
53	1	1	0	1	0	0	0	1	0	0	0	4	3.6	11.6	1.2	6	6.0	4.7	14.7
54	1	1	0	0	0	0	0	1	0	0	0	4	3.5	11.2	1.5	6	6.0	3.8	14.9
55	1	1	0	0	0	0	0	1	0	0	0	3	2.9	12.1	1.2	6	6.2	4.2	9.1
56	1	1	0	0	0	0	0	1	0	0	0	5	3.0	11.1	1.3	5	5.2	4.5	9.0
57	1	1	0	0	0	0	0	1	0	0	0	3	2.9	12.2	.9	5	6.0	3.7	24.1
58	1	1	0	0	0	0	0	1	0	0	0	4	3.6	10.8	1.5	7	6.0	4.1	16.0
59	1	1	0	0	0	0	0	1	0	0	0	4	2.9	10.7	1.2	5	6.0	3.0	13.0
60	1	1	0	0	0	0	0	1	0	0	0	3	2.9	11.5	.8	5	4.0	3.8	19.7

OTUs 31-60 = PURPUREUM

APPENDIX

Continued

OTUs	CHARACTER NO.																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
61	0	0	0	1	1	0	1	1	0	0	0	6	4.7	9.3	1.7	6	4.8	3.9	18.1
62	0	0	0	1	1	0	1	1	0	0	0	5	3.0	5.7	3.2	5	5.0	4.0	17.5
63	0	0	0	1	1	0	1	1	0	0	0	5	3.4	7.3	3.1	5	4.8	4.0	22.3
64	0	0	0	1	1	0	1	1	0	0	0	4	3.9	8.8	1.7	4	5.0	4.1	22.1
65	0	0	0	1	1	0	1	1	0	0	0	6	6.4	11.7	1.7	6	4.7	3.9	19.1
66	0	0	0	1	1	0	1	1	0	0	0	4	4.5	10.2	1.2	5	5.2	3.8	17.6
67	0	0	0	1	1	0	0	1	0	0	0	5	4.0	7.9	2.2	7	4.9	4.0	18.5
68	0	0	0	1	1	0	1	1	0	0	0	5	3.5	6.8	1.7	5	3.4	3.9	12.2
69	0	0	0	1	1	0	1	1	0	0	0	5	3.9	8.8	1.6	6	4.1	3.5	15.9
70	0	0	0	1	1	0	1	1	0	0	0	6	5.0	9.2	1.8	6	4.8	5.6	17.2
71	0	0	0	1	2	0	1	1	0	0	0	5	3.6	8.4	1.1	5	4.0	3.8	20.1
72	0	0	0	1	1	0	1	1	0	0	0	4	3.9	9.4	.8	5	5.0	3.0	25.4
73	0	0	0	1	1	0	1	1	0	0	0	5	4.2	7.5	1.6	5	5.1	4.2	27.9
74	0	0	0	1	1	0	1	1	0	0	0	6	5.3	11.2	2.6	5	5.0	3.8	19.5
75	0	0	0	1	1	0	1	1	0	0	0	6	3.4	8.6	3.1	4	4.9	3.0	25.4
76	0	0	0	1	1	0	1	1	0	0	0	5	4.1	10.2	.8	6	5.2	3.9	13.4
77	0	0	0	1	1	0	1	1	0	0	0	4	3.7	6.6	2.0	5	4.8	4.2	11.5
78	0	0	0	1	1	0	1	1	0	0	0	5	4.1	9.3	1.4	5	4.7	3.0	17.2
79	0	0	0	1	1	0	1	1	0	0	0	6	3.4	6.8	3.2	7	4.5	4.0	21.8
80	0	0	0	1	0	0	1	1	0	0	0	5	6.2	13.1	1.0	6	4.8	3.9	11.4
81	0	0	0	1	1	0	0	1	0	0	0	5	7.4	11.9	.4	5	4.9	3.9	17.3
82	0	0	0	1	1	0	1	1	0	0	0	3	5.1	7.7	1.8	6	4.5	3.9	16.4
83	0	0	0	1	1	0	1	1	0	0	0	5	5.6	9.7	1.6	5	4.8	3.9	20.1
84	0	0	0	1	1	0	1	1	0	0	0	6	4.9	10.3	1.0	5	4.7	4.0	19.2
85	0	0	0	1	1	0	0	1	0	0	0	5	6.1	10.1	.9	8	4.7	4.4	27.4
86	0	0	0	1	1	0	1	1	0	0	0	4	4.3	7.8	1.7	6	5.0	3.9	23.1
87	0	0	0	1	1	0	1	1	0	0	0	6	3.7	8.4	1.7	6	5.0	4.0	19.1
88	0	0	0	1	1	0	1	1	0	0	0	5	6.8	11.4	.6	5	4.8	3.4	24.9
89	0	0	0	1	1	0	1	1	0	0	0	4	4.6	8.7	1.7	5	5.2	3.7	12.8
90	0	0	0	1	1	0	1	1	0	0	0	6	4.9	9.5	2.5	5	5.0	3.9	13.8

OTUs 61-90 = FISTULOSUM

APPENDIX

Continued

OTUs	CHARACTER NO.																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
91	1	1	0	1	2	0	0	1	0	0	1	4	5.0	7.6	1.0	11	4.6	3.5	8.0
92	1	1	0	1	2	0	0	1	0	0	1	4	3.6	7.1	1.7	12	4.0	3.6	8.3
93	1	1	0	1	2	0	0	1	0	0	1	4	3.2	5.3	.7	15	4.8	3.1	12.6
94	1	1	0	1	1	0	0	0	0	0	1	5	3.5	5.9	1.2	8	4.8	4.3	9.4
95	1	1	0	1	2	1	0	1	0	0	1	4	3.5	7.2	1.4	17	3.0	3.0	13.1
96	1	1	0	1	2	0	0	1	0	1	1	3	4.5	8.4	1.3	13	4.6	4.0	8.5
97	1	1	0	1	2	0	0	1	0	0	1	5	3.0	5.4	1.0	14	4.9	3.0	7.7
98	1	1	0	1	2	0	1	1	0	0	1	5	6.5	11.4	.7	10	4.3	3.3	10.9
99	1	1	0	0	2	0	0	1	0	0	1	5	3.3	6.1	.4	11	4.5	3.5	7.7
100	1	1	0	1	1	0	0	1	0	0	1	4	6.3	10.2	.8	12	5.0	3.6	14.2
101	1	1	0	1	2	0	0	1	0	0	1	4	5.3	7.2	1.0	13	4.3	3.3	12.0
102	1	1	0	1	2	0	0	1	0	0	1	5	5.0	8.9	2.4	18	4.6	3.1	11.4
103	1	1	0	1	2	0	0	1	0	0	1	6	3.6	6.8	.5	15	4.9	4.5	14.8
104	1	1	0	1	2	0	0	1	0	0	1	5	4.1	8.1	1.0	14	4.6	4.0	12.5
105	1	1	0	1	2	0	0	1	0	0	1	5	4.1	5.9	1.0	12	4.8	3.9	8.9
106	1	1	0	1	2	0	0	1	0	0	1	4	3.8	7.1	1.0	13	4.5	4.0	10.6
107	1	1	0	1	2	0	0	1	0	0	1	5	1.9	5.1	1.6	16	4.6	3.0	18.9
108	1	1	0	1	2	0	0	1	0	1	1	4	4.7	6.8	1.2	11	5.1	3.4	12.0
109	1	1	0	1	2	0	0	1	0	0	1	3	5.1	10.1	1.3	9	4.9	3.7	9.1
110	1	1	0	1	0	0	0	1	0	0	1	5	4.7	8.3	1.2	14	4.0	3.6	13.4
111	1	1	0	1	2	1	0	0	0	0	1	4	5.6	11.3	.9	12	4.8	3.3	8.4
112	1	1	0	1	2	0	0	1	0	0	1	3	4.1	7.6	1.1	13	4.7	3.3	12.1
113	1	1	0	1	2	0	0	1	0	0	1	5	4.4	5.3	1.0	12	4.5	3.8	19.4
114	1	1	0	1	2	0	0	1	0	0	1	4	3.4	5.2	.8	13	4.2	3.8	16.2
115	1	1	0	1	2	0	0	0	0	0	1	5	2.7	3.4	.7	10	5.0	4.0	9.2
116	1	1	0	1	1	0	0	1	0	0	1	4	6.7	8.2	.8	16	4.8	3.5	13.8
117	1	1	0	1	2	0	0	1	0	0	1	5	2.9	5.1	1.2	11	4.4	3.0	12.4
118	1	1	0	1	2	0	0	1	0	0	1	4	4.2	6.6	.3	20	4.8	3.8	14.9
119	1	1	0	1	2	1	0	1	0	0	1	4	4.7	5.9	.4	12	4.7	3.0	12.2
120	1	1	0	1	2	0	0	1	0	0	1	4	5.9	10.4	.9	14	4.6	3.6	11.6

OTUs 91-120 = MACULATUM

APPENDIX

Continued

OTUs	CHARACTER NO.																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
121	1	1	1	1	0	0	0	1	1	0	0	3	3.1	2.2	.7	6	4.0	3.8	9.0
122	1	1	1	1	0	0	0	0	1	0	0	4	2.7	1.8	2.8	9	6.0	4.1	24.3
123	1	1	1	1	1	0	0	1	1	0	0	3	4.1	2.2	1.4	6	5.2	4.5	8.5
124	1	1	1	1	0	0	0	1	1	0	0	3	4.1	2.9	2.7	7	6.0	3.8	12.6
125	1	1	1	1	0	0	0	1	1	0	0	3	3.6	2.9	2.8	8	6.6	3.1	24.1
126	1	1	1	1	0	0	0	0	1	0	0	3	4.3	2.6	2.3	6	5.8	3.6	12.9
127	1	1	1	1	0	0	0	0	1	0	0	4	3.7	2.1	1.4	9	5.1	3.9	21.4
128	1	1	1	1	1	0	0	0	1	0	0	3	3.9	2.4	2.3	5	5.8	3.6	14.8
129	1	1	1	1	0	0	0	1	1	0	0	3	4.3	2.8	2.3	5	5.0	3.1	18.0
130	1	1	1	1	0	0	0	1	1	0	0	4	3.5	2.6	2.2	6	4.8	3.6	13.6
131	1	1	1	1	0	0	0	0	1	0	0	3	3.1	2.0	2.8	7	4.1	3.6	11.4
132	1	1	1	1	0	0	0	0	1	0	0	3	3.3	2.3	1.8	6	5.2	3.7	11.5
133	1	1	1	1	0	0	0	1	1	0	0	2	3.2	2.1	1.3	6	6.0	3.0	15.9
134	1	1	1	1	0	0	0	0	1	0	0	4	3.1	2.2	2.2	5	5.7	3.0	9.7
135	1	1	1	1	2	0	0	0	1	0	0	4	3.7	2.2	3.6	6	6.0	3.2	20.4

OTUs 121-135 = STEELEI

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