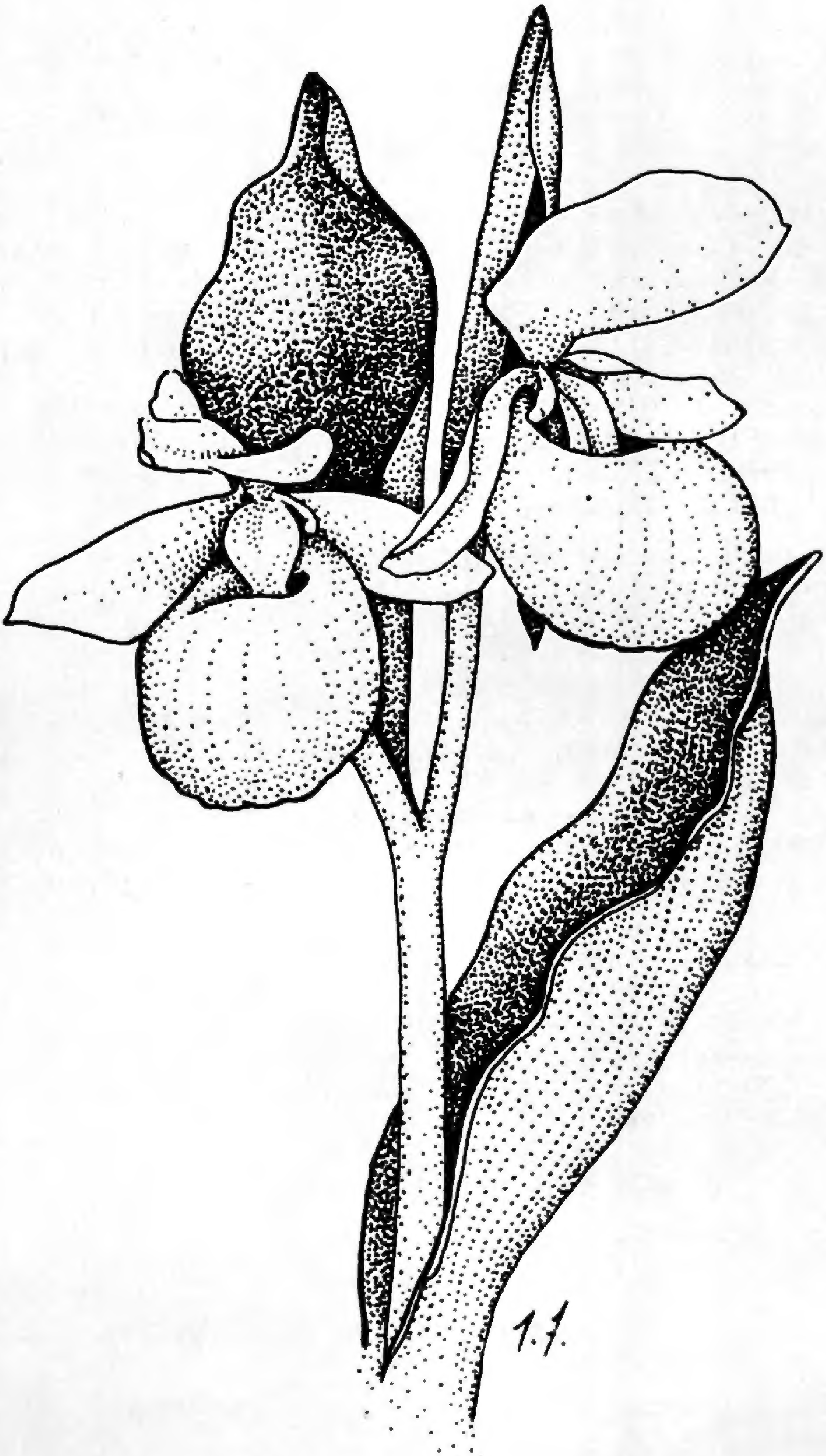
Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB



Vol. 87 January 1985 No. 849

The New England Botanical Club, Inc.

Botanical Museum, Oxford Street, Cambridge, Massachusetts 02138

Conducted and published for the Club, by
NORTON H. NICKERSON, Editor-in-Chief

RHODORA.—Published four times a year, in January, April, July, and October. A quarterly journal of botany, devoted primarily to the flora of North America. Price $20.00 per year, net, postpaid, in funds payable at par in the United States currency at Boston. Some back volumes and single copies are available. Information and prices will be furnished upon request. Subscriptions and orders for back issues (making all remittances payable to RHODORA) should be sent to RHODORA, Botanical Museum, Oxford Street, Cambridge, Mass. 02138. In order to receive the next number of RHODORA, changes of address must be received prior to the first day of January, April, July or October.

Scientific papers and notes relating to the plants of North America and floristically related aras will be considered by the editorial committee for publication. Articles concerned with systematic botany and cytotaxonomy in their broader implications are equally acceptable. Brevity is urged whenever possible in all papers. Short items will be published on otherwise blank end pages as soon as possible, even if they appear ahead of longer articles already accepted. All manuscripts should be submitted in TRIPLICATE AND MUST BE DOUBLE (AT LEAST 3/8 OF AN INCH) OR TRIPLE-SPACED THROUGHOUT. **Please conform to the style of recent issues of the journal. See "Instructions to Contributors to RHODORA" at the end of each issue. Extracted reprints, if ordered in advance, will be furnished at cost. RHODORA assesses modest page charges.**

Address manuscripts and proofs to:
Joan Y. Nickerson
Managing Editor, RHODORA
Phippen-LaCroix Herbarium, Dept. of Biology
Tufts University
Medford, Mass. 02155

Second Class Postage Paid at Boston, Mass.

PRINTED BY
THE LEXINGTON PRESS, INC.
LEXINGTON, MASSACHUSETTS

Cover illustration

Cypripedium reginae Walt., the Showy Lady's-slipper, was presumed until recently to be extirpated from New Hampshire; five sites for this exquisite orchid are now known.

Original artwork by Tess Feltes, Illustrator.

Rhodora
(ISSN 0035-4902)
JOURNAL OF THE
NEW ENGLAND BOTANICAL CLUB

Vol. 87 January 1985 No. 849

THE ORCHIDS OF NEW HAMPSHIRE[1],[2]

FRANCES E. BRACKLEY

ABSTRACT

The distribution, pollination ecology, and habitats of representatives of the Orchidaceae which occur naturally in New Hampshire, USA are discussed. The information was compiled from historic records and new field studies.

Key Words: Orchids, floristics, pollination, New Hampshire

TABLE OF CONTENTS OF GENERA

---

[1] Based on a thesis submitted to the University of New Hampshire in partial fulfillment of the requirements for the degree of Master of Science.

[2]

INTRODUCTION

New Hampshire is located in the northeastern United States between Lat. 42° 15′ N and Lat. 45° 15′ N. It encompasses 9,304 square miles, over 85% of which is presently forested. New Hampshire is known as the "Granite State", an appropriate nickname, as one-third of all the state's rock is granite or closely related igneous rock.

The landscape and soils of the state reflect effects of total glaciation experienced during the Pleistocene. Evidence of glacial activity is especially noticeable in the rugged White Mountains which occupy the central portion of the state and include the tallest peak in the northeast, Mount Washington (6,280 ft.).

From the 22 miles of seacoast on its southeastern border to the boreal forest adjacent to Canada, New Hampshire supports a diversity of habitats. New Hampshire's flora consists of species with many different geographical affinities, and several orchids reach their northern or southern limits within the state.

New Hampshire is one of the fastest-growing states in terms of population; as a result, wildlife habitats are being altered or destroyed at an increasing rate. This account of the Orchidaceae records many extant locations which will surely disappear because of human activity.

In the preparation of this work, every attempt was made to identify species carefully and to use correct nomenclature according to the rules of the *International Code of Botanical Nomenclature* (Stafleu *et al.*, 1978). As often as possible the original description of each taxon was studied and, in some cases, the type specimen examined. Not all synonyms of each plant are listed, but only those that were, at one time, in general enough use to be commonly encountered.

Plant descriptions, unless otherwise indicated, are based upon plants that I have collected and/or examined from New Hampshire. In cases where the number of specimens was few, plants from Maine and Vermont were also examined. The distributions and flowering dates of New Hampshire orchids were gathered from collections, observations, and the literature. Specimens from the following herbaria were studied: AMES, HNH, KESC, MASS, MAINE, NHA, NEBC, VT, and YU. Voucher specimens of my collection are deposited in NHA.

All the known chromosome numbers of taxa occurring in New Hampshire are listed in the discussions of individual species. Unless otherwise indicated, all chromosome counts are taken from *A Chromosome Atlas of Flowering Plants*, Darlington and Wylie, 1956.

THE ORCHIDS OF NEW HAMPSHIRE

Key to Genera

1. Lip saccate or slipper-shaped .... (2)
    2. Lip slipper-shaped; flowers 1–3, pink, pink and white, or yellow (rarely white) .... (3)
        3. Plant with 2 or more pubescent leaves clasping stem; edges of lip opening in-rolled .... **1. Cypripedium**
        3. Plant with one basal petiolate leaf; edges of lip opening turned out and forming a white apron .... **16. Calypso**
    2. Lip saccate; flowers several to many, whitish to mauve .... (4)
        4. Leaves alternate in a cluster at the base of the stem; flowers whitish................................**8. Goodyera**
        4. Leaves alternate along the stem; flowers whitish to mauve .... **5. Epipactis**
1. Lip variously shaped but not saccate or slipper-shaped ... (5)
    5. Leaf, when present solitary or undeveloped, sheath-like, or absent; stems with or without sheaths .... (6)
        6. Leaf undeveloped or absent .... (7)
            7. Inflorescence from a corralline-like rhizome; flowers many, variously colored, sepals and petals spreading .... **17. Corallorhiza**
            7. Inflorescence from a corm; flowers usually solitary, rose-pink (rarely white), sepals and petals forming a loose hood over the column .... **12. Arethusa**
        6. Leaf well developed .... (8)
            8. Leaf-blade ovate to obovate; flowers greenish-white or yellowish .... (9)
                9. Lip spurred............. **4. Platanthera (Habenaria)**
                9. Lip without a spur .... **14. Malaxis**

8. Leaf-blade linear to lanceolate; flowers pink to magenta (rarely white) .... (10)
    10. Lip in lowermost position (resupinate) .... **11. Pogonia**
    10. Lip in uppermost position (non-resupinate) .... **13. Calopogon**

5. Leaves two or more .... (11)
  11. Leaves two .... (12)
    12. Leaves located near the middle of the stem; flowers small, greenish to purplish .... **6. Listera**
    12. Leaves basal .... (13)
      13. Leaves broadly elliptic to orbicular, lying flat on the ground.............. **4. Platanthera (Habenaria)**
      13. Leaves oblong-elliptic, ascending .... (14)
        14. Stems without foliaceous bracts; flowers green, lateral petals reflexed and thread-like .... **15. Liparis**
        14. Stems with foliaceous bracts; lateral petals connivent with sepals to form a hood .... **2. Galearis (Orchis)**
  11. Leaves more than two .... (15)
    15. Leaves at the summit of the stem, appearing whorled ....**10. Isotria**
    15. Leaves scattered along the stem or appearing basal .... (16)
      16. Leaves appearing basal; plant slender with small white spiralled flowers .... **9. Spiranthes**
      16. Leaves cauline .... (17)
        17. Leaves ovate; flowers nodding, pink or white, without spurs; tiny delicate flowers of Beech woods .... **7. Triphora**
        17. Leaves clasping stem, linear-lanceolate to oblanceolate, becoming reduced to bracts; flowers not nodding, with spurs; plants of various habitats .... (18)
          18. Lip with long slender spur .... **4. Platanthera (Habenaria)**
          18. Lip with short sac-like spur .... **3. Coeloglossum (Habenaria)**

GENERA AND THEIR INDIVIDUAL TAXA

1. **Cypripedium** L. Species Plantarum 2:951.1753.

The genus *Cypripedium* was named by Linnaeus who based his description on the Yellow Lady's-slipper, *C. calceolus*. The generic name is from two Greek words, *kypris* and *podion*, that have been Latinized [incorrectly, according to Schultes and Pease (1963)]. A traditional translation is "Venus's shoe" from which the common name "Lady's-slipper" or "Lady-slipper" is derived.

The Lady's-slippers are the largest and most conspicuous of our native orchids. Flowers may be borne singly, or there may be several on one stalk. The blossoms are yellow, pink and/or white. They are composed of three sepals, two of which are usually fused together, and three free petals. Two of the petals are usually narrow and spreading, while the third petal, the labellum, or lip, is expanded into an inflated pouch (the "slipper").

The pistil and stamens are fused together into a compound structure known as the column. The two fertile stamens, which are laterally located on the column, produce the sticky masses of pollen grains. Pollen in this genus is not organized into pollinia but is loose, granular, and embedded in a viscid secretion (Garay, 1960). On the front of the column, the large sterile stamen, the "staminode," is found.

Cypripediums possess fibrous roots that have a characteristic acrid odor. The stems grow annually from subterranean rhizomes and bear two or more plicate, conspicuously ribbed leaves. Plants of most species in this genus are covered with glandular hairs which occasionally can cause an itchy rash. In the past, a drug was extracted from the roots of *Cypripedium* plants for use in treatment of nerve disorders (Hocking, 1955). This medicinal use formed the basis for the old common name, "nerve root."

World-wide, there are 30–50 species of *Cypripedium*, all found in the Northern Hemisphere. The genus is cytologically uniform in those species for which chromosome numbers have been determined. Diploid counts recorded by Stoutamire (1967) are $2n = 20$ or 22. Both natural and artificial hybrids have been reported within *Cypripedium* (Curtis, 1932). Eleven different species, several varieties, and a few hybrids occur in North America. Of these, five species grow wild in New Hampshire.

The *Cypripedium* flower displays bright color(s), fragrance, and a landing platform, attributes that are most attractive to bees. All of these attributes suggest the presence of nectar, a food source for insects. Since no nectar is actually present, the attractions are deceitful, and the blossom serves as a trap for the deluded insect. Once the visitor enters through the opening in the pouch it is prevented from retreating by the involute edges and downward-pointing hairs. To exit from the flower the insect must crawl up through a narrow channel toward the base of the lip. There, two small openings, one under each anther, provide a means of egress. As the pollinator approaches one of the openings, its back must brush against the column. The rough column scrapes off any pollen that the insect may earlier have picked up from another flower. The insect must next squeeze past an anther. In doing so, it dislodges a fresh pollen mass which then becomes firmly cemented to the insect's back. The insect finally attains freedom via one of the small apertures, carrying with it the pollen necessary to fertilize another Lady's-slipper, thus effecting cross-pollination.

Adaptation to an efficient system of outcrossing means that size of the insect visitor must be compatible with the dimensions of the entire escape route through the flower. L. A. Nilsson (1979) found that some bees are able to lift themselves back out through the entrance of smaller slippers, but an oversized insect visitor may become imprisoned within the slipper and die (Arthur, 1962).

When the ovules are fertilized an elongate capsule is formed. Populations of Lady's-slippers usually produce many flowers but very few fruits. Bingham (1939) and Correll (1950) have suggested as a possible explanation for the low percentage of seed pod formation that there may be a lack of locally available pollinators to transmit the pollen. They also noted that during the lag-period between pollination and fertilization (up to four weeks) the plants are vulnerable to various factors which might prevent fertilization and cause the capsule to abort. Case (1964a) noted that late frosts are a factor in preventing some seed capsules from ripening in the area of the western Great Lakes.

A ripened *Cypripedium* capsule can contain as many as 54,180 seeds (Stoutamire, 1964). However, the time period from seed germination to a mature flowering plant encompasses many years, and seedling mortality rate is very high (Curtis, 1943). In general, wild Cypripediums in New Hampshire do not take well to transplantation. Even those plants which at first appear to survive transplantation die after a few seasons and meantime may not reproduce. Clearly, Cypripediums are best left and enjoyed in their natural environments.

Further discussion of the North American Yellow Lady's-slippers is in order. They are generally recognized as varieties of *Cypripedium calceolus*, a Eurasian species described by Linnaeus (1753). His epithet *calceolus* means "little shoe." Although the two taxa of Yellow Lady's-slippers occurring in New Hampshire originally were described as separate species, most manuals treat them as *C. calceolus* variety *pubescens* (Large Yellow Lady's-slipper) and *C. calceolus* variety *parviflorum* (Small Yellow Lady's-slipper). Another taxon, *C. calceolus* variety *planipetalum*, found in Newfoundland and Quebec, is considered to be most like the Eurasian *C. calceolus* var. *calceolus* (Fernald, 1950a). Willdenow described the larger North American Yellow Lady's-slipper as *C. pubescens* in 1804. In 1930 this taxon was transferred to *C. calceolus* as variety *pubescens* by D. S. Correll.

The Small Yellow Lady's-slipper was first described as *Cypripedium parviflorum* by R. A. Salisbury based upon a specimen from Virginia. In 1946 Fernald treated it at the varietal level as *C. calceolus* variety *parviflorum*.

Many workers have speculated on the relationship between *Cypripedium pubescens* and *C. parviflorum*. Ilitis (1965) listed them as a vicarious species pair that probably diverged during Pleistocene glaciation. He theorized that post-glacial migration produced an overlapping of the range of the two races. The resulting hybrids display an intergradation of morphological characters that can be observed today in some populations of Yellow Lady's-slipper. In New Hampshire the two Yellow Lady's-slippers appear quite distinct. While the morphological characters of size, coloration, pubescence, and overall appearance may be attributed to genotypical response to environmental conditions, these same environmental conditions operate as the primary selective factors in the course of speciation (Sanford, 1974). Sanford also noted that with "small, spatially scattered populations, the development of slight differences in blooming time becomes an important isolating mechanism."

Mayr (1969) characterized species as groups of interbreeding natural populations that are reproductively isolated. The two races of Yellow Lady's-slippers in New Hampshire are apparently reproductively isolated by flowering time, habitat, and pollinators; they are therefore here recognized as distinct species.

Key to Species of *Cypripedium* in New Hampshire

1. Plants with two basal leaves; flowers solitary; pouch pink or sometimes white, cleft longitudinally down the front .... 1. *C. acaule*
1. Plants with 2 or more leaves borne on the stem above the base; flowers 1–3; pouch yellow, pink or white, often streaked with purple (rarely pure white), not cleft, opening above circular .... (2)
    2. Lateral sepals separate almost to base; pouch cone-shaped, prolonged downward, white streaked with purple .... 2. *C. arietinum*
    2. Lateral sepals fused for entire length, or nearly so; pouch slipper-shaped, erect, yellow or pink (rarely pure white).... .... (3)
        3. Pouch yellow; lateral petals conspicuously twisted, acute at apices, longer than the pouch.................... (4)
            4. Plants densely glandular-pubescent; sepals and lateral petals greenish-brown or yellow; pouch 3–5 cm long; plants of mesophytic woods, usually flowering in May ....3. *C. pubescens*
            4. Plants scarcely pubescent; sepals and lateral petals reddish-brown to purple; pouch 2–2.5 cm, plants of circumneutral or calcareous wetlands, usually flowering in June .... 4. *C. parviflorum*
        3. Pouch pink or pink-and-white (rarely pure white); lateral petals straight, white, ovate, shorter than the pouch; plants of circumneutral or calcareous wetlands........ .... 5. *C. reginae*

1. *Cypripedium acaule* Ait., Hort. Kew., ed. 1, 3: 303. 1789.

The Pink Lady's-slipper was first described by British botanist and gardener William Aiton from a specimen obtained in North America. This species has also been known as *Fissipes acaulis.* The literal meaning of the specific epithet *acaule* is "stemless."

Common names: Pink Lady's-slipper, Moccasin flower

Flowering dates in new hampshire: late May through June

Description: Plant from a short rhizome with thick, fibrous roots having a pungent odor. Leaves two, opposite, basal, elliptic to oblong-elliptic, 1–2.5 cm long, strongly ribbed, and sheathing the flowering stalk. Flower terminating scape, solitary, nodding, subtended by an erect bract. Lateral petals and sepals yellowish-green to brownish, often tinged with purple. Lateral sepals joined entirely beneath. Lateral petals narrow, loosely spiraled, inner surfaces pubescent near base. Lip an inflated pouch 4–6 cm long, lightly fragrant, pink (sometimes white in forma *albiflorum*) with a longitudinal fissure down the front. Edges of opening infolded. Capsule ellipsoid, ribbed, 3–4.5 cm long, held nearly horizontal to ground.

Chromosome number: $2n = 20$

In late spring and early summer, the woods of New Hampshire are lit up by the large, nodding blossoms of the Pink Lady's-slipper. It is our most conspicuous and familiar orchid, a delight of the wildflower enthusiast.

Cypripedium acaule thrives in the sandy, acidic soil that prevails in most of the state. It commonly grows in open pine or mixed woods, but can be sometimes found in damper, mossy habitats. Occasionally there are years of spectacular blooms. Stuckey (1967) found that unusually large numbers of blossoming plants occurred in areas of Rhode Island 10–15 years after a brush fire. This observation corresponds with the reported average number of years required between seed germination and the production of the first flower in *C. acaule* (Curtis, 1943). Burning may have a favorable influence in reducing competition for young seedlings and/or releasing necessary nutrients to the soil.

In New Hampshire *Cypripedium acaule* is widespread and can be found in every county. The color of the lip is commonly pink, although white-lipped plants [forma *albiflorum* Rand and Redfield (1894)] become increasingly more frequent in the mountains and the northern areas of the state, even to the point of being the dominant form in some populations (Anderson, 1936). Double-flowering forms have been found where the two slippers occur side-by-side or back-to-back on a single, doubly thick stalk.

The light, sweet frangrance of the Pink Lady's-slipper has been found by Stoutamire (1967) to be predominantly produced by the sepals and lateral petals. In the same study it was found that the most common pollinators of this species are bees of the genus *Bombus* (Apidae). In the White Mountains I have observed many blossoms of *C. acaule* with their lips filled with scores of small beetles, identified as *Anthobium pothos* (Staphylinidae) (W. Morse, personal communication). The beetles appeared to be feeding on pollen, but are seemingly too small to serve as effective pollinators. However, Smith (1863) reported that small flower-beetles pollinated the Showy Lady's-slipper by moving minute particles of pollen from the anther to the stigma. The insects he observed were later identified as *Anthobium convexium* (Guignard, 1886). A type of self-pollination may be effected by the tiny beetles, but the major cross-pollinator of the Pink Lady's-slipper is the larger *Bombus* bee.

In any New Hampshire population of *Cypripedium acaule,* the percentage of plants that set fruit is consistently low, usually less than ten percent.

GENERAL DISTRIBUTION: Northeastern North America, Newfoundland west to Alberta, south in the mountains of Georgia and Tennessee, west to northern Indiana, northern Illinois and Minnesota.

2. *Cypripedium arietinum* R. Br., Hort. Kew., ed. 2, 5: 222. 1813.

British botanist Robert Brown originally described the Ram's Head Orchid from a North American specimen. The species has also been known as *Criosanthes arietina* (R. Br.) House (1905). The epithet *arietinum* means "of a ram."

COMMON NAMES: Ram's Head Orchid, Ram's Head Lady's-slipper

FLOWERING DATES IN NEW HAMPSHIRE: May to early June

DESCRIPTION: Plant small, averaging (in this area) 20 cm tall, from a short rhizome with fibrous, musky-smelling roots. Leaves 3–5, spirally arranged, elliptic-lanceolate, purplish-brownish, lateral sepals and petals narrow, slightly twisted, greenish-purplish. Lip protuberant, prolonged downward, netted with magenta veins. Edges of the circular orifice folded in, covered with a white silky pubescence. Capsule ellipsoid, about 2 cm, prominently ribbed.

CHROMOSOME NUMBER: $2n = 20$ (Moore, 1973)

Looking at the unusually-shaped flower of *Cypripedium arietinum,* one can observe an image of the head of a tiny ram in the position for a charge. The Ram's Head Orchid is the smallest and rarest of all the Lady's-slippers in New Hampshire. The protuberant lip is "small enough to be put in a child's thimble" according to Baldwin (1894). *Cypripedium arietinum* is so inconspicuous as to be difficult to discern fron its surroundings even in blossom. In bud it is almost impossible to find. I have walked by several flowering plants before "discovering" the tiny orchid in a well-known Maine location.

Cypripedium arietinum occurs mostly in wet Northern White Cedar (*Thuja occidentalis*) woods but is also found on well-drained, ledgy slopes under deciduous trees. Cool soils and partial shade are a necessary prerequisite for this species. Although the Ram's Head Orchid may be locally abundant in some places, none of the New Hampshire stations has ever yielded more than a few plants. There are voucher specimens of *C. arietinum* from only eleven towns in New Hampshire, and most of these specimens were collected well over 50 years ago.

Cypripedium arietinum is listed as "declining" and "vulnerable" in New Hampshire by Storks and Crow (1978), and as "threatened" or "endangered" in New England by Crow *et al.* (1981). Despite the scarcity of *C. arietinum* in New England there are apparently sufficient populations of this species on a national scale to warrant its being dropped from consideration as an Endangered or Threatened species of the United States (Federal Register, Vol. 45, No. 242, Monday, December 15, 1980). At present, there is only a single known New Hampshire station for this species. However, I am reasonably confident that more of these dainty orchids are living and blooming in secret haunts within the state.

The Ram's Head Orchid is considered structurally primitive because there is no fusion of the lateral sepals as in other *Cypripedium* species. Since the flower is so small, only a correspondingly small insect can be an effective pollinator. Stoutamire (1967) observed two bees of the genus *Dialictus* (Halictidae) visit and carry off pollen masses of *C. arietinum* on their thoraxes. Van der Pijl and Dodson (1966) list another small bee, *Megachile* sp. (Megachilidae) as a pollinator. Though short lived, the flowers of the Ram's Head Orchid are not literally ephemeral as once believed. If pollination occurs, the upper sepal drops down over the lip, sealing off the entrance way to further insect visitors (Case, 1964a).

GENERAL DISTRIBUTION: Quebec west to Manitoba, south to Maine, New Hampshire, Vermont, and New York, west to Michigan, Wisconsin,' n. Illinois to Minnesota. *Cypripedium plectrochilon* of western China may be synonymous with *C. arietinum* (Leur, 1975).

3. *Cypripedium pubescens* Willd., Sp. Pl. 4: 143. 1805.

The name *pubescens* means "downy," in reference to the many fine hairs that cover this plant.

COMMON NAMES: Large Yellow Lady's-slipper, Downy Yellow Lady's-slipper, Whippoorwill Shoe

FLOWERING DATES IN NEW HAMPSHIRE: May to early June

DESCRIPTION: Plant robust, densely glandular-pubescent, 10–70 cm tall, from a cylindrical rhizome with fibrous, musky-smelling roots. Leaves 3–5, elliptic to ovate-lanceolate, strongly ribbed, bright green, sheathing the stem. Flowers 1 or 2, terminating the stalk, subtended by a large foliaceous bract that usually exceeds the flower in height. Lateral sepals united beneath lip, almost to apex. Dorsal sepal largest, 3–8 cm long, slightly spiralled with undulating margins. All sepals yellowish-green with streaks of brown. Lateral petals narrow, acuminate, loosely twisted to spiralled, yellowish-green. Lip ovate or "slipper-shaped," usually pale yellow, although all shades of yellow occur. Edges of round opening turned under, inner pouch with reddish-purple spots. Staminode triangular, yellow spotted with madder. Capsule ellipsoid, ribbed, almost erect.

CHROMOSOME NUMBER: $2n = 20$

In New Hampshire the Large Yellow Lady's-slipper is most often found in rich deciduous woods along the edges of spring run-off streams. This species prefers a substrate nearly neutral in pH, one reason why it is listed as "infrequent" (Storks and Crow, 1978) here in New Hampshire, the "Granite State." Curtis (1943) found plants growing in soils which ranged in reactions from pH 5.7 to pH 7.0, but reported that seedlings were most abundant in moist soils that ranged fron pH 6.9 to pH 7.2. Curtis also noted that the average time period between seed germination and flowering in *Cypripedium pubescens* is 12 years.

It has been claimed that many populations of the Large Yellow Lady's-slipper in New Hampshire have been commercially exploited by persons digging up and selling the plants. For whatever reasons, the records indicate that the numbers of Large Lady's-slipper populations have declined in the state; there are only 12 stations documented by specimens.

The pollination biology of *Cypripedium pubescens* has been studied by Robertson (1928) who observed two long-tongued bees of the genus *Ceratina* (Anthophoridae) visiting the flowers. In Oakland County, Michigan, Stoutamire (1967) also observed a male *Ceratina calcarata* enter a slipper and subsequently exit with a pollen mass on its thorax. As with all Cypripediums, percentage of seed set in the Large Yellow Lady's-slipper is small and propagation is assumed to be largely vegetative.

GENERAL DISTRIBUTION: Nova Scotia to Minnesota, south to New England, along the mountains to Georgia, Alabama, Tennessee, and Missouri.

4. *Cypripedium parviflorum* Salis. Trans. Linn. Soc. I: 77. 1791.

The name *parviflorum* means "small flower."

COMMON NAME: Small Yellow Lady's-slipper

FLOWERING DATES IN NEW HAMPSHIRE: June

DESCRIPTION: Plant slight and dainty, 35 cm or less, not as leafy as the preceding, scarcely pubescent. From a small rhizome with fibrous roots that have a pungent odor. Leaves small, 3 5, (usually 4 here), bluish green, strongly ribbed, ovate-lanceolate, sheathing the stem. Floral bracts small, usually not exceeding the flower in height. Flowers usually solitary, strongly fragrant, borne high above the leaves and terminating the stem. Sepals and lateral petals madder-purple. Lateral sepals united almost to the apex. Dorsal sepal 2–4 cm long with undulating edges. Lateral petals lanceolate, tightly spiralled, spreading. Lip small, saccate, bright yellow with purple stripes or spots. Opening circular with inrolled edges, claret spots within. Staminode triangular, bright yellow, spotted with purple. Capsule ellipsoid, almost erect.

CHROMOSOME NUMBER: $2n = 20$

Unlike the almost scentless Large Yellow Lady's-slipper, the dainty, wax-like blossoms of the Small Yellow Lady's-slipper possess a strong, sweet fragrance. This species also prefers a wetter, more calcareous habitat and is often found growing in association with *Thuja occidentalis*. There are only eight stations in New Hampshire where specimens designated "var. *parviflorum*" have been collected. However, this species may be even more infrequent than the records indicate. Some determinations are mistakes based on confusion over changes in nomenclature, and there are a few specimens which are actually small individuals of the polymorphic *Cypripedium pubescens*.

Van der Pijl and Dodson (1966) listed the bee *Ceratina* sp. (Anthophoridae) to be the pollinator of *Cypripedium parviflorum* as observed by Robertson. This information could be misleading if it is interpreted as referring to the Small Yellow Lady's-slipper. Robertson (1928) listed the long-tongued bee, *Ceratina* sp., as a visitor to "*Cypripedium parviflorum pubescens*," a synonymous name in use at the time for the Large Yellow Lady's-slipper (Robinson and Fernald, 1908). Robertson's published blooming dates (May 7–30) correspond more closely to the flowering time of *C. pubescens* than to the later blooming *C. parviflorum*.

Stoutamire (1967) lists no pollinator specifically for *Cypripedium parviflorum*. I have observed several small bees visiting the blossom of the Small Yellow Lady's-slipper. One bee, *Lasioglossum zonatum* (Halictidae) was captured with a pollen-smear on its thorax. The smaller size of the pouch in this species indicates that for effective cross pollination to occur, the pollen vector should be smaller than the insects observed visiting *C. pubescens.* Indeed, one visitor to the blossom made repeated attempts to enter the pouch but couldn't fit through the opening. This larger bee was identified as *Megachile melanophoea melanophoea* (Megachilidae) (J. Burger, personal communication).

GENERAL DISTRIBUTION: Restricted to the northeast. Newfoundland west to Minnesota, south to New Jersey, Pennsylvania and a few isolated stations in the Appalachian Mountains (Case, 1964a).

5. *Cypripedium reginae* Walt. Fl. Carol. 222. 1788.

American botanist Thomas Walter first described the Showy Lady's-slipper in *Flora Caroliniana* based on a type specimen from Carolina. This species has also been known as *Cypripedium spectabile* Salis. and *C. hirsutum Miller.* All three names are appropriately descriptive for this beautiful plant. *Reginae* means "of the queen," *spectabile* means "showy," and *hirsutum* translates as "hairy."

COMMON NAMES: Showy Lady's-slipper, Queen Lady's-slipper, Big Pink and White

FLOWERING DATES IN NEW HAMPSHIRE: Mid-June to mid-July

DESCRIPTION: Plant from a black cylindrical rhizome with fibrous roots. Leaves 3–6, ovate-lanceolate, strongly ribbed and hirsute, closely sheathing the stem, bright green. Inflorescence 1 2 (occasionally more) large flowers on pedicels arising from axils of erect bracts. Lateral petals and sepals white, ovate, shorter than the lip, spreading. Lateral sepals united entirely. Lip inflated, spherical with infolded edges around the circular opening, deep rose with white markings. Staminode cordate-ovate, white with yellow spots. Capsule ellipsoid, almost erect.

CHROMOSOME NUMBER: $2n = 20$.

Truly the queen of the Lady's-slippers, *Cypripedium reginae* is the largest (up to 90 cm) and most spectacular of our native orchids. Since it usually occurs in large colonies, observing the Showy Lady's-slipper in flower affords an unforgettable experience. The large, lightly fragrant, rose and white blossoms are framed advantageously by a background of soft green foliage. Morris and Eames (1929) stated that not even gorgeously colored tropical orchids can compare with the beauty of this species "for they lack their terrestrial sister's dower of rich green foliage."

Cypripedium reginae requires a wetter habitat than the other Lady's-slippers of the region. This species prefers neutral to alkaline soil conditions, but can grow in sphagnum if the roots are able to penetrate to a lower, sweeter soil layer (Case, 1964a). Seedlings, especially those that have developed close to the soil surface, have a very high mortality rate. Curtis (1943) has found that seedlings of the Showy Lady's-slipper require a three-year growing period before the first green leaf appears above the ground, and that the first flowers may take as long as sixteen years after seed germination to appear. According to Waterman (1949), seeds of this species germinate best when planted deeply (2.5–5 cm). His work in central Michigan suggests that the Showy Lady's-slipper thrives in those sites where the seeds are pressed into the soil by the feet of deer (Waterman, 1950). Another reported ecological requirement of *C. reginae* is availability of light. In some localities lumbering may provide the necessary open areas for the plant to prosper. However, Harvais (1980) found in northwestern Ontario that the Showy Lady's-slipper is more tolerant of shade than it is of low moisture conditions.

Historically, only one station for *Cypripedium reginae* was documented for the state of New Hampshire. The orchid was found growing in Bottomless Pit Bog in Hanover, Grafton County, adjacent to the Lebanon town line and erroneously assigned to that town on many herbarium labels. The most recent collection of the Showy Lady's-slipper from that site was made in 1891. In a span of 90 years the site has changed from an open-water bog to a Black Spruce (*Picea mariana*)-shrub community (J. Poole, personal communication). Because conditions have changed to the extent that the bog no longer supports an orchid population, *C. reginae* was considered "possibly extinct" for the state (Storks and Crow, 1978).

During the course of my field-work, I received information concerning a possible population of Showy Lady's-slippers in New Hampshire from Frederic L. Steele, a well-known local botanist. After two days of searching through swamps in the given location I came upon a population of over 200 plants of *C. reginae* in full flower. The new station is a rather ordinary swamp with Cinnamon

Fern (*Osmunda cinnamomea*), Sensitive Fern (*Onoclea sensibilis*) and Swamp Saxifrage (*Saxifraga pensylvanica*) growing in abundance (Brackley, 1979).

Subsequently, I have found two other sites in New Hampshire for the Showy Lady's-slipper. Both these populations are found in Cedar (*Thuja occidentalis*) swamps that support other orchids and associated northern elements of the flora as well. Because of the striking beauty of this species there is a danger of exploitation by private and commercial cultivators. In New Hampshire, such a practice could readily cause the demise of this most elegant plant.

The report that hirsute stems and foliage of the Showy Lady's-slipper can cause a dermatitis reaction in some people was supported by a colleague who developed "poison-ivy" on two occasions after accompanying me to a station in northern N. H. where poison-ivy is rarely found.

Guignard (1886) observed bees of the genus *Megachile* (Megachilidae) pollinating the Showy Lady's-slipper. Stoutamire (1967) also observed a medium-sized black bee enter the pouch and quickly force its way out under the anther and carry off a pollen load. In the same study, the fact was noted that although the opening in the labellum allows access to large bees, the exit canal in *Cypripedium reginae* is smaller than in *C. acaule*. This situation suggests that the larger bees of the genus *Bombus* (Apidae) better "fit" *C. acaule*. As previously mentioned, Smith (1863) found the small beetle *Anthobium pothos* (Staphylinidae) effecting self-pollination in a population of Showy Lady's-slippers in Norway, Maine. In Ontario, Arthur (1962) has found that adults of the European Skipper Butterfly *Thymelicus lineola* (Hesperidae) commonly become trapped within the pouch of the Showy Lady's-slipper where they eventually starve or are drowned in rainwater.

General distribution: Newfoundland west to Manitoba, south to New England, and southward along the Appalachian Mountains to Tennessee, west through Ohio to Missouri.

2. **Galearis** Raf., Herb. Raf. 71. 1833.

Originally, Linnaeus placed the Showy Orchis in the genus *Orchis*, a large group of European orchids that provided the basis for the family name, Orchidaceae. Because of morphological differences (see Vermeulen, 1953) between the European and eastern North American plants, the genus *Galearis* was segregated from *Orchis* almost 150 years ago by Rafinesque, the Constantinople-born naturalist who did most of his botanical work in the United States. Because of his eccentricities and his abandonment of the Linnaean principles of taxonomy, Rafinesque's work was not accepted by botanists of the day. One of his contemporaries described his prolific writings as "the wild effusians of a literary madman" (Humphrey, 1961). In such an atmosphere, Rafinesque's new genus *Galearis* was ignored and the Showy Orchis continued to be known by its original name of *Orchis spectabilis.*

When Rydberg revised the genus in 1901, he placed the Showy Orchis in the genus *Galeorchis* but his generic segregation was not widely accepted. Time has since vindicated some of Rafinesque's ideas on a natural system of classification and some of his generic segregations, such as *Galearis,* have been substantiated.

Galearis is derived from the Latin word for "helmet," which fittingly describes the hood-like shape made by convergence of the sepals and lateral petals over the column. There are but two species in this genus, the eastern North American *G. spectabilis,* and an eastern Asian representative, *G. cyclochita.*

1. *Galearis spectabilis* (L.) Raf., Herb. Raf. 71. 1833.

This species is based upon a type specimen from Virginia. The specific epithet means "showy."

COMMON NAMES: Showy Orchis, Showy Orchid, Preacher-in-the-pulpit

FLOWERING DATES IN NEW HAMPSHIRE: May to early June

DESCRIPTION: Low plant from a short rhizome with fleshy, narrow roots. Leaves 2, large, basal, sub-opposite, obovate-oblong, narrowing into petioles that sheath the 4–5 angled stem. Raceme 2-several flowered, each subtended by a lanceolate floral bract that exceeds the height of the flower. Ovaries thick, sessile, 1–2 cm long. Sepals and lateral petals shell-pink to mauve. Sepals ellipitic, concave, connivent to the linear-lanceolate lateral petals, together forming a hood over the column. Lip white (rarely pink in forma *Willeyi*), entire, dilated, ligulate, having undulating margins and a conspicuously broad, club-shaped spur at the base. Capsule ellipsoid, erect, 2 cm long.

CHROMOSOME NUMBER: $2n = 42$

The Showy Orchis prefers a humus-rich, hardwood forest habitat where it blooms before the leafy canopy fully develops. Although it bears an impressive name, the plant is quite inconspicuous in the dappled light of early spring woods. The shiny basal leaves are often half-concealed under leaf litter, and the nodding, delicately colored flowers are tucked beneath the leafy bracts. Usually, only scattered individual plants are found in flower, accompanied by one or two vegetative plants. Occasionally one finds a small colony of several plants all flowering at once. Blossoming seems to be related to cyclic patterns or specific environmental parameters, as there are "good years" for finding flowering plants; during some growing seasons, vegetative plants predominate and flowering individuals are rarely found.

In New Hampshire, the Showy Orchis is generally restricted to the Connecticut River Valley. That area's alluvial soils tend to be more neutral than the acidic soils which prevail throughout the rest of the state. The Showy Orchis grows with other plants of rich wooded hillsides, such as Maidenhair Fern (*Adiantum pedatum*), Blue Cohosh (*Caulophyllum thalictroides*), and Hepaticas (*H. acutiloba* and *H. americana*).

Of the ten historical sites for *Galearis spectabilis* in New Hampshire, only two are outside the Connecticut River Valley. One of these stations, a population discovered by Herbert Sargent in Tuftonboro in 1935, seems to have disappeared. A third previously unrecorded population of Showy Orchis in Franklin, Merrimack County was shown to the author in 1982.

In New Hampshire the natural habitat of the Showy Orchis occurs within a climax forest community, dominated in this area by Beech (*Fagus grandifolia*), Sugar Maple (*Acer saccharum*), and Hemlock (*Tsuga canadensis*). In this section of its range, the response of this species to disturbance is highly negative (Auclair, 1972). Unfortunately, the number of undisturbed areas remaining in the eastern deciduous forest is declining rapidly and this loss contributes to the decline of *Galearis spectabilis*. The species is listed as "vulnerable" by Storks and Crow (1978). The Showy

Orchis apparently has animal predators too, as the last known plant of this species growing in Rhode Island was reported to have been eaten, presumably by a skunk, about 1963 (Stucky, 1967)!

Attempts to germinate seeds of the Showy Orchis in the laboratory have proven unsuccessful. There exists a dormant condition in the ripe seed that is obviously broken in nature, but the means of breaking this dormancy is presently unknown to researchers (Stoutamire, 1964).

Galearis spectabilis is a true food plant for insects (L. A. Nilsson, 1980). It offers rewards to visitors in the form of nectar which is pooled in the broad spur. Robertson (1928) recorded visits by females of *Bombus separatus* and *B. americanorum* (Apidae), two species of long-tongued bees.

An unusual pink-lipped form of *Galearis spectabilis* has been named forma *Willeyi* for Herman Willey (Seymour, 1970).

GENERAL DISTRIBUTION: Eastern North America: New Brunswick south to Georgia and Alabama, west through the southern Great Lake states to Minnesota, and the Mississippi embayment region of Missouri and Arkansas.

3. **Coeloglossum** Hartman, Handb. Skand. Fl. 329. 1820.

The genus *Coeloglossum* was described in 1820 by Hartman based on *Coeloglossum viride,* originally included in the genus *Satyrium* by Linnaeus (1753). The name *Coeloglossum* is derived from the Greek for "hollow tongue," referring to the saccate spur that characterizes this genus. The genus is currently treated as having a single species which includes two ecotypes that have been variously interpreted as separate species, subspecies, or varieties; they are here treated on the subspecies level.

1. *Coeloglossum viride* (L.) Hartman subspecies *bracteatum* (Muhl. *ex* Willd.) Hultén.

Coeloglossum viride is a polymorphic species with a widespread distribution throughout the colder regions of the Northern Hemisphere. In southern areas of Europe, Asia, and North America it is confined to cool montane regions (Meusel *et al.*, 1965; Leur, 1975). In Europe *C. viride* is commonly known as the "Frog Orchid" or "Die Hohlzunge" (Hollow-tongue) (Summerhayes, 1951; Schrenk, 1975). The epithet *viride* is Latin for "green," the color of the flowers.

The North American plant referred to *Coeloglossum* was originally designated as a distinct species, *Orchis bracteata,* by Muhlenberg. He sent a specimen of Long-bracted Orchid from Pennsylvania to Willdenow who published a description of the plant in his *Species Plantarum* (1805). In 1813, R. Brown transferred the species to the genus *Habenaria.* Until recently most American botanists have treated the Long-bracted Orchid as *Habenaria viridis* var. *bracteata.* The conspicuous long floral bracts give this subspecies of *C. viride* its common name.

COMMON NAMES: Long-bracted Orchid, American Frog Orchid.

FLOWERING DATES IN NEW HAMPSHIRE: Late may through July.

DESCRIPTION: Plant stout, glabrous, from a thickened rhizome, 10–60 cm tall. Roots fleshy. Leaves dark green, 3–5, oblanceolate to lanceolate, clasping the stem. Floral bracts linear, acuminate, much exceeding the length of the flowers. Inflorescence a spike of inconspicuous green flowers. Ovaries sessile, stout, 5–10 mm long. Dorsal sepal ovate, concave. Lateral sepals obliquely oblong. Lateral petals lanceolate. Lip oblong, 3–8 mm long, bi-lobed (sometimes with a small, often obscure tooth in the open sinus), with a thickened median ridge. Spur saccate, greenish-white, approximately 2 mm long. Capsule ellipsoid, ascending.

CHROMOSOME NUMBER: $2n = 40$

Terrestrial orchids are known for producing inconspicuous flowers that are often curious-looking rather than aesthetically pleasing. The Long-bracted Orchid is one such species; it is even difficult to determine without a close inspection whether or not the Long-bracted Orchid is blooming. When flowering occurs the sepals and lateral petals barely expand and retain a bud-like form. Only the presence of the green lip extending downward from beneath the hood of sepals and petals verifies that the plant is in full bloom.

Ostensibly this species has a wide range of flowering dates, but I have found the Long-bracted Orchid to be an early (May) bloomer, as did Morris and Eames (1929). Microclimatic influences such as moisture and light availability are apparently important factors in determining flowering time. In New Hampshire, *Coeloglossum viride* ssp. *bracteatum* is most often found in rich deciduous woods. The plants tend to grow singly with only a few scattered individuals at each location. The Long-bracted Orchid is a boreal species and occurs more frequently in the northern areas of the state. Soil reaction studies indicate that this species grows in soils where the pH is between 5.0 and 6.0 (Stuckey, 1967; Wherry, 1918).

In addition to the distinctively long floral bracts, the Long-bracted Orchid is characterized by a small, saccate spur, often described in manuals as "scrotoform." In a study of *Ceologlossum viride* in the Faroes, Hagerup (1951) found that the wide throat of the nectar-filled spur is covered by a thin membrane. The membrane has only one narrow opening which is hidden behind the thickened base of the lip. In order to partake of the nectar an insect must squeeze its proboscis through the tiny aperture, or penetrate the membrane. Insects with strong biting mandibles, such as beetles, can easily break the thin membrane (Hagerup, 1952).

In Finland, Silen (1906) reported that *Coeloglossum viride* was pollinated by beetles of the genus *Cantharis* (Cantharidae). He also observed visits to the flowers by wasps and mosquitoes. I have seen no reports listing pollinators specifically for subspecies *bracteatum*. The Long-bracted Orchid obviously attracts sufficient pollinators to perpetuate itself; it is one of the most common and widely distributed northern orchids.

GENERAL DISTRIBUTION: Boreal North America; south in the mountains to North Carolina and New Mexico; west to Alaska and the Aleutian Islands; Japan and China.

4. **Platanthera** L. C. M. Rich., Mem. Mus. Paris. 4: 48. 1818.

Most species in this genus were originally described as members of the genus *Orchis*. Although Richard segregated those plants with caudicles of the pollinaria adnate to the column into his genus *Platanthera* in 1818, most botanists, until very recently, treated these plants as members of the genus *Habenaria*. *Habenaria* was described by Willdenow (1805) to accommodate two tropical American orchids with projecting anther caudicles (Stoutamire, 1974). The tropical genus *Habenaria* as now understood is distinguished from *Platanthera* by its two stigmatic lobes borne on stalks beside or below the nectary opening. *Platanthera* has a single median stigma above the nectary opening, and is largely composed of plants with temperate distributions (Stoutamire, 1974).

Platanthera consists of about 200 species (Leur, 1975). Typically, the base of the lip is spurred, and the length of the spur usually corresponds to the tongue-length of a specific pollinator. In this genus the pollinia are attached to caudicles which are distally united to a sticky disc of cells called the viscidium (L. A. Nilsson, 1978). The entire complex structure has the shape of a drumstick or club, and has been termed a "pollinarium" or a "hemipollinarium" (Dressler, 1981). The two pollinaria are embedded in locules on either side of the opening of the nectary, with the sticky discs of the viscidia facing each other. The distance between the viscidia usually corresponds with the size of the head of a specific pollinating insect. As the insect probes the nectar-containing spur with its proboscis, the viscidia adhere to the pollinator, and the pollinaria are pulled from their locules. At this point, one of the most amazing adaptations for cross-pollination occurs. As the insect flies to another flower to partake of more nectar, the caudicles rotate downward and inward resulting in the pollinaria being in a position to come directly in contact with the stigma of the next visited flower. This phenomenon was studied by Darwin (1877) and by Gray (1862–1863). Most Platanthera species are pollinated by moths and butterflies (Lepidoptera).

The name *Platanthera* is derived from two Greek words signifying "wide-anther."

Key to the Species of *Platanthera* in New Hampshire

1. Lip fringed or lacerate along margin .... (2)
   2. Flowers white; lip entire; plants of sphagnum bogs .... 1. *P. blephariglottis*
   2. Flowers rose, pink, purple or green (rarely white), lip divided into three segments; plants usually not occurring in sphagnum bogs .... (3)
      3. Flowers green; plants of hayfields and roadsides (occasionally woods) .... 4. *P. lacera*
      3. Flowers pink, rose or purple (rarely white); plants of wet ditches, marshes and woods .... (4)

4. Lip typically shallowly fringed; opening of nectary oblong, constricted and appearing as 2 lateral openings . . . . 2. *P. psycodes*
4. Lip typically deeply fringed; opening of nectary circular and unobstructed . . . . 3. *P. grandiflora*

1. Lip margin entire . . . . (5)
   5. Leaves basal, with or without bracts on stem . . . . (6)
      6. Leaf solitary, ovate; plants of northern woods . . . . 7. *P. obtusata*
      6. Leaves two, oblong to orbicular, at or near the surface of the ground; plants of mixed or deciduous woods. . . .(7)
         7. Flowers white; lip curved downward; stem with several small bracts . . . . .5.*P. orbiculata*
         7. Flowers greenish-yellow; lip curved upward; stem with one bract or naked . . . . 6. *P. hookeri*
   5. Leaves cauline; bracts present . . . . (8)
      8. Plant with a single prominent leaf; flowers askew, greenish; spur club-shaped; plant of wet woods and moist ditches . . . . 8. *P. clavellata*
      8. Plant with two or more prominent leaves; flowers not askew, white, yellowish or greenish; spurs variously shaped but not club-shaped; habitats various . . . . . . (9)
         9. Flowers whitish-yellowish; lip bearing a prominent tubercle, apex blunt . . . . 9. *P. flava*
         9. Flowers white or greenish; lip lacking a tubercle, apex acute . . . . (10)
            10. Flowers white, strongly fragrant; lip abruptly dilated at base. . . . . 10. *P. dilatata*
            10. Flowers green, only slightly fragrant; lip gradually widened at base . . . . 11. *P. hyperborea*

1. *Platanthera blephariglottis* (Willd.) Lindl., Gen. Sp. Orchid. 291. 1835.

Willdenow (1805) described this species as *Orchis blephariglottis* from plants collected in Pennsylvania. This orchid has also been known as *Habenaria blephariglottis* and *Blephariglottis blephariglottis*. The epithet *blephariglottis* translates as "eyelid-tongue," in reference to the tongue-shaped fringed lip.

COMMON NAME: White Fringed Orchid

FLOWERING DATES IN NEW HAMPSHIRE: July through August

DESCRIPTION: Plant from many fleshy roots, glabrous. Stem leafy, strongly ribbed. Leaves 2–3, sheathing the lower stem, elliptic-lanceolate, somewhat keeled, becoming bracteate above. Inflorescence a raceme. Floral bracts lanceolate. Flowers snow-white with a cream colored column. Dorsal sepal ovate, concave. Lateral sepals ovate, oblique. Lateral petals linear to oblong, erose at apex. Lip tongue-shaped, fringed at margins. Spur slender, slightly curved. Capsule ellipsoid, ascending.

CHROMOSOME NUMBER: $2n = 42$ (Moore, 1973).

Platanthera blephariglottis is an orchid of Black Spruce-Tamarack bogs. It is seldom found on the open mat near the water's edge where Rose Pogonias, Grass-pinks, and cranberries thrive; its preference is the partial shade of small shrubs and tall grasses. The snow-white spires of the White Fringed Orchid are in bright contrast with the bog greenery. Inspecting an individual flower, one can see that the oval lip is copiously cut along the margins into a feathery fringe. Occasionally plants of this species appear with an unfringed lip, a form that was segregated by Lindley, and graphically named *P. holopetala.*

In *Platanthera blephariglottis,* the projections of the column in which the pollinaria are embedded are a creamy light-gold color. The tips of the long curved spurs are also of a golden color, indicating the presence of nectar within.

Smith and Snow (1976) reported that in Michigan, *Platanthera blephariglottis* is predominantly pollinated by several species of moths. Insects that were captured in their study carrying pollinaria of the White Fringed Orchid include *Darapsa versicolor, Haemorrhagia thysbe* (Sphingidae), *Papilio troilus* (Papilionideae), and *Bombus* sp. (Apidae). In the same study, the Spicebush Swallowtail, *Papilio troilus* was also found to be a pollinator of the Yellow Fringed Orchid *P. ciliaris.* This orchid is closely related to the White Fringed Orchid, the major difference being the color of the flowers. When sympatric, the two species occasionally hybridize, most probably through the services of the Spicebush Swallowtail. Although the Yellow Fringed Orchid was reported from the state of New Hampshire in 1872, it has not been found here since. It is possible that the determination documenting the report was incorrect, as it is difficult to distinguish the two taxa on the basis of dried herbarium material.

At the southern end of its range, the White Fringed Orchid is sometimes segregated as var. *conspicua* on the basis of larger flowers and longer spurs (Correll, 1950).

Although the White Fringed Orchid is often locally abundant in the state, the species seems to be experiencing a decline in its numbers in New Hampshire. Over an eight-year period, I have observed a drop in the number of individual plants at established locations. Reports of new stations for this orchid are rare. Perhaps the ostensible decline of this species is more apparent than real; there may be many populations of White Fringed Orchids hidden in undiscovered bogs throughout the state.

GENERAL DISTRIBUTION: Newfoundland south through New England and the mid-Atlantic states, west to Ontario and Michigan, south to Florida, west to Texas.

2. *Platanthera psycodes* (L.) Lindl., Gen. Sp. Orchid. 294. 1835, as to synonymy and name, excluding description.

Linnaeus (1753) described this species, which was collected by Peter Kalm in Canada, as *Orchis psycodes.* Lindley transferred the taxon to the genus *Platanthera,* but his accompanying description was of the species that is known today as *P. lacera.* This orchid is perhaps most well known by American botanists as *Habenaria psycodes.* The species name *psycodes* is a misspelling of "psychodes," the Greek word for "butterfly," perhaps alluding to the shape of the flowers.

COMMON NAMES: Small Purple Fringed Orchid, Butterfly Orchid

FLOWERING DATES IN NEW HAMPSHIRE: late July to mid-August

DESCRIPTION: Plant glabrous, leafy, from fleshy roots. Leaves 2–5, elliptic to lanceolate, becoming bracteate above. Inflorescence a densely flowered raceme. Floral bracts lanceolate. Flowers mauve or purplish (rarely white), fragrant. Sepals elliptic. Lateral petals ascending, spatulate with denticulate margins. Lip cleft into 3 divisions, fringed, reflexed. Spur slender, slightly clavellate. Opening of nectary constricted by a projection with the resulting appearance of 2 openings. Capsule ellipsoid, ascending.

CHROMOSOME NUMBER: $2n = 42$ (Stoutamire, 1974).

Platanthera psycodes occurs in New Hampshire in wet grassy areas and along stream sides. This showy species lends its various shades of pinkish-purple flowers to the mid-summer July landscape. In large colonies of the Small Purple Fringed Orchid one can sometimes find a rare albino form (forma *albiflora*). In our area this species flowers later than the Large Purple Fringed Orchid, *P. grandiflora,* with which it is often confused. This confusion arises because the two taxa have been treated by many botanists as varieties of a single species. Distinctions between the two taxa in the past have been based largly on size, which, despite the common names, is not a reliable criterion.

Stoutamire (1974) did a comparative study of the two orchids and found that in most areas where both occur, the mean height of *P. psycodes* exceeds that of *P. grandiflora.* I have never encountered such a situation in New Hampshire perhaps owing to a relatively small number of populations of the Small Purple Fringed Orchid in the state (map 9). An easily observable difference between typical individuals of each species is found in the appearance of the raceme. In *P. psycodes* the raceme is tightly packed with many small individual flowers; it has the overall shape of a cylinder. The inflorescence in *P. grandiflora* is loosely flowered with fewer, larger blossoms, and is noticeably wider. The tripartite lip of the Small Purple Fringed Orchid is typically reflexed downward while the lip of the Large Purple Fringed Orchid is more widely spreading and curved upward.

While these attributes may vary, Stoutamire (1974) found basic morphological differences between the two species that are functionally important. He found that the structure of the column and the shape of the nectary are characters that consistently separate the two taxa and determine their pollination biology. The nectary opening in *Platanthera psycodes* is oblong in shape but partially constricted so as to produce "two lateral openings, one beneath each viscidium" (Stoutamire, 1974), whereas the circular opening of the nectary in *P. grandiflora* is unobstructed. These seemingly slight differences in floral morphology dictate different pollinators for each species, and thus the two taxa remain reproductively isolated.

S. I. Smith of Norway, Maine, observed the Hawkmoths *Sesia* (*Haemorrhagia*) *thysbe* and *S.* (*H.*) *diffinis* (Sphingidae), and a Swallowtail *Papilio polyxenes asterias* (Papilionidae) visit the flower of *Platanthera psycodes.* The insects had "their probosces so encumbered with the pollinia, that it was impossible for them to be coiled up between their palpi" (Smith, 1863). In Michigan, Stoutamire (1974) also observed the Hawkmoth *Haemorrhagia thysbe* visiting the Small Purple Fringed Orchid, as well as the Skipper *Polites mystic* (Hesperiidae), each carrying pollinaria of the orchid.

Although the scent of the Small Purple Fringed Orchid has been described as sweet (Gray, 1862–1863), I am inclined to agree with Baldwin (1894) who described the odor as "rank." To Ramsey (1966) the scent of this species is like "fresh calico."

Platanthera psycodes forms natural hybrids with the more widespread Ragged Orchid. A hybrid plant was first discovered by M. W. White and A. L. Andrews in a "very wet meadow in Pownal, Vermont, July 22, 1898" (Andrews, 1901). White (1904) named the hybrid *Habenaria ×andrewsii* in honor of his friend, Andrews, a well known bryologist, and published it in Niles (1904). The hybrid is intermediate between the two parents and most often occurs in the northern areas of this state. In Nova Scotia, I have seen roadside ditches filled with flowering plants of *P. psycodes, P. lacera,* and hybrids of every conceivable intermediate form.

GENERAL DISTRIBUTION: Newfoundland west through the Great Lakes area to Ontario and Minnesota, south through New England and the mid-Atlantic states to Virginia; continuing southward in the mountains to Georgia.

3. *Platanthera grandiflora* (Bigelow) Lindl. Gen. Sp. Orchid. 294. 1835.

Investigating the nomenclatural history of this taxon is a confusing and frustrating ordeal. Fortunately, Stoutamire (1974) has assiduously researched the subject recently and has determined that the correct name for this species is *P. grandiflora.* He reported that, due to inadequate descriptions and lack of type materials, older names previously ascribed to this taxon must be rejected, thus Bigelow's (1824) combination of *Orchis grandiflora* must be taken as the basionym. Bigelow based his description on plants found in

Massachusetts and Enfield, New Hampshire. The lectotype is deposited in AMES.

American botanists have long known this species as *Habenaria fimbriata.* The epithet *grandiflora* means "large-flowered."

COMMON NAME: Large Purple Fringed Orchid

FLOWERING DATES IN NEW HAMPSHIRE: late June to early August

DESCRIPTION: Plant from fleshy roots, glabrous, leafy. Leaves 2–6, elliptic at base, becoming lanceolate and then bracteate above. Inflorescence a loosely-flowered raceme, approximately 2–4 times longer than broad. Floral bracts lanceolate. Flowers lilac to rose-purple. Sepals ovate-elliptic. Dorsal sepal erect, lateral sepals spreading. Lateral petals oblong with finely dentate margins. Lip cleft into 3 fan-shaped segments, deeply fringed. Spur slender, slightly clavellate. Capsule ellipsoid, ascending.

CHROMOSOME NUMBER: $2n = 42$ (Stoutamire, 1974).

Robert Frost (1964) referred to the Purple Fringed Orchid as "the far sought flower." It is the largest of our orchids, and one of the most beautiful. Thoreau (1884) stated that Bigelow thought it to be the most beautiful of all the orchids, and added "Is it not significant that some rare and delicate and beautiful flowers should be found only in unfrequented wild swamps?" In New Hampshire, swampy areas are not the only habitats for *Platanthera grandiflora.* The tall purple wands can often be found along wet, unmowed roadsides, while less robust forms inhabit wet woodlands, sometimes flourishing in the darkness of a coniferous forest. It is in open areas that this species attains its greatest size. Ramsey (1966) reported an individual plant of the Large Purple Fringed Orchid a full five feet tall, and Morris and Eames (1929) observed flowers with lips more than 1 1/8 inches in width.

The loosely flowered racemes of lilac to rose-purple flowers are typically more deeply fringed then in *Platanthera psycodes* and suggested to Baldwin (1894) "a flock of birds struggling to get foot-hold on the same branch." Such abundance of form and beauty alone would make this species exceptional, but the scent of the flowers elevates the Large Purple Fringed Orchid to a thing of perfection. The fragrance is reminiscent of the sweetest-smelling roses, only it is much nicer.

Flowers of *Platanthera grandiflora* are adapted for pollination by long-tongued Lepidoptera which transport the pollinaria attached to their compound eyes (Stoutamire, 1974). Van der Pijl and Dodson (1966), and Moldenke (1949) reported the Large Purple Fringed Orchid as being pollinated by moths. Various species of Swallowtail butterflies have also been reported as visiting the orchid (Stoutamire, 1974; Ramsey, 1966). I have also observed these butterflies on the flowers of *P. grandiflora.*

Occasionally, plants of the Large Purple Fringed Orchid occur with narrow and fringeless middle lip divisions. Fernald (1946b) has called such individuals forma *menotonsa* (with shaved chin). I saw this form, as well as an albino form, in the same swampy area of Rumney, Grafton County, in 1978.

General distribution: Newfoundland west through the Great Lakes area to Ontario and Minnesota, south to Virginia, and continuing southward in the mountains to Tennessee; west to Iowa.

4. *Platanthera lacera* (Michx.) G. Don in Sweet, Hort. Brit. ed. III. 650. 1839.

This species was described by Michaux (1803) from plants collected in Carolina. It has also been known as *Habenaria lacera* and *Blephariglottis lacera.* The epithet *lacera* is Latin for "torn," descriptive of the deeply fringed lip.

Common names: Ragged Orchid, Green Fringed Orchid

Flowering dates in New Hampshire: July through mid-August

Description: Plant from fleshy roots, glabrous, leafy, up to 60 cm tall. Leaves rigid, 2–5, sheathing lower stem below, oblong to lanceolate, becoming bracteate above. Inflorescence a loosely flowered raceme of greenish-white to yellowish flowers. Floral bracts lanceolate. Dorsal sepal ovate. Lateral sepals oblong, oblique, reflexed. Lateral petals linear-oblong, ascending. Lip deeply tripartite. Lateral lobes deeply cut into thread-like fringes. Mid-lobe linear-spatulate, cut about half-way into fringes. Spur slender, slightly clavellate. Capsule ellipsoid, ascending.

Chromosome number: $2n = 42$ (Stoutamire, 1974).

The Ragged Orchid is a widespread and common midsummer orchid in New Hampshire. This species often grows in open, grassy areas where it is hidden in tall grasses. The greenish flowers seem inconspicuous at first, but a closer look reveals a most delicate and lacy blossom. The British horticulturist Robert Sweet described the Ragged Orchid as being "elegantly jagged" (Gibson, 1905).

Platanthera lacera is tolerant of a wide variety of habitats. It occurs in both damp and drier habitats, in the open and, sometimes, in the woods. The favored habitat of this species is hayfields where it usually blossoms just before the hay is cut. Several times I have plucked a specimen only minutes before the mower flattened the waving herbage. Morris and Eames (1929), in their discussion of *P. lacera,* referred to the "deadly swarth of the mower's scythe," but I have found that, just as the grasses reappear the following year, so do these hardy orchids.

Stoutamire (1974) found the Hawkmoth *(Haemorrhagia thysbe* (Sphingidae) carrying the pollinaria of both *Platanthera lacera* and *P. psycodes.* These insects are probably the agents responsible for producing the hybrid between the two taxa, *P.* ×*andrewsii.* Gray (1862 1863) observed that nectar was more plentiful in the spurs of older flowers ("almost full"), especially those individuals which had their pollinaria removed and stigma fertilized.

In Newfoundland *Platanthera lacera* var. *terrae-novae,* a robust plant with less dissection of the lip, replaces the typical var. *lacera* (Fernald, 1926b).

General distribution: Newfoundland west to Ontario and Wisconsin, south to Georgia, west to eastern Texas.

5. *Platanthera orbiculata* (Pursh) Lindl. Gen. Sp. Orchid. 286. 1835.

Pursh (1814) originally described this orchid from plants found in shady Beech woods in the mountains of Pennsylvania and Virginia. He noted that the plant was known "in the mountains by the name of Heal-all." The name *orbiculata* is Latin for "round," referring to the two large, round leaves.

Common name: Large Round-leaved Orchid

Flowering dates in new hampshire: late June through early August

Description: Plant from long, fleshy roots, glabrous, scapose. Leaves 2, lying flat on the ground, subopposite, basal, elliptic to orbicular, shiny blue-green above, silvery beneath. Stem stiffly erect with one or two small bracteate leaves. Inflorescence a loosely-flowered raceme. Floral bracts linear-lanceolate. Flowers white, few to 25 or more. Dorsal sepal erect, sub-orbicular. Lateral sepals oblong, obtuse, reflexed. Lateral petals ovate-lanceolate, oblique, spreading. Lip linear-oblong, pendant, recurved. Spur long and slender. Column large with 2 wing-like projections on each side. Capsule ellipsoid, ascending.

CHROMOSOME NUMBER: $2n = 42$ (Moore, 1973).

The Large Round-leaved Orchid is a species that, in our region, is confined to woodlands. It is most common in rich deciduous woods but can also be found in mixed or coniferous forests. A favored spot for *Platanthera orbiculata* is by the base of a large tree. I once found it blossoming in an open, slash-filled area in a cut-over Cedar woods in Coos County. The Large Round-leaved Orchid is not uncommon in the higher, cooler regions of the state, but is rarer in the southeastern lowlands.

Platanthera orbiculata is a large and impressive plant, even in the vegetative state. The twin leaves, which range in shape from oblong to perfectly round, are sometimes as large as 19 cm in diameter. The shiny, blue-green leaves hug the forest floor closely, but if pried up they reveal a silver surface on their undersides. In a population of Large Round-leaved Orchids, there are usually more vegetative plants than flowering individuals.

Exceptionally large plants of the Large Round-leaved Orchid have been described as a separate species, *Platanthera macrophylla,* which Ames (1906) distinguished on the basis of spur length. Leur (1975) treated the larger plants as *P. orbiculata* var. *macrophylla,* while Morris and Eames (1929) referred to them as forma *macrophylla.* The majority of plants that I have seen from New Hampshire approach the larger form. Additionally, a dwarfed plant of this species from Newfoundland has been described as var. *lehorsii* (Fernald, 1950b). It is apparent that *P. orbiculata* is exceedingly plastic in regard to size.

The large curious-looking flowers have elongated lips and spurs. By night, the white blossoms are conspicuous and lightly fragrant. Night-flying Hawkmoths are lured to the flowers to sip from the nectar-filled spurs. The moth *Sphinx drupiferanun* (Sphingideae) is listed by van der Pijl and Dodson (1966) as a pollinator of *Platanthera orbiculata.* Stoutamire (1971) also reported the moths *Autographa ampla* and *Plusia balluca* (Noctuidae) to be pollinators of this species. According to Gray (1862–1863) self-fertilization in this species is "out of the question." The Large Round-leaved Orchid does reproduce vegetatively and it is common to find colonies where the large leaves of several plants overlap.

GENERAL DISTRIBUTION: Woodlands from Newfoundland, following the tree-line to Alaska and the Aleutians, south to Virginia and continuing southward in the mountains to Georgia, west to Washington and Oregon.

6. *Platanthera hookeri* (Torr.) Lindl., Gen. Sp. Orchid. 286. 1835.

This species was described from plants collected in New York, and was named for William Jackson Hooker (1785–1865), an English botanist who published, among other works, a flora of northern "British" America (Stafleu, 1967). This species has also been known as *P. hookeriana* and *Habenaria hookeri.*

COMMON NAME: Hooker's Orchid

FLOWERING DATES IN NEW HAMPSHIRE: late May to early July

DESCRIPTION: Plant from long, fleshy roots, glabrous, scapose. Leaves 2, basal, sub-opposite, oval to orbicular, light green. Stem olive-colored, naked or with a solitary bract. Inflorescence a loose, elongate raceme of few to many flowers. Floral bracts lanceolate. Flowers yellowish-green, erect. Dorsal sepal ovate to triangular. Lateral sepals oblong-lanceolate, strongly reflexed. Lateral petals linear, falcate, connivent with dorsal sepal. Lip triangular, acute, strongly upcurved. Spur slender. Column with a tubercle above stigma. Capsule ellipsoid, ascending.

CHROMOSOME NUMBER: $2n = 42$ (Moore, 1973).

Hooker's Orchid is one of our early-blooming woodland species with a habitat preference for rich deciduous woods of Sugar Maples and Beech. It is often associated there with other orchids; I have found this orchid growing near the Showy Orchid, reaching its peak bloom a few days after *Galearis spectabilis.* In New Hampshire this species is widespread but does not occur as often as the Large Round-leaved Orchid.

Superficially, Hooker's Orchid resembles *Platanthera orbiculata* but can be distinguished by its smaller leaves that are not typically as flattened as those of the latter. The stem is an olive-green color and is usually naked. The flowers of *P. hookeri* are quite distinct, being closer to the rachis, yellowish in color, and with a wider, upturned lip. The whole appearance of the flower has been likened to a "gargoyle" (Correll, 1950), or termed "grotesque" (Schrenk, 1977). The most practical description for determining this species is given by Morris and Eames (1929) who coined the phrase "Hooker's hooks" as an "identity-tag." The pair also stated that the origin of the hooked lip is from the crease of its folding in the bud.

In *Platanthera hookeri* the viscidia are more widely divergent than in our other Platantheras, and an insect would be quite able to steal nectar without coming in contact with the pollinaria if it were not for the upturned lip that prevents a direct approach to the nectary (Gray, 1862–1863). An insect must approach the nectary from the side and in doing so "its face will almost certainly be brought into contact with one of the discs" (Darwin, 1877). Darwin (1877) also reported that Gray observed a butterfly, *Nisoniades* (Hesperiidae) in Canada with the pollinaria of *P. hookeri* attached to its eyes. Since the genus *Nisoniades* is tropical in distribution, only rarely reaching southern Texas, Gray must have seen another Skipper in Canada.

General distribution: Nova Scotia west through the Great Lakes area to Iowa, Michigan and Manitoba, south to Pennsylvania.

7. *Platanthera obtusata* (Banks ex Pursh) Lindl., ssp. *obtusata* Gen. Orchid. 284. 1835.

This species was collected by the British naturalist Sir Joseph Banks, and was described in Pursh's *Flora Americae Septentrionalis* in 1814. The type specimen was collected from Hudson Bay in Canada. The name *obtusata* means "blunt," and refers to the rounded apex of the solitary leaf.

Common names: Blunt-leaf Orchid, Small Northern Bog Orchid

Flowering dates in new hampshire: July to early August

Description: Plant from a few fleshy roots, small (usually not over 20 cm tall), glabrous. Leaf solitary (rarely 2), obovate to oblanceolate, blunt at apex. Stem naked or with 1–2 bracteate leaves.

Inflorescence a few-flowered raceme of greenish-white flowers. Floral bracts lanceolate. Dorsal sepal concave, ovate with rounded apex. Lateral sepals lanceolate-elliptic, oblique, reflexed. Lateral petals triangular-lanceolate, apiculate, connivent with dorsal sepal. Lip fleshy, linear-lanceolate, pendant, with a callus in the center of the base that serves to divide the nectary opening. Spur triangulate, elongated, curved. Capsule ellipsoid, ascending.

CHROMOSOME NUMBER: $2n = 126$ (ssp. *oligantha*).

The Blunt-leaf Orchid is a small and inconspicuous *Platanthera*. It is a true plant of the north, being distributed beyond the tree-line into the alpine zone of mountains and tundra of the arctic. This species also occurs in sections of northernmost Eurasia where those plants have been segregated as ssp. *oligantha*. Subspecies *oligantha* is a smaller plant with fewer flowers than our ssp. *obtusata*. Intermediates between the two races have been reported from Alaska (Moore, 1980). In eastern North America, the southern limit of the Blunt-leaf Orchid is reached in northern New England. This species is not widespread in New Hampshire as it requires a habitat where midsummer soil temperatures rarely exceed 15° C. (Stoutamire, 1968). Accordingly, *P. obtusata* is found in the montane locations in the upper-middle region of New Hampshire, and in the cold, swampy woods of the northern part of the state. To find this orchid, one must explore wet, northern woods floored with mosses and humming with insects. Once a plant of *P. obtusata* is discovered, a quick search of the area will often reveal many more individuals as this species, once established, forms large populations. The whitish-green flowers of the Blunt-leaf Orchid are described as "galeate," or helmet-shaped, in reference to the hood formed by the convergence of the lateral petals and the dorsal sepal. Although Raup (1930) described this species as possessing scent, I have not been able to detect an odor. It is possible that the flower may become more fragrant toward the end of the day.

Platanthera obtusata has the distinction of being one of the few plants known that is pollinated by mosquitoes. I have often observed mosquitoes resting on orchid flowers, but in this case mosquitoes have actually been observed carrying the pollinaria of this species (Raup, 1930; Stoutamire, 1968; Thein, 1969; Thein and Utech, 1970). Although mosquitoes are not well known as pollinators, there is evidence that these insects obtain nectar for food in the higher latitudes (Hocking, 1968). Kevan (1972) reported mosquitoes of the genus *Aedes* (Culicidae) carrying pollen of the Mountain Avens (*Dryas integrifolia*) in the high Canadian arctic. Stoutamire (1968) and Thein (1969) found *Aedes* spp. with the pollinaria of *P. obtusata* in Michigan and Wisconsin respectively.

The callus on the base of the lip of this orchid which divides the nectary opening makes it necessary for the insects to approach the nectary from the side. Mosquitoes probing the nectary come in contact with a viscidium which attaches the pollinarium to the insect's eye. Moths of the genus *Xanthorhoe* (Geometridae) have also been observed on the flowers of the Blunt-leaf Orchid, and with the pollinaria attached to their eyes (Stoutamire, 1968; Thein and Utech, 1970).

GENERAL DISTRIBUTION: Woodlands, Labrador and Newfoundland, west to the Aleutians, south to northern New England, west through the Great Lakes area, south in the western mountains to Colorado; Norway, Sweden, northern parts of central and eastern Asia.

8. *Platanthera clavellata* (Michx.) Leur, Native Orchids Fla. 148. 1972.

Michaux (1803) named this species *Orchis clavellata,* which he described from plants collected in Carolina. At one time it was called *Habenaria tridentata* for the three small teeth at the apex of the lip. The epithet *clavellata* means "little club," referring to the club-shaped spur.

COMMON NAMES: Little Club-spur Orchid, Small Green Wood Orchid

FLOWERING DATES IN NEW HAMPSHIRE: July through August

DESCRIPTION: Plant glabrous, small (5–35 cm tall), from slender, fleshy roots. Stem angled, with several linear-lanceolate bracts and one lower, well-developed leaf, oblong to oblanceolate. Inflorescence a few- to many-flowered raceme. Floral bracts lanceolate. Flowers whitish to yellowish-green, askew. Sepals ovate, obtuse. Petals ovate, oblique, obtuse. Lip oblong-cuneate, truncate, with 3 obscure notches at apex. Spur slender, clavellate, curved. Capsule ellipsoid, ascending.

CHROMOSOME NUMBER: $2n = 42$ (Moore, 1973).

One of our most common orchids, *P. clavellata* is distinct; no other orchid in our flora carries its flowers at such an angle ("askew"), a feature that is seldom captured in drawings of this species. In New Hampshire, the Little Club-spur Orchid is widespread and common. One reason for its abundance is that it can occur in a wide variety of habitats. I have found this orchid in acidic roadside seeps that later yielded prodigious numbers of Nodding Ladies'-tresses (*Spiranthes cernua*), and in boggy open habitats in the company of Rose Pogonias (*Pogonia ophioglossoides*). In deeply shaded woods the Blunt-leaf Orchid appeared with the fruiting Early Coral-root (*Corallorhiza trifida*), and the flowering Large Purple Fringed Orchid (*Platanthera grandiflora*).

In *Platanthera clavellata*, there is usually only one well-developed leaf-blade near the base of the plant, and 2–5 small bracteate leaves higher on the stem. The flowers seem to be of a more whitish-yellowish color when growing in the open, and more of a greenish hue under shade. The broad wedge-shaped lip has three small notches at the apex. The long curved spur widens at the end into the club-shape that gave this orchid its name.

Gray (1882–1883) observed that packets of pollen in *Platanthera clavellata* often detach themselves from the pollinaria and fertilize the stigma before the flower opens. Because the Little Club-spur Orchid is self-fertilizing, almost all of the flowers form fruit. No doubt, this reproductive strategy is partially responsible for the abundance of *P. clavellata* in New Hampshire.

GENERAL DISTRIBUTION: Newfoundland west through the Great Lakes area to Ontario and Minnesota, south to northern Florida, west to Texas.

9. *Platanthera flava* (L.) Lindl. Gen. Sp. Orchid. 293. 1835.

From plants collected in Virginia, Linnaeus described this species as *Orchis flava*. It has had an interesting history of nomenclature, often being confused with *Coeloglossum viride*. Some of the many names by which it has been known include *Habenaria flava* and *P. herbiola*. Some authors (Senghas, 1973) place this species in a separate genus as *Tulotis flava*. The name *flava* means "yellow" and refers to the yellowish flowers.

COMMON NAME: Tubercled Orchid

FLOWERING DATES IN NEW HAMPSHIRE: late June through July

DESCRIPTION: A glabrous, leafy plant from several fibrous roots. Leaves 2–5, oblong-elliptic to lanceolate, spreading, becoming bracteate above. Inflorescence sub-scapose. Floral bracts lanceolate, acuminate, longer than the lower flowers, equalling or shorter than the upper flowers. Flowers yellowish-white. Dorsal sepal ovate, concave. Lateral sepals ovate, oblique. Lateral petals ovate, forming a loose, wide hood with the dorsal sepal. Lip oblong-quadrate with a lobe-like tooth on each side near the base, and a projecting tubercle at the middle in front of the nectary. Capsule ellipsoid, ascending.

CHROMOSOME NUMBER: $2n = 42$ (Moore, 1973).

Platanthera flava is an orchid that is neither beautiful nor common in New Hampshire. It is primarily a species with a more southern distribution, with our more robust northern plants being referred to var. *herbiola.* In New Hampshire the Tubercled Orchid grows in swales, or in wet or rocky woods. It is most often found in swales where it grows amongst a tangle of grasses, sedges, and ferns. To distinguish the orchid from the surrounding herbage takes a sharp eye, and it is helpful if one has a previous acquaintance with the Tubercled Orchid.

The majority of New Hampshire stations for this species are in Strafford County, but it has also been found in Cheshire and Coos County. *Platanthera flava* is listed as "threatened" in *Endangered and Threatened Plants of the United States* (Ayensu and DeFilipps, 1978) and is presently considered "rare" in New England (Crow *et al.*, 1981). However, the federal government has dropped it from further consideration (Federal Register , Vol. 45, No. 242, Monday, December 15, 1980).

Ames and Correll (1943) have reported on the taxonomic problems in this taxon that have been exacerbated by the superficial resemblance of it to *Coeloglossum viride,* especially in dried materials. Baldwin (1894) offered an easy way to separate the two species by stating that *Platanthera flava* "carries a spur, and *H. viridis* [*C. viride*] a bag." It is true that the short sac-like spur of the latter species is a consistent character that is usually still apparent in dried plants.

I have found the flowers of the Tubercled Orchid to be lightly fragrant, but Morris and Eames (1929) found them "deliciously sweet-scented, with the fragrance of Madonna Lilies." The characteristic tubercle, described by Gray (1862–1863) as a "nasiform protuberance," is located at the base of the lip at about the point where the lip turns sharply downward. This projection apparently functions to deflect pollinators so that they must approach the nectary laterally. The Tubercled Orchid is reported to be pollinated by several moths, and is also visited by mosquitoes (Leur, 1975). Offset plants may be formed vegetatively as well (Case, 1964a).

GENERAL DISTRIBUTION: Nova Scotia west to Ontario, south to central Florida, west to Texas.

10. *Platanthera dilatata* (Pursh) Lindl. ex Beck, Bot. U.S. 347. 1833.

This northern plant was described from a specimen collected in Labrador and was originally named *Orchis dilatata* by Pursh (1814). American botanists have traditionally treated this taxon as *Habenaria dilatata.* The name *dilatata* is derived from Latin and means "widened," referring to the broad base of the lip.

COMMON NAMES: Bog Candle, Tall Leafy White Orchid

FLOWERING DATES IN NEW HAMPSHIRE: June through August

DESCRIPTION: Plant from fleshy roots, glabrous, leafy, slender or stout. Leaves several, linear to lanceolate, clasping stem below becoming bracteate above. Inflorescence a loosely or densely flowered cylindrical raceme. Floral bracts lanceolate, usually ascending. Flowers white, fragrant. Dorsal sepal ovate, obtuse, concave. Lateral sepals elliptic-lanceolate, falcate, connivent with dorsal sepal. Lip linear-lanceolate, abruptly dilated at base. Spur cylindrical, about equal in length with the lip. Capsule ellipsoid, ascending.

CHROMOSOME NUMBER: $2n = 42$ (Moore, 1973).

The Bog candle is a species that presents itself in a variety of forms. Sometimes it appears as a small, delicate wand with a few crystalline blossoms, while a neighboring plant from the same habitat may be a robust, leafy individual, with a stout raceme crowded with scores of flowers. Schrenk (1975) stated that the floral proportions remain constant despite the wide range of dimensions in *P. dilatata,* therefore the characters that distinguish it will hold true. The major difficulty in the identification of this taxon is caused by the similarity of the Bog Candle to the Tall Leafy Green Orchid, *Platanthera hyperborea.* In the field there is no problem as the flowers of the Bog Candle are snow-white and fragrant, whereas those of the Tall Leafy Green Orchid are green and scentless. Another character that serves to distinguish the two taxa is the shape of the lip, which in *P. dilatata* is typically abruptly widened at the base. In contrast, the lip in *P. hyperborea* gradually widens toward the base.

The confusion between *Platanthera dilatata* and *P. hyperborea* is further amplified by the fact that the two frequently hybridize. Plants with intermediate attributes can be ascribed to *P.* ×*media.* In western North America many forms of the Bog Candle occur, some of which have been described as varieties.

As the common name implies, this species prefers wet, peaty habitats. "No orchid loves better to dig its toes in the ooze and even paddle over the ankles in flood pools" (Morris and Eames, 1929). While it can be found in the southern sections of the state, it is most frequently found in Coos County (Pease, 1964), where it grows rather commonly in sloping graminoid fens and waysides. Another common habitat of this species is the damp, misty ravines of the White Mountains.

Platanthera dilatata displays an interesting phenomenon in that the apex of the lip is often "caught-up" in the hood formed by the dorsal sepal and the lateral petals. As a result the flower has an odd, half-opened appearance.

The strong fragrance of the flowers is usually described as "clove-like," and is both sweet and spicy-smelling. Fernald (1926) reported that *P. dilatata* is locally called "Scent-bottle" in Newfoundland. Although the Bog Candle attracts "armies" of Tiger Swallowtails [*Papilio glaucus* (Papilionidae)] to its blossoms (Morris and Eames, 1929), the only verified pollinators at this date are several species of moths and skippers (Leur, 1975).

GENERAL DISTRIBUTION: Greenland, west through boreal North America to the Aleutians, south to New Jersey in the east, extending southward in the western mountains to California, Colorado, and New Mexico.

11. *Platanthera hyperborea* (L.) Lindl., Gen. Sp. Orchid. 287. 1835.

Linnaeus originally named this species, known to him from Iceland, *Orchis hyperborea*. Like all of our other Platantheras, it was formerly referred to the genus *Habenaria*. The epithet *hyperborea* means "beyond the north," as this orchid grows within the arctic circle (Correll, 1950).

COMMON NAMES: Tall Leafy Green Orchid, Tall Northern Green Orchid

FLOWERING DATES IN NEW HAMPSHIRE: July through August

DESCRIPTION: Plant from fleshy, fusiform roots, glabrous, leafy, slender or stout. Leaves several, cauline, oblong-elliptic to linear-lanceolate, gradually reduced to bracts. Inflorescence a spike cylindrical in shape, elongated, few- to many-flowered. Floral bracts lanceolate, usually spreading. Flowers green to greenish-yellow, not fragrant. Dorsal sepal ovate-elliptic, concave. Lateral sepals lanceolate, oblique, spreading, reflexed. Lateral petals lanceolate, falcate, acute, erect, connivent with dorsal sepal. Lip elliptic, fleshy, gradually tapering from widened base to obtuse apex. Spur cylindrical, usually shorter than lip. Capsule ellipsoid, ascending.

CHROMOSOME NUMBER: $2n = 42$

The Tall Leafy Green Orchid, like the Bog Candle, is a polymorphic species. Often plants of *Platanthera hyperborea* that occur in the woods are small and slender with only a few flowers, but in wet, open, roadside ditches it is often tall, thick and robust, even to the point where it has been compared to "vigorous young stalks of maize" (Case, 1964a). Some of this dimorphism is probably related to age of individual plants, as both forms may occur in the same habitat.

Our plants of *Platanthera hyperborea* are referable to var. *huronensis*, an overall larger and more robust plant than the typical var. *hyperborea*. In New Hampshire, the Tall Green Leafy Orchid occurs in wet, peaty soils, often along with *P. dilatata* and the hybrid *P.* ×*media*. There are locations where the hybrids have been observed to greatly outnumber the parent species (Schrenk, 1978).

The green flowers of this orchid are scentless. It is reported that the Tall Leafy Green Orchid regularly self-fertilizes (Gray, 1862–1863; Hagerup, 1952); however, some insects must find the flowers, attractive enough to carry pollinaria to *Platanthera dilatata,* or vice-versa.

General distribution: Arctic and Boreal North America, south to Pennsylvania, west through the Great Lakes area to Washington, southward in the western mountains to California, Colorado, and Arizona; Iceland and east Asia.

5. Epipactis Zinn, Catal. 85. Mai, 1757. (conserved name)

The name *Epipactis* goes back to Theophrastus, who applied the name to a plant (of uncertain identity) which was used to curdle milk. There is some confusion as to the correct author of this genus but it appears that the first publication of the name after the starting point for nomenclature was in *Catalogus plantarum horti academici et agri gottingensis* (Zinn, 1757). Although Zinn did not use binomials for the species he described, his generic names must be accepted if they are otherwise in accordance with the International Code of Botanical Nomenclature (Stafleu, 1967).

The genus is comprised of about 20 species. One of these, *Epipactis gigantea,* is a native of western North America. The common Helleborine orchid of northeastern North America is not indigenous but an exotic, a plant introduced from Eurasia which has naturalized here.

1. *Epipactis helleborine* (L.) Crantz, Strip. Austr. ed. 2. Fasc. 6: 467. fig. 6. 1769.

This species was called *Serapias helleborine* by Linnaeus, who based his description on European material. In 1769 the species was renamed by von Crantz. The specific epithet *helleborine* means "like a hellebore," referring to a group of plants in the buttercup family which the orchid supposedly resembles.

Common name: Helleborine

Flowering dates in new hampshire: July through August

Description: Plant leafy, from a short rhizome with many fibrous roots. Leaves clasping, spirally arranged, variable but usually elliptic-lanceolate, reduced above and changing into floral bracts. Inflorescence few- to many-flowered, a one-sided raceme. Rachis lightly pubescent. Flowers small with thick, sessile ovaries subtended by lanceolate bracts that exceed the flowers in length. Sepals ovate-lanceolate, spreading, concave, greenish-white often with rose-purple streaks. Lateral petals ovate-elliptic, greenish-white to pink. Lip divided into two sections by a central constriction, lower half (epichile) thickened, saccate, triangular, dark purple; apical section (hypochile) thin, triangular-ovate, concave, pink. Column short, white, fleshy. Capsule obovate-ellipsoid, pendant.

CHROMOSOME NUMBER: $2n = 38$.

Long used as a medicinal herb in Eurasia, *Epipactis helleborine* was best known in the Old World as a remedy for gout. The Helleborine is the only widespread non-native orchid in our flora.* How it first immigrated to this continent is a mystery, but when Helleborine was discovered in 1879, it had already become established in a deciduous woods near Syracuse, N.Y. (Anon., 1879). Mrs. M. P. Church of the Syracuse Botanical Club surprised the professional botanists of her day by making this remarkable find. Three years later, another amateur botanist recorded a well-established colony of Helleborine near Scajaquada Creek, Buffalo (Zenkert, 1950). In subsequent years populations of Helleborine were reported from Toronto and Montreal (Leur, 1975). *Epipactis helleborine* was clearly here to stay.

In aggressive, weed-like fashion, Helleborine continued to extend its range. One state after another—Massachusetts, 1902; Indiana, 1931; Missouri, 1940—added the "new" orchid to their state lists (Doyon and Cayouette, 1966).

Helleborine was found in Hartland, Vermont near the New Hampshire state line in 1925, but was not recorded in this state until 17 years later. In 1942, in Plainfield (Sullivan County), directly across the river from Hartland, Vermont a single plant of Helleborine growing on a shaded bank provided the first record of its occurrence in New Hampshire (Upham, 1942).

In the Jessup Herbarium at Dartmouth College in Hanover, N. H., there is a map of the state studded with colored pins which represent

---

*The recent reports from Canada (Elliott and Cook, 1970; Anderson and Goltz, 1982) of the occurrence of the European orchid *Listera ovata* indicate that a similar invasion may be taking place by that species.

records of the occurrence of *E. helleborine;* each color designates an interval of time since 1942. Dr. James Poole, Professor Emeritus of Botany at that institution, has provided a graphic illustration of the procession of this orchidaceous weed through time within the state. Today, Helleborine can be found in every county in New Hampshire.

Helleborine is reported to prefer circumneutral soils (Correll, 1950), but Stucky (1967) indicated that the presence of free carbonates in the substrate is a more important ecological requirement. I have found, as she did, Helleborine growing amongst old foundations, but the most likely place to encounter this orchid in New Hampshire is in rich, deciduous woods. In testimony to its aggressiveness, Helleborine is able to flourish in a wide variety of habitats. The most robust specimens I ever observed were waist-high, growing in open pine woods in Belknap County.

Immature Helleborine plants produce only a leafy stalk which somewhat resembles that of *Cypripedium arietinum.* Each year the plants become larger until they become reproductive (Leur, 1975). A mature plant produces many, rather inconspicuous, small flowers.

Epipactis helleborine produces large amounts of nectar in the cup-like hypochile (L. A. Nilsson, 1978). The lower half of the lip, the epichile, provides a platform for insects to perch on while partaking of the nectar. As the insect (in this case a wasp) backs out of the flower, its head comes in contact with the sticky rostellum. The rostellum wall ruptures and its sticky effluent glues the pollinia to the insect's head (Darwin, 1877).

In Europe, Darwin (1877) observed the wasp *Vespa sylvestris* (Vespidae) pollinate *Epipactis helleborine.* On this continent wasps of the genus *Vespula* (Vespidae) have been reported as the most important pollinators (Judd, 1972; Leur, 1975). Hagerup (1952) has found that populations of Helleborine in Denmark are autogamous, and that this process takes place directly before or just after the flower opens.

Helleborine produces abundant ripe capsules filled with many microscopic seeds. The fact that the seeds are easily dispersed far and wide is documented by the rapid spread in northeastern North America of this most interesting and delightful orchid.

GENERAL DISTRIBUTION: Eurasia and northeastern North America, west to Michigan and Missouri.

6. Listera R. Brown in W. *et* W. T. Aiton, Hort. Kew. ed. 2, 5: 201. 1813. (conserved name)

This genus of minute orchids was named in honor of Martin Lister, a 17th century English naturalist and physician. Although the genus is widely distributed in temperate regions, most of the approximatley 25 species are rare and local.

Twayblades are extremely small and have tiny, inconspicuous flowers. All the Listeras that occur in the northeast have an elongated somewhat bifurcated lip which secretes nectar along a central groove. While some Listeras are apparently scentless, most of our species produce fetid odors that have been described as "truly repulsive" (Ramsey, 1950; Ackerman and Mesler, 1979).

Pollination biology of the Twayblades is especially fascinating as it features an active attachment of the pollinia to the pollinator. This process begins in the bud when the anther opens and drops the two pollinia onto the concave back of the rostellum (Baldwin, 1894). The rostellum, which forms a hood-like cover over the stigmatic surface, has tiny projections on the front margin that act as triggers (Ramsey, 1950). When the triggers are touched, even lightly, the rostellum explosively expels a viscid, quick-drying fluid onto "the object whose touch caused the exudation" (Müller, 1883). Instantly, the margins of the rostellum fold back releasing the pollinia which fall precisely onto the drop of quick-drying cement (Ackerman and Mesler, 1979). When this mechanism acts on a pollinator, it frightens the insect which quickly flies away bearing a crown of pollinia.

In their study of *Listera cordata,* Ackerman and Mesler (1979) found that after the pollinia are removed, the rostellum spreads flat over the stigma for approximately one day. This position of the rostellum assures that the flower does not become self-pollinated by a returning insect. Gradually the rostellum rises to expose the now-receptive stigmatic surface. Cross-pollination occurs when an insect bearing pollinia from another Twayblade alights to partake of the nectar and brings a pollinium in contact with the stigma. Since only small pieces of the pollen-masses adhere to the sticky stigma, it is possible for several flowers to be pollinated by a single insect (Ackerman and Mesler, 1979). This precise pollination mechanism of *Listera* is adapted for use with unspecialized pollinators (Proctor, 1978). European Twayblades are pollinated by ichneuman wasps, beetles, and small flies (Summerhayes, 1951).

In our flora, there are three species of *Listera*. In addition, a hybrid between *L. convallarioides* and *L. auriculata* has been recently described as *L.* ×*veltmanii* (Case, 1964b). Cody and Monro (1980) reported this hybrid as occurring in Coos County, N.H.

Key to the Species of *Listera* in New Hampshire

1. Lip linear-oblong with a pair of horn-like teeth at the base, divided at least half-way to base into 2 linear prongs; leaves ovate-cordate .... 1. *L. cordata*
1. Lip oblong to obovate without horn-like teeth, cleft less than half-way to base into oblong or broadly rounded lobes; leaves ovate-elliptic to suborbicular........................ (2)
    2. Lip oblong, broadest at base with auricles clasping the column; pedicels glabrous .... 3. *L. auriculata*
    2. Lip obovate, broadest at apex with a slender claw at base and a triangular tooth on each side near claw; pedicels glandular ....2. *L. convallarioides*

1. *Listera cordata* (L.) R. Brown in W. *et* W. T. Aiton, Hort. Kew., ed. 2, 5: 201. 1813.

The Heart-leaved Twayblade was described by Linnaeus based upon European plants of cold, moist forests. He placed this species (and another European Twayblade, *L. ovata*) into the genus *Ophrys*. Robert Brown realized that the Twayblades were distinct from *Ophrys* and separated them to the genus *Listera*. As the common name indicates, the specific epithet means "heart-shaped."

COMMON NAME: Heart-leaved Twaybade

FLOWERING DATES IN NEW HAMPSHIRE: June through July

DESCRIPTION: Plant slight, 10–20 cm tall, mostly glabrous. Roots few, fibrous. Leaves two, opposite, ovate-cordate, midway up stem. Inflorescence a slender raceme. Flowers inconspicuous, greenish to reddish-purple, subtended by minute bracts. Sepals and lateral petals ovate-oblong to elliptic, spreading, 2–3 mm long. Lip linear with two horn-like teeth at base, deeply cleft for half of its length into two spreading, lanceolate prongs. Column small, stubby, 0.5 mm long. Capsule ovate, ribbed, semi-erect.

CHROMOSOME NUMBERS: $2n = 38, 42$.

The circumboreal distribution of *Listera cordata* makes it the most widespread species of the genus. A diminutive inhabitant of wet, mossy Spruce-Fir woods and Cedar swamps, the Heart-leaved Twayblade is easily overlooked by the orchid hunter. The plant is often buried so deeply in loose moss that the twin heart-shaped leaves appear to be basally located. The minute flowers are spread widely to expose the nubby column and the curious pair of horn-like teeth at the base of the lip. The microscopic dimensions of the Heart-leaved Twayblade and its production of a fetid odor usually prevents this species from being sought out as an addition to wildflower gardens.

Ackerman and Mesler (1979) stated that the flowers of *Listera cordata* are self-compatible but not autogamous. In their study of northern Californian populations of the Heart-leaved Twayblade, they found the most common pollinator to be fungus gnats of the genera *Mycetophila* (Mycetophilideae), *Sciara* and *Corynoptera* (Sciaridae). That these small diptera can serve as effective pollinators, was illustrated by the high percentage of fruit set in *L. cordata*, especially when contrasted with percentage fruit set for other allogamous orchids (Mesler *et al.*, 1980).

The Heart-leaved Twayblade is a prolific seed producer. One plant can yield as many as 2,860 seeds a year (Stoutamire, 1964). Vegetative reproduction may also occur in this species (Case, 1964a).

In New Hampshire, *L. cordata* has been most often collected in the White Mountains and northern Coos County. There have been few modern collections of the Heart-leaved Twayblade in the state. Two of the most recent records are from the northernmost town of Pittsburg, collected by the late Albion R. Hodgdon of the University of New Hampshire.

Storks and Crow (1978) listed *Listera cordata* as "widespread but infrequent." It is possible that in some areas of the White Mountains where hiking (and botanizing) activities are high, some populations of the Heart-leaved Twayblade may have been diminished, but other populations of *L. cordata*, with their delicate stems and tiny flowers, surely grow unnoticed in scattered locations within the state.

General distribution: Circumboreal; in North America extending south along the mountains to North Carolina, California, and Colorado.

2. *Listera convallarioides* (Sw.) Torrey, Comp. Fl. North and Middle States. 320. 1826.

A North American specimen was described by Swartz (1800) as *Epipactis convallarioides.* In 1818, Nuttall simply listed *L. convallarioides* as the third species in the genus *Listera* without a description or reference to the original author and description. Because of Nuttall's lack of description, his name must be regarded as invalid, according to Article 33 of the *International Code of Botanical Nomenclature* (Stafleu et al., 1978). Therefore, Torrey, who described *Listera convallarioides* in 1826, can technically be considered the author of this species, but the matter needs further study. Torrey's use of the epithet *convallarioides* indicates that he was familiar with Swartz's taxon, and may have intended to transfer it to *Listera.* The epithet *convallarioides* means "like a *Convallaria,*" referring to a supposed resemblance to Lily-of-the-Valley.

Common names: Broad-leaved Twayblade, Lily-leaved Twayblade

Flowering dates in new hampshire: July

Description: Plant usually slender, 5–30 cm tall (averaging 16 cm tall here), glabrous below leaves, pubescent above. Leaves 2, opposite, about half-way up stem, elliptic to sub-orbicular. Inflorescence a loose, many-flowered raceme. Floral bracts lanceolate, semitranslucent. Flowers yellowish-green, translucent, on slender glandular pedicels. Sepals linear-lanceolate, reflexed. Lateral petals narrower than the sepals, linear, reflexed. Lip conspicuous, much elongated, wedge-shaped with a central groove, widely flared and bilobed with a minute tooth in the sinus, auriculate near the base and narrowing into a slender claw. Margins of lip minutely ciliate. Column recurved, winged. Capsule ellipsoid.

Chromosome number: $2n = 36$ (Moore, 1973).

The Broad-leaved Twayblade is a northern plant of cold soils (Case, 1964a). In New Hampshire this species inhabits mossy woods and Cedar (*Thuja occidentalis*) swamps. The shiny, broad green leaves appear early in the summer well before the flowering spike elongates. The unusual-looking flowers have inconspicuous sepals and lateral petals that are reflexed from the oversized bilobed lip and overhanging column. The blossom is stiffly perched on the thread-like pedicel with the lip held at a 45 degree angle from the stem.

Unfortunately, I have found no specific references to insect visitors of *Listera convallarioides* and have not observed pollination in this species myself. An interesting observation on the inflorescence of the Broad-leaved Twayblade is that it strongly resembles a raceme of small diptera with their wings held in a resting position. Comparing a dorsal view of a fungus gnat (Mycetophilideae) with the lip of *L. convallarioides*, similarities of color, translucence and the ciliated margins are apparent. The dark central line of the lip corresponds to the very narrow body of the insect. A detailed study of the pollination biology of this species might reveal some interesting relationships with insect visitors.

All locations for the Broad-leaved Twayblade in New Hampshire are within Coos County. There have been very few collections of this species in the state in the past 50 years. Case (1964a) reported finding many individuals of *Listera convallarioides* in the western Great Lakes area with blackened stems, and Wherry stated that this species is "extraordinarily susceptible to attack by parasitic fungi" (Correll, 1950).

General distribution: Boreal North America; mostly Canada, reaching northern New England and the northern Great Lakes states. Disjunct to the mountains of North Carolina and Tennessee. In the west; north to Alaska, south to the mountains of Utah and Arizona. Closely related to *L. makinoana* of Japan (Leur, 1975).

3. *Listera auriculata* Wiegand. Bull. Torr. Bot. Club 26: 166, pl. 356, fig. 2. 1899.

Wiegand described *L. auriculata* from material collected in Quebec, New Hampshire, and Maine. The epithet *auriculata* means "ear-like," in reference to ear-like appendages which curl around the column.

Common name: Auricled Twayblade

Flowering dates in new hampshire: Mid-June to mid-July

DESCRIPTION: Plant slight, slender. Stem glabrous below leaves, pubescent above. Leaves 2, opposite, ovate-elliptic, dark green, situated above the middle of the stem. Inflorescence a loosely flowered raceme. Floral bracts small, approximately 5 mm, oblong-lanceolate. Flowers watery blue-green on stout, glabrous pedicels. Sepals and lateral petals reflexed from column and lip. Dorsal sepal elliptic-obovate, blunt at apex. Lateral sepals lanceolate-elliptic. Lateral petals linear, obtuse. Lip oblong, somewhat narrowed in the center, ciliate at margins, cleft at apex into two blunt lobes with a narrow sinus. Base of lip forming two auricles which curve behind the column. Column stout, curved toward lip. Capsule ellipsoid.

CHROMOSOME NUMBER: $2n = 36$.

Listera auriculata is a rare orchid with a distribution restricted to northeastern North America. It is quite close in appearance to *L. borealis*, the Northern Twayblade, which occurs in Canada and western North America. Where the two species grow together they can be distinguished by the shape and position of the auricles. In *L. auriculata*, the rounded auricles curve behind the column while in *L. borealis* the oblong auricles diverge from the column.

The Auricled Twayblade has a distinctive habitat preference for alluvial thickets where it grows under Alder (*Alnus viridis* var. *crispa*) shrubs. In such a thicket, I discovered a population of Auricled Twayblades pushing through leaf litter that had accumulated on the sandy soil. The largest plant was less than 10 cm tall, yet their pale blue-green flowers were beginning to unfurl. This riverside site is only the fifth station and the only known extant site in New Hampshire for this rare, small orchid. All recorded locations in the state for this species occur within Coos County.

Northern sections of Maine, New Hampshire and Vermont form the southeastern limit of the range of this boreal species. The scarcity of the Auricled Twayblade has earned it a listing as "Endangered" for New England (Crow et al., 1981). On a national scale, *L. auriculata* is currently under review for listing as an Endangered or Threatened Species of the United States (Federal Register, Vol. 45, No. 242, Monday, Dec. 15, 1980).

GENERAL DISTRIBUTION: Northeastern North America; Newfoundland south to northern New England, west to Michigan.

7. Triphora Nuttall, Gen. N. Am. Pl. 2: 192. 1818.

Once included within the genus *Pogonia,* this genus of small woodland orchids was segregated in 1818 by Nuttall. The genus occurs exclusively in the Western Hemisphere and includes about 10 species. Case (1964a) stated that "structurally and physiologically members of this genus appear to be intermediate between independent, free-living plants and dependent saprophytes." The name *Triphora* is from two Greek words meaning "three-bearing," referring to the number of flowers per plant in bloom at one time.

1. *Triphora trianthophora* (Sw.) Rydb. in Britton, Man. 298. 1901.

This North American species was first described in 1800 by Swartz as *Arethusa trianthophora.* The Three-birds Orchid has also been known as *Pogonia pendula* which translates as "Nodding Pogonia," another common name for this species. The specific epithet *trianthophora* is somewhat repetitive as it means "bearing three flowers."

COMMON NAMES: Three-birds Orchid, Nodding Pogonia

FLOWERING DATES IN NEW HAMPSHIRE: mid-August to early September.

DESCRIPTION: Plant stoloniferous, producing white ovoid tubers and slender white roots. Stem glabrous, greenish-purple, succulent. Leaves alternate, ovate, clasping stem. Inflorescence a raceme of 1–6 pedicellate flowers borne in the axils of the upper leaves. Flowers fragile, spreading, white or pinkish-white. Dorsal sepal oblanceolate. Lateral sepals and lateral petals oblanceolate, falcate. Lip with a slender claw, three-lobed. Lateral lobes ovate, obtuse. Mid-lobe ovate with sinuate margins. Column white with terminal anther. Capsule ellipsoid, erect.

CHROMOSOME NUMBER: $2n = 18$ (Baldwin and Speese, 1957).

The Three-birds Orchid is so named for the three flowers on each plant that are usually in bloom at the same time—"one perfect bloom with a fading flower below and an opening bud above" (Morris and Eames, 1929). The blossoms of the tiny, fragile orchid range in color from waxy white to rosy pink. Instead of the usual yellow-colored pollen, the Three-birds Orchid is unique in having pollen masses that are violet. In keeping with the scheme of threes, the lip has three lobes and a median trio of long green crests.

The only member of the genus that occurs north of Florida, *Triphora trianthophora* is widespread but uncommon throughout its range (Porcher, 1977). In addition to being uncommon, sizes of known populations of the Three-birds Orchid fluctuate widely from year to year. The plant may be abundant at a particular station during one year and be absent or scanty for the next few years (Eastman, 1976). An example of the varying size of *Triphora trianthophora* populations is furnished by one well-known New Hampshire station where 5000 plants were found in 1916 but only 5 of the orchids were located in 1978 (Lowenstein, 1917; Storks and Crow, 1978). At the same location in 1980 I counted approximately 200 plants in flower.

The reason for the elusive occurrence of flowering plants of *Triphora* is attributed to the largely subterranean existence of this orchid (Ames, 1922a). During most of its life, this species reportedly remains underground in a tuberous condition. In this state the plant exhibits a saprophytic mode of existence, deriving its nourishment from the mycorrizal association present in the tissues of the tuber. Because colonies of the Three-birds Orchid also produce green stems and leaves capable of photosynthesis during its brief life above ground, the plants have been termed "hemisaprophytes" or "semisaprophytes" (Batchelder, 1909; Case, 1964a).

Triphora trianthophora requires a specialized habitat in northern New England. It is often found in nearly pure stands of Beech (*Fagus*), where it grows in hollows and depressions that have filled up with fallen leaves. Prince (1902) described the Three-birds Orchid at Intervale (Conway) New Hampshire as "often pushing up through the Beech leaves and carrying them like an unwieldly collar at a little distance below the flowers." The companion herbs of this species are also largely saprophytic and parasitic. Indian Pipes (*Monotropa uniflora*), Spotted Coral-root (*Corallorhiza maculata*) and Beech-drops (*Epifagus virginiana*) commonly share the same Beech grove.

In late August *Triphora trianthophora* begins to make its transient appearance above ground. The plants grow rapidly for about two weeks and quickly develop buds. A drop in the average night temperature may serve as a stimulus to flowering, as 48 hours later all of the mature buds in a colony will simultaneously open (Leur, 1975). Leur also stated that the strategy of mass flowering increases the chance for the (literally) ephemeral flowers to be cross-pollinated. Lowes (1920) listed the small bee *Halictus quadrimaculatus* (Halictidae) as a pollinator of the Three-birds Orchid in New Hampshire. A number of seed capsules are commonly observed after the flowering season. *Triphora trianthophora* also reproduces vegetatively by the production of stolons that develop new tubers (Ames, 1922a).

In New Hampshire, the Three-birds Orchid is listed by Storks and Crow (1978) as "widespread but infrequent." Although it has been occasionally found in scattered locations throughout the state, most populations of this orchid occur within Carroll County.

GENERAL DISTRIBUTION: New England and southern Ontario, west to Michigan and Wisconsin, south to Florida, west to Texas.

8. Goodyera R. Br. in W. *et* W. T. Aiton, Hort. Kew. ed. 2, 5: 197. 1813. (conserved name).

This genus was proposed by Robert Brown who named it in honor of the botanist John Goodyer (1592 1664) who "englished" Dioscorides' herbal (Freeman, 1943). There are about 25 species of *Goodyera* widely distributed in temperate and tropical regions of the world (Correll, 1950). Members of this genus are characterized by creeping rhizomes and rosettes of evergreen leaves. The leaves are similar in shape, though much smaller, to the Common Plantain (*Plantago*) and are marked with reticulations reminiscent of the patterns of snakeskins, hence the common name of Rattlesnake Plantains. Of the four North American species, three are found in New Hampshire.

The Rattlesnake Plantains are capable of hybridizing and apparently do so quite often in the Great Lakes region (Case, 1964a). Because of slightly different habitat preferences and less geographical overlap this phenomenon is less likely to occur in our area.

Key to the species of *Goodyera* in New Hampshire

1. Raceme one-sided or loosely spiralling .... (2)
   2. Leaves less than 3 cm long; raceme one-sided .... 1. *Goodyera repens* var. *ophioides*

  2. Leaves 2–7 cm long; raceme loosely spiralling .... 2. *Goodyera tesselata*
1. Raceme densely flowered, cylindrical in overall appearance... .... (3)
  3. Beak of rostellum equal in length or greater than body of stigma; leaves bluish-green .... 2. *Goodyera tesselata*
  3. Rostellum essentially beakless; leaves dark green .... 3. *Goodyera pubescens*

1. *Goodyera repens* (L.) R. Br. in W. *et* W. T. Aiton, Hort. Kew. ed. 2, 5: 198. 1813.

Described by Linnaeus as *Satyrium repens* from plants collected in Sweden and Siberia, this species is widespread in the cool moist coniferous forests of Eurasia. The typical var. *repens* with plain green leaves is also found in western North America. Our eastern North American plants are referable to var. *ophioides* Fern. This variety (Fernald, 1899) is distinguished from var. *repens* by its smaller size and conspicuous white markings that border the veins of the leaf. The epithet *repens* translates as "creeping," descriptive of the growth habit of the rhizome. In Europe this species is known as "Creeping Ladies'-tresses" (Summerhays, 1951). The name *ophioides* means "snake-like," alluding to the patterns on the leaves which "strongly suggest the markings of a serpent" (Fernald, 1899).

COMMON NAMES: Lesser Rattlesnake Plantain, Creeping Rattlesnake Plantain

FLOWERING DATES IN NEW HAMPSHIRE: mid-July through August.

DESCRIPTION: Plant from a creeping rhizome, scapose, rosette-forming, approximately 16 cm tall. Leaves 3–7 on short pedicels, ovate to oblong-elliptic with white reticulations. Inflorescence a one-sided raceme, loosely flowered. Floral bracts lanceolate, acuminate. Flowers white to geenish-white, pubescent on outer surfaces. Dorsal sepal ovate, concave. Lateral sepals oblique. Lateral petals oblong-spatulate, connivent with dorsal sepal and forming a hood over lip. Lip globose-saccate with flaring margins and an elongated recurved tip. Column with beak shorter than body of stigma. Capsule ovoid.

CHROMOSOME NUMBER: $2n = 30$.

This orchid is found in dark coniferous woods throughout its range. The creeping manner of growth in this and in all *Goodyera* species derives from horizontally-growing rhizomes which are located just below the surface of the forest floor. Upright plants develop at the tips of rhizomes. According to Summerhays (1951) the production of a rosette of green leaves takes five years from the time of germination, and it is only after eight years that a flowering stalk appears. Other workers believe that there may be a shorter time requirement for the initiation of flowering (Case, 1964a). Vegetative plants of this species are more commonly observed than flowering individuals. Downie (1940) found that plants of *G. repens* remain dependent on mycorrhizae for nourishment throughout their lives.

The slender, one-sided flower stalk has up to 20 small sweet-smelling blossoms subtended by bracts. A close look at one of the white pubescent flowers reveals a lip in the form of a boat-like pouch. The apex of the lip extends out into a pointed channel, much like the pouring groove of a pitcher. Nectar is produced inside this vessel, an apparent adaptation for insect pollination.

Goodyera species are protandrous, a reproductive syndrome which promotes cross-fertilization. In the newly-opened blossoms of the Lesser Rattlesnake Plantain the column is bent forward, covering the stigma and almost touching the lip. This arrangement provides an opening only large enough for a bee's proboscis. A bee stopping to sip nectar will immediately come in contact with a viscid gland which glues the pollen-masses to the bee's mouth (Gibson, 1905).

As the blossoms age the column turns upward and backward causing the flower to open wider and expose the newly receptive stigma (Gray, 1862–1863). Any pollinia-bearing bee will now come in direct contact with the stigma and effect cross-pollination. This same process apparently occurs in the other North American members of this genus (Ackerman, 1975). Bumblebees (Apidae) are responsible for fertilizing the Lesser Rattlesnake Plantain. Darwin (1877) observed *Bombus pratorum* with pollinia from *Goodyera repens,* and Müller (1883) saw this orchid being visited by *B. mastrucatus* in the Alps. There are also reports of *Bombus* visiting North American plants of the Lesser Rattlesnake Plantain (Ackerman, 1975).

Because of the relatively high percentage of seed set in *Goodyera repens*, it has been suggested by Hagerup (1952) that, in Denmark, this species may be autogamous. Bagging experiments on *G. repens* var. *ophioides* by Kallunki (1976) in northern Michigan indicated that this is not the case in eastern North American plants. The Lesser Rattlesnake Plantain is a successful plant from the standpoint of reproduction with a high (for orchids) percentage seed-set and the additional ability to propagate vegetatively by its horizontal rhizomes.

Of our Goodyeras, *Goodyera repens* is by far the most widely distributed. Variety *repens* is found throughout Eurasia and in western North America. Our var. *ophioides* very rarely occurs in Europe but is known from Asia, especially in the Himalayan Mountains in India (Correll, 1950). On this continent var. *ophioides* grows in the northeast and in Alaska. Kallunki (1976) proposed that the taxon survived glaciation in refugia near the glacial edge, perhaps in the Appalachian Mountains. The Alaskan plants may well have been an element of the boreal forest flora that survived glaciation in the ice-free area connecting Alaska and Siberia, known as Beringia (Murray, 1980).

In New Hampshire the Lesser Rattlesnake Plantain favors the cool forests of the White Mountains and northern New Hampshire. *Goodyera repens* var. *ophioides* can grow in dark moist woods where its tolerance of such conditions often results in its being one of the only herbs present in the community.

GENERAL DISTRIBUTION: In the formerly glaciated areas of eastern North America, south along the Appalachians to North Carolina and Tennessee, disjunct to Alaska. Intermediate forms between the two varieties occasionally found in the western mountains (Kallunki, 1976). Rarely from Europe, occasionally from Asia. Very close to *G. japonica* from Japan (Hultén, 1962).

2. *Goodyera tesselata* Lodd. Bot. Cab. 10: pl. 952. Apr. 1825.

Goodyera tesselata was first described by Loddiges, who published a colored figure of the plant in his *Botanical Cabinet* (1824) that was drawn from plants found in New York and Philadelphia. However, Loddiges' species remained unknown to most botanists until it was included in the seventh edition of *Gray's Manual of Botany* (Robinson and Fernald, 1908). Northeastern plants of *G.*

tesselata collected prior to this publication were labeled either *G. menziesii* (presently known as *G. oblongifolia*) or *G. repens* (Fernald, 1899). Some of these old designations still remain on herbarium sheets, causing much confusion about the true distribution of *G. oblongifolia;* this species does not occur in New Hampshire. The epithet *tesselata* means "checkered," describing the pattern on the leaves in this species.

COMMON NAMES: Tesselated Rattlesnake Plantain, Checkered Rattlesnake Plantain

FLOWERING DATES IN NEW HAMPSHIRE: late July to early September.

DESCRIPTION: Plant erect, up to 30 cm tall, densely glandular-pubescent, from a creeping rhizome with fibrous roots. Leaves with short broad petioles, in a basal rosette, light bluish-green reticulated with white. Inflorescence a loosely or densely flowered raceme, somewhat one-sided, loosely spiralled or (occasionally) cylindrical. Floral bracts lanceolate. Flowers with stout ovaries, white to greenish-white, pubescent on outer surfaces. Sepals oblong-lanceolate, oblique. Lateral petals spatulate, oblique, connivent with dorsal sepal to form a hood. Lip saccate with recurved beak. Column with slender beak equal in length or longer than body of stigma. Capsule ovoid.

CHROMOSOME NUMBER: $2n = 60$ (Kallunki, 1976).

The Tesselated Rattlesnake Plantain is the most common *Goodyera* in northern New England. It was suggested by Fuller (1933) and Case (1964a) that *G. tesselata* may have originated through post-glacial hybridization of *G. oblongifolia* and *G. repens* var. *ophioides.* Kallunki (1976) researched this hypothesis for her thesis and the results of her study supported the theory of a past hybrid origin for *G. tesselata.* Her research showed the Tesselated Rattlesnake Plantain to be intermediate in morphological characters between the two putative parents and to share their respective phenolic compounds. *Goodyera tesselata,* with a diploid chromosome number of 60, is reported to be an allotetraploid derived from the diploids *G. repens* var. *ophioides* and *G. oblongifolia* (both $2n = 30$), and that morphologically intermediate triploids exist (Kallunki, 1976). The presence of these triploid plants in the area of the Great Lakes states are the cause of much difficulty in identification.

The establishment and proliferation of the Tesselated Rattlesnake Plantain in regions where the parental species are scanty or absent (i.e., New Hampshire) indicates that *Goodyera tesselata* is not just a hybrid swarm, but is clearly a distinct species (Case, 1964a).

This species is larger and stouter than the Lesser Rattlesnake Plantain and is better adapted to drier situations. Instead of growing in colonies, as is the habit of other Goodyeras, plants of *Goodyera tesselata* are most apt to grow singly and at some distance from each other. The late summer orchid hunter is almost certain to be rewarded by the presence of this species. This species is common in mixed or coniferous woods, especially when few other herbs are present. The narrow, white-flowered stalks are quite noticeable in shady woods.

Dried flower stalks from the previous year are often found next to fresh rosettes of the watery blue-green leaves. In contrast, the flowering plants that I have observed never have an old inflorescence in evidence. From these observations it appears that at least one year elapses between production of a new rosette of leaves and the onset of flowering.

The pollination mechanism in the Tesselated Rattlesnake Plantain is probably much the same as in *Goodyera repens* var. *ophioides*. Bagging experiments on this species done by Kallunki (1976) indicated that *G. tesselata* does not normally self-pollinate. In the same study, bees of the genus *Bombus* (Apidae) were observed visiting the fragrant flowers.

GENERAL DISTRIBUTION: Newfoundland west to Ontario and Minnesota, south through New York.

3. *Goodyera pubescens* (Willd.) R. Br. in W. *et* W. T. Aiton, Hort. Kew. ed. 2. 5: 198. 1813.

Willdenow (1805) first described this species as *Neottia pubescens*, and it has also been known as *Epipactis pubescens*. The epithet *pubescens* stands for "downy" describing the densely pubescent flowering stalk.

COMMON NAME: Downy Rattlesnake Plantain

FLOWERING DATES IN NEW HAMPSHIRE: late July through August.

DESCRIPTION: Plant from a creeping rhizome with fibrous roots, densely pubescent, erect, up to 37 cm tall. Leaves with a short, broad petiole, dark green with many white reticulations, ovate-lanceolate. Inflorescence a stout, cylindrical, densely flowered raceme. Floral bracts lanceolate. Flowers globose, white, with stout ovaries. Sepals ovate, concave, narrowed into a blunt apex. Lateral petals oblong-spatulate, oblique, connivent with the dorsal sepal to form a hood. Lip scrotiform with a short recurved beak. Column short, rostellum essentially beakless. Capsule globose.

CHROMOSOME NUMBER: $2n = 26$ (Kallunki, 1981).

This species, with its dark green leaves embossed with delicate white markings, has the most handsome foliage of all our native orchids. Because of these attractive leaves, plants are often taken for terraria. *Goodyera pubescens* is our counterpart of the southeast Asian Jewel Orchids (*Macodes* spp.) that are cultivated for their foliage. All of our Rattlesnake Plantains are termed "evergreen" but only in this species are the leaves a rich green color; our other two species have pale bluish-green leaves.

The type location of this species was listed by Willdenow (1805) as "from Canada to Florida," but the range of *Goodyera pubescens* only extends south to the mountains of Tennessee. This species is quite common in New Hampshire where it grows in mixed woods. Often a colony of the Downy Rattlesnake Plantain will be found nestled at the bottom of a large old Pine tree. *Goodyera pubescens* grows in colonies so dense that the leaves of individual plants often overlap. Ames (1922b) investigated this habit of growth and stated that the compactness of the colony derives in part from the constant replenishment of seedlings. He concluded that only those seeds that fall within an established colony will be assured of successful germination owing to the already established presence of mycorrhizal fungi. This species also perpetuates itself vegetatively and colonies of *G. pubescens* usually are composed of plants in different stages of maturity with only a few flowering shoots per colony. During one season Baldwin (1894) counted 572 plants of *G. pubescens,* of which 103 flowered.

The Downy Rattlesnake Plantain has long been used as a medicinal plant, as evidenced by one of its old common names "Scrofula

Weed." Baldwin (1894) quoted the *American Herbal* published in Walpole, New Hampshire in 1801:

> Country people use a decoction of the leaves for skin diseases, and Captain Carver says the Indians are so convinced of its power as an antidote that they allow a snake to drive its fangs into them, then chew the leaves and apply them to the wound.

It is fortunate that poisonous snakes have only been rarely reported in New Hampshire. Pursh (1814) reported that, "This plant has lately made a great noise among the country people, as infallibly curing the bite of a mad dog."

Whigham and McWethy (1980) reported that *Goodyera pubescens* is not self-pollinating and that cross-pollination is effected by *Bombus* spp. (Apidae). It appears that all of our *Goodyera* species have evolved reproductive strategies involving bumblebees of the genus *Bombus*. The Downy Rattlesnake Plantain produces a relatively high percentage of seeds, and, as previously stated, can also propagate vegetatively. Ames (1938) noted that in this species the ovaries of the fading flowers tend to untwist returning the lip to a more upright position.

GENERAL DISTRIBUTION: Quebec and Ontario south through the Appalachian uplands to Georgia and Alabama, west through the Great Lakes states to Minnesota.

9. Spiranthes L. C. M. Rich., De Orch. Europe. Annot. 28. 1817. (conserved name)

A large genus of about 300 species, the majority of which are confined to the New World, *Spiranthes* is closely allied with the morphologically similar *Goodyera*, although the Ladies'-tresses lack the evergreen leaves and saccate lips which characterize the Rattlesnake Plantains (Case, 1964a). In most species of *Spiranthes* the leaves begin to wither at, or before, flowering time.

In old botany books, this genus is referred to as *Gyrostachys* or *Ibidium*, two generic names that pre-date the name *Spiranthes*. The name *Spiranthes* is conserved over the other earlier names according to the *International Code of Botanical Nomenclature* (Stafleu *et al.*, 1978).

The species of *Spiranthes* that occur in our geographic area have more or less basal leaves and a spike of small flowers. All of the northeastern species have white or whitish flowers.

The name *Spiranthes* is from two Greek words, and means "coiled flower," referring to spiralling of the flower spike which occurs in most species. If the inflorescence appears to be composed of one vertical row of flowers spiralled around the stem, the floral arrangement is termed "one-ranked" or "single-ranked." Two vertical rows of spiralling flowers are said to be "two-ranked," and so forth. The spirals may be "right-handed" or "left-handed." Correll (1950) found the majority of single-ranked inflorescences he examined to be "right-handed."

In this genus the dorsal sepal and lateral petals usually overlap to form a hood over the lip. The base of the lip has two small round knobs called "callosities" or "tuberosities," which are sometimes diagnostic in determining a taxon.

The majority of our species are protandrous. While the flower is still in bud, the anther, which is pressed over the rostellum, matures and releases the two pollen-masses. The pollinia fall into a boat-shaped disk that is embedded in a furrow on the rostellum (Gibson, 1905). The pollination biology of *Spiranthes* was studied by Darwin (1877) who found that when the furrow is touched it instantly splits open and exudes a milky adhesive. In a matter of seconds the adhesive dries, cementing the pollen-bearing disk to the bee's proboscis.

The column in newly opened flowers is pressed down against the lip, blocking the passage-way to the immature stigma and nectary. A probing insect coming in contact with the rostellum may collect several pollen-bearing disks from different flowers before landing on a wide-open, older flower with a sticky, receptive stigma. Darwin (1877) also observed that the insects first visited the lowermost, most mature flowers on a *Spiranthes* spike and worked up to the uppermost, younger blossoms. On the higher blossoms the bees encounter the pollinia and carry them off to the wide-open lowermost flowers of another plant, thus effecting cross-pollination. The pollinators of most *Spiranthes* species are reported to be bumblebees (Darwin, 1877; Ames, 1921). *Spiranthes lucida* is the exception to the above information. This distinctive species is not protandrous and is pollinated by halictine bees (Catling, Ph.D. thesis, U. Toronto, 1980).

Most of our *Spiranthes* are pioneer species that can thrive in nutrient-poor soils where competition from other plants is minimal. The majority of the Ladies'-tresses are able to colonize open, disturbed areas such as gravelly shores and highway ditches. Some of these plants display the aggressiveness associated with "weedy" species. Apparently, there is a comparatively short interval between germination and flowering in this genus, as Ames (1921) reported flowering plants that were only three years old.

This genus is taxonomically difficult in the northeast; many species are similar in morphology, and there is a wide range of morphological variation within each species. Ames (1921) attributed some of this intraspecific variation to different stages of development, as one plant may have a slender few-flowered inflorescence during its first flowering season and an elongated many-flowered inflorescence the next year.

Hybrids are often formed between species that share similar habitats and overlap in blooming dates. This phenomenon makes identification difficult and should be borne in mind whenever plants appear to be intermediate between two species. There are also individual races within species that differ in chromosome counts and reproductive strategies. All of these factors contribute to a situation that led Ames (1921) to exclaim: "*Spiranthes* is the most perplexing orchid genus in our flora."

Key to the Species of *Spiranthes* in New Hampshire

1. Flowers appearing in a single-ranked spike; plants slender...(2)
  2. Leaves linear to oblong-elliptic, sessile; lip cream-colored or yellow .... (3)
    3. Lip cream colored to yellowish; plants of upland habitats .... (4)
      4. Spike loosely flowered; lip cream-colored .... 5. *Spiranthes casei*
      4. Spike densely flowered; lip yellowish .... 3a. *Spiranthes cernua* var. *ochroleuca*
    3. Lip with bright yellow center; plants of riverside seeps... .... 1. *Spiranthes lucida*

2. Leaves ovate, petioled; lip with green center .... 4. *Spiranthes lacera*

1. Flowers appearing in several-ranked spike; plants stout ... (5)
    5. Lip less than 6 mm long with a bright yellow center; flowering in early summer .... 1. *Spiranthes lucida*
    5. Lip longer than 6 mm, white to yellowish; flowering in late summer to autumn .... (6)
        6. Lip pandurate, markedly constricted near middle, apex dilated; sepals and petals connivent into a hood .... 2. *Spiranthes romanzoffiana*
        6. Lip oblong to ovate, slightly constricted near middle, gradually tapered towards apex; lateral sepals free, petals and dorsal sepal adherent .... (7)
            7. Flowers white, nodding; plants of mesic to wet sites... .... 3. *Spiranthes cernua* var. *cernua*
            7. Flowers cream-colored to yellowish, ascending; plants of drier sites .... 3a. *Spiranthes cernua* var. *ochroleuca*

1. *Spiranthes lucida* (H. H. Eaton) Ames, Orch., fasc. 2: 258. 1908.

This species, originally described by Rafinesque as *Neottia plantaginea* was based on specimens found in Troy and other parts of New York. It has also been known as *Spiranthes latifolia.* The name *lucida* means "shining," in reference to the broad, glossy leaves.

COMMON NAME: Shining Ladies'-tresses

FLOWERING DATES IN NEW HAMPSHIRE: late June through July.

DESCRIPTION: Plant small, slender, glabrous below to sparsely pubescent above, usually about 20 cm tall. Roots fleshy. Leaves 2 4 of graduated size, clustered near the base, oblong-elliptic to elliptic-lanceolate, shiny. Inflorescence cylindrical with few to 20 flowers in 1-2 ranks, spiralled. Floral bracts lanceolate, longer than the ovaries. Flowers white, tubular. Sepals linear-oblong. Lateral sepals oblique, free. Lateral petals linear-oblanceolate, connivent with dorsal sepal forming a hood. Lip oblong, folded around column with a small basal callosity on each side and a bright yellow floor. Apex of lip rounded with undulating margins. Column white with 2 bright yellow pollinia. Capsule ellipsoid.

CHROMOSOME NUMBER: $n = 22$ (±2) (P. Catling, personal communication).

The Shining Ladies'-tresses is the earliest member of this genus to flower in New Hampshire. Most *Spiranthes* are late summer and fall bloomers but this dainty little orchid begins to open its tubular flowers in June. The Shining Ladies'-tresses is unique among our *Spiranthes* in that the leaves do not begin to wither at flowering time but remain green and functional for the duration of the growing season (Case, 1964a). Although *S. lucida* is the smallest Ladies'-tresses in the state, it is the most striking in appearance. Snow-white flowers are accented by a sunshine-bright, yellow stripe on the lip that is often bordered with fine green lines. The stem is surrounded by a basal cluster of two to four bright green, glossy leaves of graduated size, the smallest one being nearest the bottom of the stem. Unlike the majority of *Spiranthes* species in our region, *S. lucida* is pollinated by halictine bees (Catling, Ph.D. thesis, U. Toronto, 1980).

Because this species prefers a substrate that is neutral or calcareous, its distribution is limited in New Hampshire. In Vermont, where sweeter soils prevail, the Shining Ladies'-tresses grows abundantly on river banks and in wet meadows. In that state, I have seen a proliferation of plants of *Spiranthes lucida* growing along the side of a small stream at the edge of a pasture.

In New Hampshire, there are only two known stations where the Shining Ladies'-tresses have been found, both along rocky shores of the Connecticut River just downstream from dams. The habitats are rocky, seepy areas in full sunlight. Companion plants found at these sites are, for the most part, species considered unusual for the state and are generally restricted to the same two stations. These uncommon plants include False Asphodel (*Tofieldia glutinosa*), Grass-of-Parnassus (*Parnassia glauca*) Musky Monkey-flower (*Mimulus moschatus*) and Jesup's Milk-vetch (*Astragalus robbinsii* var. *jesupi*).

Because of the restricted occurrence of this species, *Spiranthes lucida* is listed in "Rare and Endangered Vascular Plant Species in New Hampshire" (Storks and Crow, 1978). The Shiny Ladies'-tresses is limited in its range to northeastern North America but disjunct stations from Missouri and Kansas have been reported

(Correll, 1950). It may well be that this species is overlooked in some areas because of its diminutive proportions and its preference for rather mundane habitats.

GENERAL DISTRIBUTION: New Brunswick west through Ontario, south to Virginia, west to Indiana, disjunct to Missouri and Kansas.

2. *Spiranthes romanzoffiana* Cham. Linnaea 3: 32. 1828.

Chamiso first described this species from plants collected in the lowermost valleys of Unalaska, an island in the Aleutians. He gave the orchid the name of his patron, Nicholas Romanzoff, a Russian minister of state.

COMMON NAMES: Hooded Ladies'-tresses, Romanzoff's Ladies'-tresses

FLOWERING DATES IN NEW HAMPSHIRE: July through August.

DESCRIPTION: Plant with long fleshy, almost tuberous roots; erect; glabrous below, pubescent above, averaging approximately 25 cm tall. Leaves 3–6, clustered at base, linear to oblanceolate, becoming reduced to bracts on the upper stem. Inflorescence a densely flowered cylindrical spike of 3-ranked flowers. Floral bracts thin, ovate-lanceolate, acuminate. Flowers creamy-white to yellowish-green, gaping. Sepals and lateral petals connivent into a hood. Sepals oblong-lanceolate. Lateral petals linear. Lip with minute basal callosities, pandurate, markedly constricted near middle. Apex of lip dilated, recurved. Capsule ellipsoid.

CHROMOSOME NUMBER: $2n = 30$ (Moore, 1973).

The Hooded Ladies'-tresses has the widest range of all our *Spiranthes*. In North America it has a classic boreal distribution with southward extensions into the western mountains. *Spiranthes romanzoffiana* also occurs in Ireland, the Scottish Hebrides, and in southwest England (S. Nilsson, 1979). The "hood" of this species is formed by the complete convergence of the sepals and lateral petals, giving the plant a "two-lipped" appearance (Case, 1964a). The lip is strongly constricted in the middle and rounded at the base and apex resulting in the characteristic "fiddle-shape." The lip is also deflected sharply downward from the middle of the flower "with the effect of a receding chin" (Morris and Eames, 1929).

Because *Spiranthes romanzoffiana* superficially resembles the Nodding Ladies'-tresses, *S. cernua*, the two taxa are often confused. In comparing plants of the two species, the spike of the Hooded Ladies'-tresses is usually denser and more tapering toward the top. The 3-ranked greenish-white flowers of *S. romanzoffiana* are ascending, whereas in *S. cernua* they are nodding and pearly-white. On the lip of the Hooded Ladies'-tresses the callosities are minute, but in the Nodding Ladies'-tresses they are prominent.

Flowering times and microhabitats also separate the two species. In his botanical notebook of 1891, H. E. Sargent (unpubl., deposited in NHA) wrote: "Found in Plymouth (Aug. 21) two or three dried up plants that I called *S. Romanz.* About Sept. 1st began to find plants of *S. cernua.* That problem is solved." As Sargent noted, the Hooded Ladies'-tresses is the earlier bloomer, usually beginning to flower in July and often "gone-by" at the beginning of September when the Nodding Ladies'-tresses bloom. Occasionally the blooming times of the two taxa do overlap.

Spiranthes romanzoffiana prefers a wetter habitat than *S. cernua* and commonly is found at the edges of ponds and swales. In these wet sandy or sparsely grassy areas, the Hooded Ladies'-tresses grow along with the Bog Clubmoss (*Lycopodium inundatum*), the Little Green Wood Orchid (*Platanthera clavellata*) and the tiny, flycatching sundews (*Drosera* spp.). Often *S. romanzoffiana* shares a community with *S. cernua*, the latter occupying areas that could be termed "moist" rather than "wet." In 1940, Steiger discovered such a locality in the town of Warner in Merrimack County, New Hampshire. He collected several plants that appeared to be intermediate between the two species. These putative hybrids were named *Spiranthes* ×*steigeri* by D. S. Correll (1941) in honor of their discoverer. The largest hybrid of the population was a monstrosity with abnormally developed callosities and two extra abortive lips. Case (1964a) reported a large colony of the hybrid growing in Michigan's Upper Peninsula. Hybrids between *S. romanzoffiana* and *S. lacera* var. *lacera* were recently reported by Simpson and Catling (1978) as occurring in Ontario and Maine.

Ladies'-tresses has a delightful fragrance but descriptions of the scent are varied. Morris and Eames (1929) had it almond-scented; Gibson (1905) claimed it smelled like violets; Wherry (Correll, 1950) likened it to cumarin; Summerhayes (1951) reported it to be reminiscent of either Hawthorn or vanilla; while to Bingham (1939) the odor was similar to lilacs.

The pollinators of this species are listed by van der Pijl and Dodson (1966) as being bees of the genera *Halictus* and *Chlorhalictus* (Halictidae) as observed by Godfrey in the British Isles.

In western North America a separate variety of *Spiranthes romanzoffiana* has been described as var. *porrifolia* ("leek-green"). This variety is distinguished by its prominent callosities and a lip that is not significantly dilated at the apex.

GENERAL DISTRIBUTION: Boreal North America; Newfoundland west to Alaska, south to New York in the east, through the Great Lakes area; extending south in the western mountains to California and New Mexico. Also Ireland, Scottish Hebrides, and southwest England.

3. *Spiranthes cernua* (L.) L. C. M. Rich., De Orchid. Europe. Annot. 37. 1817.

Linnaeus (1753) named this species *Ophrys cernua* from plants collected in Virginia and Canada. The specific epithet *cernua* is Latin for "nodding," referring to the appearance of the flowers.

COMMON NAME: Nodding Ladies'-tresses

FLOWERING DATES IN NEW HAMPSHIRE: September to early October

DESCRIPTION: Var. *cernua* (3). Plants quite variable, from slender, fleshy roots, erect, glabrous below, downy pubescent above, up to 45 cm tall. Leaves 3–6, glabrous, clustered at base, linear-lanceolate, acuminate, becoming bracteate above. Inflorescence a densely flowered spike of nodding white flowers in 2–4 ranks. Floral bracts lanceolate, acuminate. Dorsal sepal lanceolate. Lateral sepals lanceolate, oblique, free. Lateral petals linear-lanceolate, connivent with the dorsal sepal. Lip with prominent basal callosities, ovate-oblong, somewhat constricted at the middle, directed downward with undulating margins at apex. Capsule ellipsoid.

Var. *ochroleuca* (3a). This variety differs from the typical in the following attributes: straw-yellow, non-dilated lip; longer, narrower, more tapering floral bracts; longer, more recurved callosities; ascending flowers; greater ascension and separation of lateral and dorsal sepals; leaves that are more apt to be sessile; slightly later flowering time; drier habitats (Sheviak and Catling, 1980).

CHROMOSOME NUMBERS: var. *cernua:* $2n = 60$; var. *ochroleuca:* $2n = 30$; intermediate or undetermined plants: $2n = 45$ (Sheviak and Catling, 1980).

Probably our most common orchid, *Spiranthes cernua* is widespread throughout the state. The lucky combination of abundance and beauty makes the Nodding Ladies'-tresses one of the most popular wildflowers of our region. The snow-white, fragrant flowers have a crisp crystalline appearance and are usually tightly spiralled in two to four ranks. The "nodding" impression of the blossom, which is really more or less horizontal, derives from downward deflection of the lip. The flowering spike varies in size from 10 to 45 cm and is surrounded by grass-like basal leaves.

Spiranthes cernua is the last orchid to bloom during the flowering season in New Hampshire. All summer long the fields and roadsides are dominated by naturalized plants that are European in origin, such as Daisies (*Chrysanthemum leucanthemum*), Buttercups (*Ranunculus* spp.), and Dandelions (*Taraxacum officinale*). With the coming of Autumn, our native herbs display their bouquets. The Nodding Ladies'-tresses is not found in the company of tall and leafy Asters and Goldenrods, but instead grows in roadside ditches, old sand pits, and mowed, moist meadows.

The most common habitat of this species is in roadside ditches where summer mowing keeps competition with grasses to a minimum. Apparently, modern highway systems have been instrumental in making this orchid widespread by providing long stretches of appropriate habitats. A roadside area where Milkwort (*Polygala sanguinea*) and Gerardia (*Agalinis* spp.) are blooming generally means that plants of the Nodding Ladies'-tresses are likely to be nearby. At especially favored sites one can find Bottle and/or Fringed Gentians (*Gentiana* spp.) in the vicinity of populations of *Spiranthes cernua.*

It takes a heavy killing frost to nip plants of the Nodding Ladies'-tresses. I have seen flowers of this orchid in Pinkham's Grant, Coos County, completely encased in ice in the early morning. By noon, the warm late-September sun of Indian Summer had freed the plants of the ice and the flowers looked fresh and unwilted.

The annual appearance of this species seems to be dependent upon rainfall. During the early part of September in 1980, I was unable to find the Nodding Ladies'-tresses in its usual haunts. In mid-September the rains finally came, and the next weekend the roadsides were dotted with the white spikes. So abundant and noticeable are these plants that it is quite possible to botanize when driving along and stopping when populations of the Nodding Ladies'-tresses appear by the side of the road.

Polyembryony, the production of more than one embryo per seed, was reported long ago in *Spiranthes cernua* by Leavitt (1901). Swamy (1948) also investigated embryo formation in the Nodding Ladies'-tresses. He found that three separate races, sexual, asexual, and intermediate, occur in this species. The predominant race (4068 out of 5000 specimens studied) is the asexual one in which 2–6 embryos per seed arise without fertilization (agamospermy). Out of the 5000 plants that he studied, 520 were a normal sexual race in which a single embryo is produced (monoembryony) as a result of sexual fusion. Swamy found that the sexual race was mostly confined to the New England area. The remaining 412 plants that he studied were termed "intermediates," as in these individual plants some embryos were produced as the result of sexual fertilization while others arose by agamospermy. Further studies have shown that the polyembryonic, asexual race is a polyploid ($2n = 60$) and that the sexual, monoembryonic race is diploid ($2n = 30$) (Sheviak and Catling, 1980).

3a. *Spiranthes cernua* var. *ochroleuca*

In 1899, Andrews reported a variant of *Spiranthes cernua* in which the flowers were a yellowish color, rather than the usual pure-white. This color form, along with other subtle morphological differences led Rydberg (Britton, 1901) to describe a new species of Ladies'-tresses which he called *Gyrostachys ochroleuca*. Rydberg's species corresponds to the sexual, monoembryonic race of *S. cernua*. Ames (1906) reduced this taxon to *S. cernua* var. *ochroleuca* because the one reliable character of differentiation between the two taxa is the type of embryo present, an impractical taxonomic character. Recently Leur (1975) reinstated *S. ochroleuca* to species status. Sheviak and Catling (1980) attempted to illustrate through a statistical analysis of floral morphology that morphological characters alone could serve to distinguish the two taxa.

I have collected hundreds of specimens of the *Spiranthes cernua* complex and have found very few that neatly fall into the *ochroleuca* category. Many characteristics are apparently dependent upon habitat (i.e., *S. cernua* sometimes has ascending flowers). Two plants of the same species, one growing in the bottom of a wet roadside in full sunlight, the other growing at the top of the roadbank in partial shade, might be expected to look somewhat different. Although the two races may sometimes be distinguished by morphology, the polyploid race is usually best differentiated from the diploid race by an examination of embryos. As Correll (1950) stated, "Such ultratechnical characters are not readily usuable." Both varieties of the Nodding Ladies'-tresses are visited by bees of the genus *Bombus* (Apidae) (Leur, 1975; Ames, 1921).

GENERAL DISTRIBUTION: Nova Scotia west through Ontario to Minnesota, south to Florida, west to Texas.

4. *Spiranthes lacera* (Raf.) Raf., Herb. Raf., 44. 1833. (Slender Ladies'-tresses)

A somewhat variable taxon probably best treated as a single species composed of two varieties, var. *lacera* and var. *gracilis*. Rafinesque first described this species as *Neottia lacera* from plants found in New York State. Six years later it was also described as *Neottia gracilis* by Bigelow in his *Florula Bostoniensis* (1824), a compendium of plants found in the vicinity of Boston. In this work Bigelow included a description of a plant he called *N. gracilis* var. *secunda*. In this plant, which was collected in Conway, Carroll County, New Hampshire, the spike was hardly twisted and the flowers more slender than the typical plant.

For many years, both varieties of this species were referred to *Spiranthes gracilis*. In 1946, Fernald accorded specific rank to the two entities, calling the more northern plants *S. lacera*, and those plants more southern in distribution *S. gracilis*. Other botanists (Correll, 1950; Case, 1964a) felt that this complex was best treated as a single species, *S. gracilis*. It has been pointed out by Fernald (1946a) and Voss (1966) that Rafinesque's name *S. lacera* has priority over *S. gracilis*, and those who prefer to treat the taxon as a single species must use the earlier name.

The name *lacera* means "torn," describing the margins at the apex of the lip. The Latin word for "slender" is *gracilis,* referring to the very slender flowering spike.

COMMON NAMES: Slender Ladies'-tresses, Green Pearl-twist

FLOWERING DATES IN NEW HAMPSHIRE: July through August (occasionally earlier or later).

DESCRIPTION: (var. *lacera*) Plants from fleshy, fasciculate roots, very slender, moderately pubescent, up to 50 cm tall. Leaves basal, 2–5, short-petioled, ovate, present at flowering time. Inflorescence an elongated, loosely spiralled or secund spike. Flowers white, distantly spaced. Floral bracts ovate, acuminate. Sepals lanceolate, acute. Lateral petals linear, adherent to dorsal sepal. Lip oblong with a green stripe and small callosities. Apex of lip with finely lacerate margins. Capsule ellipsoid.

Variety *gracilis* differs from the above in the following attributes: Plant essentially glabrous; leaves rarely present at flowering time; inflorescence strongly spiralled; flowers closely spaced.

CHROMOSOME NUMBER: $2n = 30$ (Tanaka and Kamoto, 1975).

Disregarding the subtle varietal differences, the Slender Ladies'-tresses is a distinctive plant in our area and is unlikely to be mistaken for another species of *Spiranthes.* The common name is most appropriate as this plant is so slender and elongate that it resembles a wand of grass. *Spiranthes lacera* is a plant that is apt to be overlooked as it often blends in with its surroundings. I have walked by a group of Slender Ladies'-tresses, oblivious to their existence, only to be astounded by their "sudden" appearance when returning along the same path.

When the sunlight strikes a patch of *Spiranthes lacera,* the wispy little flowers look like tiny flags blowing in the wind. The blossoms have a sweet fragrance and a lip that sports a green stripe. The shape of the basal leaves resembles that of the Rattlesnake Plantains, but they usually begin to wither around the time of flowering.

In New Hampshire, *Spiranthes lacera* is most often found in dry, open pastures, especially on slopes, or in open, rocky woods. I have found this orchid at the edges of ski-slopes in the mountains. The occurrence of this species is widespread throughout the state. Because of its inconspicuous nature it is probably more prevalent than collected specimens indicate.

The two varieties of *Spiranthes lacera* are somewhat separated geographically, with var. *lacera* a more northern element and var. *gracilis* found in more southern locations. Fernald (1946a) claimed that all specimens that he examined from northern and central New Hampshire were referable to *S.* [var.] *lacera* and that *S.* [var.] *gracilis* was only present in the southern counties of Hillsborough and Strafford. While this separation may be the general case the situation unfortunately is not quite so clear-cut, as each variety occasionally occurs in the "wrong" end of the state.

The Slender Ladies'-tresses usually blossom in July and August but a few plants have been recorded in flower during June and September in New Hampshire. On this long flowering season Baldwin (1894) commented: "Nature must be fond of the Slender Spiranthes or she would not permit it to flourish in comparatively dry soil and to enjoy a four months lease of life." As tiny as the flowers are, they attract many insect visitors. Robertson (1928) observed a male Long-tongued Bee, *Bombus americanorum* (Apidae) and a female Short-tongued Bee *Calliopsis andreniformis* (Andrenidae) visiting the orchid. The Slender Ladies'-tresses propagates readily from seeds, becoming abundant once it is established in an area (Case, 1964a). This species can apparently achieve the flowering state in only three to five years (Correll, 1950).

Spiranthes lacera var. *gracilis* has been reported to hybridize with *S. vernalis*, in those areas where both taxa grow and flower at the same time, to produce *S. ×intermedia* (Catling, 1978). This hybrid is unlikely to be encountered in this state because one of the putative parents, *S. vernalis* apparently does not grow in New Hampshire. As previously mentioned, *S. lacera* var. *lacera* has been reported to hybridize with *s. romanzoffiana* (Simpson and Catling, 1978).

GENERAL DISTRIBUTION: Nova Scotia west through Ontario to Saskatchewan, south to Florida, west to Texas.

5. *Spiranthes casei* Catling and Cruise, Rhodora 76: 526. 1974.

This is the most recently described species among the orchids of New Hampshire. *Spiranthes casei* was described by Catling and Cruise to eliminate the problem of a group of northern plants which were previously referred to *S. vernalis*. These plants are morphologically quite distinct from the *S. vernalis* that occurs in the southwestern United States. The species was named for the orchid specialist Frederick W. Case, Jr., author of *Orchids of the Western Great Lakes Region* (1964a).

COMMON NAME: Case's Orchid

FLOWERING DATES IN NEW HAMPSHIRE: August to early September.

DESCRIPTION: (from Catling and Cruise, 1974; and Catling, 1978) Plants erect, glabrous below, pubescent above, 27–33 cm tall at flowering time. Leaves glabrous, often glaucous, oblanceolate or linear-lanceolate, reduced to sheaths below the inflorescence, ascending up to 1/3 the length of the stem, present at flowering and withering soon after. Inflorescence a spike of loosely arranged flowers, often in a single spiral, the rachis with septate, reddish-glandular hairs. Floral bracts ovate to ovate-lanceolate, acuminate, pubescent at the base. Ovary obliquely swollen on the upper side at anthesis, pubescent. Sepals lanceolate, barely upcurved. Lip obovate, apically truncated and occasionally notched. Base of lip cordate. Basal callosities stout, incurved. Capsule elliptical.

CHROMOSOME NUMBER: $2n = 60$–70, 65–75 (P. Catling, personal communication).

In one section of his discussion of New England orchids, Ames (1921) noted that the northern *Spiranthes vernalis* may not be comparable to the southwestern form of *S. vernalis*, as originally described by Englemann and Gray. Ames postulated that the northern *vernalis* may be a hybrid between *S. cernua* and *S. gracilis*, as the plants in question seemed to him to be intermediate between the two. Catling and Cruise (1974) do not deny the possibility of a hybrid origin of this species but point out that the taxon maintains itself in the abscence of one or both putative parents, shows no evidence of back-cross-swamping of its distinctiveness, and is fertile. Additionally, *Spiranthes casei* has cream-colored flowers, whereas *S. cernua* and *S. lacera* both have white flowers.

While plants clearly referable to *Spiranthes vernalis* occur in southeastern Massachusetts, these populations seem to constitute the northern limit of this species. It appears that *S. vernalis* (*sensu* Englemann and Gray) has not been found in New Hampshire to date. The specimens identified as *S. vernalis* from this state that I have seen are referable to *S. casei*, or are hybrids of uncertain affinities. Catling has placed the hybrid *S. cernua* × *S. gracilis* Ames and *S. neglecta* Ames in synonymy with *S. vernalis*. He has also indicated that the name *S.* ×*intermedia* Ames (*pro* hybr.) should be retained for hybrids between *S. vernalis* and *S. lacera* var. *gracilis*. All of the above taxa are similar to each other but differ from *S. casei* in the light-colored and non-glandular pubescence of the rachis (Catling, 1978). The pubescence of *S. casei* is a dark-reddish color, septate, and glandular. *Spiranthes intermedia*, as recently circumscribed by Leur (1975), is actually synonymous with *S. casei*.

Spiranthes casei is a tall, robust plant that grows in dry open areas such as roadside banks and along power lines. I have found this species growing in an old field in Colebrook, Coos County, in August. Apparently, this orchid flowers earlier than the Nodding Ladies'-tresses with which it sometimes grows (Catling and Cruise, 1974).

An examination of herbarium specimens of *Spiranthes* from the state turned up some plants from northern New Hampshire that easily fall into the *S. casei* category. The situation becomes more complicated in the southern counties as a few plants labeled "*S. vernalis*" appear to be neither *S. vernalis* nor *S. casei*, and are most probably hybrids.

In their study of their new species, Catling and Cruise found *S. casei* to be partially apomictic. Flowers from which insects were excluded demonstrated 10–25% seed germination.

GENERAL DISTRIBUTION: A broad band from Nova Scotia west through northern New England to Michigan and Ontario (Catling and Cruise, 1974).

10. Isotria Raf., Med. Repos. II 5: 357. 1808.

This genus consists of two eastern North American species which were originally referred to *Arethusa*. In 1808 Rafinesque segregated these species into his genus *Isotria* but his generic concept did not gain acceptance until about 70 years ago. In the interim most botanists followed Nuttall's (1818) treatment which included the two species within the genus *Pogonia*.

The apparently* whorled arrangement of the leaves at the summit of the stem is unique to this genus of the orchid family. The

---

*Homoya (Master's thesis, So. Ill. Univ., 1977) reported that "careful inspection reveals staggered leaf insertion on the stem."

name *Isotria* is from two Greek words meaning "equal" and "three," referring to the nearly identical size and shape of the sepals.

Key to the species of *Isotria*

1. Flowers on a pedicel over 2 cm long; sepals purplish, more than 3 cm long; stem purplish; in fruit the pedicel is about twice the length of the capsule .... 1. *Isotria verticillata*
1. Flowers on a very short pedicel, appearing almost sessile; sepals light green, less than 3 cm long; stem greenish-white, in fruit the pedicel is about the same length as the capsule .... 2. *Isotria medeoloides*

1. *Isotria verticillata* (Muhl. ex Willd.) Raf., Med. Repos. II 5: 357. 1808.

Muhlenberg first collected this species in the Blue Ridge Mountains of Pennsylvania; he sent the specimens along to Willdenow in Germany who then published the description of the plant (as *Arethusa verticillata*) in his *Species Plantarum* (1805). The epithet *verticillata* is Latin for "whorled," describing the apparent arrangement of the leaves.

COMMON NAME: Large Whorled Pogonia.

FLOWERING DATES IN NEW HAMPSHIRE: mid-May to mid-June.

DESCRIPTION: Plant erect with extremely long, hairy roots that produce root-shoots which give rise to new plants. Stem glabrous, hollow, purplish, 10–30 cm tall. Leaves 5–6, green, oblong-lanceolate, whorled at summit of stem. Inflorescence consists of 1 or 2 pedicellate flowers terminating the stem. Sepals purplish, narrowly lanceolate, acuminate, spreading. Lateral petals yellow-green, elliptic-obovate. Lip 3-lobed, oblong-cuneate, yellowish-white, streaked with purple, crested along median ridge. Column approximately 1 cm long with a denticulate apex. Capsule erect, ellipsoid, on a pedicel nearly twice the length of the capsule.

CHROMOSOME NUMBER: $2n = 18$ (Baldwin and Speese, 1957).

The Larger Whorled Pogonia presents an exotic-looking flower. Elevated on a pedicel above the circle of leaves, the dramatically long and spreading purple sepals serve to focus attention on the yellowish-green petals which they surround.

Isotria verticillata is primarily a more southern species that reaches its northern limit in New England. In the more optimum southern environments the Large Whorled Pogonia is considered uncommon but it is truly rare here at the northeastern edge of its range. The historic occurrence of this species in the southern part of New Hampshire is verified by three specimens, all collected before 1909. In the literature *I. verticillata* has been mentioned as occurring in Auburn and Manchester in 1900 (Batchelder, 1900). Unfortunately the station in Manchester at which the Large Whorled Pogonia was described by Batchelder (1900) as being locally abundant, was transformed into a potato field "doubtless more profitable to the owner of the land than the orchids, but less interesting to the botanist" (Batchelder, 1909). Presently there is one known extant station for this species in New Hampshire. The report of the orchid's occurrence in Rockingham County by Storks and Crow (1978) proved to be the Small Whorled Pogonia, *Isotria medeoloides*.

Although the Large Whorled Pogonia is found in a variety of habitats throughout its range, in New Hampshire it has been consistently reported as growing in second (or third) growth acidic woodland habitats dominated by Red Maple (*Acer rubrum*) and Hemlock (*Tsuga canadensis*). Companion herbs include Canada Mayflower (*Maianthemum canadense*), Goldthread (*Coptis groenlandica*) and Wintergreen (*Gaultheria procumbens*) "for which the Pogonia seemed to have a fondness" (Morris and Eames, 1929). *Isotria verticillata* very closely resembles the Indian Cucumber-root (*Medeola virginiana*) which is also commonly associated with the orchid.

In a recent study of the breeding systems and pollination biology of the genus, Mehrhoff (1980) found that *I. verticillata* is pollinated by bees of the families Andrenidae, Anthophoridae and Halictidae. In the same study it was noted that percentage seed set in this species was only 15% owing to low pollinator activity. The Large Whorled Pogonia regularly propagates by means of root-shoots and often forms large colonies (Ames, 1922a; Leur, 1975).

Isotria verticillata is reported as being subject to long periods of dormancy but Case (1964) has observed a colony of this species that has produced plants annually for 13 years. Flowering is reported to be sporadic in the Large Whorled Pogonia but this behavior can probably be attributed to factors such as lack of maturity and non-optimum environmental parameters.

General distribution: New England west to Michigan, south to northern Florida, west to eastern Texas.

2. *Isotria medeoloides* (Pursh) Raf. Fl. Tellur. 4: 47. 1838.

This species was first described by Pursh in 1814 as *Arethusa medeoloides*. The Small Whorled Pogonia has also been known as *Pogonia affinis* and *Isotria affinis*. The specific epithet *medeoloides* means "resembling *Medeola*," the Indian Cucumber-root, a common liliaceous plant of the eastern deciduous forest.

Common names: Small Whorled Pogonia, Little Five Leaves.

Flowering dates in New Hampshire: June

Description: Plant erect, glabrous, up to 27 cm tall, elongating in fruit up to 36 cm. Roots fibrous, hairy. Stem stout, pale green, glaucous, hollow. Leaves terminal, 5 or 6 in a whorl, elliptic, apiculate, slightly drooping when flowering begins and becoming horizontal in fruit. Inflorescence of 1 or 2 nearly sessile flowers, the short pedicel only becoming noticeable in fruit. Flowers yellowish-green. Sepals linear-oblanceolate. Petals oblanceolate. Lip whitish-yellow with greenish veins, three lobed. Lateral lobes triangular. Mid-lobe rounded, cuneate, with a median crest. Plant greatly elongating in fruit. Capsule erect, ellipsoid, on a short pedicel about equaling the capsule in length.

Chromosome number: $2n = 18$ (Baldwin and Speese, 1957).

"Our rarest orchid," state Gleason and Cronquist (1975) of *Isotria medeoloides* in their *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*. Leur (1975) concurred that the Small Whorled Pogonia is the rarest orchid east of the Mississippi, excluding Florida. Many botanists have never seen this species in the wild. I am fortunate to be among those that Ames (1922) called the "favored few" who have actually found *I. medeoloides*. In other parts of the country reports of new *I. medeoliodes* stations have often turned out to be *I. verticillata*, whereas in New Hampshire the opposite situation has occurred.

A review of the characters that serve to distinguish the two taxa seems appropriate here. Their very names suggest a size differential but in newly discovered populations of *Isotria medeoloides* in Maine and New Hampshire, many individuals exceed the height heretofore listed in published descriptions (E. Briggs, personal communication). A better indicator is the length and shape of the sepals which, in *I. verticillata,* are over 3 cm long, purplish in color, and are widely spreading. In *I. medeoloides* the sepals smaller, not spreading, and greenish-colored. The flowers of the former are borne on a pedicel but in the latter they appear to be almost sessile. In the Large Whorled Pogonia the stem is purplish while in the Small Whorled Pogonia it is a pale greenish color. When the plants are in fruit the pedicel of *I. verticillata* is twice the length of the capsule whereas in *I. medeoloides* they are about equal in length (Case, 1971).

Another interesting difference between the two species is the position of the whorled leaves when blossoming is taking place. As flowering begins the leaves of the Large Whorled Pogonia are pointed upward and gradually drop to a horizontal position. In the Small Whorled Pogonia the leaves are pointed toward the ground when the flowers first open and slowly rise to become horizontal. Plants of *Isotria verticillata* are described as growing in clumps within a few inches of each other, while *I. medeoloides* is said to commonly occur as solitary plants growing several feet apart (Case, 1971). Although this report may be generally true, I have observed clumps of three to four flowering plants of the Small Whorled Pogonia growing up from almost the same point in the ground.

In the past, most known populations of the Small Whorled Pogonia have consisted of very few individuals. Mehrhoff (1980) reported that in all of the populations of this species known as of 1979, the mean average number of plants per population was five, and the median average was listed as being only three. At the other extreme, some newly-located stations in N.H. and Maine have well over 200 plants. Because *I. medeoloides* is so rare throughout its range, it has been listed by the U.S. Fish and Wildlife Service (Federal Register, Vol. 47, No. 176, Sept. 10, 1982) as "Endangered" under the Endangered Species Act of 1973. Until recently, it was believed that there were a greater number of dried specimens of this taxon in herbaria than there are living plants (Federal Register, Vol. 45, No. 242, December 15, 1980). Of all the individual plants known to exist in the world today, approximately 80% occur in Maine and New Hampshire (R. Dyer, personal communication).

Isotria medeoloides grows in acidic soil conditions and is most often found in second growth mixed deciduous forest communities. The preferred habitat appears to be in areas of thick organic duff associated with vernal streams. In other words, this species may be found in a forest habitat typical of many areas of New Hampshire. Two small sub-populations of *Isotria medeoloides* have recently been found in dark, fairly wet, coniferous forests in New Hampshire, but none of the plants flowered in that situation.

It has been claimed that the Small Whorled Pogonia remains dormant underground without flowering for up to 20 years, but this supposition has not been supported by detailed observations. One New Hampshire station has been observed since 1965 by Mr. and Mrs. Ring, a naturalist couple in Merrimack County. They have made a valuable contribution to the knowledge of the biology of this species by keeping careful records of its occurrence. Though the number of flowering plants varied from year to year, the population made a showing every year. When the plants were discovered, the area (which had been previously logged) was composed mainly of saplings about 12 feet tall and a few scattered larger trees. The Rings have found that the percentage of plants blossoming increased between 1965 and 1973. Since that time the number of flowering individuals has steadily declined. These data seem to suggest that light intensity may provide at least one stimulus for flowering. These observations have been reinforced by Mehrhoff's recent work on the genus. He found that flowering individuals of the Small Whorled Pogonia occurred in locations with only a low herbaceous cover while sites with relatively dense shrub coverage, or many saplings, only produced vegetative individuals (Mehrhoff, 1980). One station of Small Whorled Pogonia that I located in 1980 consisted of only two small plants. In 1981 this area was hard hit by an invasion of Gypsy Moths which had devoured much of the canopy. The population has doubled in size and vigor each year since then, a phenomenon that I believe to be related to the increased amount of sunlight reaching the forest floor.

Lacking scent, nectar guides and brightly colored flowers, the Small Whorled Pogonia has been found to be self-pollinating by

Mehrhoff (1980) who also noted that seed set was 83% in this species. Despite this relatively high percentage of seed set, a study of an Illinois population suggests that *I. medeoloides* exhibits reduced reproductive potential owing to early termination of capsule development and late summer mortality, at least at that particular site (Homoya, Master's thesis, So. Ill. Univ., 1977). I have also observed many cases of arrested flower development in this species, where flower buds were formed but eventually withered away.

That this orchid is exceedingly rare is indisputable, but its presence also just may be overlooked much of the time. A small green plant that resembles many other herbs and lives in an ordinary, unspecialized habitat (where few botanists concentrate their field work) can easily go unnoticed. Perhaps the secret of its continued existence, despite the low numbers of known populations which would seem to indicate imminent extinction, lies in the fact that the Small Whorled Pogonia is able to avoid detection by would-be exploiters.

DISTRIBUTION: Ontario, Canada; Connecticut, Georgia, Illinois, Massachusetts, Michigan, Missouri, New Hampshire, New Jersey, New York, Maine, Maryland, North Carolina, Pennsylvania, Rhode Island, South Carolina, Vermont and Virginia.

11. **Pogonia** Juss. Gen. Pl. 65. 1789.

Pogonia is a small genus of acid-loving orchids which occurs in eastern North America and eastern Asia. The first-described species of this genus was originally included within the genus *Arethusa* by Linnaeus (1753); de Jussieu transferred a section of Linnaeus's genus *Arethusa* to his new genus *Pogonia*. Several species were formerly referred to *Pogonia* but are now segregated in distinct genera, including *Cleistes, Isotria, Triphora* and *Psilochilus* (Ames, 1922a).

In this genus the pollen grains of the pollinia characteristically are separate (simple) rather than being grouped into tetrads. The name of the genus is taken from the Greek word for "beard," referring to the bristles on the lip.

1. *Pogonia ophioglossoides* (L.) Juss. Gen. Pl. 65. 1789.

The only eastern North American species in this genus is the Rose Pogonia, *Pogonia ophioglossoides*. The specific name *ophioglos-*

soides means "like the Adder's-tongue," referring to the plant's single leaf which is reminiscent of the solitary leaf of *Ophioglossum*, the Adder's-tongue fern.

COMMON NAMES: Rose Pogonia, Snake-mouth, Adder's-tongue Orchid

FLOWERING DATES IN NEW HAMPSHIRE: Mid-June through July

DESCRIPTION: Plant slender, glabrous, 8–30 cm tall. Stem green, arising from fibrous roots. Leaf solitary, fleshy, ovate-lanceolate, almost half-way up stem. Floral bracts leaflike, oblong-lanceolate. Ovary sessile, slender. Flowers terminal, usually solitary (occasionally 2), rose to pink (rarely white, in forma *albiflora*), fragrant. Sepals narrow, linear-oblong to elliptic. Lateral petals wider than the sepals, oblong-elliptic, obtuse. Lip spatulate, narrowing at base, fringed along margins at apex, bearded along the three main veins with fleshy yellow bristles which become longer and fuchsia-colored at the apex. Column approximately 1 cm long, pink, curved, toothed at apex. Capsule ellipsoid, ribbed, erect.

CHROMOSOME NUMBER: $2n = 18$ (Moore, 1973).

Our eastern North American bog-orchid, *Pogonia ophioglossoides*, was brought to the attention of the world when Ker published a description and drawing of the species in *The Botanical Register* "consisting of Colored Figures of Exotic Plants cultivated in British Gardens with their history and Mode of Treatment" (1916). The slender plant, bearing a beautiful pink blossom with an elaborately fringed lip, understandably captured the fancy of English nurserymen.

The acid-loving Rose Pogonia occurs quite frequently in our region in wet meadows and open bogs. In the former habitat the delicate pink flowers seem to magically appear amoung the grasses. Robert Frost (1964), in his poem "Rose Pogonias" described such a scene:

> "For though the grass was scattered
>   Yet every second spear
> Seemed tipped with wings of color
>   That tinged the atmosphere"

The presence of *P. ophioglossoides* is more noticeable in sphagnum bogs where many vegetative plants, consisting only of solitary leaves on small petioles, rise straight up from the bog mat. The Rose Pogonia can reproduce vegetatively by rootshoots and is able to form large colonies in favorable habitats.

The fragrance of the Rose Pogonia has elicited a wide variety of descriptions. Thoreau (1884) found the odor offensive and declared that it smelled "exactly like a snake." Others have likened its perfume to raspberries (Barker, 1931) or violets (Baldwin, 1894). I have found the Rose Pogonia to possess a sweet odor that smells uniquely like Rose Pogonia.

The structure of the flower of *Pogonia ophioglossoides* is adapted for outcrossing (Scudder, 1862). The pollen-masses in this species are located within a pouch-like recess, covered by a hinged lid (Bingham, 1939). To reach the nectar that is located deep within a narrow passage-way, a visiting insect must first press its head against the sticky stigma. Any pollen that the bee carried into the blossom is thus removed and, at the same time, its head is smeared with the sticky substance. In the process of backing out of the small opening the head of the insect catches the projecting edge of the lid. As the bee continues to back out, the lid raises to expose the pollen-masses, parts of which adhere to the front of its head. When the bee has completely emerged the anther lid snaps shut again (Scudder, 1862). Heinrich (1979) found that the odor, fragrance, and presence of nectar in *P. ophioglossoides* attracts bees of the genus Bombus (Apidae), and they serve as pollinators for the orchid. The percentage of seed set in this species is quite variable, ranging from 10–100%. The higher figure has led to speculation that some populations of the Rose Pogonia may be apomictic (Thein and Marks, 1972).

GENERAL DISTRIBUTION: eastern North America; Newfoundland, west through the Great Lakes region to Minnesota, south along the Coastal Plain to Florida, west to Texas. Closely related to *P. japonica* of eastern Asia (Li, 1952).

12. **Arethusa** L. Sp. Pl. 950. 1753.

In Greek mythology Arethusa was a beautiful river nymph. Gronovius appropriately applied the name to this orchid in his pre-Linnaean publication *Flora virginica* (1743). Linnaeus subsequently used the same name, *Arethusa bulbosa,* in his *Species Plantarum.*

1. *Arethusa bulbosa* L. Sp. Pl. 950. 1753.

Arethusa bulbosa is the only species within the genus. A closely related Japanese plant *Eleorchis japonica* (Sawa-ran) has sometimes been treated as *Arethusa japonica* (Ohwi, 1965). The specific epithet *bulbosa* refers to the bulb-like corm from which the plant arises.

COMMON NAMES: Arethusa, Dragon's-mouth

FLOWERING DATES IN NEW HAMPSHIRE: late May through June

DESCRIPTION: Plant slender, arising from a bulbous corm, glabrous, scapose, 10–40 cm tall. Leaf solitary, grass-like, enclosed in a sheath at flowering time and emerging after the flower fades. Floral bracts scalelike, triangular, minute. Ovaries sessile, erect. Flowers terminal, solitary (rarely 2), deep rose (rarely white as in forma *albiflora,* or lavender in forma *subcaerulea*). Dorsal sepal oblanceolate, connivent with the linear-oblong lateral petals, all curved over the column. Lateral sepals oblong-lanceolate, oblique, only slightly curved foreward. Lip pale pink streaked with purple, clawed, oblong, recurved, often indistinctly 3-lobed. Margins of lip crenulate-undulate, erose. Disks of lip with yellow, fleshy, fringed crests. Column pink, flattened, linear-spatulate, erose at apex. Capsule ovoid, erect, approximately 2 cm long.

CHROMOSOME NUMBER: $2n = 44$ (Thein and Marks, 1972).

All who have had the good fortune to see this orchid in bloom acclaim its beauty. Morris and Eames (1929) stated: "To our mind this is the most exquisitely beautiful of all single-flowered orchids." With all the orchids in the United States and Canada to choose from, Dr. C. A. Leur selected photographs of *Arethusa* to grace the cover of his recent book *The Native Orchids of the United States and Canada excluding Florida.* This colorful denizen of bogs and wet meadows is sometimes called "Dragon-mouth," for its animal-like countenance.

The distribution of *Arethusa* is restricted to northeastern North America with one disjunct population in the mountains of North Carolina. In New Hampshire the number of known populations of this striking orchid has significantly decreased since the turn of the century. Fernald (1950a) stated that *A. bulbosa* is "rapidly becoming extinct S. of Nfld. and Canada."

Reasons for the drastic reductions of our *Arethusa* populations are circumstantial; unlike most orchids in our flora, *Arethusa* seldom reproduces vegetatively and depends primarily upon seed production to perpetuate itself (Case, 1964a). In addition, the bulb-like corm is only loosely attached in the mossy substrate where the slightest disturbance may dislodge it (Fernald, 1950a). In Rhode Island, Stuckey (1967) noted that the "changing patterns of land use away from pasturing and mowing would seem to be the direct cause of the decline in numbers of *Arethusa.*

Some of the old *Arethusa* stations are no longer suitable habitats for the orchid due to the natural tendency of wetlands in our area to become drier over a long period of time (Jorgensen, 1971). One *Arethusa* location in Carroll County prompted Wolfboro botanist H. E. Sargent to write in his botanical notebook, in 1917, "never saw so much of it" (Sargent, unpublished notebook, NHA). During the summer of 1980 the same location yielded only two *Arethusa* blossoms in the now drier meadow. An aesthetically pleasing plant like *Arethusa* is unfortunately vulnerable to the possessiveness of man; many hundreds of these orchids have been taken from their boggy habitats only to perish in wildflower gardens or plant presses.

Arethusa attracts pollinators to its showy, fragrant flowers which produce a small amount of nectar. Thein and Marks (1972) found that *A. bulbosa* requires a large insect to effect pollination, and this role is usually filled by queens of the genus *Bombus* (Apidae). The mechanism of pollination is similar to that of *Pogonia.* In this case it is the bee's thorax that comes in contact with the sticky stigma, forces the anther lid open, and receives the (usually whole) pollinia.

Percentage seed-set is quite low for *A. bulbosa,* approximately 5% in northern Wisconsin (Thein and Marks, 1972).

Baldwin (1894) quoted "the unsentimental Hooker" (Sir William Jackson Hooker) as stating that Arethusa bulbs are used as a cure for toothache. In our era of preventive dentistry one hopes that the corms of this striking orchid are safe from such cure seekers.

GENERAL DISTRIBUTION: northeastern North America; Newfoundland west through the Great Lakes region to Wisconsin, south to Pennsylvania, disjunct to North Carolina.

13. Calopogon R. Br. *In* W. *et* W. T. Aiton. Hort. Kew ed. 2, 5:204. 1813. (conserved name).

Originally named *Limodorum* by Linnaeus (1753), this genus was removed to *Calopogon* by British botanist Robert Brown. There are four species in this genus, of which 3 are confined to the southeastern United States. The fourth species, *C. tuberosus,* is more widespread. *Calopogon* is distinct in having non-resupinate flowers. In this genus the lip occupies the uppermost position in the blossom. The name *Calopogon* means "beautiful beard" referring to the bristles on the lip.

1. *Calopogon tuberosus* (L.) BSP, Prel. Cat. N. Y. 52. 1888.

The Grass-pink was named by Britton, Sterns and Poggenberg (abbreviated BSP). This species has also been known as *Calopogon pulchellus,* a most descriptive appelation meaning "little beauty."

COMMON NAMES: Grass-pink, Calopogon

FLOWERING DATES IN NEW HAMPSHIRE: mid-June through July

DESCRIPTION: Plant arising from a small ovoid corm with many fibrous roots. Scape slender, glabrous, 9–50 cm tall. Leaves 1 (rarely 2), grass-like, basal, linear, ribbed. Inflorescence a loosely-flowered terminal raceme of 1–8 successively opening blossoms. Flower buds sickle-shaped. Floral bracts small, approx. 6 mm long, ovate-lanceolate, acuminate. Flowers deeply colored magenta or rose-purple (rarely white). Middle sepal oblong-elliptic, acute. Lateral sepals ovate, oblique, acute, concave. Lateral petals short-clawed, oblong-pandurate, narrower than the sepals. Lip uppermost, linear with 2 basal side knobs (obscure lobes), dilated into a triangular or rounded "whale-tailed" apex, retuse. Disk bearded along the 3 veins with spreading clavellate hairs that are white with yellow tips. Column incurved, winged, spoon-shaped. Capsule ellipsoid, erect, ribbed.

CHROMOSOME NUMBER: $2n = 40$ (Thein and Marks, 1972).

It is always a pleasant surprise to find a population of the deeply-colored Grass-pinks in bloom. To describe more accurately such intense color, the common name of this orchid should be "Grass-magenta" or "Grass-rose-purple." There have been other complaints concerning the names of orchids. "Pogonia! Calopogon!!" grumbled Thoreau (1884) in his journal entry for July 7, 1852, "They would blush still deeper if they knew what names man had given them."

Although this showy plant is abundant in many places within its range it is, unfortunately, yet another orchid that appears to be declining in New Hampshire. I have never found *Calopogon* growing in any other habitat than a quaking spruce-tamarack bog. There, among the cranberries and carnivorous Pitcher-plants the grass-like leaves and bright flowers of *Calopogon* are found, most often growing alongside Rose Pogonias. In those rare sites where *Arethusa* also grows, the three orchids provide a succession of rose-colored flowers from late May through July.

Calopogon tuberosus is pollinated by bees of the genus *Bombus* (Apidae) (Thein and Marks, 1972). When the bee alights on the lip its weight causes the hinged-like lip to fall downward, lowering the insect onto the column. In this way the bee's back comes in contact with the sticky stigma and then the pollen-masses of the anther. When the insect flies away the lip springs back up to its original position. *Bombus* bees are the proper weight and proportion to effect pollination in *Calopogon* whereas smaller insects are not heavy enough to cause the lip to drop.

Without scent or nectar, one might ask how the Grass-pink can attract pollinators. It is believed that the yellow bristles (beard) found on Calopogon, Arethusa, and Rose Pogonia mimic the yellow anthers of non-orchid flowers that serve as a food reward for insects (Dressler, 1981). Indeed, like anthers, the beards of these three orchids show ultraviolet reflectance patterns that are important for orientation of bees on flowers (Thein and Marks, 1972).

The co-occurrence of the three orchid species in the same habitat with staggered but overlapping blooming times (first Arethusa, then Rose Pogonia and finally Calopogon) leads bees to expect that the Grass-pink will also be a source of nectar. Heinrich (1979) has found that where plant species with similar flowers bloom in close succession of each other, the first to blossom has more nectar than those following. Dressler (1981) has termed the pollination tactic of Calopogon a case of "empty promises."

GENERAL DISTRIBUTION: southeastern Canada; Newfoundland west through Ontario. Eastern U.S. west to Minnesota and Texas; Cuba and the Bahamas.

14. Malaxis Soland., Prodr. Veg. Ind. Occ. 119. 1788.

A widely distributed genus of about 200 species most of which are concentrated in Asia and Oceania (Correll, 1950). All the species are small and uncommon. The name *Malaxis* is Greek for "softening," probably referring to the texture of the leaves. Only two species occur in our area. Our plants have also been referred to the genera *Microstylis* ("little column") and *Achroanthes* ("colorless flowers"), two appropriately descriptive names.

Key to the species of *Malaxis* in New Hampshire

1. Leaf sheathing base of stem; flowers in a loose raceme with pedicels less than 3 mm long; mid-lobe of lip long and pointed at apex .... 1. *Malaxis monophylla* var. *brachypoda*
1. Leaf clasping stem almost half-way; flowers in a dense raceme with slender pedicels 3 mm or longer; apex of lip cleft into 2 triangular lobes with a minute tooth in the sinus .... 2. *Malaxis unifolia*

1. *Malaxis monophylla* (L.) Sw., Kongl. Svens. Vetens. Nya Handl. 21: 234, t. 3, fig. P. 1800.

This species was described by Linnaeus (1753) as *Ophrys monophyllos* from type material collected in the swampy forests of Prussia. In 1830 Lindley transferred the species to the genus *Microstylis*, where it is still retained by some workers (*see* Moore, 1980).

Our eastern North American plant was described in 1835 as a separate species *Microstylis brachypoda* by Asa Gray, who subsequently changed his concept of this taxon and viewed it as a variety. In 1926 Fernald (1926a) reinstated the taxon to species status as *Malaxis brachypoda*, a synonym by which it is most well known. Morris and Eames (1929) designated the taxon as *Malaxis monophylla* var. *brachypoda*, a name that has only recently gained wide acceptance.

The eastern North American var. *brachypoda* has resupinate flowers, thus differing from the European var. *monophylla* in which the pedicels twist a full 360 degrees, returning the lip to an uppermost ("hyper-resupinate") position (Dressler, 1981). The epithet *monophylla* means "single-leaved", *brachypoda* signifies "short-pedicelled."

COMMON NAME: White Adder's-mouth

FLOWERING DATES IN NEW HAMPSHIRE: mid-June to mid-July.

DESCRIPTION: Plant small, less than 20 cm, from an ovoid corm covered with leaf-sheaths. Leaf solitary, broad, ovate-elliptic, with a long sheathing petiole. Raceme slender, elongate, loosely flowered. Floral bracts minute. Flowers tiny, pale greenish-white to yellowish-green, on short, thread-like pedicels. Sepals linear-oblong, acuminate. Lateral petals linear, acute, reflexed. Lip lowermost, 3-lobed, slightly cordate. Lateral lobes small, rounded, inrolled. Mid-lobe longer, lanceolate, sharply pointed. Column short, stout. Capsule ellipsoid, ascending.

CHROMOSOME NUMBER: $2n = 28$ (Moore, 1973).

Malaxis monophylla is a circumboreal species that probably survived the Ice Age close to the margins of the glacier (Correll, 1950). Accordingly, our variety prefers cold wet soils and doesn't venture further south than the glacial boundary. In Europe *M. monophylla* is extremely rare, occurring in calcareous swamps under dense growths of alders (S. Nilsson, 1979).

The White Adder's-mouth has the distinction of possessing the smallest flowers of all our native orchids. The tiny, pale flowers are almost colorless or "faded like withered tissue" (Morris and Eames, 1929). It is so well camouflaged by its surroundings that it is surprising that this species is ever found by orchid hunters. The majority of specimens of *Malaxis monophylla* that I have seen were collected in fruit. The light brown capsules are evidently more noticeable that the almost colorless flowers.

The habitat preference of *Malaxis monophylla* var. *brachypoda* is reported to be wet, swampy woods, especially of Cedar (*Thuja*). Case (1964a) suggested that the simplest way to locate this orchid is to search in the very wettest deer trails and rabbit runs. This variety seeks the shade of the forest in this state, but toward the northern edge of its range the White Adder's-mouth can be found growing in open areas. I was recently surprised to come upon this species in a decidedly acidic mixed-forest along the edge of a vernal stream. *Malaxis monophylla* var. *brachypoda* has been verified from only three places in the state. Because of its scarcity it is regarded as an endangered species in New Hampshire by Crow and Storks (1980).

On a regional level the White Adder's-mouth is classified as "Rare" in New England (Crow *et al.*, 1981).

The members of this genus appear to be adapted for insect pollination. In a *Malaxis* species from India, Hooker found a projection which, when touched, turned into a drop of viscid material (Gibson, 1905). Hagerup (1951) reported that the exclusion of insects of another small member of this genus, *M. paludosa,* prevented the formation of seeds. Although I have found no record of specific pollinators for *Malaxis monophylla,* it may well be that small flies and gnats effect pollination in this species, as has been long suspected by other workers. On the European continent the common name of this orchid is "Gnat Flower" (S. Nilsson, 1979).

GENERAL DISTRIBUTION: Newfoundland south to Pennsylvania, west through the Great Lakes region to Minnesota and Manitoba, north to Alaska.

2. *Malaxis unifolia* Michx., Fl. Bor. Am. 2: 157. 1803.

This species was discovered by Michaux and described in his *Flora Boreali-americanae* (1803). The plants on which he based his description were collected in wooded areas of Pennsylvania, Carolina, and Florida. This plant has also been known by the specific epithet *ophioglossoides,* meaning "like the Adder's-tongue fern." The name *unifolia* refers to the single leaf produced by this species.

COMMON NAME: Green Adder's-mouth

FLOWERING DATES IN NEW HAMPSHIRE: July through August.

DESCRIPTION: Plant erect, glabrous, bright green, up to 27 cm tall in our area. Stem arising from a basal corm which is covered by leaf sheaths. Leaf solitary, sheathing stem about half-way, ovate, dark green. Inflorescence a densely flowered raceme of long pedicelled green flowers loosely arranged below and crowded near summit. Floral bracts minute, triangular. Sepals filiform, strongly reflexed, curled under lateral sepals. Lip auricled, oblong-quadrate, divided at apex into 2 triangular lobes with a small tooth in the open sinus. Column a minute stub. Capsule ellipsoid.

CHROMOSOME NUMBER: unknown

Malaxis unifolia has an unusual distribution. It occurs in eastern temperate North America, Jamaica, Cuba, and in sections of Central America. The Green Adder's-mouth is yet another orchid so small and inconspicuously flowered that it led Baldwin (1894) to complain that he "scarcely knew how to describe or make my finest pointed pencil flatter." With a magnifying glass and some imagination one can perceive in the flower the flattened head of a viper from which the fanciful common name is drawn.

In our range the Green Adder's-mouth is adapted to a wide variety to habitats including rich deciduous woods, wet woods, moist pastures, and dry rocky slopes. Wherry (1918) stated that *M. unifolia* prefers soils that are acid in reaction, a requirement readily fulfilled in New Hampshire as demonstrated by the many specimens collected in the state. In compiling the records for this plant I was struck by the abundance of older collections; almost half of them are from the 19th century. Of the 85 New Hampshire specimens (many of them from the same town) deposited in New England herbaria, only 15 were collected in the past 50 years.

It is difficult to assess the situation with regard to the dearth of modern collections of *Malaxis unifolia*. It is possible that the numbers of this species have declined owing to changing land use patterns in the state. In Rhode Island Stuckey (1967) recorded a stand of *Malaxis unifolia* growing with other orchids under some power lines. During a three-year period the amount of woody plants increased and the stand of orchids declined, leading her to conclude that the loss of orchid plants was caused by competition from the woody species. Similar changes have taken place in New Hampshire where many formerly open areas have reverted to forest lands during the past 100 years.

It is also probable that the number of botanists working in the state, especially serious "amateurs," has declined. This loss has greatly influenced the amount of botanical collecting now going on in New Hampshire. For the most part these individuals earned their livings in other professions but were able to spend long summer holidays in New Hampshire, where they actively pursued their avocation of botany. Without such collectors as Walter Deane, C. F. Batchelder, E. F. Williams and many others, our flora would be considerably less well represented in the major herbaria of the area.

My first experience with the Green-Adder's-mouth came on a collecting trip specifically for ferns. The day was quite warm and the myriad of old logging roads kept us moving in circles instead of heading for the cliffs we hoped would yield some "good" pteridophytes. The forest floor was carpeted with plants of Canada Mayflower (*Maianthemum canadense*) and, sitting down to take a sip of water, I noticed one "*Maianthemum*" that looked a little different. Closer inspection revealed the plant to be the tiny Green Adder's-mouth, a single orchid in a sea of Canada Mayflower. It is often characteristic of orchids to grow with "look-alike" plants, non-orchid species that have a similar morphology.

There apparently has been no study of the pollination biology of *Malaxis unifolia.* Seeds are regularly produced in the Green Adder's-mouth, an occurrence that seems to initiate the lengthening of the stem, for plants with seed capsules are generally much taller than flowering plants (Correll, 1950).

GENERAL DISTRIBUTION: Newfoundland west to Ontario and Minnesota, south to Florida, Cuba, and Jamaica, west to the Gulf Coast of Texas; Mexico, Honduras, and Guatemala.

15. **Liparis** L. C. M. Rich., De Orchid. Eur. Annot. 38. 1817. (conserved name.)

A large genus of approximately 250 species distributed throughout temperate and tropical regions, *Liparis* is represented in eastern North America by only two species. The genus is characterized by its fleshy, oily-looking leaves, a feature that gave the genus its name; *Liparis* derives from a Greek word for "greasy."

Linnaeus (1753) originally placed those members of this genus which he described into the genus *Ophrys*. *Liparis* is closely related to the genus *Malaxis* and can be distinguished from that genus by its elongated column.

Liparis lilifolia, the Lily-leaved Twayblade, is a plant of the eastern deciduous forest. Batchelder (1909) reported the presence of this species in Manchester, Hillsborough County, N. H., and this record has been documented by a specimen collected by him. Since this orchid no longer appears to be part of our flora, *L. lilifolia* is not included in this treatment of the orchids of New Hampshire.

1. *Liparis loeselii* (L.) L. C. M. Rich., Orchid. Europ. Annot. 38. 1817.

This species was described by Linnaeus (1753) as *Ophrys Loeselii,* from plants collected in the swamps of Sweden and Prussia. Linnaeus named the plant for Loesel who originally described this species in his flora of Prussia.

COMMON NAMES: Fen Orchid, Loesel's Orchid

FLOWERING DATES IN NEW HAMPSHIRE: mid-June through July.

DESCRIPTION: Plant from a bulbous corm, erect, glabrous, fleshy, up to 16 cm tall. Leaves 2, basal, sheathing corm and stem, oblong-elliptic, keeled beneath. (Leaves reduced, broader in open situations.) Inflorescence a slender raceme, few flowered, with minute floral bracts. Flowers yellowish-green on thread-like pedicels. Sepals lanceolate, slightly recurved. Lateral petals linear, curved, spreading. Lip narrowly-cuneate to oblong, arcuate-recurved with an apiculate apex. Column stout, approximately 2 mm long. Capsule ellipsoid, ascending.

CHROMOSOME NUMBER: $2n = 32$.

Liparis loeselii is a small, inconspicuous plant, often only attaining a height of 6 cm in this area, although more robust forms may grow as tall as 16 cm. The base of the stem is expanded into a bulbous corm, sometimes termed a pseudobulb, a feature common to tropical tree-dwelling orchids (Summerhayes, 1951). Usually the bulb from the previous year is still apparent at the bottom of the present year's flowering shoot (S. Nilsson, 1979). The yellowish-green flowers are rather curious looking with their widely spreading, thread-like petals and sepals. When growing among grasses, as this plant often does, the Fen Orchid is difficult to spot. The shiny, somewhat greasy-looking leaves vary in form depending on the habitat. In shady, moist situations the leaves tend to be longer and narrower while in plants growing in drier, more open areas the leaves tend to be shorter and broader.

The common name "Fen Orchid" is European in origin and is descriptive of the habitat in which this species grows. A fen is a wet area that is neutral or alkaline in nature (Summerhayes, 1951). In

New England *Liparis loeselii* is often found growing in circumneutral grassy pastures and damp meadows. It is unusual among the orchids of our flora in that it also flourishes in sterile, sandy drainage areas. I found this species in 1972 in a sandy seepage depression on the banks of the Connecticut River. Here, with little competition from other vegetation, a small population of flowering plants grew scattered among the rocks. When I returned to this station in 1978 only a few vegetative individuals were seen. In 1980 the plants were nowhere in evidence. Since *Liparis loeselii* cannot withstand a hot, dry habitat, the population was probably a victim of the recent drought-like situation to which the state has been subjected.

Storks and Crow (1978) listed *Liparis loeselii* as "widespread but infrequent" in New Hampshire. In this state the Fen Orchid has most often been found in Coos County or along the lower Connecticut River Valley, indicating its preference for neutral soils. This orchid certainly must be frequently overlooked because of its small size and overall "greenness."

The inconspicuous flowers of the Fen Orchid have no odor and produce no nectar (Kirchner, 1922). Hagerup (1941) studied the reproductive biology of *Liparis loeselii* in Denmark and found the species to be autogamous. His experimental plants were sheltered from insects but still developed seeds. In his description of the process of self-pollination he reported that the anther cap lifts up to expose the pollen-masses and subsequently collapses, forcing the pollen-masses down onto the stigma.

More recently Catling (1980b) carried out a series of pollination experiments with plants of *Liparis loeselii* from Ontario. He observed no insect visitors in the field and determined through experiments that the North American plants are also self-pollinating. In addition, Catling demonstrated experimentally that raindrops greatly increase the incidence of autogamy, a fascinating adaption to the cool, rainy climates which best support this orchid.

General distribution: Central Europe and northeastern North America, Nova Scotia west through the Great Lakes region to Ontario, disjunct to Saskatchewan and Washington, south to the mountains of North Carolina and disjunct to the Piedmont Plateau of Alabama. Closely related to *L. hawaiensis* of Hawaii (S. Nilsson, 1979).

16. Calypso Salis. Par. Lond. Pl. 89. 1807. (conserved name).

Because the single species in this genus possesses a sac-like lip, Linnaeus (1753) included it within the genus *Cypripedium.* It is now believed that the two genera evolved quite independently and are not closely related. *Calypso* appears to represent a unique line of development in the family.

In 1807 Salisbury placed this species in a separate genus and named it for the sea-nymph of Homer's *Odyssey.*

1. *Calypso bulbosa* (L.) Oakes in Z. Thompson, Hist. Vermont 1: 200. 1842.

Originally described from plants of Lapland, Russia and Siberia, this orchid is circumboreal in distribution. At various times this species has been called *Calypso borealis* and *Cytherea bulbosa.* Oakes made the presently accepted combination in Thompson's *History of Vermont* (1842), a rather unusual avenue of botanical publication. The eastern North American representative has been treated by Leur (1975) as var. *americana.* The epithet *bulbosa* is Latin for "bulbous," referring to the bulb-shaped corm (sometimes termed a pseudobulb) at the base of the stem.

COMMON NAMES: Calypso, Fairy Slipper

FLOWERING DATES IN NEW HAMPSHIRE: mid-May to early June.

DESCRIPTION: Plant erect, glabrous, from a bulbous corm, up to 16 cm tall. Stem purplish, glaucous, enveloped about half-way by 2 or 3 transparent sheaths. Leaf from top of corm, petiolate. Blade ovate to cordate, plicate, dark bluish-green. Floral bract lanceolate, pink. Flower showy, solitary, on a slender pedicel. Sepals and lateral petals linear-lanceolate, spreading, pinkish-purple. Lip saccate, pendant, with a bicornuate apex, purplish. Margins of sac folded outward forming a whitish apron. Apron spotted with purple, bearded with yellow bristles in the center. Column petaloid, convex, semiorbicular, inverted over opening of lip. Capsule erect, ellipsoid, approximately 2 cm long.

CHROMOSOME NUMBER: $2n = 28$.

The exquisite beauty of this orchid is renowned. The story is often told of the great naturalist John Muir who, upon finding

Calypso for the first time, shed tears of joy over its beauty. Correll (1950) characterized Calypso as "the most beautiful terrestrial orchid in North America." Morris and Eames (1929) penned the following:

> The extraordinary delicacy of the whole blossom, the miraculous blend of so many diversly gay colors, the structure of the lip, its multiplicity of detail and unique form, serve to create a thing of beauty unmatched in all of the world of flowers.

In the northeast Calypso is most often found in dark, mossy woods of Northern White Cedar (*Thuja occidentalis*) and Spruce (*Picea*). There it often grows in the company of Creeping Snowberry (*Gaultheria hispidula*) and the flower so favored by Linnaeus, the delicate, trailing Twinflower (*Linnaea borealis*). My only vision of the diminutive Calypso was in such a habitat in Vermont, where the orchid was found growing on a moss-covered log. Despite having seen many herbarium specimens of Calypso, I was still unprepared for its diminutive proportions and bright coloration.

One of the earliest of our wildflowers to bloom, Calypso is unaffected by early spring frosts of Northern New England (Nylander, 1935). Outside North America this species tolerates the cold climates of Sweden, Finland, northern Russia, and northern Asia (S. Nilsson, 1979). Through most of its range Calypso is rare and local. Only in some areas of western North America can Calypso be termed "rather frequent" (Correll, 1950). It is in these western locations that the plant attains a larger, more robust form which has been referred to as var. *occidentalis* Leur (Leur, 1975).

In the three northern New England states, which delineate the southeastern range limit of Calypso, the orchid is considered "Endangered/Threatened" (Crow *et al.,* 1981). Of the three, the state of Maine boasts the most stations for the showy little plant. In the past Calypso was locally abundant in many localities in Vermont, but at the present time populations of this orchid have dwindled to just a few extant sites in the northeastern section of the state (Countryman, 1978).

In New Hampshire Calypso has been found at only two locations. There is a record from Hanover, Grafton County, dated 1893 but it is unlikely that this population still exists. Our only other record is from Columbia, Coos County. In 1931, Thomas W. Wallace, a native of Columbia, discovered Calypso at the edge of Lime Pond in that town (Wallace, unpubl. letter in NHA files). He sent a photograph of the plant to Arthur Stanley Pease, author of the *Flora of Coos County*, who at that time was president of Amherst College in Massachusetts. Pease went to the site in 1946 and made a collection of Calypso, but when he returned to the same spot in 1952, and again in 1961, the orchid was not in evidence (Pease, 1964).

In the past 25 years many nature lovers in the state have made the pilgrimage to Lime Pond attempting to rediscover Calypso in New Hampshire. To date, the site has not yielded the beautiful orchid again and the seekers return from their expeditions with only white lime-encrusted boots and scores of black-fly bites.

The brightly-colored flower and position of the column suggest that Calypso is pollinated by bees. Although the orchid produces no nectar it does display the yellow bristles that are believed to mimic anthers. The European plants are reported to have a vanilla-like scent which attract bees who feed on the blueberry (*Vaccinium*) flowers that bloom at the same time (S. Nilsson, 1979). Mosquin (1970) has studied the reproductive biology of *Calypso bulbosa* in Alberta, Canada, and has identified bumblebees of the genera *Bombus* and *Psithyrus* (Apidae) as carrying pollinia of Calypso on their thoraxes. Stoutamire (1971) listed the bumblebees *Bombus ternarius* and *B. vagans* (Apidae) as pollinators of Calypso.

Unlike the apparent situation in northwestern North America, few plants in the northeast form fruit, a factor which may account for the rarity of the species here. Nylander (1922) observed birds attacking the flowers of Calypso in Woodland, Maine, a practice that he believed accounted for the low percentage of seed-set in this species. When the flower is not pollinated it remains fresh for about three weeks (Nylander, 1935; Mosquin, 1970). Calypso propagates vegetatively through the production of coralline rhizomes (Mously, 1925).

Correll (1950) reported that the Indians of British Columbia eat the corms of Calypso which contain a large amount of a mucilaginous substance.

Every year during my orchid hunting forays in New Hampshire, I discover new locations with habitats suitable for Calypso and faithfully return the following May to seek the elusive plant. That I have not yet met with success is not surprising when one considers that it was only after 25 years of searching that Calypso revealed itself to Morris and Eames (1929). The thought of finding Calypso lingers long after its blooming dates have passed and the lines from Frost's (1964) poem "The Encounter" keep returning to my mind.

> "Sometimes I wander out of beaten ways
> Half looking for the orchid *Calypso*"

GENERAL DISTRIBUTION: Circumboreal, extending southward in the Rocky Mountains to Arizona and California.

17. Corallorhiza [Hall.] Chatelain, Spec. Inaug. de Corallorhiza 6. 1760.

A small genus of eight to ten species which have a center of distribution in Mexico (Leur, 1975), the name for the genus was already well established when Haller used it in his pre-Linnean work published in 1742. The author of *Corallorhiza* must be attributed to Chatelain who published the first description of this genus after 1753.

Corallorhiza is from two Greek words signifying "coral-root." Although the members of this genus do not actually have roots they do possess an intricately branched underground rhizome that is coralline in appearance. Corrallorhizas have little or no chlorophyll and are saprophytes associated with mycorrhizal fungi and/or indirect parasites on the roots of living trees.

Two species of *Corallorhiza* commonly occur in New Hampshire and there is a historic record for a third, *Corallorhiza odontorhiza.*

Key to the common species of *Corallorhiza* in New Hampshire

1. Plant yellowish, usually less than 20 cm tall; lip 3 5 mm long; blossoming in spring or early summer; plants of wet areas. . . . . 1. *Corallorhiza trifida*
1. Plant purplish, usually greater than 20 cm tall; lip 5–9 mm long; usually blossoming in late summer; plants of upland woods . . . . 2. *Corallorhiza maculata*

1. Corallorhiza trifida Chat. Spec. Inaug. de Corallorhiza 8. 1760.

Linnaeus (1753) originally described this species as *Ophrys corallorhiza*, and it has also been known as *Corallorhiza innata*. *Corallorhiza trifida* is circumpolar in distribution with the Eurasian and northernmost North American plants referable to var. *trifida*. Variety *verna* (Nutt.) Fern. occurs in our area and is distinguished by a lighter, more yellowish color and a white, unspotted, abruptly-tipped lip. This difference was sufficient to lead Nuttall to consider it as a separate species, which he called *C. verna*.

The specific epithet *trifida* is from Latin and means "split into three," referring to the three-lobed lip. The varietal name *verna* means "spring," the season of flowering.

COMMON NAME: Early Coral-root

FLOWERING DATES IN NEW HAMPSHIRE: May through June.

DESCRIPTION: Plant from a fragile much-branched rhizome, erect, yellowish, glabrous, averaging approximately 18 cm in height, with 2–3 tubular sheaths enclosing the stem. Inflorescence a loosely flowered raceme of few–20 flowers. Floral bracts minute, acute. Flowers spreading yellowish-white on short slender pedicels. Sepals lanceolate, concave. Lateral petals linear-lanceolate. Lip white, unspotted or with very few basal spots, obovate, 3-lobed. Lateral lobes of lip near base, short, triangular. Mid-lobe expanded, bluntly tipped. Column curved, slightly clavate. Capsule obovoid, pendant.

CHROMOSOME NUMBER: $2n = 42$.

One of our earliest orchids to blossom, the flowers of *Corallorhiza trifida* var. *verna* are usually in evidence by May. The yellowish to yellowish-green color of the plant signifies that this taxon does possess a small amount of chlorophyll, unlike the majority of species in the genus. The characteristic coralline rhizomes which lie beneath the surface of the forest floor are much-branched and knobby in appearance. On the surface of the rhizome of the Early Coral-root, Thomas (1893) found tiny papillae with protruding tufts of hairs. Campbell (1970) reported that various fungi, with white or yellow hyphae, enter the rhizome through the protruding hairs and advance into the cortex. Her study also revealed that some of the fungal hyphae found in the Early Coral-root are additionally attached to the roots of Cedar (*Thuja*) or Spruce (*Picea*) trees. The orchid presumably obtains some of its nourishment from the trees and therefore functions as an indirect parasite through the fungal intermediaries.

In order to see the Early Coral-root in blossom one must venture into a wet coniferous or mixed forest at the height of Black-fly season. Since this species is shade tolerant it can thrive in the darkness that characterizes our Cedar woods. In more southern areas *Corallorhiza trifida* var. *verna* is often found growing along the edges of forest streams.

The Early Coral-root can occasionally be found in bogs. My first meeting with this orchid was in a bog in Merrimack County where it was found growing tucked beneath the shrubs at the edge of the bog mat. Wherry (1927) reported that the apparent optimum soil for this species is one with a minimum-acid reaction, and Stuckey (1967) reported this species growing in soils with a pH of 5.4 in Rhode Island.

A characteristic of this genus is the joined bases of the lateral sepals, which are somewhat fused with the lip forming a small sac-like spur (Bingham, 1939). It has not been determined if nectar is produced in the Early Coral-root. On the upper surface of the lip are two longitudinal ridges that probably serve to direct insects to the spur. Corallorhizas are protandrous. The anther produces two pollen-masses which remain under the anther lid. At this time the column renders the opening of the blossom too narrow for insects to reach the spur. When an insect probes the flower, it trips open the anther lid causing the pollen-mass to become attached to its head. When the stigma is mature the flowers open widely and the next insect visitor with attached pollen-masses easily transfers them to the sticky stigma. In Europe, Silen (1906) reported that the Hover-fly *Syrphus cinctellus* (Syrphidae) visited *Corallorhiza trifida.* Catling (1980a) suggested that this species may be partly autogamous. I have found the beetle *Anthobium convexium* (Staphylinidae) on the flowers of the Early Coral-root but they appeared to be only feeding on the pollen-masses.

When fertilization occurs in the Early Coral-root the ovaries increase in size and turn a greenish color, possibly indicating that most of the chlorophyll in the plant is concentrated in this organ. *Corallorhiza trifida* var. *verna* is a good seed producer. Propagation in this species is primarily by sexual means, as vegetative multiplication in the Early Coral-root is reportedly not as effective as in most orchids (Summerhayes, 1951).

GENERAL DISTRIBUTION: Newfoundland west through the Great Lakes area to British Columbia and Oregon, south to Pennsylvania.

2. *Corallorhiza maculata* Raf., Amer. Monthly Mag. and Crit. Rev. 2: 119. 1817.

This new world species of *Corallorhiza* was originally described by Rafinesque from plants found in New York. The species has also been known as *C. multiflora.* The epithet *maculata* is Latin for "spotted," describing the purple spots on the lip.

COMMON NAMES: Spotted Coral-root, Large Coral-root

FLOWERING DATES IN NEW HAMPSHIRE: late July through early September, rarely earlier.

DESCRIPTION: (An extremely variable species). Plant from a coralline rhizome, erect, glabrous, succulent, purplish, with sheaths enclosing the stem. Raceme few- to many-flowered. Floral bracts obscure. Flowers spreading, on stout pedicels. Sepals purplish, oblong-lanceolate. Lateral sepals joined under the lip forming a small spur-like sac. Lateral petals slightly smaller and of a lighter purplish color than the sepals, oblong-lanceolate. Lip three-lobed, white with magenta spots and 2 longitudinal median ridges. Lateral lobes small, inrolled, directed forward. Mid-lobe expanded, broadly rounded. Column yellow, spotted with magenta, curved. Capsule ellipsoid, pendent.

CHROMOSOME NUMBER: $2n = 42$ (Moore, 1973).

The Spotted Coral-root is one of the most widespread of all the orchids of our flora. *Corallorhiza maculata* lacks chlorophyll entirely, a feature that led earlier writers to label the species "degenerate" (Gibson, 1905). But this species is rich in other color pigments. A typical plant usually has a purplish stem, yellowish to purplish sepals and lateral petals, and a white lip spotted with magenta. Overall, *C. maculata* is a handsome plant.

Several different color types of *Corallorhiza maculata* exist, some of which have been described as varieties (Bartlett, 1922). These are characterized as follows:

1. var. *flavida* (Peck) Farwell: this taxon lacks the purple anthocyanins which usually color the stems and sepals, resulting in a yellow plant with a white unspotted lip.

2. var. *intermedia* Farwell: an overall brownish plant, perhaps representing only older specimens of var. *maculata* (Case, 1964).
3. var. *punicea* H. H. Bartlet: a more slender version with transparent sheaths and reddish-purple stems.

The color differences in this species are noticeable in the field but, upon drying, all plants of *C. maculata* turn a uniform reddish-brown.

Usually it is late summer before the Spotted Coral-root emerges and opens its flowers. Plants of *Corallorhiza maculata* can be found growing singly or in clumps. In New Hampshire the favored habitat for this species is in Beech-Maple-Hemlock forests. At that time of year other saprophytes indigenous to this community are also apparent. Indian Pipes (*Monotropa uniflora*) and Beech-drops (*Epifagus virginiana*) are usually associated with the Spotted Coral-root. It is easy to confuse the Spotted Coral-root with Beech-drops when the plants are very young. If one remembers that Beech-drops exhibit a branching habit, whereas the Spotted Coral-root never branches, the two plants can be readily distinguished.

In 1980, when photographing the early-blooming *Corallorhiza trifida* var. *verna* in a wet streamside habitat, I noticed a clump of pale yellow succulent-looking stalks pushing up through the leaf litter. When I returned to the station two weeks later, I was greeted by the sight of a robust colony of *Corallorhiza* that was of such an unusual form, and flowering at so early a date, that I was certain I had discovered something special. The plant, however, would key out only to *C. maculata*. The entire plant was pale yellow but, unlike the description of var. *flavida*, the white lips displayed magenta spots. Never before had I encountered this species flowering so early or living in such a habitat. Later, I read of Morris and Eames (1929) being shocked to find the yellow form of the Spotted Coral-root in bloom as early as June 13th. This is truly a highly diversified species.

In her study of the fungal associations of *Corallorhiza* in Michigan, Campbell (1970) found rhizomorphs of the Honey Mushroom (*Armillariella mellea*) associated with the hairs of papillae on the Spotted Coral-root rhizomes. The same rhizomorphs were also found penetrating roots of adjacent trees. It is interesting that the fungal associates of *C. maculata* are quite different from those found in *C. trifida* var. *verna* (Campbell 1970).

The Spotted Coral-root appears to be morphologically adapted for insect pollination, but I have not found any mention of pollinators in the literature for this species. Catling (1980a), however, reported that evidence indicates this orchid may be partly autogamous. There is an obvious need for further investigation into the reproductive biology of this taxon.

GENERAL DISTRIBUTION: Newfoundland south to North Carolina, west through the Great Lakes area to Washington, and south through the mountains to Arizona; Mexico and Guatemala.

ACKNOWLEDGMENTS

I thank Garrett E. Crow, A. Linn Bogle, Owen M. Rogers and Leslie A. Garay for their helpful critisms of the manuscript. I am grateful to all the herbarium curators who gave their time and assistance to me. Many thanks are extended to John Burger and Wally Morse for identifying the insects collected in this study.

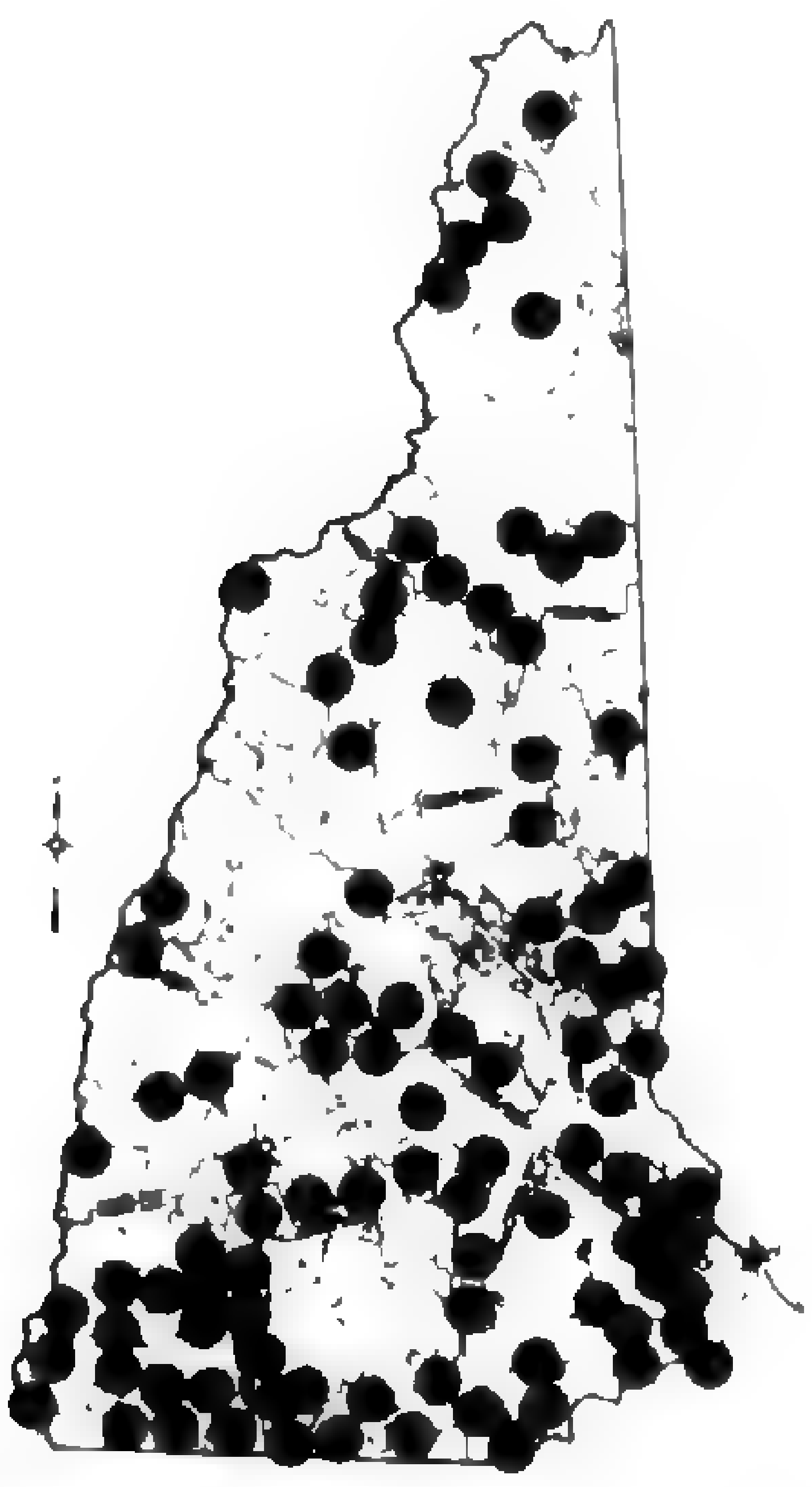
My deepest appreciation is extended to J. Korpi, C. Levesque, K. Price, C. Bartholomew and F. Smith for their help and moral support. For introducing me to the study of Botany, I thank David Boufford and David Gregory. Finally, I wish to thank the people of New Hampshire for sharing their knowledge of the flora and for their many kindnesses.

This work was supported in part by a grant from the American Orchid Society and by two UNH Central University Research Grants (CURF S135 and S167).

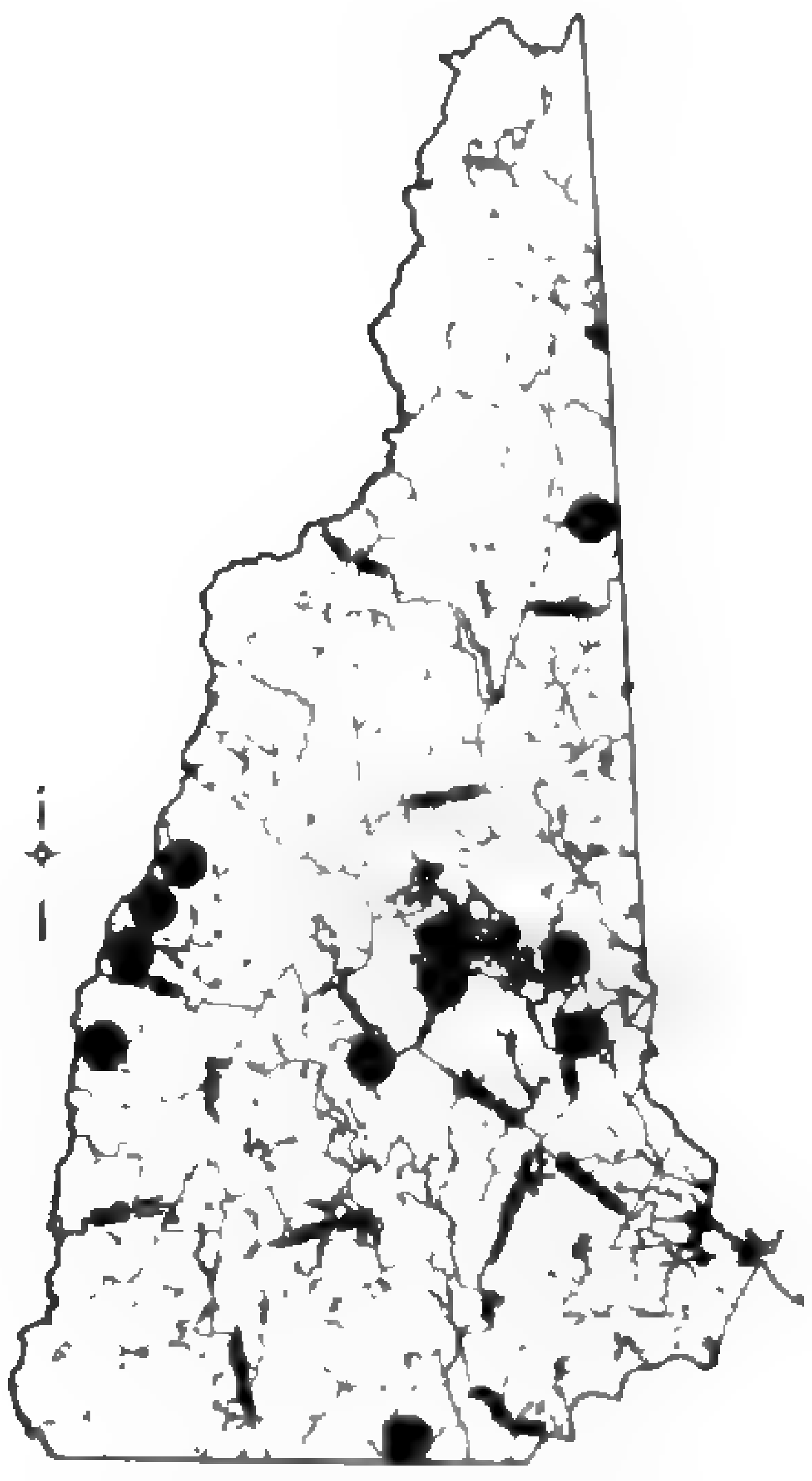
DISTRIBUTION MAPS OF 43 NEW HAMPSHIRE ORCHIDS

Bold-face numbers refer to genus in the key and text; other number is species under that particular genus.

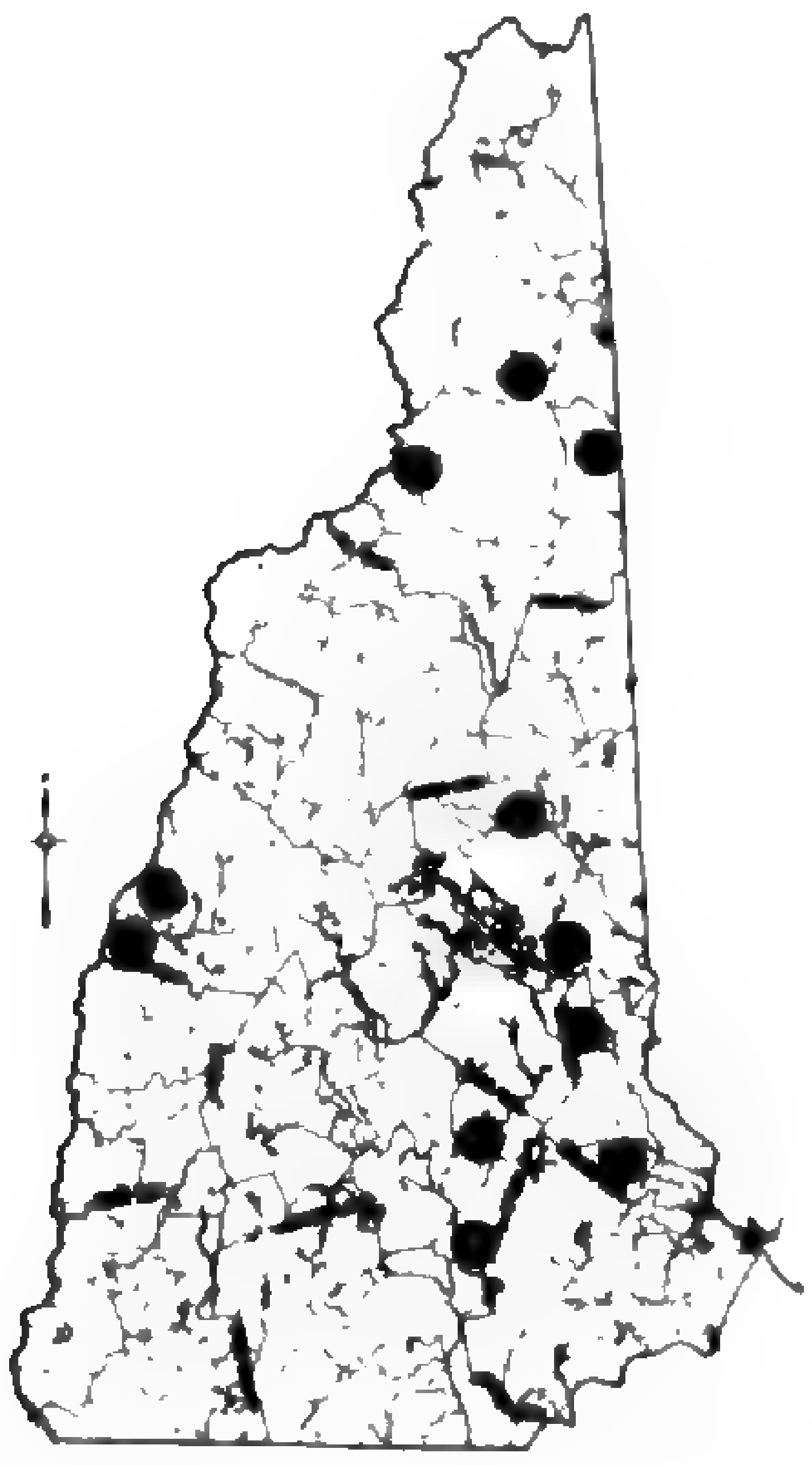
Each dot on the map represents an historic or extant record(s) for the species within that town or township. Maps have been updated to reflect field work done since 1981.



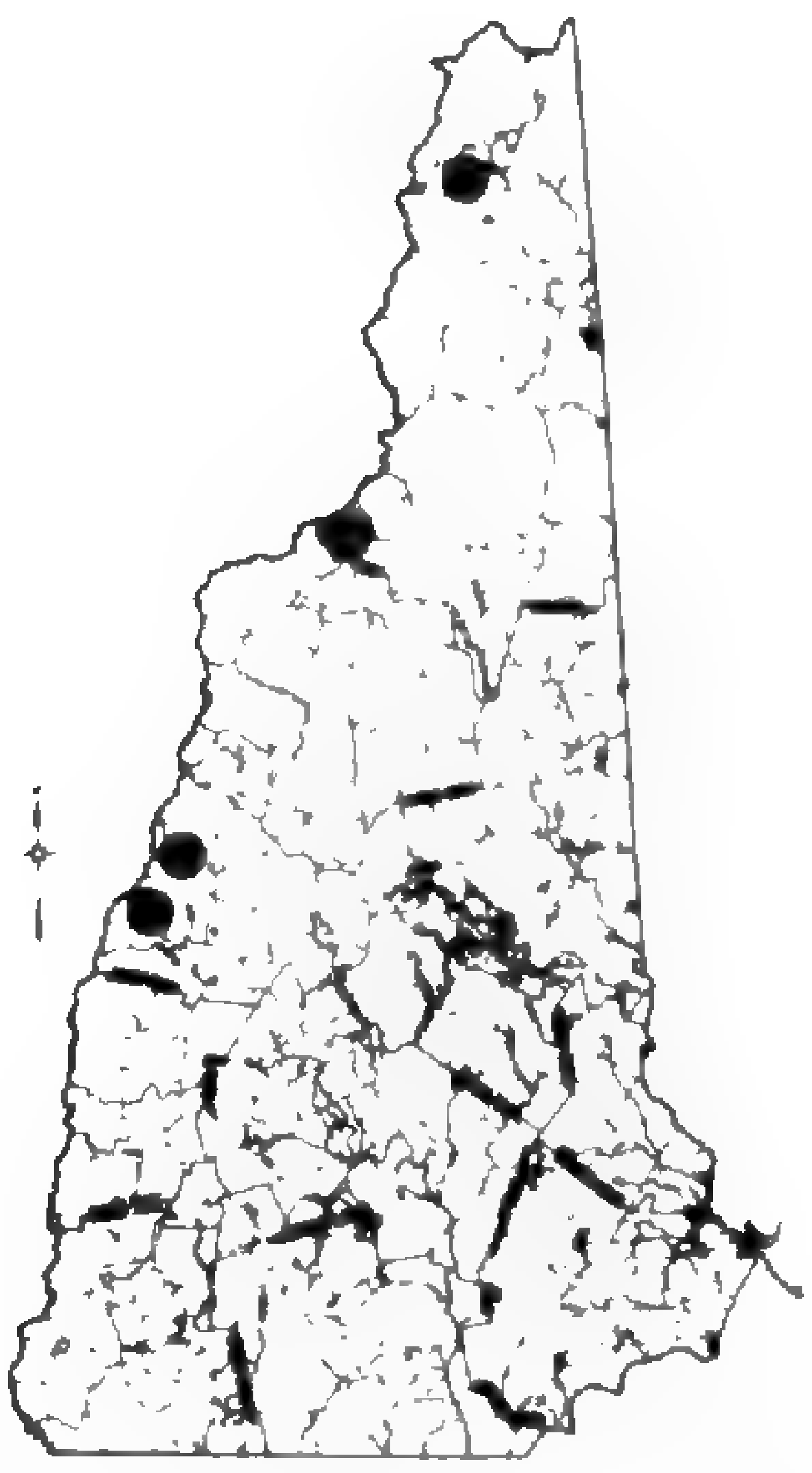
1-1 CYPRIPEDIUM ACAULE



1-2 CYPRIPEDIUM ARIETINUM

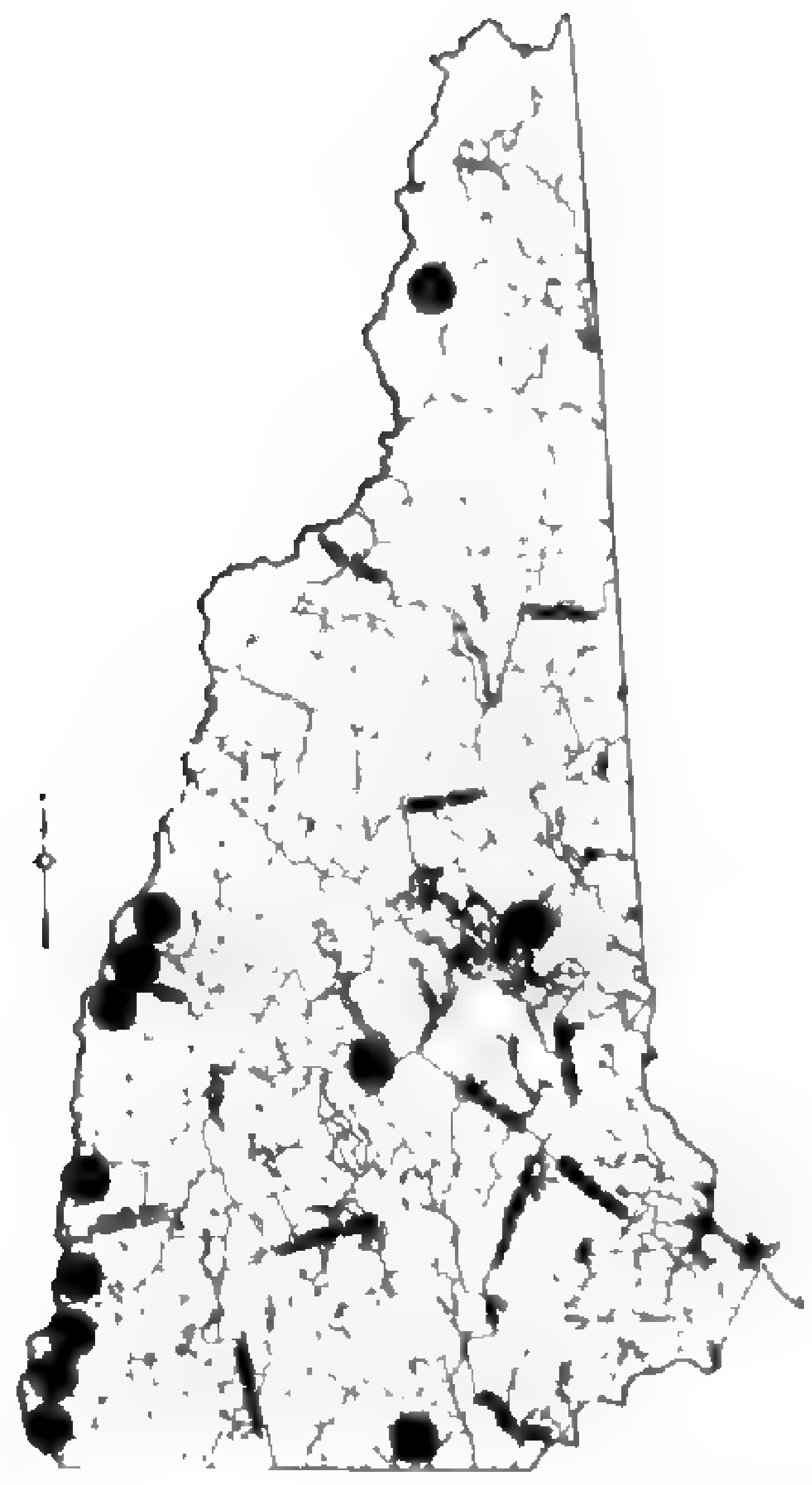


1-3 CYPRIPEDIUM PUBESCENS



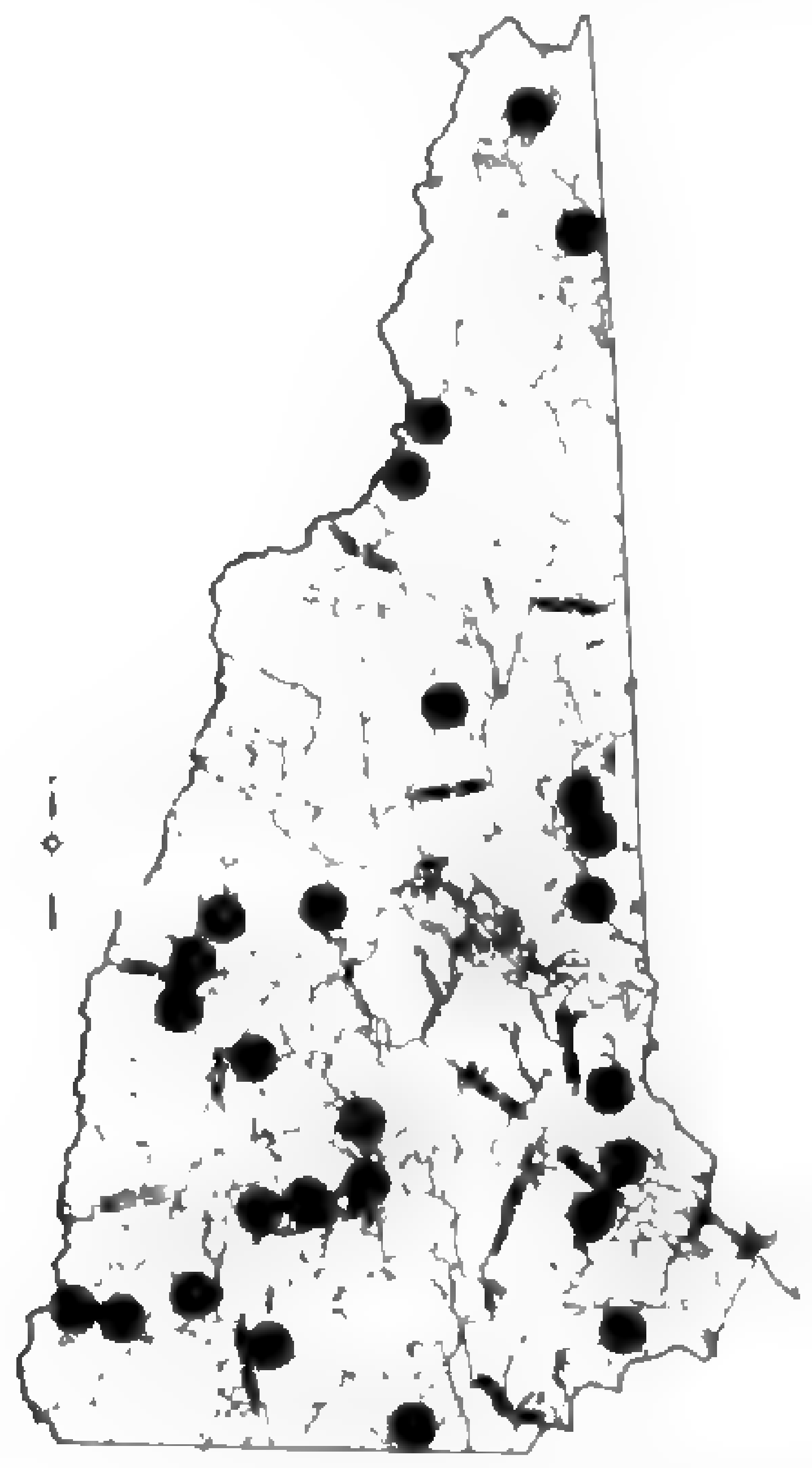
1-4 CYPRIPEDIUM PARVIFLORUM

1-5 CYPRIPEDIUM REGINAE

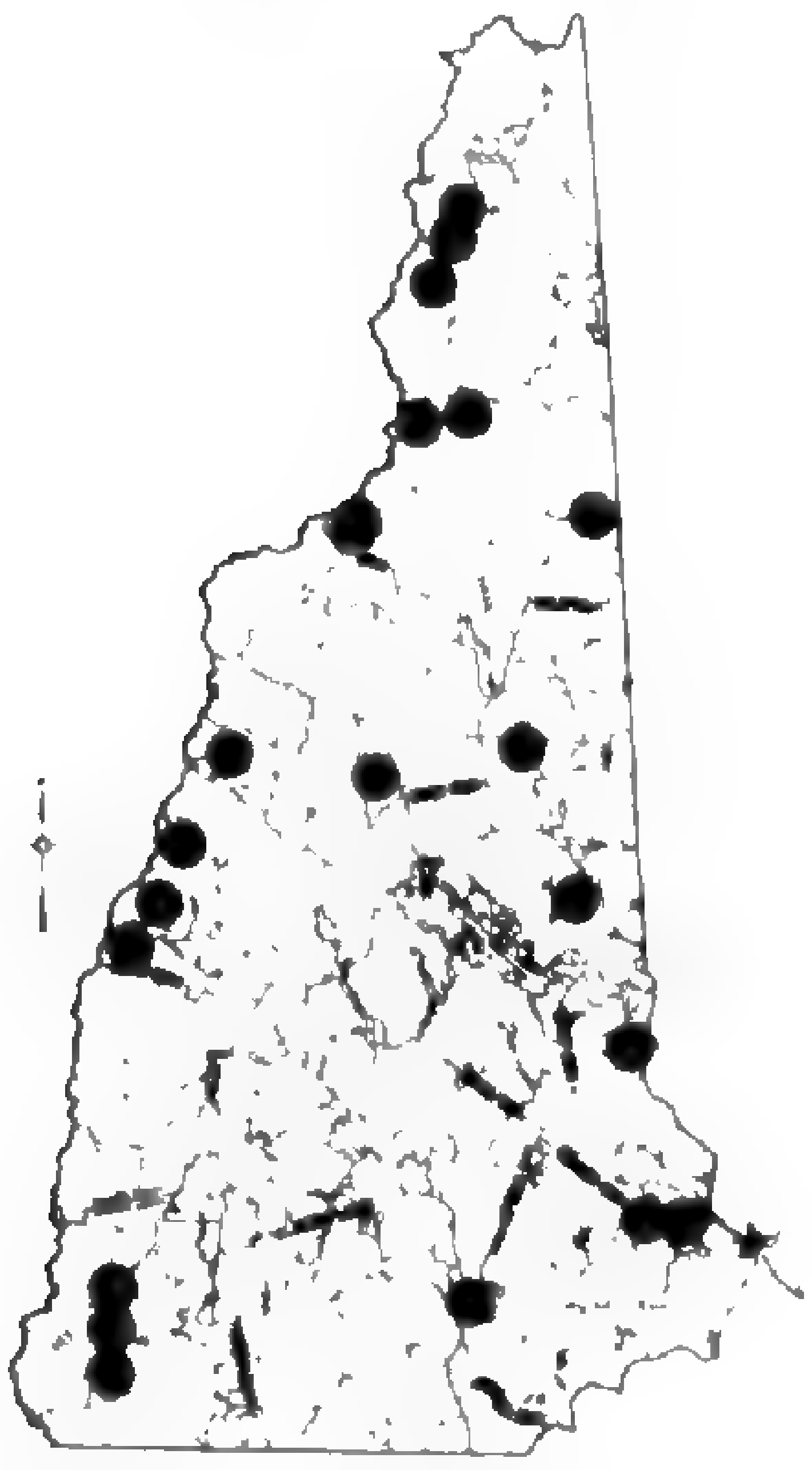


2-1 GALEARIS SPECTABILIS

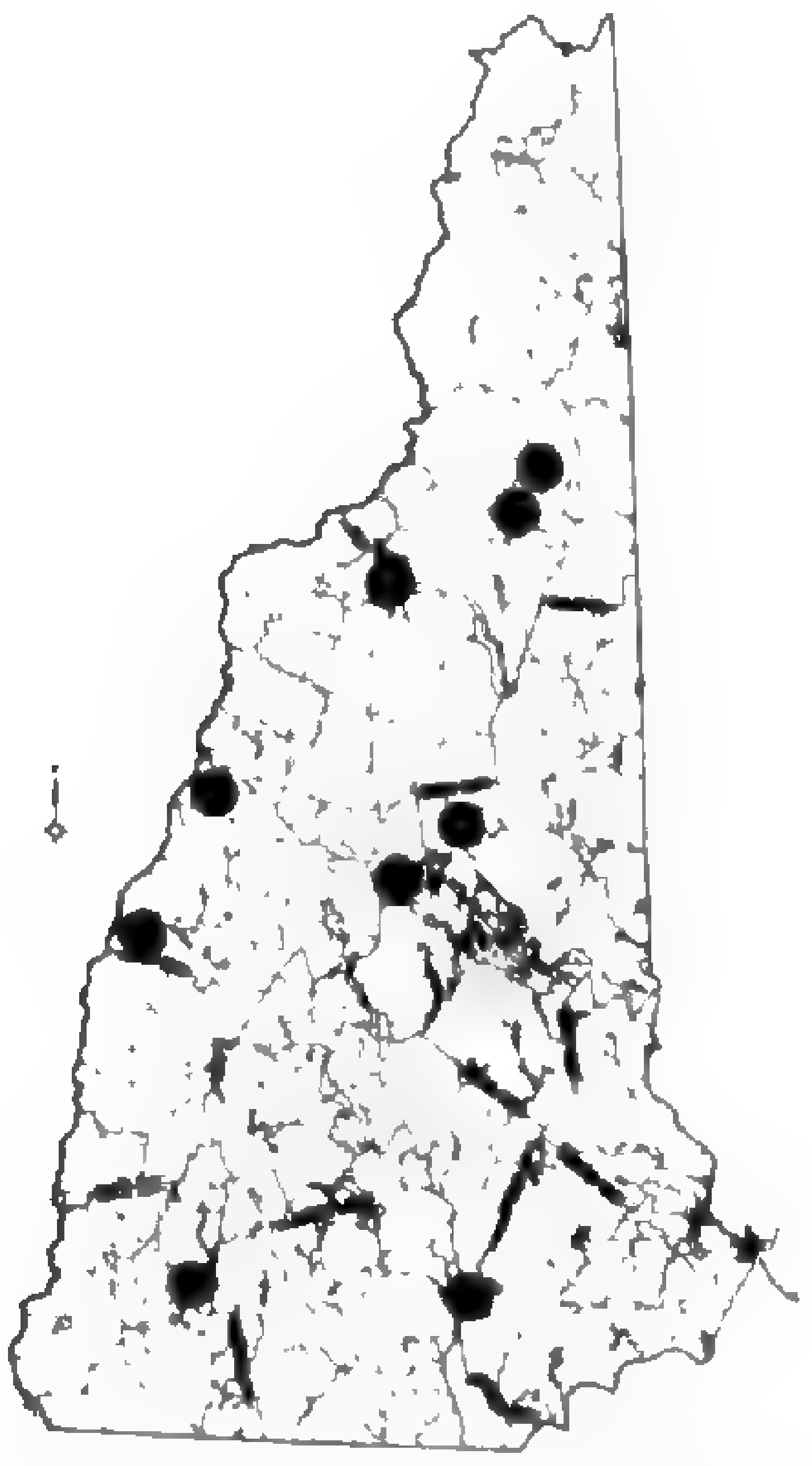
3-1 COELOGLOSSUM VIRIDE ssp. BRACTEATUM



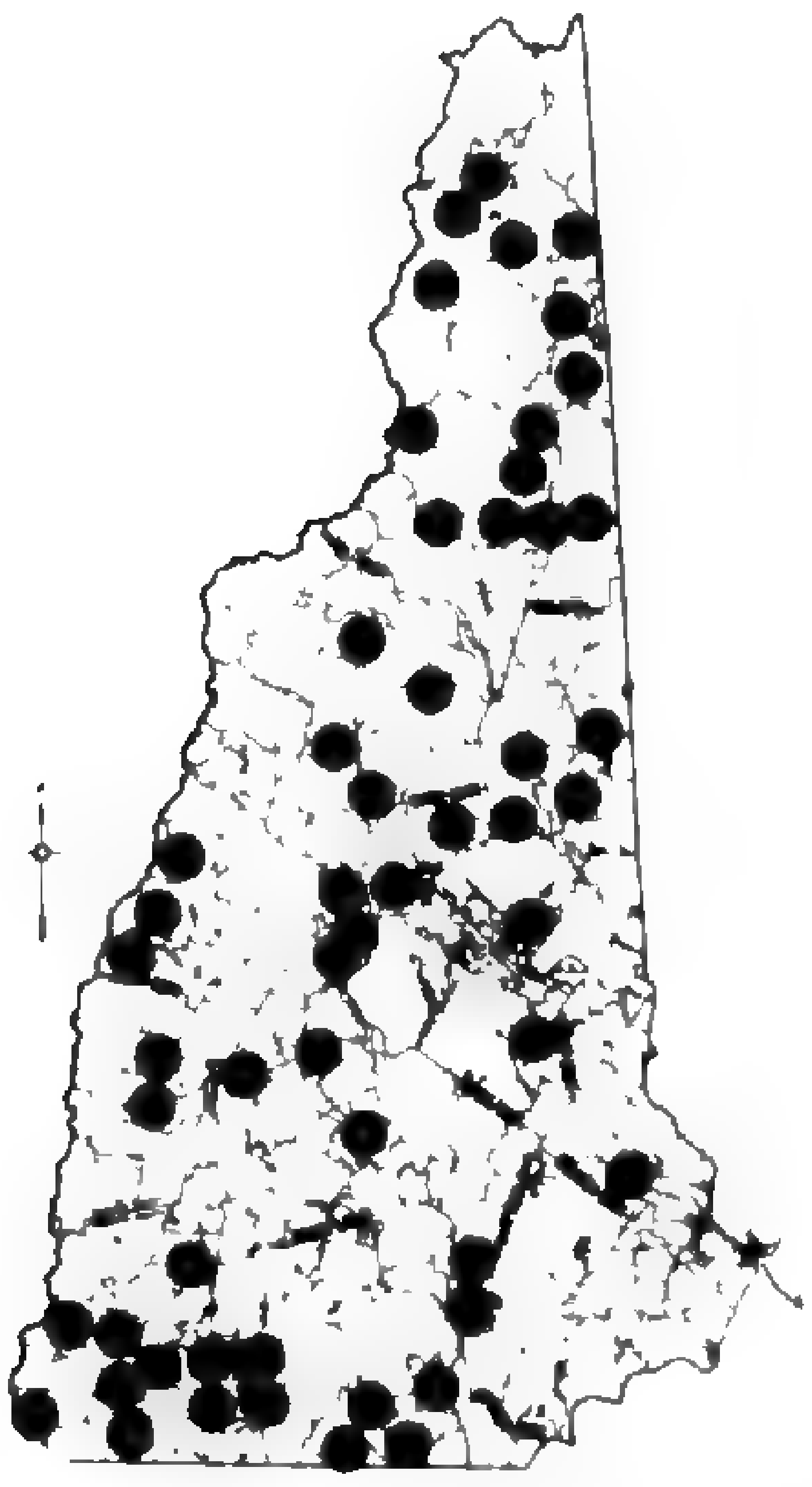
4-1 PLATANTHERA BLEPHARIGLOTTIS



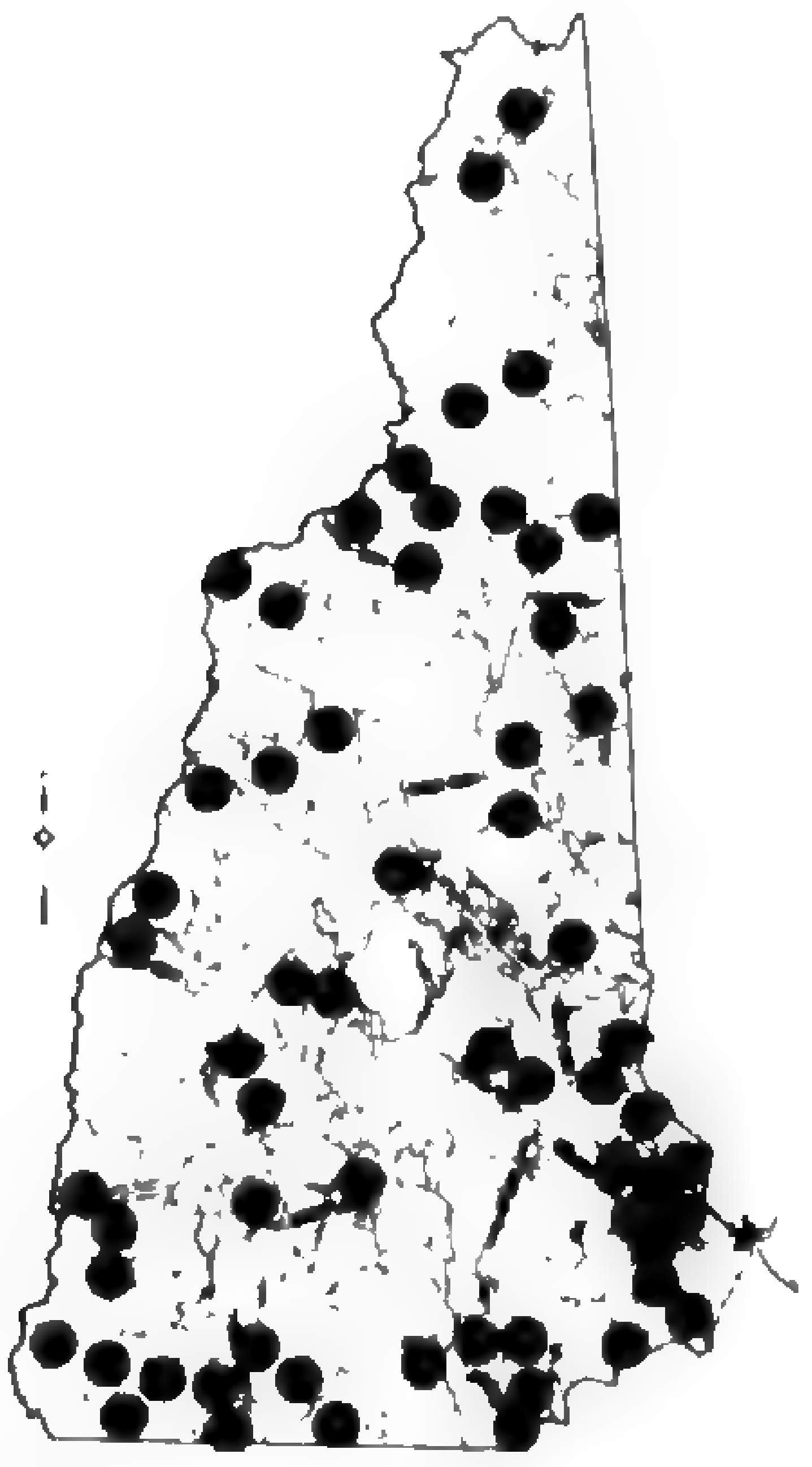
4-2 PLATANTHERA PSYCODES



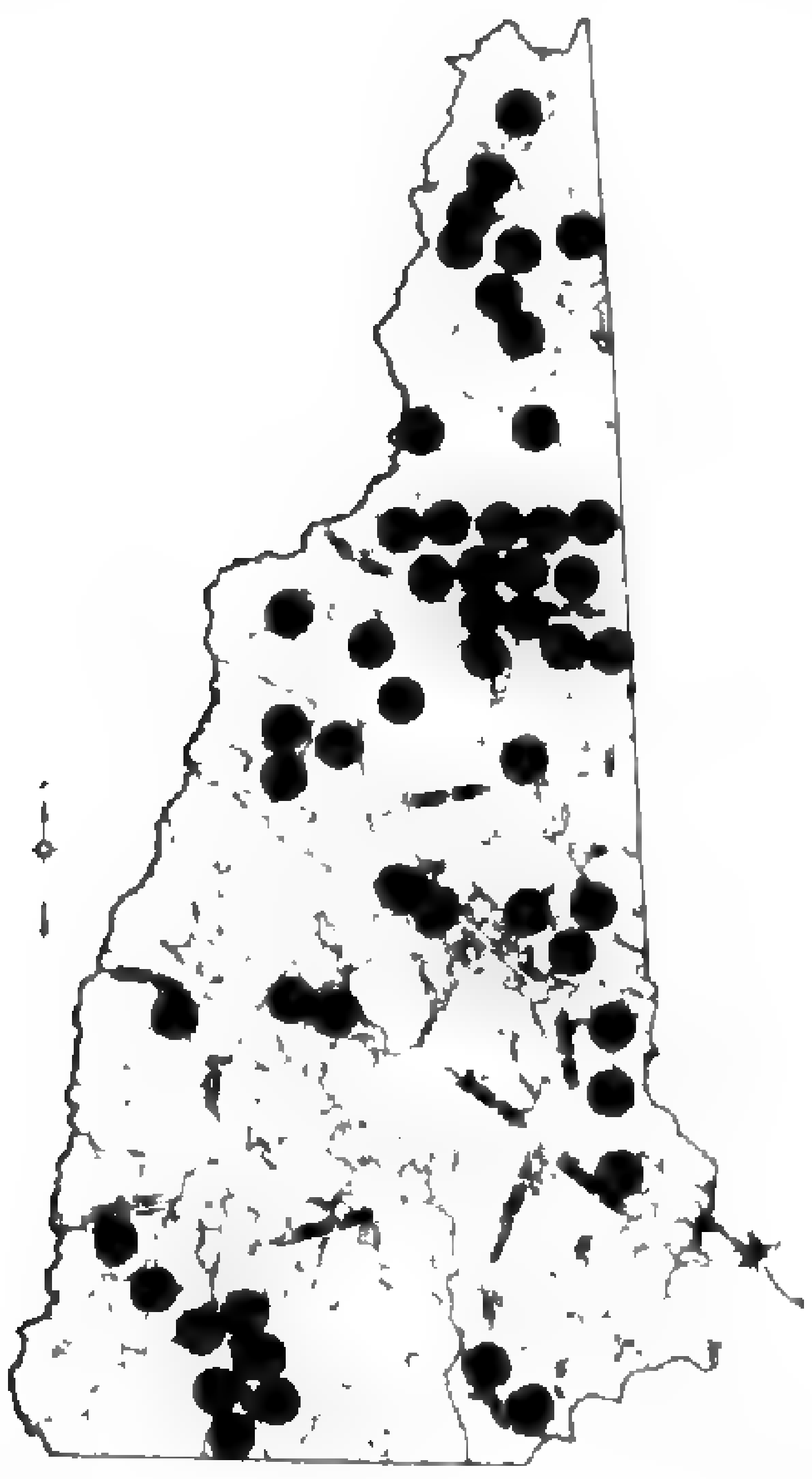
4-2x PLATANTHERA ×ANDREWSII



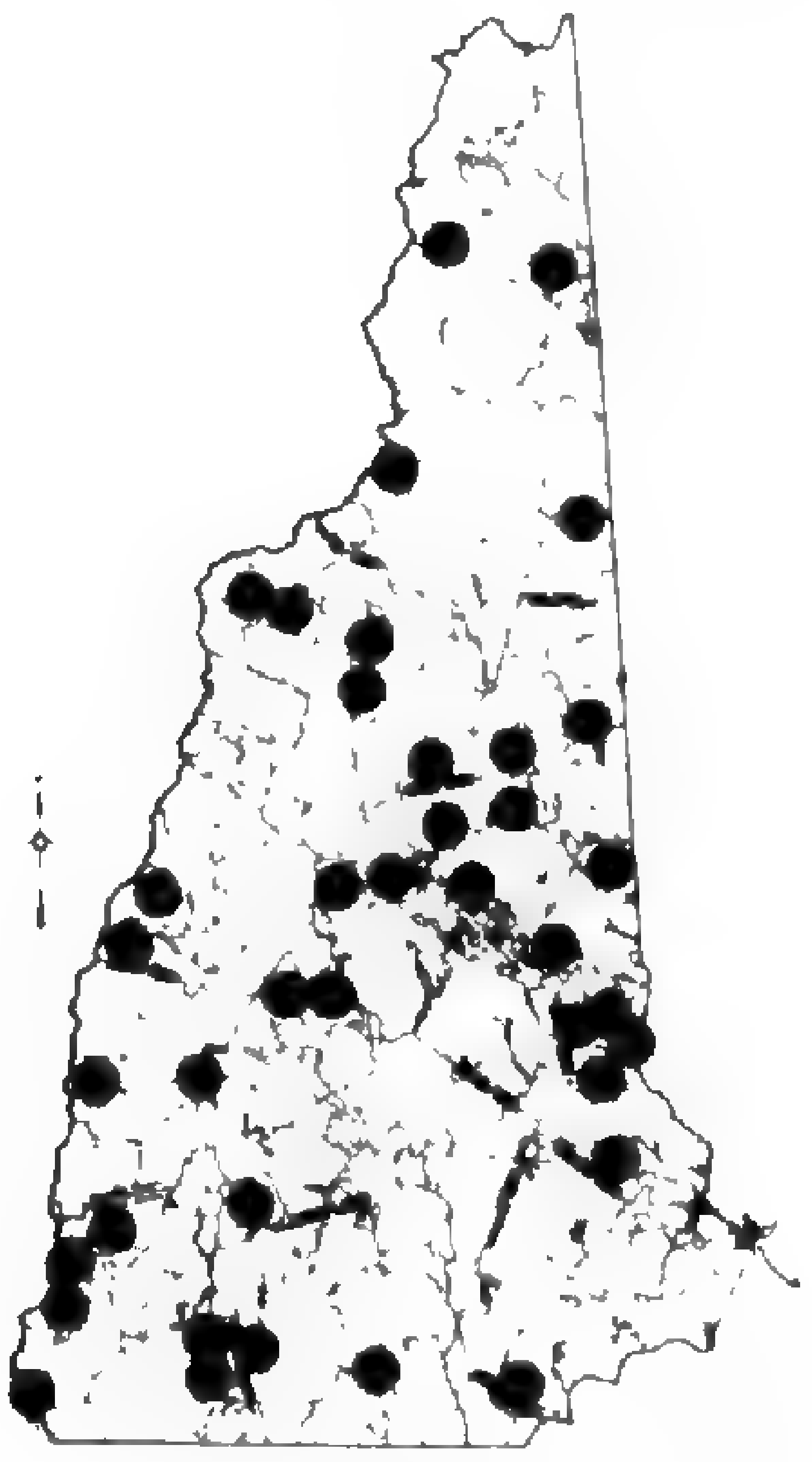
4-3 PLATANTHERA GRANDIFLORA



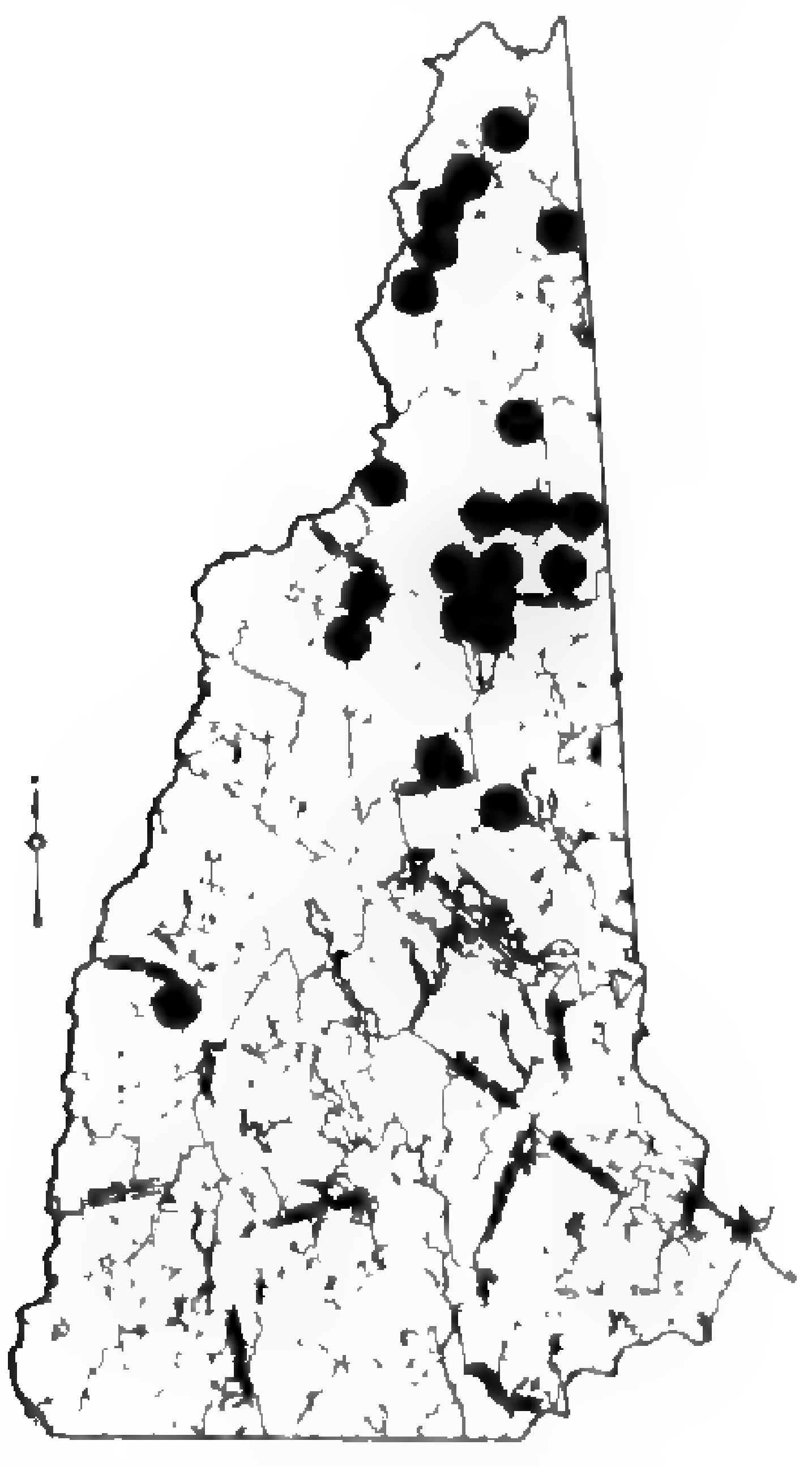
4-4 PLATANTHERA LACERA



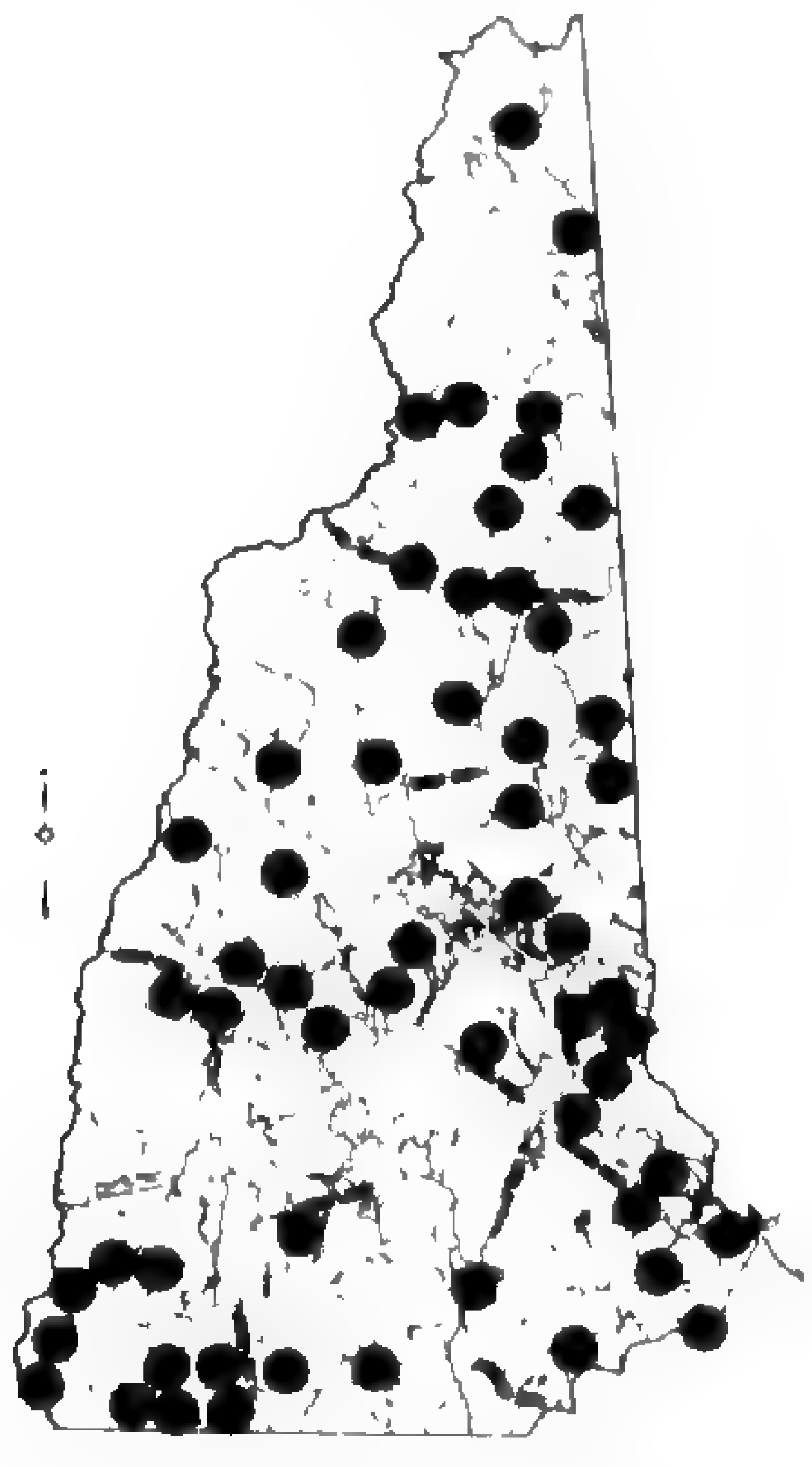
4-5 PLATANTHERA ORBICULATA



4-6 PLATANTHERA HOOKERI

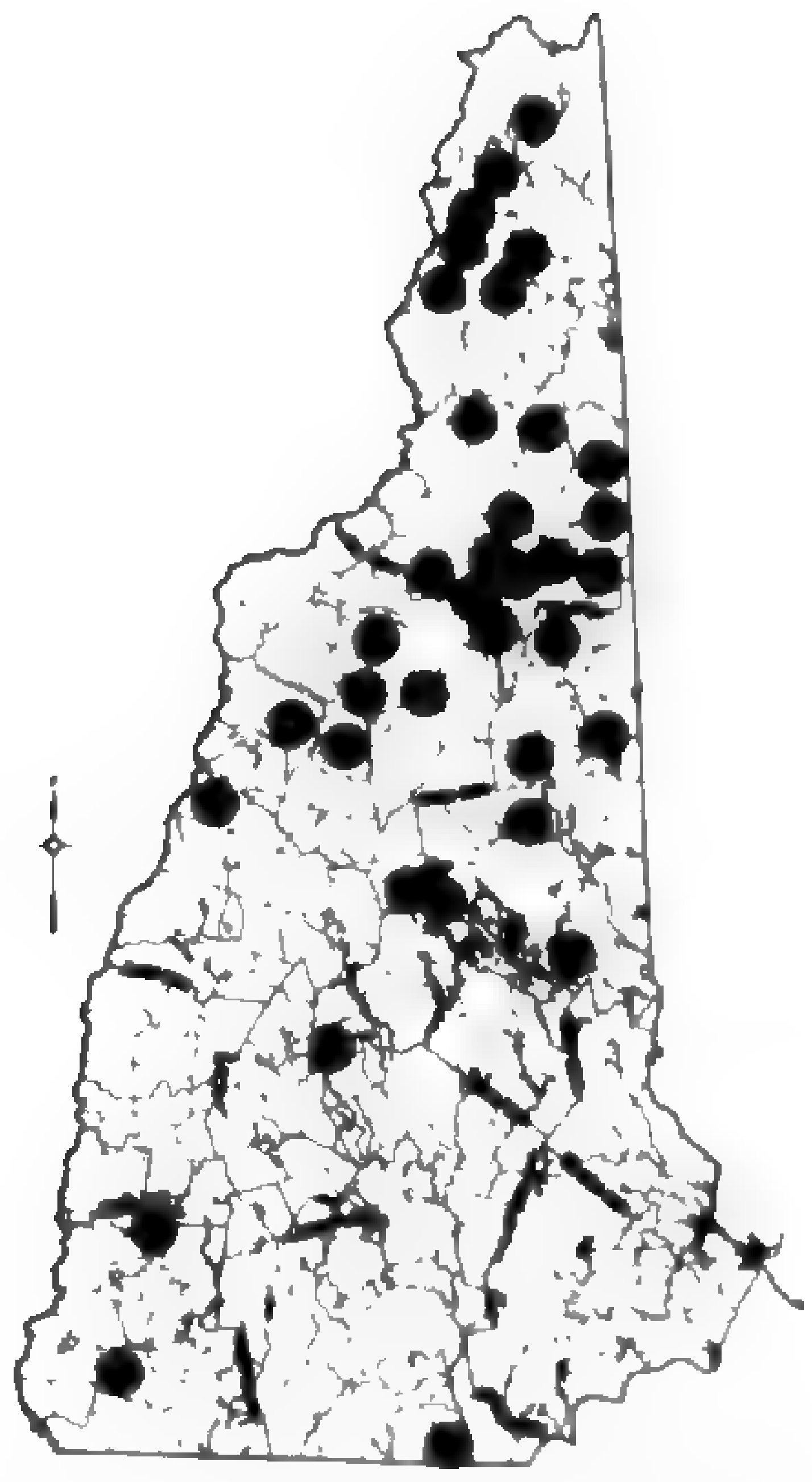


4-7 PLATANTHERA OBTUSATA
ssp. OBTUSATA



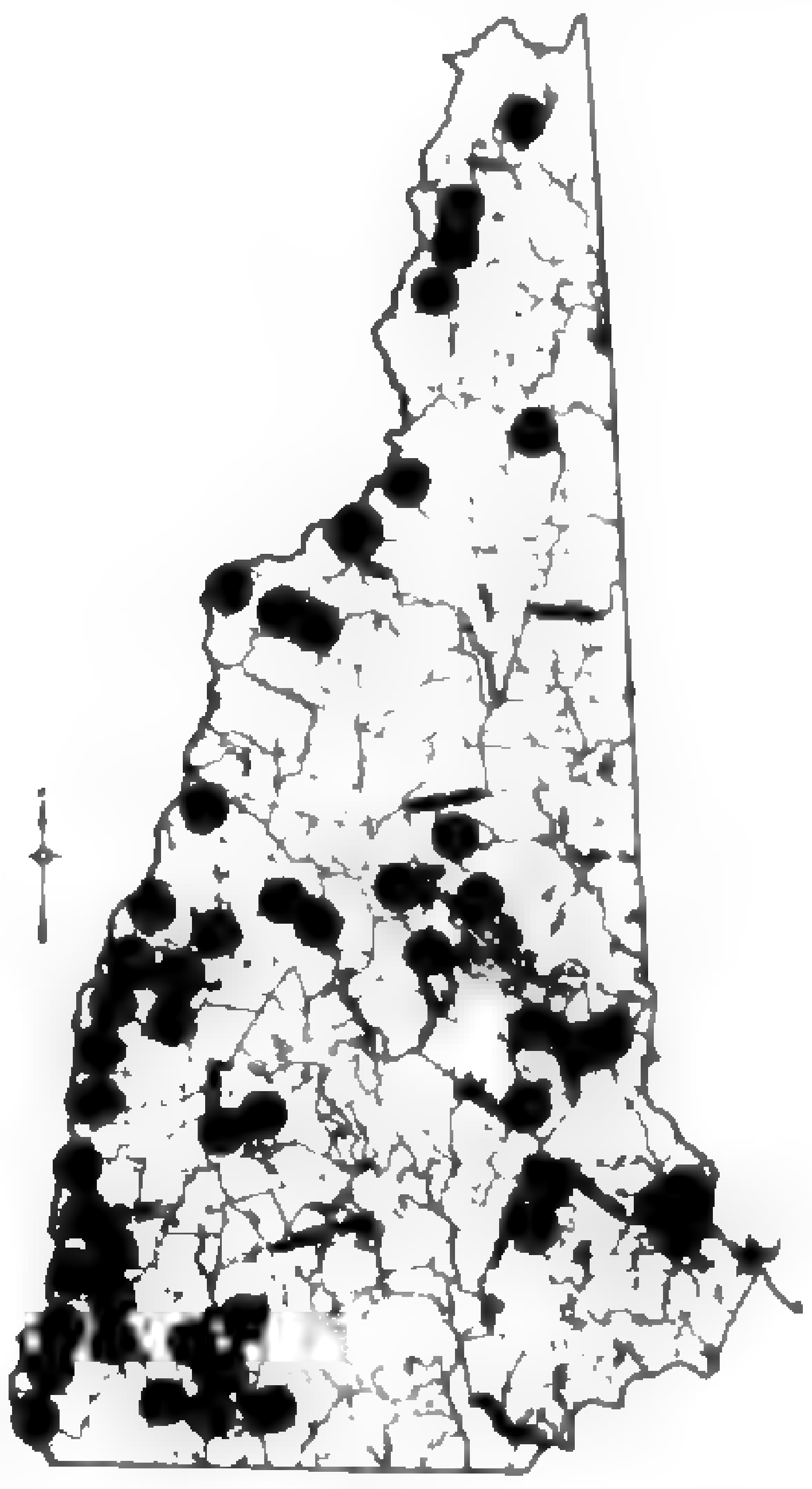
4-8 PLATANTHERA CLAVELLATA

4-9 PLATANTHERA FLAVA

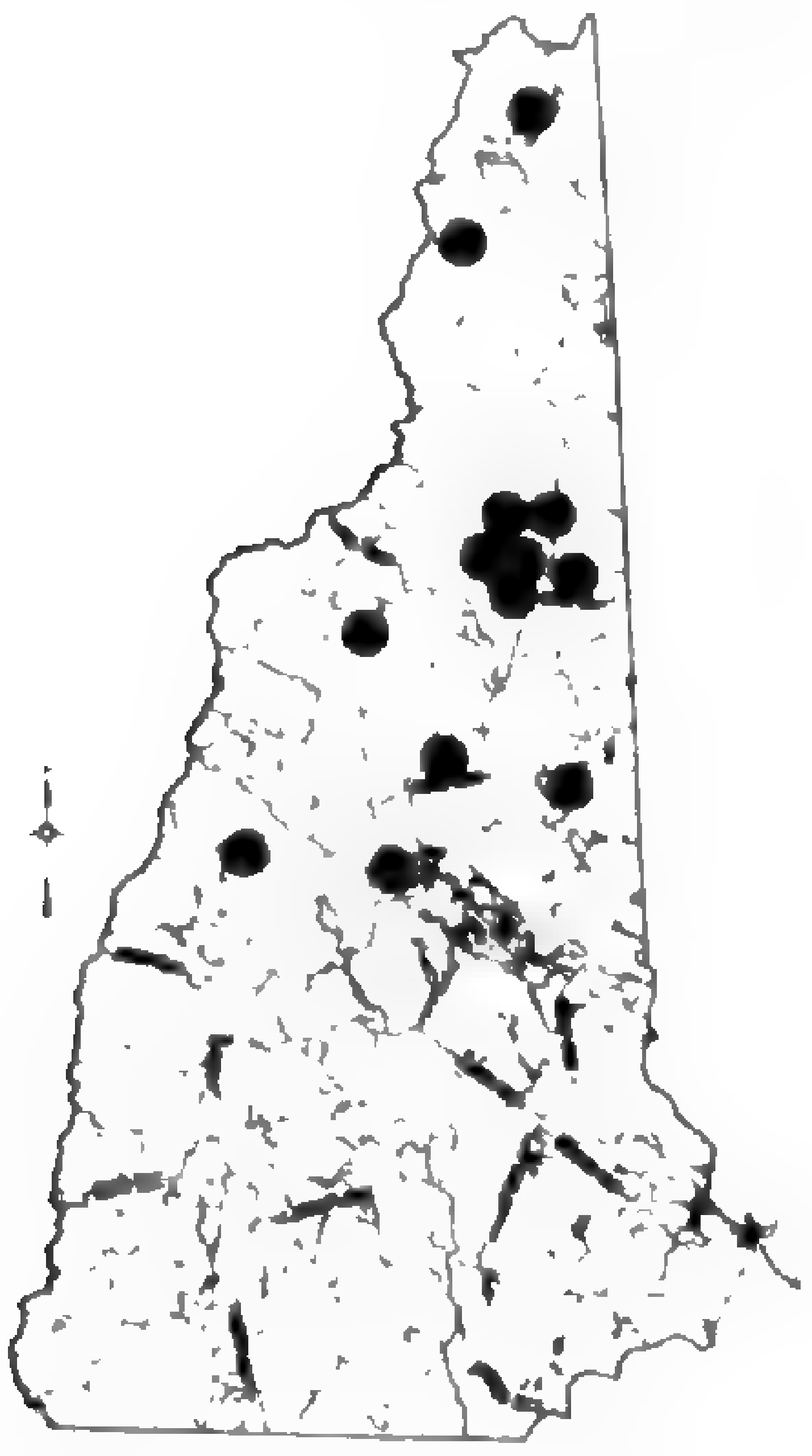


4-10 PLATANTHERA DILATATA

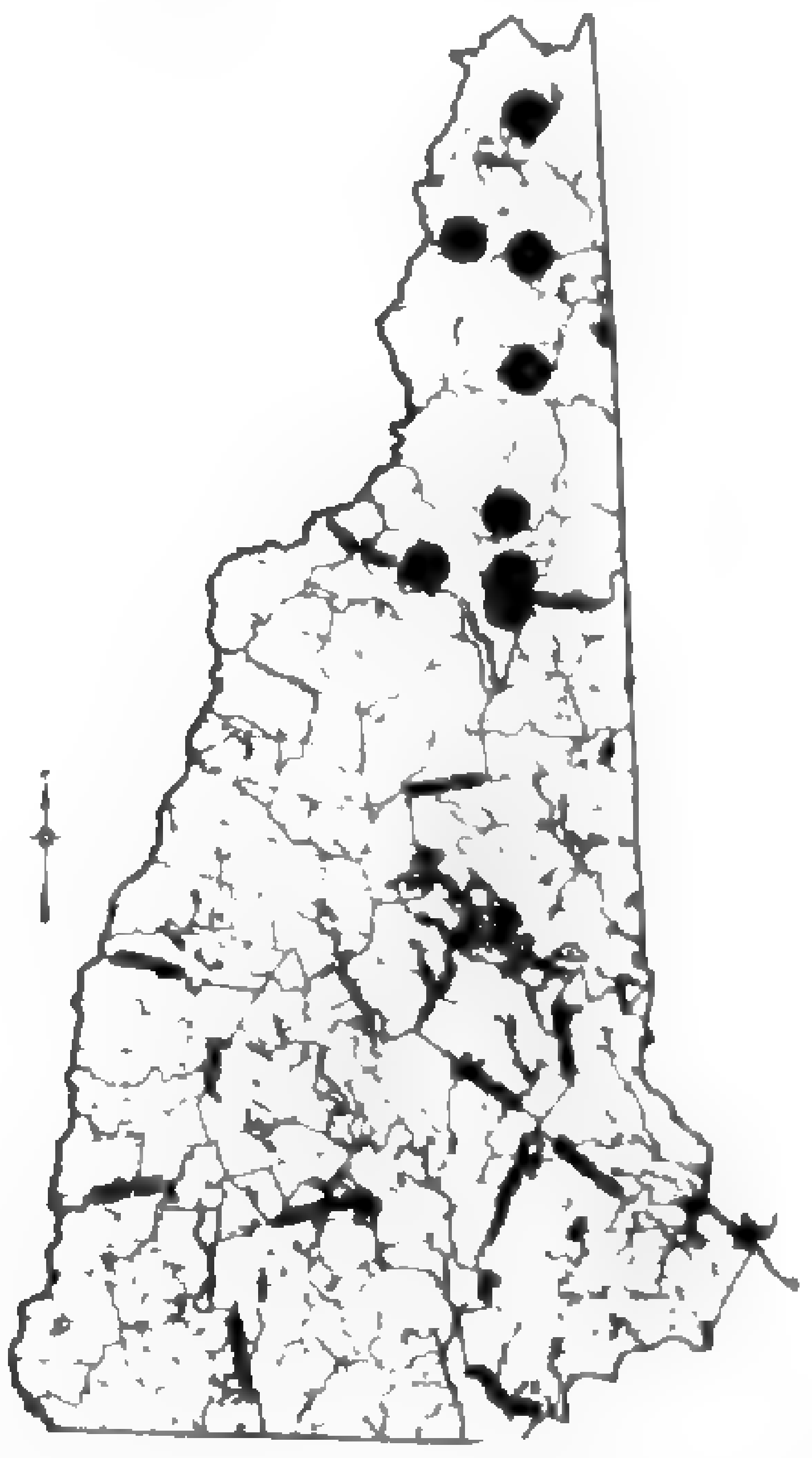
4-11 PLATANTHERA HYPERBOREA



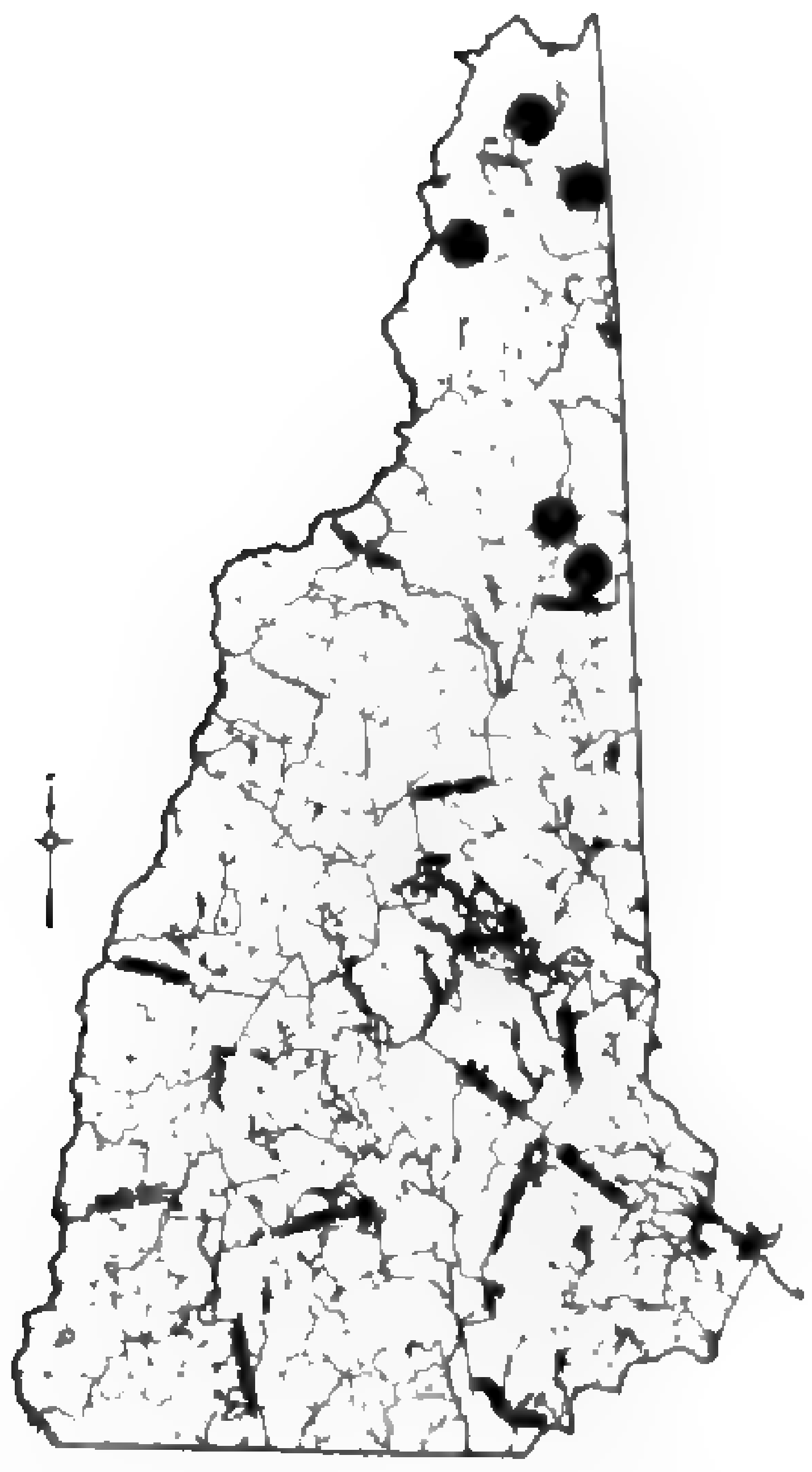
5-1 EPIPACTIS HELLEBORINE



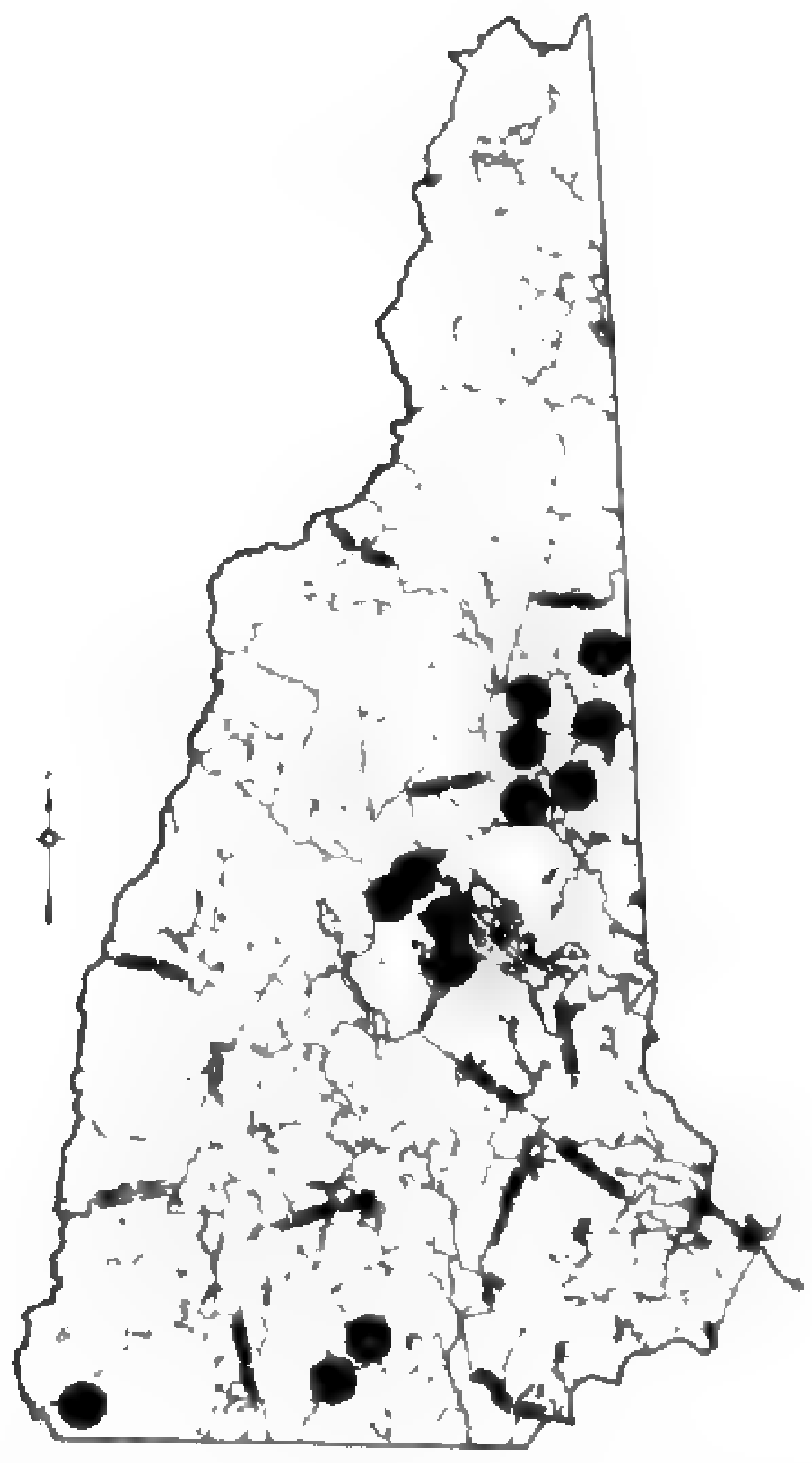
6-1 LISTERA CORDATA



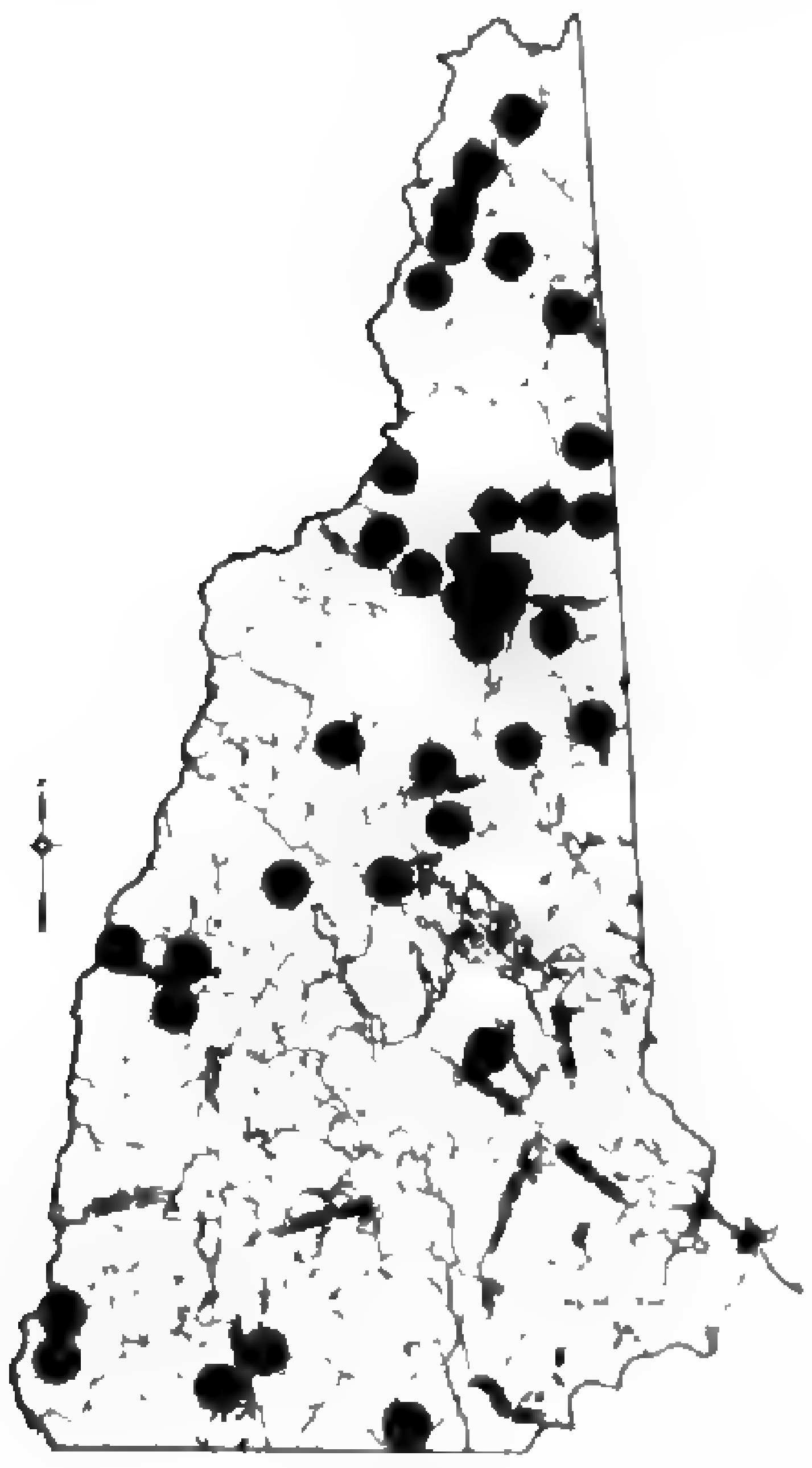
6-2 LISTERA CONVALLARIOIDES



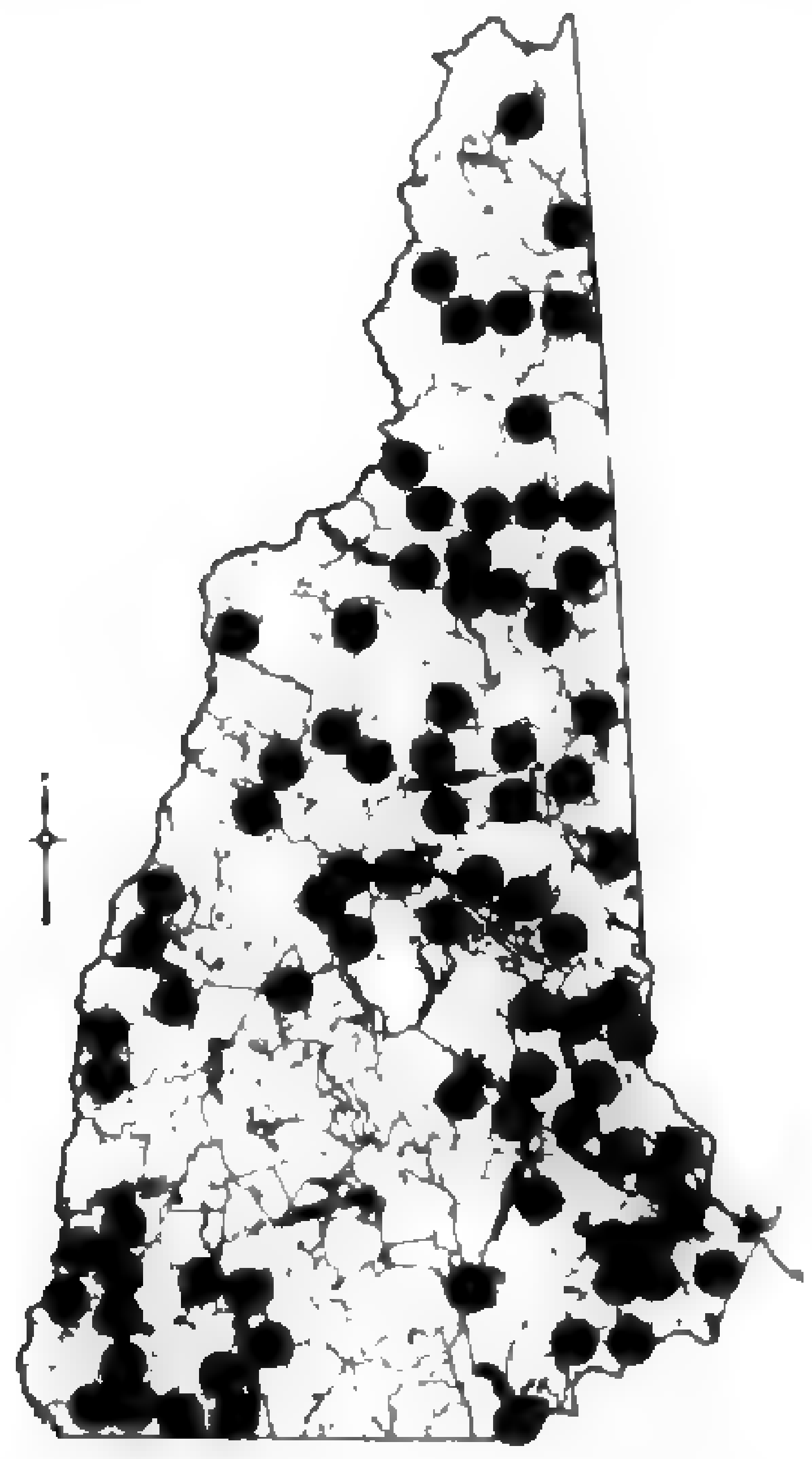
6-3 LISTERA AURICULATA



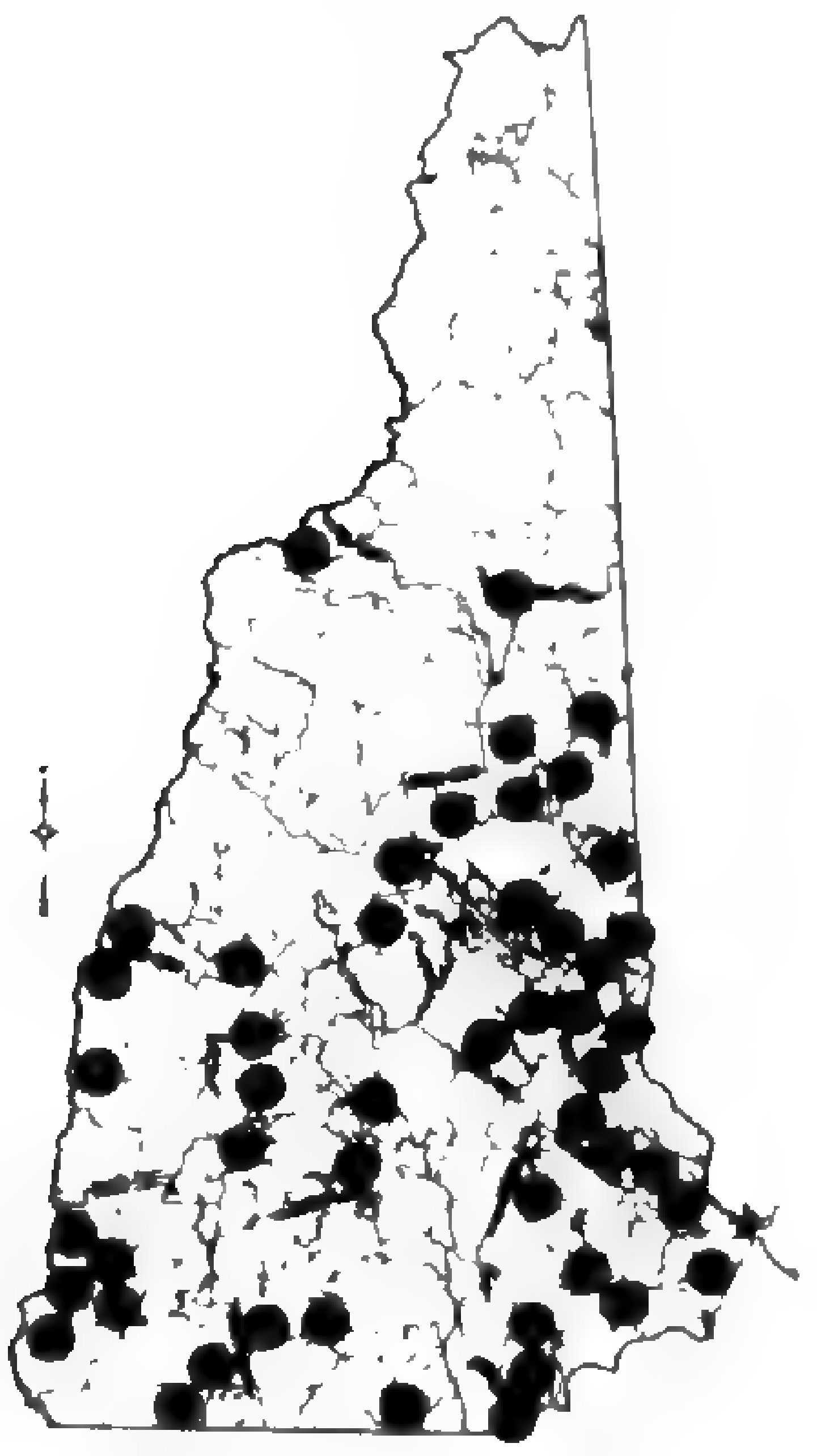
7-1 TRIPHORA TRIANTHOPHORA



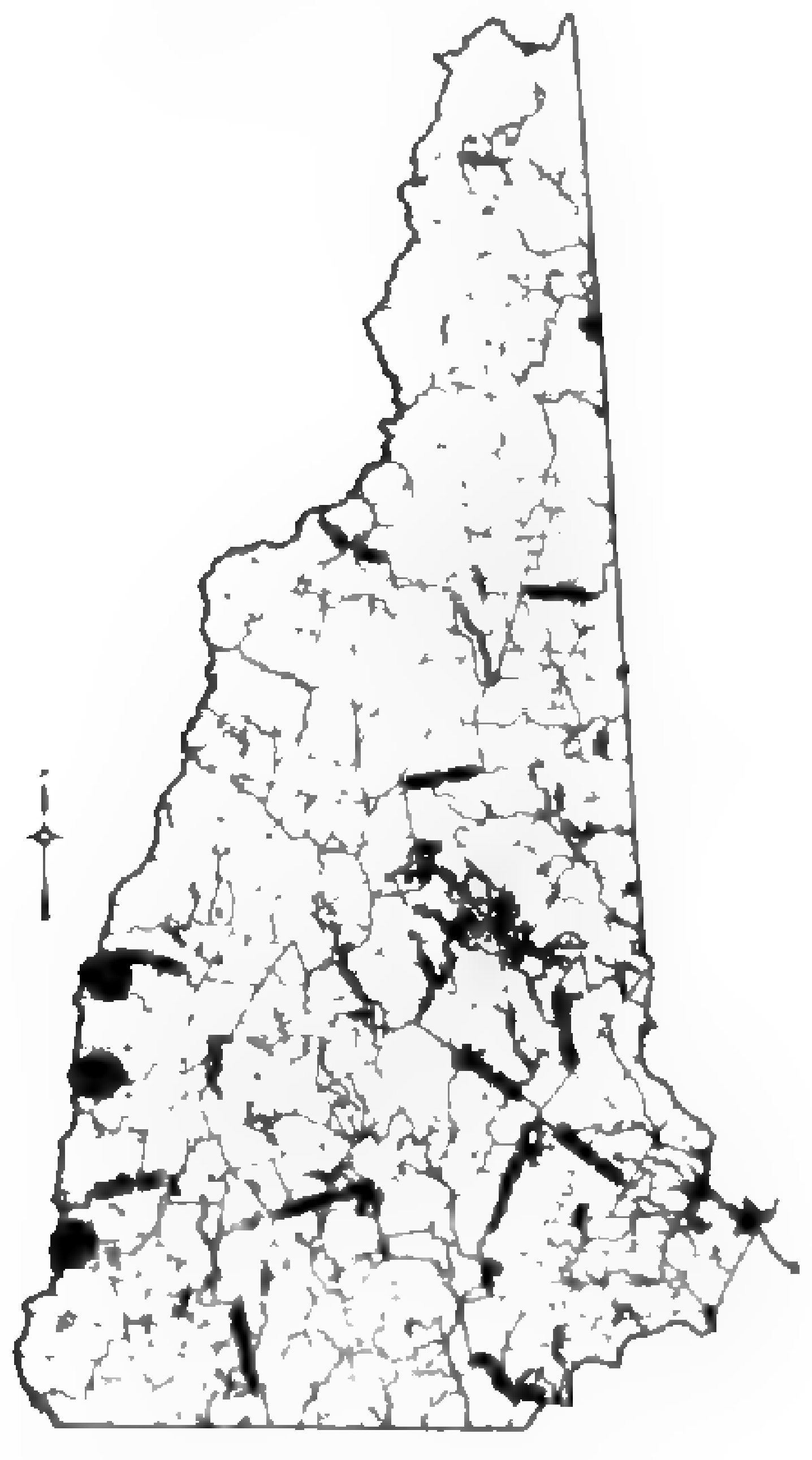
8-1 GOODYERA REPENS



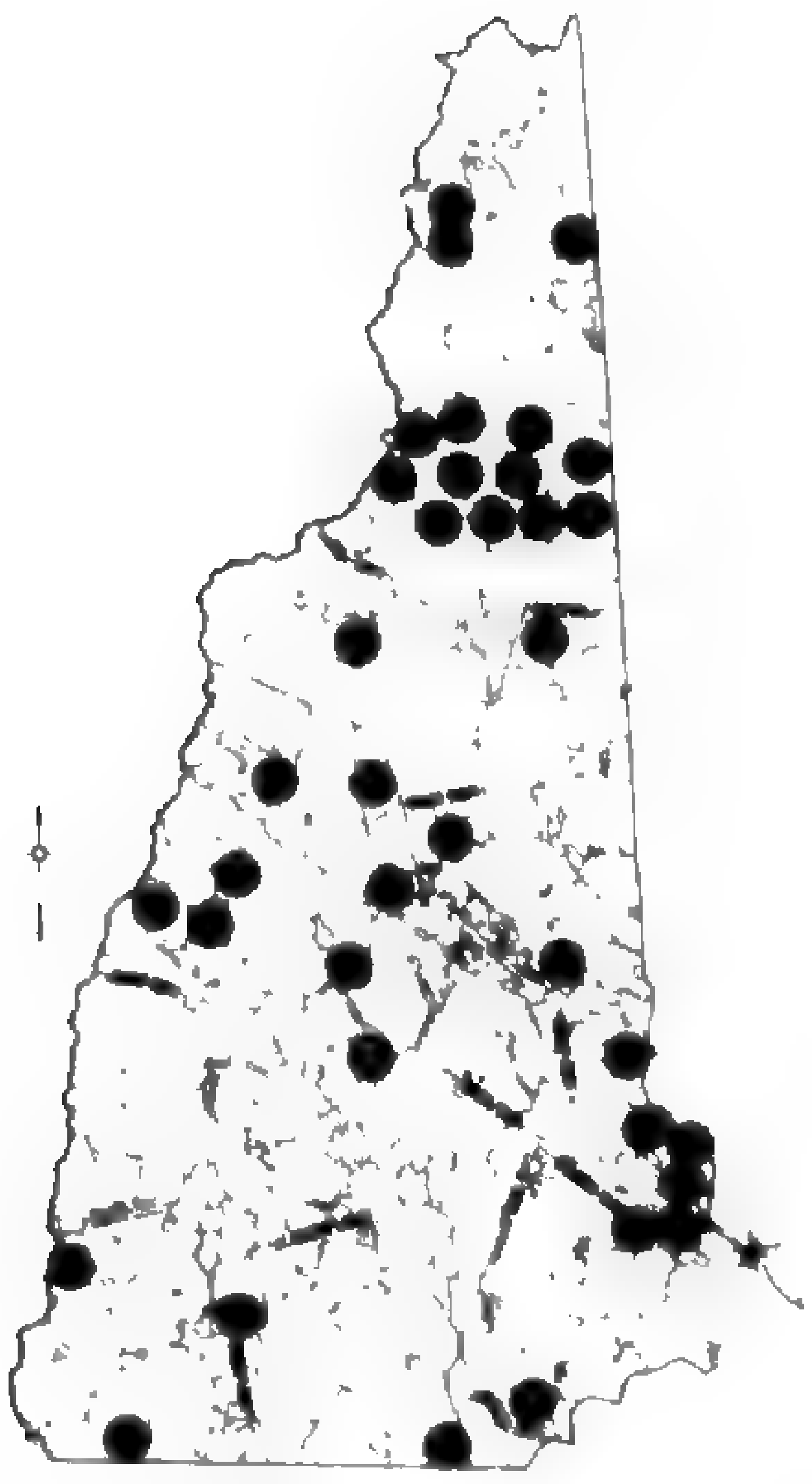
8-2 GOODYERA TESSELATA



8-3 GOODYERA PUBESCENS



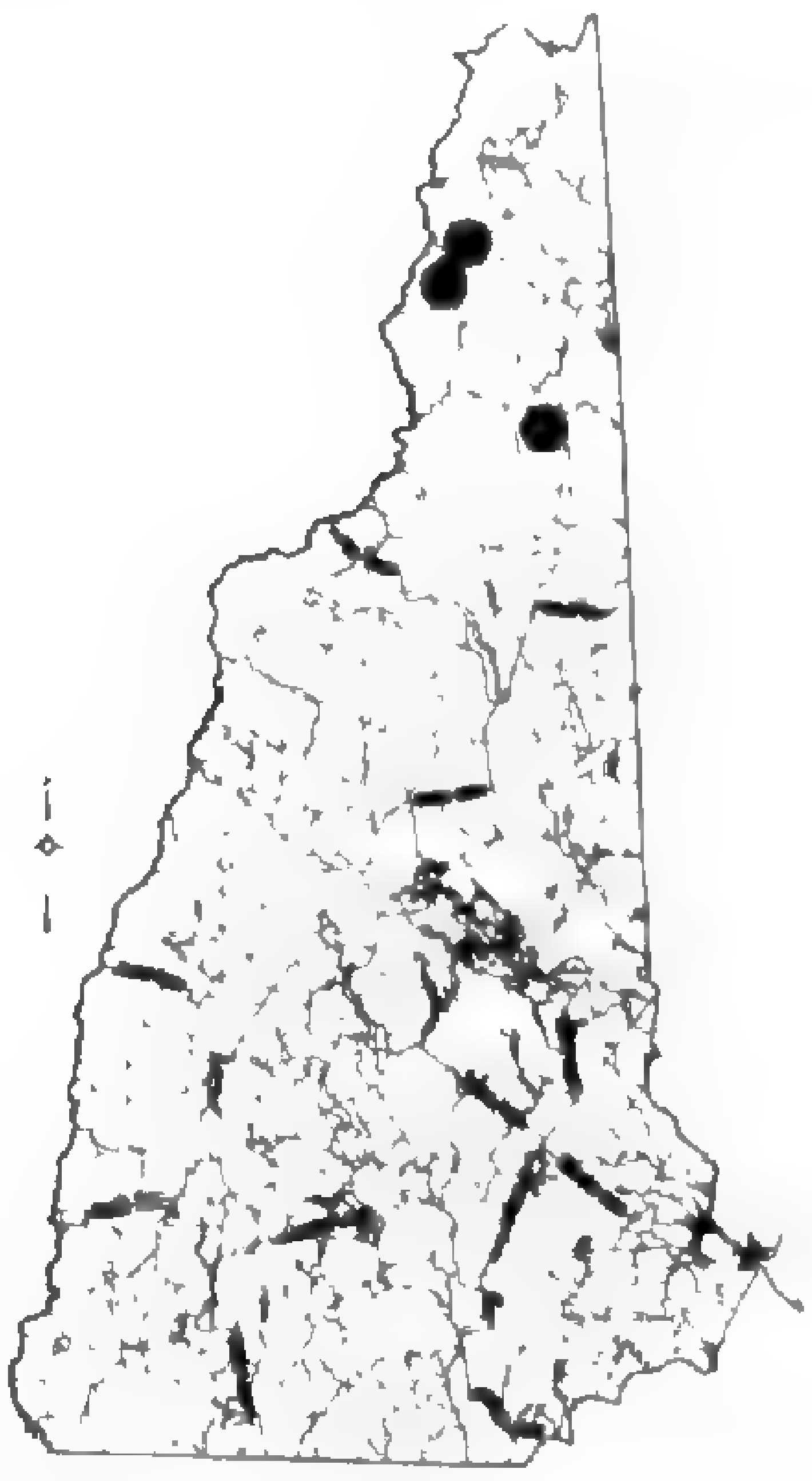
9-1 SPIRANTHES LUCIDA



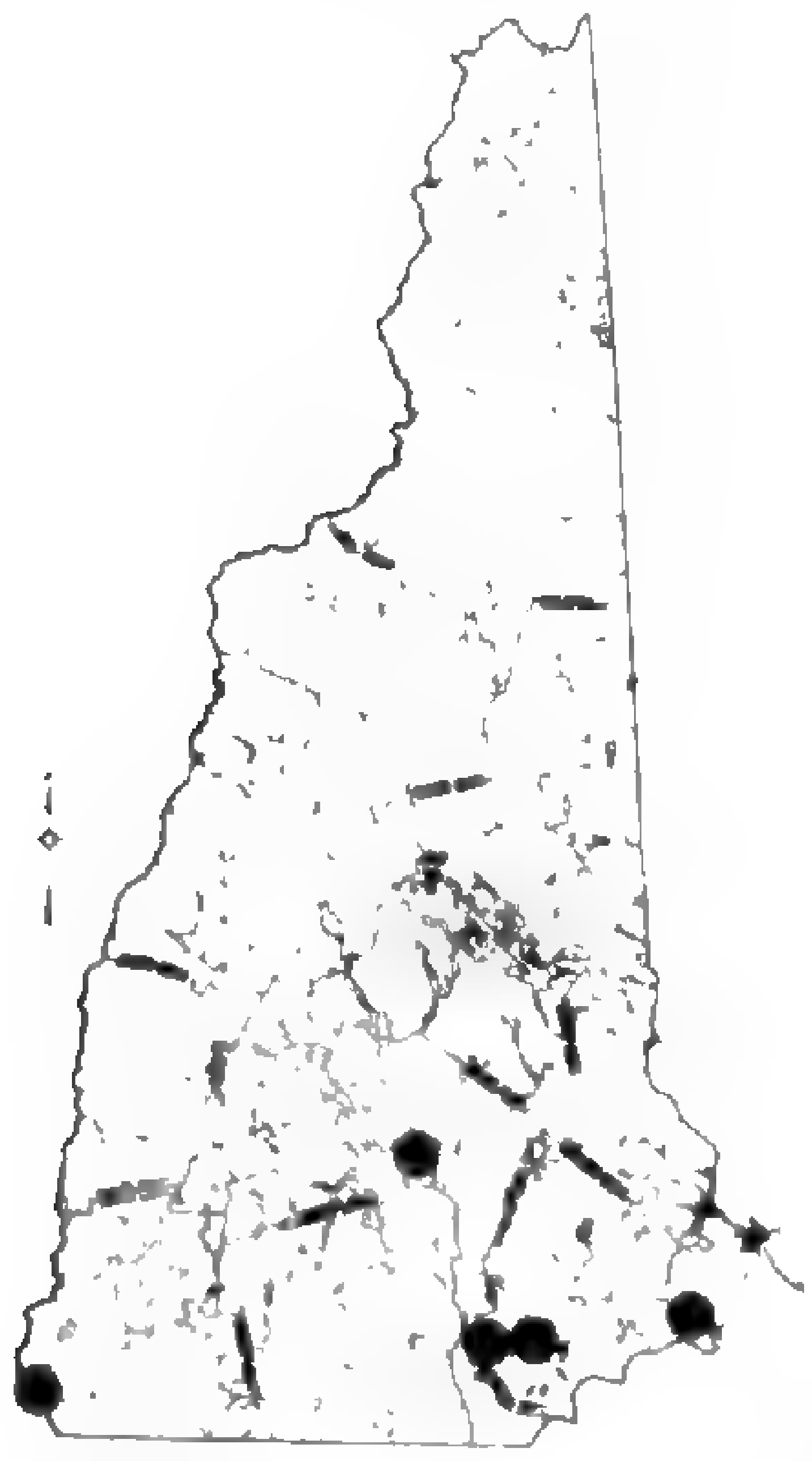
9–2 SPIRANTHES ROMANZOFFIANA

9–3 SPIRANTHES CERNUA

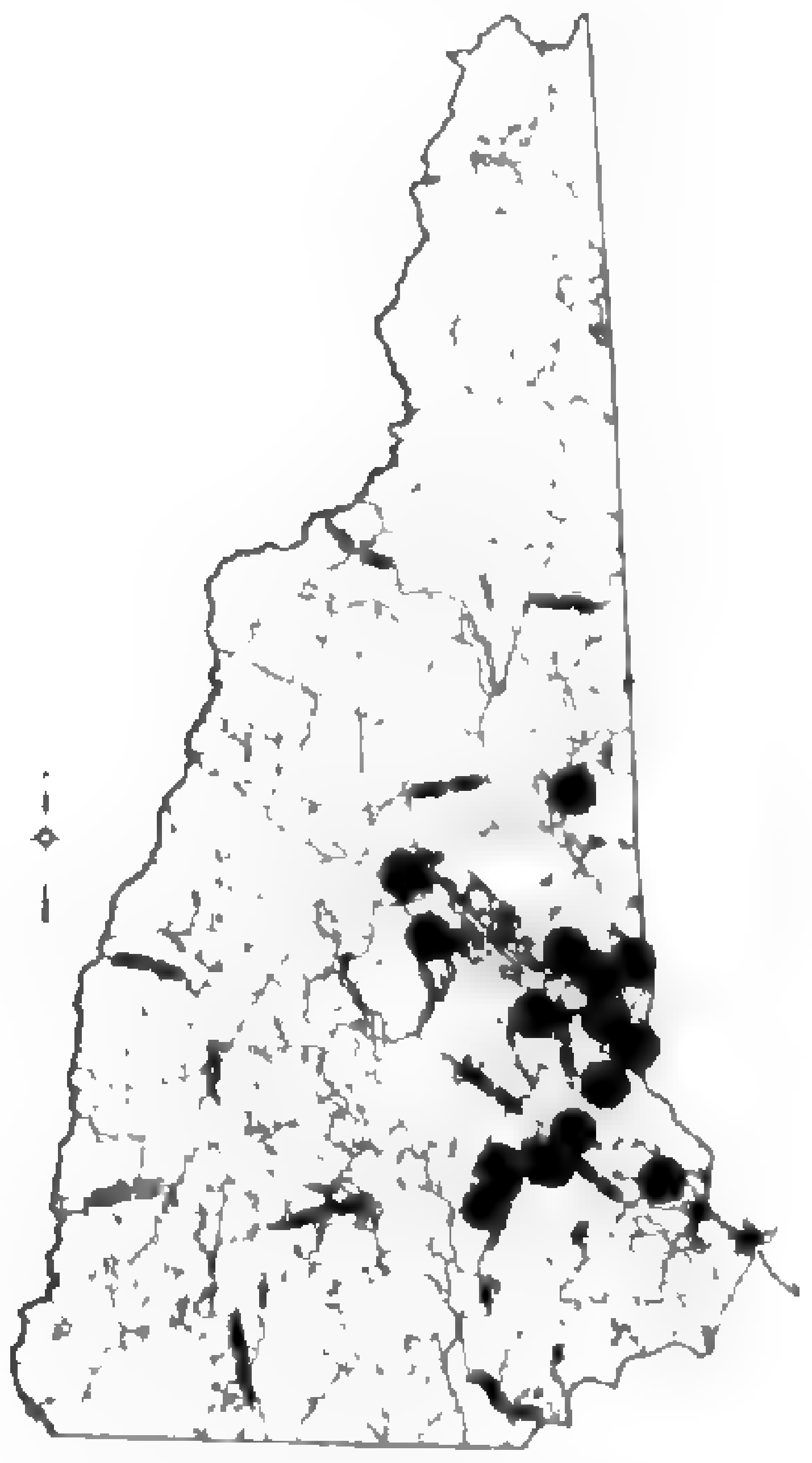
9–4 SPIRANTHES LACERA



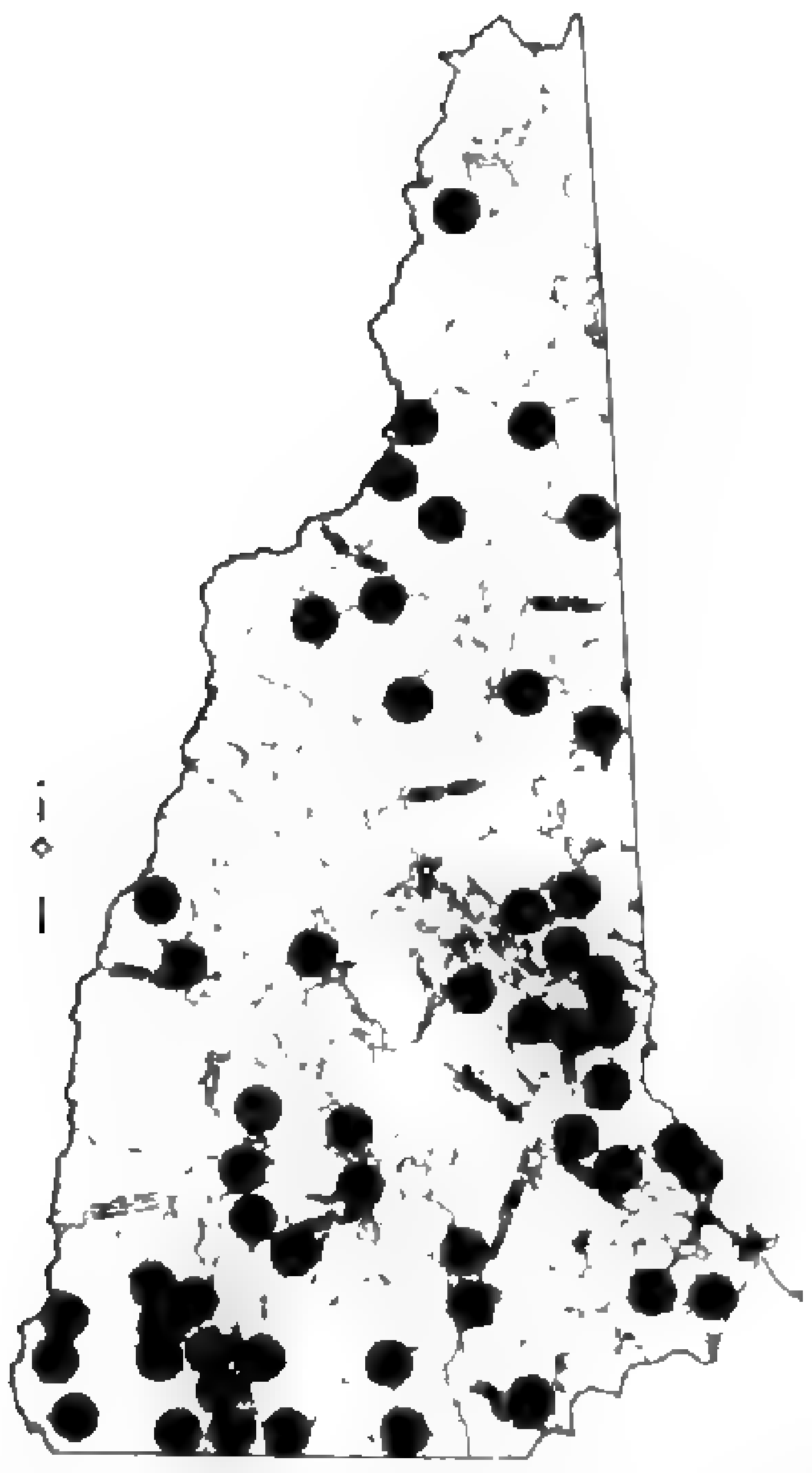
9–5 SPIRANTHES CASEI



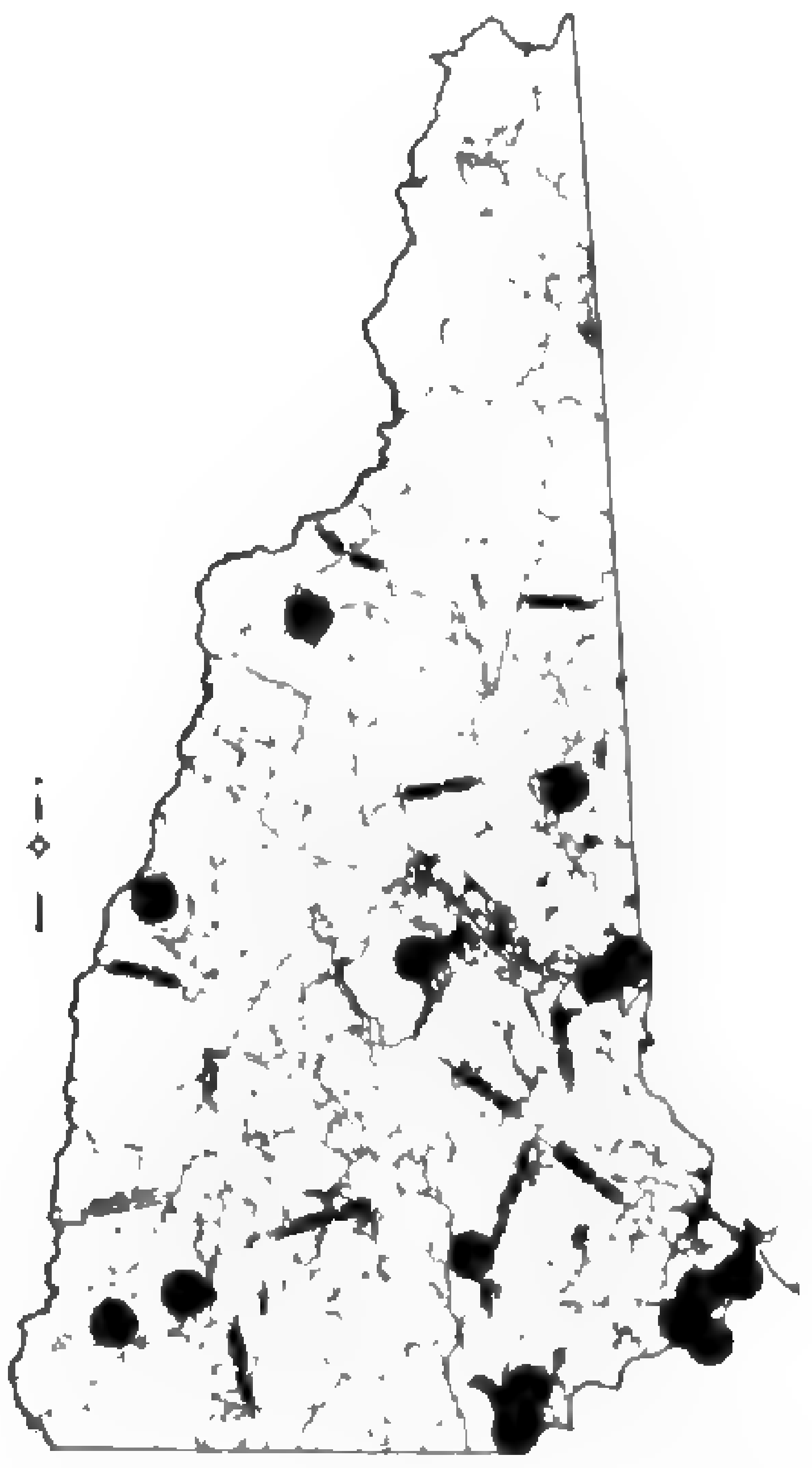
10–1 ISOTRIA VERTICILLATA



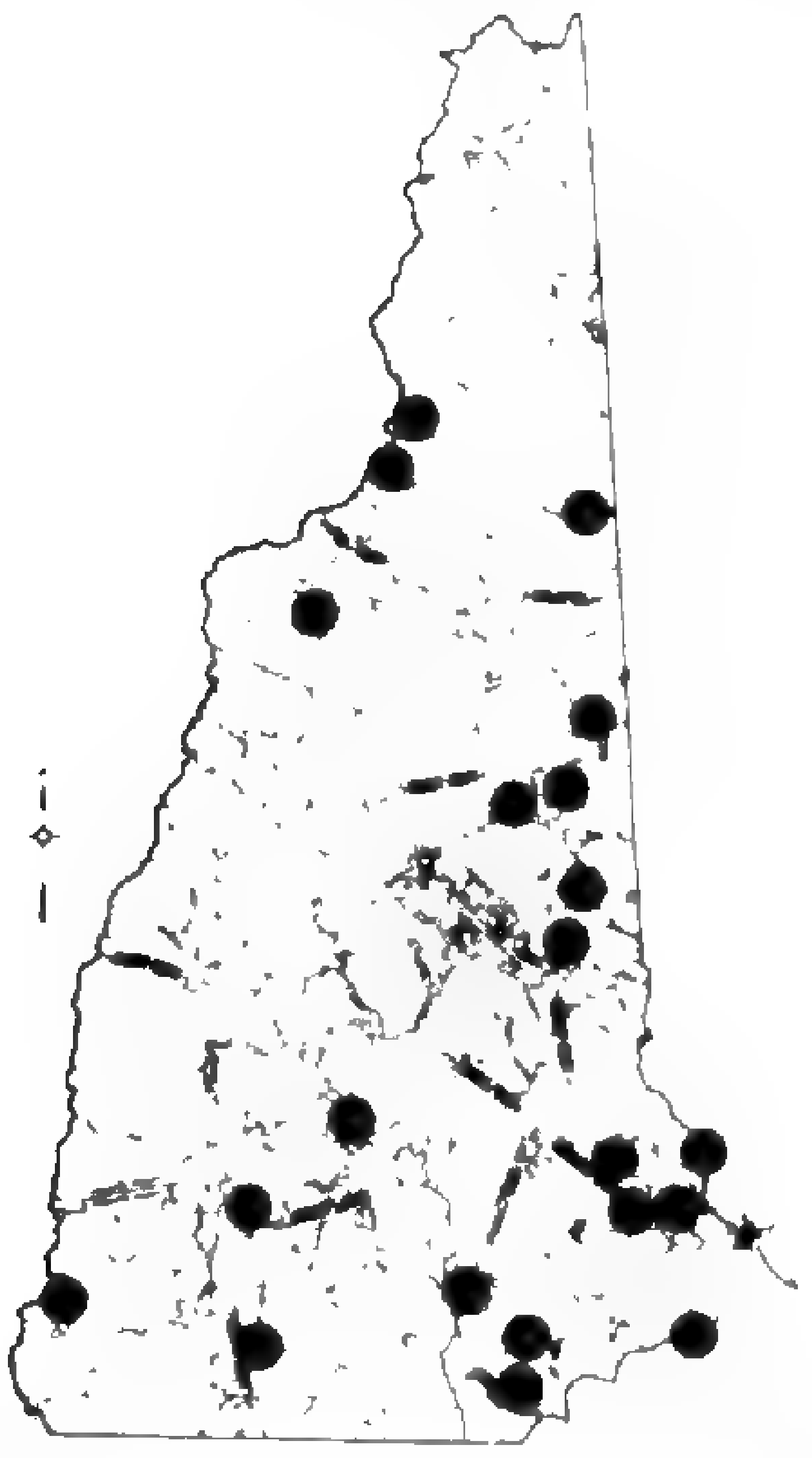
10–2 ISOTRIA MEDEOLOIDES



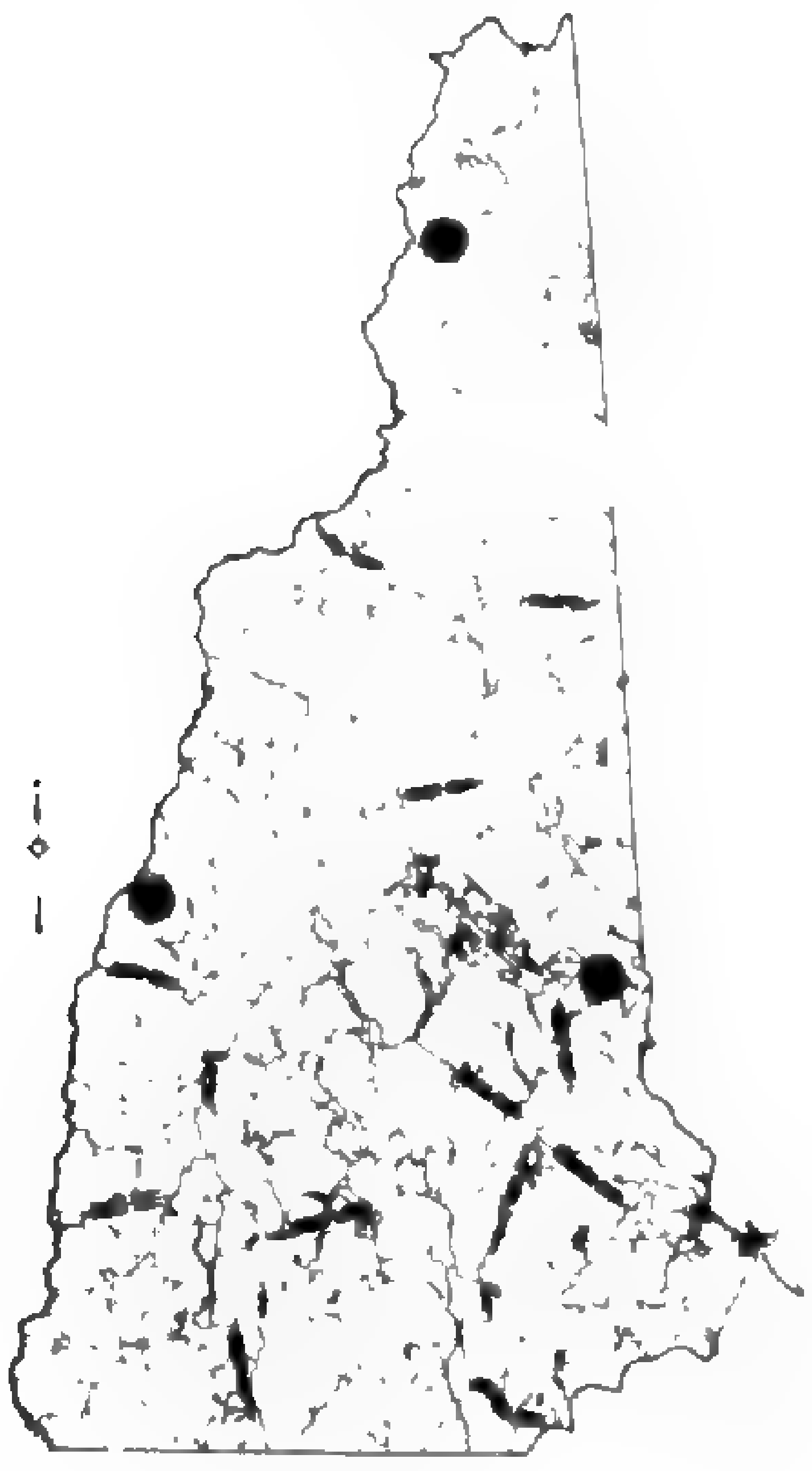
11-1 POGONIA OPHIOGLOSSOIDES



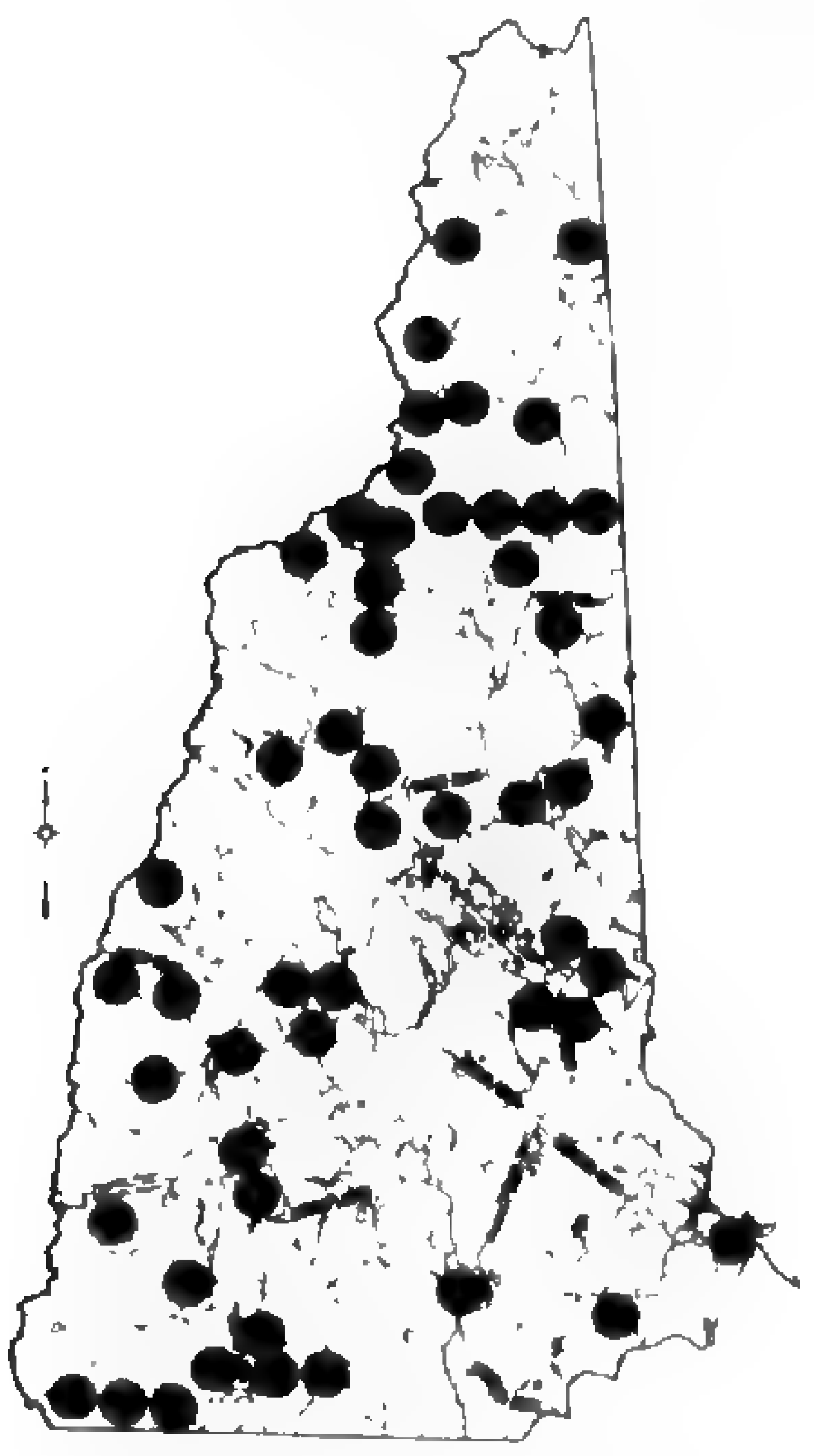
12-1 ARETHUSA BULBOSA



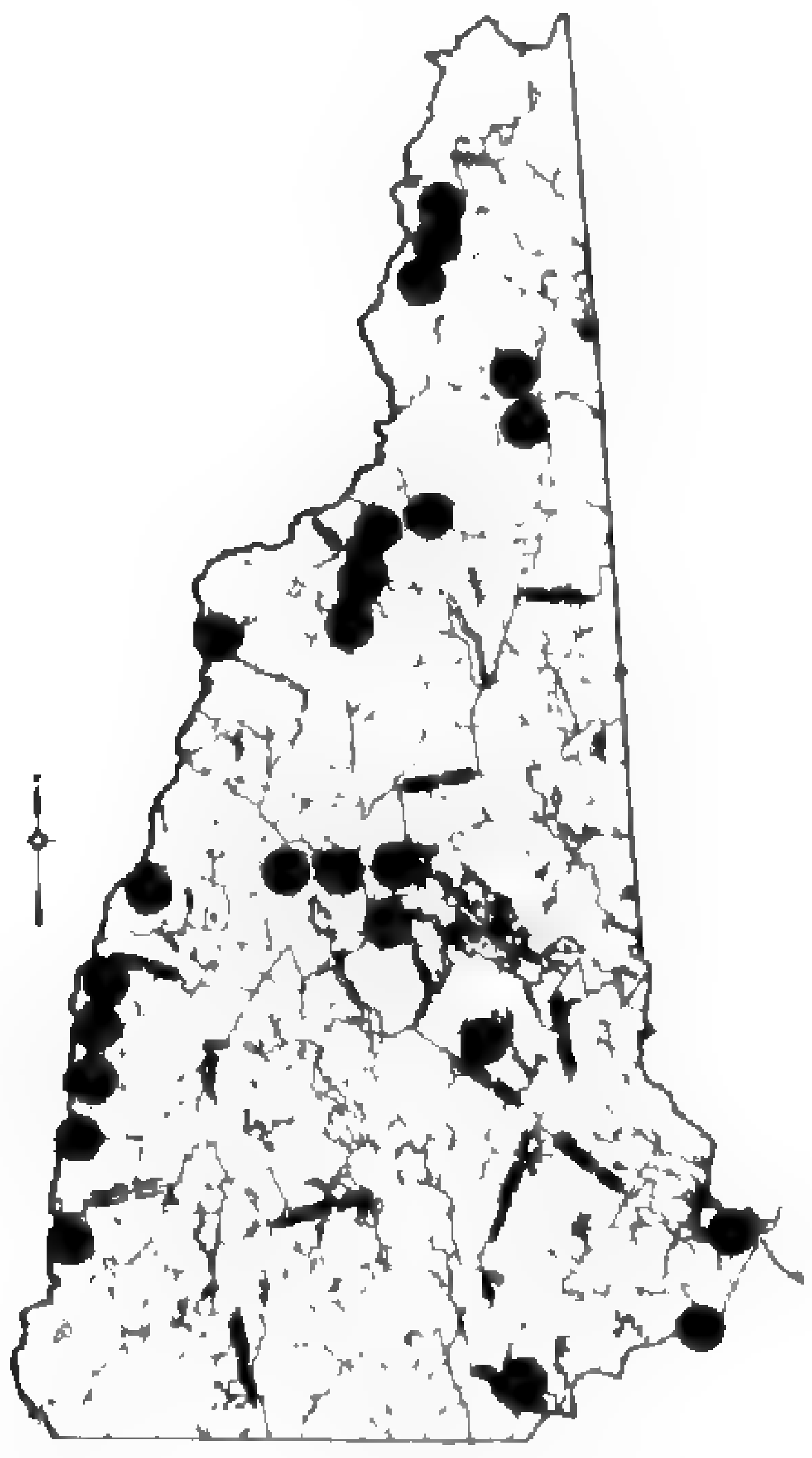
13-1 CALOPOGON TUBEROSUS



14-1 MALAXIS MONOPHYLLA

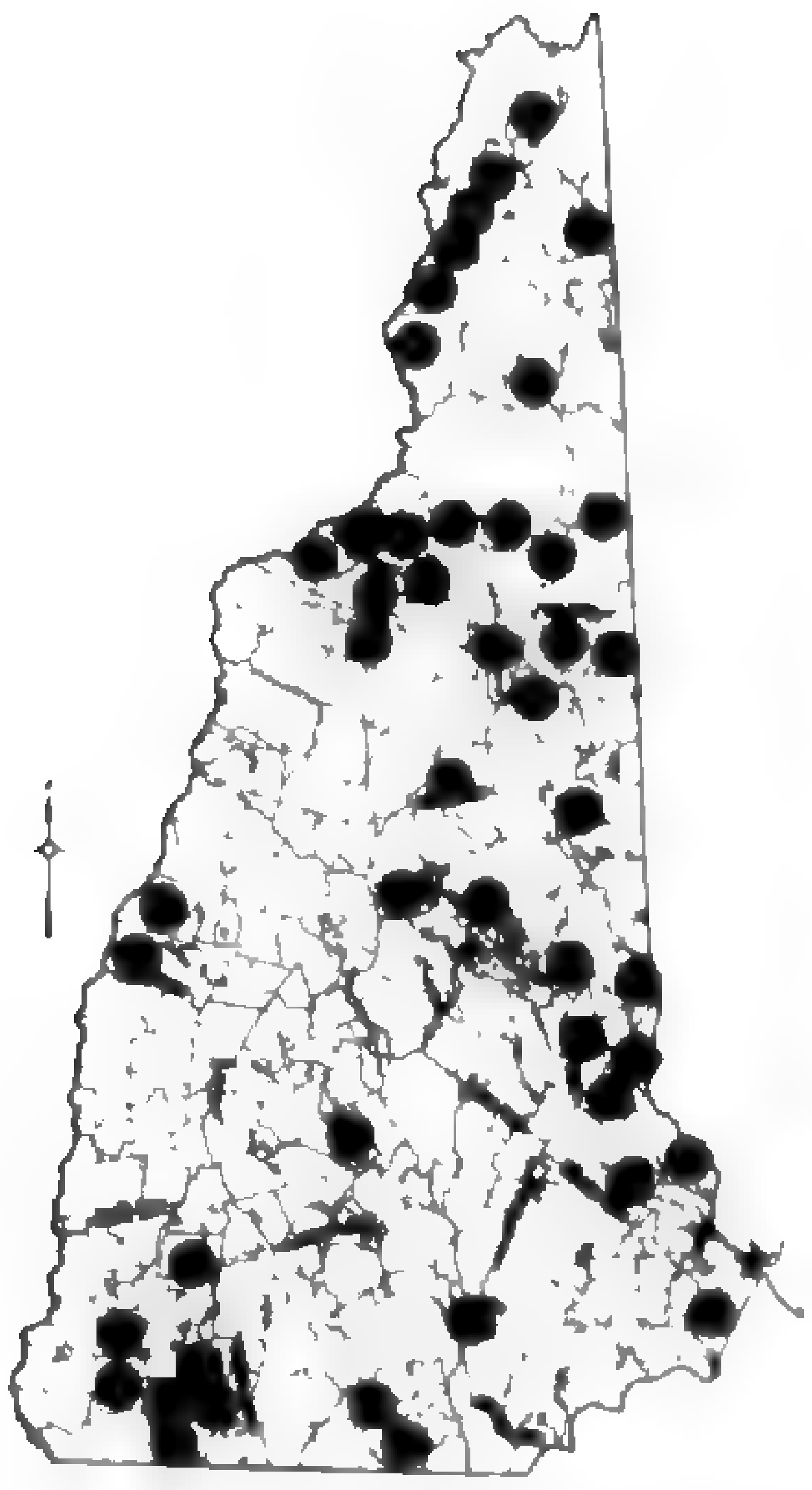


14-2 MALAXIS UNIFOLIA



15-1 LIPARIS LOESELII

16-1 CALYPSO BULBOSA



17-1 CORALLORHIZA TRIFIDA

17-2 CORALLORHIZA MACULATA

LITERATURE CITED

ACKERMAN, J. D. 1975. Reproductive biology of *Goodyera oblongifolia* (Orchidaceae). Madroño 23: 191–198.

——— AND M. R. MESLER. 1979. Pollination biology of *Listera cordata* (Orchidaceae). Amer. J. Bot. 66: 820–824.

AMES, O. 1906. *Habenaria orbiculata* and *H. macrophylla*. Rhodora 4: 1–5.

———. 1921. Notes on New England orchids—I. *Spiranthes*. Rhodora 23: 73–85.

———. 1922a. A discussion of *Pogonia* and its allies in the northeast United States with references to extra-limital genera and species. Orchidaceae 7: 3–38.

———. 1922b. Notes on New England orchids—II. The mycorrhiza of *Goodyera pubescens*. Rhodora 24: 37–46.

———. 1938. Resupination as a diagnostic character in the Orchidaceae with special reference to *Malaxis monophyllos*. Bot. Mus. Leafl. 6: 145–183.

——— AND D. S. CORRELL. 1943. Studies in *Habenaria* and *Dichaea*. Bot. Mus. Leafl. 11: 57–80.

ANDERSON, A. B., AND J. P. GOLTZ. 1982. Common Twayblade, *Listera ovata* (Orchidaceae) in Wellington County, Ontario: A second North American record. Canadian Field Nat. 96: 351–352.

ANDERSON, E. 1936. Color variation in eastern North American flowers as exemplified by *Hepatica acutiloba*. Rhodora 38: 301–304.

ANDREWS, A. L. 1901. A natural hybrid between *Habenaria lacera* and *H. psychodes*. Rhodora 3: 245–248.

ANONYMOUS. 1879. An orchid new to America. Bull. Torrey Bot. Club 6: 329–330.

ARTHUR, A. P. 1962. Adults of the European skipper *Thymelicus lineola* (Ochs.). Proc. Entomol. Soc. Ontario 92: 190–191.

AUCLAIR, A. N. 1972. Comparative ecology of the orchids *Aplectum hymale* and *Orchis spectabilis*. Bull. Torrey Bot. Club 99: 1–10.

AYENSU, E. S. AND R. A. DEFILIPPS. 1978. Endangered and Threatened Plants of the United States. Smithsonian Institution and World Wildlife Fund, Inc., Washington, DC.

BALDWIN, H. 1894. The Orchids of New England. John Wiley and Sons, New York.

BALDWIN J. T. AND B. M. SPEESE. 1957. Chromosomes of *Pogonia* and of its allies in the range of Gray's Manual. Amer. J. Bot. 44: 651–653.

BARKER, E. E. 1931. You also can grow orchids as I do in N. Y. State. Better Homes and Gardens. April issue.

BARTLETT, H. H. 1922. Color types of *Corallorrhiza maculata* Raf. Rhodora 24: 145–148.

BATCHELDER, F. W. 1900. Flora of Manchester and vicinity. Proc. Manchester Institute of Arts and Sciences 1: 1–158.

———. 1909. Preliminary list of plants growing without cultivation in the vicinity of Manchester, New Hampshire. Proc. Manchester Institute of Arts and Sciences. 4: 3–59.

BIGELOW, J. 1824. Florula Bostoniensis. 2nd ed. Cummings, Hilliard, and Co., Boston.

BINGHAM, M. T. 1939. Orchids of Michigan. Bull. Cranbrook Inst. Sci. 15: 1–87.

BRACKLEY, F. E. 1979. *Cypripedium reginae* rediscovered in New Hampshire. Rhodora 81: 579–580.

BRITTON, N. L. 1901. Manual of the Flora of the Northern States and Canada. New York.

CAMPBELL, E. O. 1970. Morphology of the fungal association in three species of *Corallorhiza* in Michigan. Mich. Bot. 9: 108–113.

CASE, F. W. JR. 1964a. Orchids of Western Great Lakes Region. Cranbrook Institute, Bloomfield Hills, Michigan.

———. 1964b. A hybrid twayblade and its rarer parent, *Listera auriculata*, in northern Michigan. Michigan Bot. 3: 67–70.

———. 1971. *Isotria medeoloides*, the smaller Whorled Pogonia, in Michigan. Michigan Bot. 10: 39–43.

CATLING, P. M. 1978. Taxonomic notes on *Spiranthes casei* Catling and Cruise and *Spiranthes* ×*intermedia* Ames. Rhodora 80: 377–389.

———. 1980a. Autogamy in north-eastern North American orchids. Bot. Soc. Amer. Misc. Ser. 158: 20.

———. 1980b. Rain-assisted autogamy in *Liparis loesellii* (L.) L. C. Rich (Orchidaceae). Bull. Torrey Bot. Club 107: 525–529.

CATLING, P. M. AND J. E. CRUISE. 1974. *Spiranthes casei*, a new species from northeastern North America. Rhodora 76: 526–536.

CODY, W. J. AND D. MONRO. 1980. The genus *Listera* (Twayblades) in New Brunswick. Canad. Field-Nat. 94: 443–446.

CORRELL, D. S. 1941. A new *Spiranthes* hybrid from New Hampshire. Amer. Orchid Soc. Bull. 9: 241.

———. 1950. Native Orchids of North America. Stanford Univ. Press, Stanford, CA.

COUNTRYMAN, W. D. 1978. Rare and endangered vascular plant species in Vermont. New England Botanical Club in cooperation with the U. S. Fish and Wildlife Service, Region 5 [Newton Corner, MA].

CROW, G. E. *et al.* 1981. Rare and endangered vascular plant species in New England. Rhodora 83: 259–299.

——— AND I. M. STORKS. 1980. Rare and endangered plants of New Hampshire: a phytogeographic viewpoint. Rhodora 82: 173–189.

CURTIS, J. T. 1932. A new *Cypripedium* hybrid. Rhodora 34: 239–242.

———. 1943. Germination and seedling development in 5 species of *Cypripedium* L. Amer. J. Bot. 30: 199–206.

DARLINGTON, C. D. AND A. P. WYLIE. 1956. A Chromosome Atlas of Flowering Plants. Macmillan, New York.

DARWIN, C. 1877. On the Various Contrivances by which British and Foreign Orchids are Fertilized by Insects. 2nd ed. London.

DOWNIE, D. G. 1940. On the germination and growth of *Goodyera repens*. Trans. Bot. Soc. Edinburgh 33: 36–51.

DOYON, D. AND R. CAYOUETTE. 1966. *Epipactis helleborine* (L.) Crantz au Quebec. Naturaliste Canad. 93: 171–176.

DRESSLER, R. L. 1981. The Orchids. Natural History and Classification. Harvard Univ. Press, Cambridge, MA.

EASTMAN, L. M. 1976. Nodding Pogonia, *Triphora trianthophora* (Sw.) Rydb., in Maine and its relevance to the Critical Areas Program. Planning Report No. 19. State Planning Office, Augusta, ME.

ELLIOTT, H. V. AND F. S. COOK. 1970. *Listera ovata* (L.) R. Br. in the Bruce Peninsula, Ontario. Rhodora 72: 274–275.

FERNALD, M. L. 1899. Rattlesnake Plantains of New England. Rhodora 1: 2–7.

______. 1926a. Botanizing in Newfoundland. Rhodora 28: 49–112, 161–178.

______. 1926b. The Ragged Orchis of Newfoundland. Rhodora 28: 21–22.

______. 1946a. Technical studies on North American plants. Rhodora 48: 5–12.

______. 1946b. Identification and reidentification of North American plants. Rhodora 48: 137–162, 184–197.

______. 1950a. Gray's Manual of Botany, 8th Ed. American Book Co., New York.

______. 1950b. A small fascicle of novelties. Rhodora 52: 61–65.

FREEMAN, M. B. 1943. Herbs for the Mediaeval Household. Met. Mus. of Art, New York.

FROST, R. 1964. Complete Poems of Robert Frost. Holt, Rinehart, and Winston, New York.

FULLER, M. A. 1933. Studies on the flora of Wisconsin. Part I: Orchidaceae. Bull. Publ. Mus. Milwaukee 14, 1: 1–248.

GARAY, L. A. 1960. On the origin of the Orchidaceae. Bot. Mus. Leafl. 19: 57–96.

GIBSON, W. H. 1905. Our Native Orchids. Doubleday, Page and Co., New York.

GLEASON, H. A. AND A. CRONQUIST. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. D. Van Nostrand Co., New York.

GRAY, A. 1862–1863. Fertilization of orchids. Amer. J. Sci. 34: 420–429, 36: 292–294.

GRONOVIUS, J. F. 1743. Flora Virginica. Pars 2. Leiden.

GUIGNARD, J. A. 1886. Insects and orchids. Annual Rep. Ent. Soc. Ont. 16: 39–48.

HAGERUP, O. 1941. Bestøvningen hos *Liparis* og *Malaxis*. Bot. Tidsskr. 45: 396–402.

______. 1951. Pollination in the Faroes—in spite of rain and poverty of insects. Biol. Meddel. Kongel. Danske Vidensk. 18: 1–48.

______. 1952. Bud autogamy in some northern orchids. Phytomorphology. 2: 51–60.

HARVAIS, G. 1980. Scientific notes on a *Cypripedium reginae* of northeastern Ontario, Canada. Amer. Orchid Soc. Bull. 49: 237–244.

HEINRICH, B. 1979. Bumblebee Economics. Harvard Univ. Press., Cambridge, MA.

HOCKING, B. 1968. Insect-flower associations in the high arctic with special reference to nectar. Oikos 19: 359–388.

HOCKING, G. M. 1955. A Dictionary of Terms in Pharmacognosy. C. C. Thomas, Pub., Springfield, IL.

HOMOYA, M. 1977. Some aspects of the life history of *Isotria medeoloides*, an endangered orchid species. Trans. Illinois State Acad. Sci. 70: 196.

HOUSE, H. D. 1905. Further notes on the orchids of central New York. Bul. Torrey Bot. Club 32: 373–382.

HULTÉN, E. 1962. Flora of Alaska. Stanford Univ. Pres., Stanford, CA.

HUMPHREY, H. B. 1961. Makers of North American Botany. Ronald Press, New York.

ILTIS, H. H. 1965. The genus *Gentianopsis* (Gentianaceae): transfers and phytogeographic comments. Sida 2: 129 154.

JORGENSEN, N. 1971. A Guide to New England's Landscape. Barre Publ., Barre, MA.

JUDD, W. W. 1972. Wasps (Vespidae) pollinating Helleborine, *Epipactis helleborine* (L.) Crantz, at Owen Sound, Ontario. Proc. Ent. Soc. Ontario. (1971) 102: 115 118.

KALLUNKI, J. A. 1976. Population studies in *Goodyera* (Orchidaceae) with emphasis on the hybrid origin of *G. tesselata.* Brittonia 28: 53-75.

———. 1981. Reproductive biology of mixed-species populations of *Goodyera* (Orchidaceae) in northern Michigan. Brittonia 33: 137 155.

KER, J. B. 1916. The Botanical Register. Vol. II. London.

KEVAN, P. G. 1972. Insect pollination of high arctic flowers. J. Ecol. 60: 831-847.

KIRCHNER, O. 1922. Über selbstbestäubung bei den Orchideen. Flora 115: 103 129.

LEAVIT, R. G. 1901. Notes on the embryology of some New England orchids. Rhodora 3: 61 63.

LEUR, C. A. 1975. The Native Orchids of the United States and Canada excluding Florida. N. Y. Botanical Garden, Bronx, New York.

LI, H. 1952. Floristic relationship between eastern Asia and eastern North America. Trans. Amer. Philos. Soc. 42: 371 429.

LINNAEUS, C. 1753. Species Plantarum. Facsimile ed. 1959. Ray Society, London.

———. 1757. Mantissa plantarum. *In:* Systema Naturae, ed. 2, Vol. 2. Stockholm.

LODDIGES, C. 1824. Botanical Cabinet. x. No. 942.

LOWENSTEIN, A. E. 1917. Orchids found in the region of Asquam Lake. Rhodora 19: 56 57.

LOWES, A. E. 1920. Notes on *Pogonia trianthophora.* Rhodora 22: 53-55.

MAYR, E. 1969. Populations, Species, and Evolution. Harvard Univ. Press., Cambridge, MA.

MEHRHOFF, L. A. 1980. Reproductive systems in the genus *Isotria* (Orchidaceae). Bot. Soc. America Misc. Series. Pub. 158: 72.

MESLER, M. R., J. D. ACKERMAN, AND K. L. LU. 1980. The effectiveness of fungus gnats as pollinators. Amer. J. Bot. 67: 564-567.

MEUSEL, H., E. JÄGER UND E. WEINERT. 1965. Vergleichende Chorologie der Zentraleuropäischen Flora. VEB Gustau Fischer Verlag, Jena.

MICHAUX, A. 1803. Flora Boreali-americana. Strasbourg, Paris. 2 vols.

MOLDENKE, H. N. 1949. American Wild Flowers. D. Van Nostrand, New York.

MOORE, D. M. 1980. *In:* Tutin, T. G. (ed.), Flora Europaea. Vol. 5. Alismataceae to Orchidaceae. Cambridge Univ. Press., Cambridge, England.

MOORE, R. J. ed., 1973. Chromosome Numbers 1967 1971. Utrecht, Netherlands. Regnum Veg. Vol. 77.

MORRIS, F. AND E. E. EAMES. 1929. Our Wild Orchids. Charles Scribner's Sons, New York.

MOSQUIN, T. 1970. The reproductive biology of *Calypso bulbosa*. Canad. Field Naturalist. 84: 291 296.

MOUSLY, H. 1925. Further notes on *Calypso*. J. New York Bot. Gard. 25: 25 32.

MÜLLER, H. 1883. The Fertilisation of Flowers. Macmillan and Co., London.

MURRAY, D. F. 1980. The role of arctic refugia in the evolution of the arctic vascular flora—a Beringian perspective. Abstracts—2nd International Congress of Evolutionary and Systematic Biology: p. 3.

NILES, G. G. 1904. Bog Trotting for Orchids. Scribner, New York.

NILSSON, L. A. 1978. Pollination ecology and adaptation in *Platanthera chlorantha* (Orchidaceae). Bot. Not. 131: 35-51.

______. 1979. Anthecological studies on the Lady's Slipper, *Cypripedium calceolus* (Orchidaceae). Bot. Not. 132: 329 347.

______. 1980. The pollination ecology of *Dactylorhiza sambucina* (Orchidaceae). Bot. Not. 133: 367-385.

NILSSON, S. 1979. Orchids of Northern Europe. Penquin Books, Ltd., England.

NUTTALL, T. 1818. Genera of North American Plants. Philadelphia, PA.

NYLANDER, O. O. 1922. Life history of the calypso. Maine Naturalist 2: 82 83.

______. 1935. Our Northern Orchids. Star-Herald Publ. Co., Presque Isle, ME.

OHWI, J. 1965. Flora of Japan (in English). Smithsonian Institution, Washington, DC.

PEASE, A. S. 1964. A Flora of Northern New Hampshire. New England Botanical Club, Inc., Cambridge, MA.

PORCHER, R. 1977. The re-discovery of *Triphora trianthophora*, 3-birds orchid, in the coastal plain of South Carolina. Castanea 42: 108 111.

PRINCE, F. E. 1902. Some plants of Intervale, New Hampshire. Rhodora 4: 61.

PROCTOR, M. C. F. 1978. Insect pollination systems in an evolutionary and ecosystemic context. *In:* Richards, A. J., ed. The Pollination of Flowers by Insects. Linnean Society Symposium Series No. 6, 1978.

PURSH, F. 1814. Flora Americae Septentrionalis. London.

RAND, E. L. AND J. H. REDFIELD. 1894. Flora of Mount Desert Island, Maine. John Wilson and Son, Cambridge, MA.

RAMSEY, C. T. 1950. The triggered rostellum of the genus *Listera*. Amer. Orchid Soc. Bull. 19: 482 485.

______. 1966. Our two purple-fringed orchids. Amer Orchid Soc. Bull. 35: 458 460.

RAUP, H. M. 1930. The pollinization of *Habenaria obtusata*. Rhodora 32: 88 89.

ROBERTSON, C. 1928. Flowers and Insects. Carlinville, Ill.

Robinson, B. L. AND M. L. FERNALD. 1908. Gray's New Manual of Botany, 7th Ed. American Book Co., New York.

RYDBERG, P. 1901. *In:* Britton, N. L., Manual of the Flora of the Northern States and Canada. New York.

SANFORD, W. W. 1974. The ecology of orchids. *In:* Withner, C. L., ed. The Orchids. Wiley and Sons, New York.

SCHRENK, W. J. 1975. Die Orchideen der nordöstlichen Vereinigten Staaten. Teil VI. Die Orchidee 27: 153-158.

______. 1977. Die Orchideen der nordöstlichen Vereinigten Staaten. Teil VII. Die Orchidee 28: 66-69.

———. 1978. North American Platantheras: Evolution in the making. Amer. Orchid Soc. Bull. 47: 429–437.

Scudder, S. H. 1862. An account of the structure of *Pogonia ophioglossoides* Nutt., and of the probable manner in which fertilization is effected. Proc. Bos. Soc. Nat. Hist. 9: 182–185.

Senghas, K. 1973. Einige neve Namen in der Unterfamilie Orchidoideae. Die Orchidee 24: 97–98.

Seymour, F. C. 1970. Notes from the Pringle Herbarium III. Rhodora 72: 47–50.

Shelford, V. E. 1963. The Ecology of North America. Univ. of Ill. Press. Urbana, Illinois.

Sheviak, C. J., and P. M. Catling. 1980. The identity and status of *Spiranthes ochroleuca* (Rydberg) Rydberg. Rhodora 82: 525–562.

Schultes, R. E., and A. S. Pease. 1963. Generic Names of Orchids. Academic Press, New York.

Silen, F. 1906. Blombiologisk iakttagelser i sodra Finnland. Meddeland. Soc. Fauna Fl. Fenn. 32: 120–134.

Simpson, P. C., and P. M. Catling. 1978. *Spiranthes lacera* var. *lacera* × *S. romanzoffiana*, a new natural hybrid from Ontario. Canad. Field Naturalist 92: 350–358.

Smith, G. R., and G. E. Snow. 1976. Pollination ecology of *Platanthera* (*Habenaria*) *ciliaris* and *P. blephariglottis* (Orchidaceae). Bot. Gaz. 137: 133–140.

Smith, S. I. 1863. Notes on the fertilization of *Cypripedium spectabile* Swartz, and *Platanthera psychodes* Gray. Proc. Boston Soc. Nat. Hist. 9: 328–329.

Stafleu, F. A. 1967. Taxonomic Literature. Regnum Vegetabile 52: 1–566.

——— *et al.*, (eds.) 1978. International Code of Botanical Nomenclature. Regnum Vegetabile 97: 1–392.

Storks, I. M., and G. E. Crow. 1978. Rare and Endangered Vascular Plant Species in New Hampshire. New England Botanical Club in cooperation with the U.S. Fish and Wildlife Service [Newton Corners, MA.]

Stoutamire, W. P. 1964. Seeds and seedlings of native orchids. Michigan Bot. 3: 107–119.

———. 1967. Flower biology of the Lady's Slippers (Orchidaceae, *Cypripedium*). Michigan Bot. 6: 159–173.

———. 1968. Mosquito pollination of *Habenaria obtusata* (Orchidaceae). Michigan Bot. 7: 203–212.

———. 1971. Pollination in temperate American orchids. Proceedings of the 6th World Orchid Conference. pp. 233–243.

———. 1974. Relationships of the Purple-Fringed Orchids *Platanthera psycodes* and *P. grandiflora*. Brittonia 26: 42–58.

Stuckey, I. 1967. Environmental factors and the growth of native orchids. Amer. J. Bot. 54: 232–241.

Summerhayes, V. S. 1951. Wild Orchids of Britain. Collins, London.

Swamy, B. G. L. 1948. Agamospermy in *Spiranthes cernua*. Lloydia 2: 149–162.

Swartz, O. 1800. Nova Genera et Species Plantarum. 1783–1787. Stockholm.

Tanaka, R. and H. Kamento. 1975. List of chromosome numbers in species of the Orchidaceae. *In:* Withner, C. L. The Orchids - Scientific Studies. John Wiley and Sons, NY.

THEIN, L. B. 1969. Mosquito pollination of *Habenaria obtusata* (Orchidaceae). Amer. J. Bot. 56: 232–237.

———, AND I. UTECH. 1970. The mode of pollination in *Habenaria obtusata* (Orchidaceae). Amer. J. Bot. 57: 1031–1035.

———, AND B. G. MARKS. 1972. The floral biology of *Arethusa bulbosa, Calopogon tuberosus*, and *Pogonia ophioglossoides* (Orchidaceae). Canad. J. Bot. 50: 2319–2325.

THOMAS, M. B. 1893. The genus *Corallorhiza*. Bot. Gaz. 18: 166–170.

THOMPSON, Z. 1842. The History of Vermont. Chauncey Goodrich, pub. Burlington, VT.

THOREAU, H. D. 1884. Summer. (edited by H. G. O. Blake) Houghton Mifflin and Co., Cambridge, MA.

UPHAM, A. U. 1942. *Epipactis latifolia* in New Hampshire. Rhodora 44: 456–457.

VAN DER PIJL, L., AND C. H. DODSON. 1966. Orchid Flowers, their Pollination and Evolution. Univ. of Miami Press, Coral Gables, FL.

VERMEULEN, P. 1953. *Orchis spectabilis* L. Amer. Orchid Soc. Bull. 22: 437–440.

VOSS, E. G. 1966. Nomenclatural notes on monocots. Rhodora 68: 435–463.

WALLACE, J. E. 1951. The Orchids of Maine. Univ. Maine Bull. 53: 1–80.

WATERMAN, W. G. 1949. *Cypripedium reginae* Walt., the showy ladyslipper. Amer. Orchid Soc. Bull. 18: 90–97.

———. 1950. Habitats of *Cypripedium reginae* Walt., in north central Michigan. Amer. Orchid Soc. Bull. 19: 588–594.

WHERRY, E. T. 1918. The reactions of the soils supporting the growth of certain orchids. Jour. Wash. Acad. Sci. 8: 589–598.

———. 1927. The soil reactions of some saprophytic orchids. Jour. Wash. Acad. Sci. 17: 35–38.

WHIGHMAN, D. F., AND M. MCWETHY. 1980. Studies on the pollination ecology of *Tipularia discolor* (Orchidaceae). Amer. J. Bot. 67: 550–555.

WHITE, M. W. 1904. *In:* Niles, G. G. Bog Trotting for Orchids. Scribner, New York.

WILLDENOW, C. L. 1804. Hortus Berolinensis. Berlin.

———. 1805. Caroli a Linne Species Plantarum. Vol 4, part 1. Berlin.

ZENKERT, C. A. 1950. The story of an immigrant Orchid. Amer. Orchid Soc. Bull. 19: 316–318.

ZINN, G. 1757. Catalogus Plantarum Horti Academici et Agri Gottingensis. Gottingen.

THE NATURE CONSERVANCY
NEW HAMPSHIRE NATURAL HERITAGE PROGRAM
54 PORTSMOUTH STREET
CONCORD, N.H. 03301

AN AWARD FOR THE SUPPORT OF BOTANICAL RESEARCH IN NEW ENGLAND, U.S.A.

The New England Botanical Club is offering an award of $1,000 in support of botanical research to be conducted in the New England region during 1985. It is being made to stimulate and encourage botanical research on the New England flora and to make possible visits to the New England region by those who would not otherwise be able to do so. The award will be given to the graduate student submitting the best research proposals dealing with field studies in systematic botany and plant ecology, but proposals for research in other areas of botany will also be considered. This award is not limited to graduate students at New England institutions. The NEBC's support must be acknowledged in any publications resulting from this study. It is encouraged that papers based on this research be submitted to RHODORA, the Club's journal, for possible publication—subject to standard review processes. The New England Botanical Club hopes to be able to make this award on an annual basis.

Applicants should submit a proposal of no more than three double spaced pages, including a budget (the budget will not affect the amount of the award), and their *Curriculum Vitae.* Two letters, one from the student's major professor, in support of the proposed research are also required. Proposals and supporting letters should be sent before 28 February 1985 to: Awards Committee, The New England Botanical Club, 22 Divinity Avenue, Cambridge, MA 02138. The recipient of the award will be notified by 30 April 1985.

ASPT HERBARIUM TRAVEL AWARDS

The American Society of Plant Taxonomists is pleased to announce the availability of competitive awards for travel by graduate students to the nation's herbaria. The awards will not exceed $500 and will be used to help pay expenses to and from any herbarium (or herbaria) in the United States and per diem expenses during the visit. Competitions for awards will be held twice a year: The first competition deadline is 1 January 1985, with the second deadline 1 July 1985. The grants program will last a minimum of three years (six competitions). Interested Master's or Ph.D. graduate students should send a curriculum vitae, two letters of recommendation (including one from the major professor), a two or three page outline of the proposed research emphasizing the role that the visit to the herbarium will play, and a letter from the Head Curator, Chairman or Director of the institution(s) to be visited indicating willingness to receive the visitor. Awards will be announced by 1 March from the January competition and during the annual banquet of the ASPT from the July competition. Students are encouraged to obtain additional funds from their home institutions (or elsewhere) to extend their research visits even further. This competition is open to students of both cryptogamic and phanerogamic groups. Completed applications and additional questions should be directed to Tod F. Stuessy, Chairman, ASPT Committee for Systematics Collections, Department of Botany, Ohio State University, 1735 Neil Avenue, Columbus, OH 43210. Phone: (614) 422-5200 or (614) 422-8952.

Vol 86, No. 848, including pages 397–554, was issued December 20, 1984

INSTRUCTIONS TO CONTRIBUTORS TO RHODORA

Submission of a manuscript implies it is not being considered for publication simultaneously elsewhere, either in whole or in part.

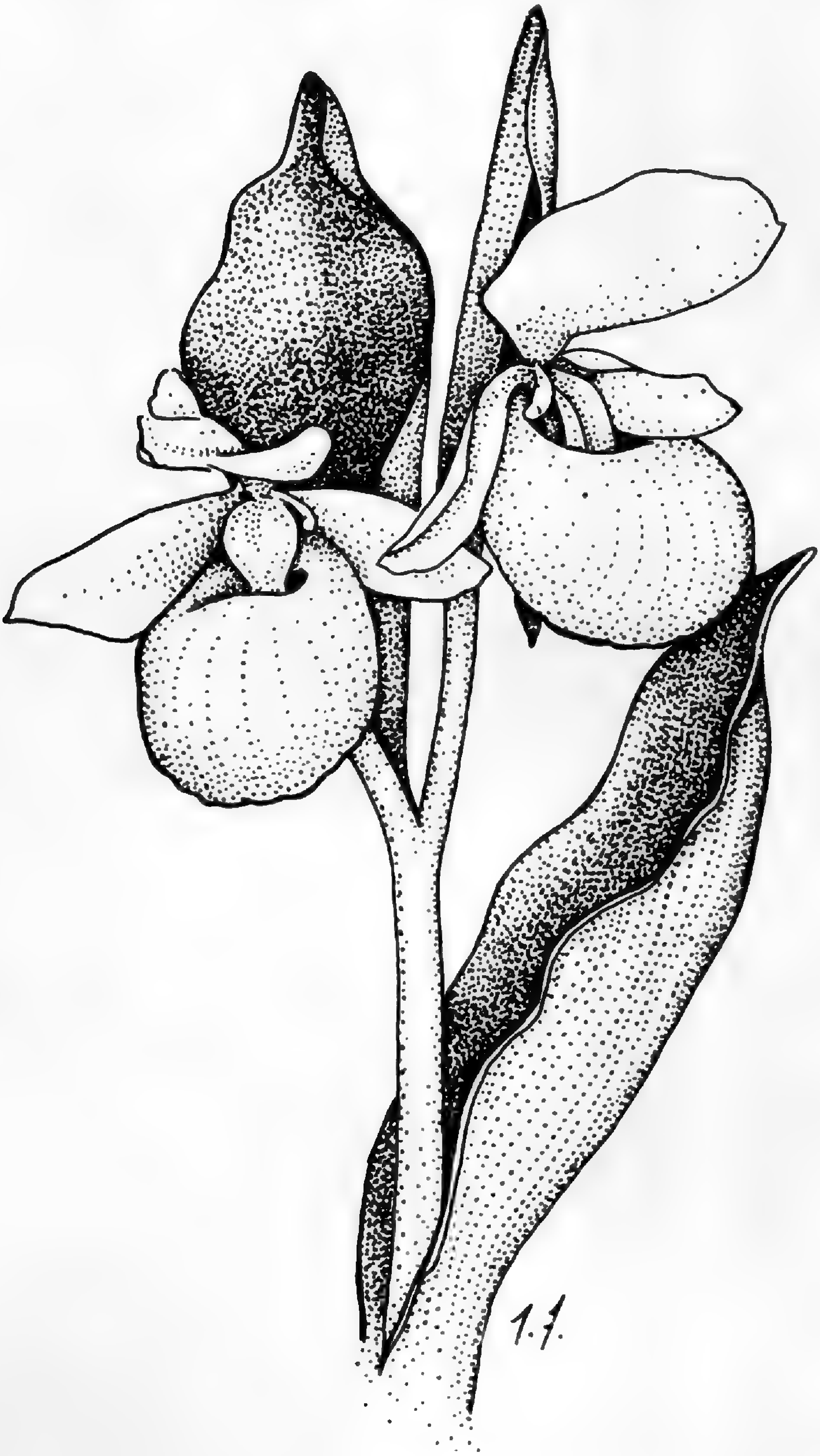
Manuscripts should be submitted in **triplicate** (an original and two xerox copies) and *must be double-spaced* (at least 3/8 of an inch) **throughout** including footnotes, figure legends, and references. Please do not use corrasable bond. The list of legends for figures and maps should be provided on a separate page. Footnotes should be used sparingly. Do not indicate the style of type through the use of capitals or underscoring, particularly in the citation of specimens. Names of genera and species may be underlined to indicate italics in discussions. Specimens citations should be selected critically, especially for common species of broad distributions. Systematic revisions and similar papers should be prepared in the format of "A Monograph of the Genus Malvastrum", S. R. Hill, Rhodora 84: 1–83, 159–264, 317–409, 1982, particularly with reference to indentation of keys and synonyms. Designation of a new taxon should carry a **Latin diagnosis** (rather than a full Latin description), which sets forth succinctly just how the new taxon is distinguished from its congeners. Papers of a floristic nature should follow, as far as possible, the format of "Annotated list of the ferns and fern allies of Arkansas", W. Carl Taylor and Delzie Demaree, Rhodora 81: 503–548, 1979. For bibliographic citations, refer to the Botanico-Periodicum-Huntianum (B-P-H, 1968), which provides standardized abbreviations for journals originating before 1966. All abbreviations in the text should be followed by a period, except those for standard units of measure and direction (compass points). For standard abbreviations and for guidance in other matters of biological writing style, consult the *CBE Style Manual,* 5th ed. (original title: *Style Manual for Biological Journals*). In preparing figures (maps, charts, drawings, photos, etc.) please remember that the printed plate will be 4 × 6 inches; be sure that your illustrations are proportioned to reduce correctly, and indicate by blue pencil the intended limits of the figures. (Some "turn-page" figures with brief legends will be 3 1/2 × 6 in.) Magnification/reduction values given in text or figure legends should be calculated to reflect the actual printed size. An Abstract and a list of Key Words should be supplied at the beginning of each paper submitted, except for a very short article or note.

RHODORA **January 1985** **Vol. 87, No. 849**

CONTENTS

Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB



Vol. 87 April 1985 No. 850

The New England Botanical Club, Inc.

Botanical Museum, Oxford Street, Cambridge, Massachusetts 02138

RHODORA.—Published four times a year, in January, April, July, and October. A quarterly journal of botany, devoted primarily to the flora of North America. Price $20.00 per year, net, postpaid, in funds payable at par in the United States currency at Boston. Some back volumes and single copies are available. Information and prices will be furnished upon request. Subscriptions and orders for back issues (making all remittances payable to RHODORA) should be sent to RHODORA, Botanical Museum, Oxford Street, Cambridge, Mass. 02138. In order to receive the next number of RHODORA, changes of address must be received prior to the first day of January, April, July or October.

Scientific papers and notes relating to the plants of North America and floristically related areas will be considered by the editorial committee for publication. Articles concerned with systematic botany and cytotaxonomy in their broader implications are equally acceptable. Brevity is urged whenever possible in all papers. Short items will be published on otherwise blank end pages as soon as possible, even if they appear ahead of longer articles already accepted. All manuscripts should be submitted in TRIPLICATE AND MUST BE DOUBLE (AT LEAST 3/8 OF AN INCH) OR TRIPLE-SPACED THROUGHOUT. **Please conform to the style of recent issues of the journal. See "Instructions to Contributors to RHODORA" at the end of each issue. Extracted reprints, if ordered in advance, will be furnished at cost. RHODORA assesses modest page charges.**

Address manuscripts and proofs to:
Joan Y. Nickerson
Managing Editor, RHODORA
Phippen-LaCroix Herbarium, Dept. of Biology
Tufts University
Medford, Mass. 02155

Second Class Postage Paid at Boston, Mass.

PRINTED BY
THE LEXINGTON PRESS, INC.
LEXINGTON, MASSACHUSETTS

Cover illustration

Cypripedium reginae Walt., the Showy Lady's-slipper, was presumed until recently to be extirpated from New Hampshire; five sites for this exquisite orchid are now known.

Original artwork by Tess Feltes, Illustrator.

Rhodora
(ISSN 0035 4902)
JOURNAL OF THE
NEW ENGLAND BOTANICAL CLUB

Vol. 87 April 1985 No. 850

SYSTEMATICS OF *TALINUM PARVIFLORUM* NUTT. AND THE ORIGIN OF *T. TERETIFOLIUM* PURSH (PORTULACACEAE)

M. Eloise Brown Carter and William H. Murdy

ABSTRACT

Talinum appalachianum Wolf, known from only one station in Alabama, is not distinct from *T. parviflorum* Nutt. Plants of *T. parviflorum* were sampled from Texas, Arkansas and Kansas and were compared with *T. appalachianum*. Plants of the four populations had the same chromosome number ($2n = 24$), very late diurnal anthesis, and were predominantly self-pollinating. Population means for four floral traits overlapped: petal length, number of stamens, style length and number of ovules. *Talinum teretifolium* Pursh appears to be an allotetraploid derivative of *T. mengesii* Wolf and *T. parviflorum*. Crosses between the latter two species produced sterile hybrids similar to *T. teretifolium* in floral morphology and pattern of diurnal anthesis. Fertile polyploid flowers, which developed after colchicine treatment, produced fertile offspring when crossed to *T. teretifolium*, selfed or sibbed.

Key Words: *Talinum*, allopolyploidy, hybridization, rock outcrop, southeastern U.S.

INTRODUCTION

Talinum (Portulacaceae) has approximately 50 species distributed in Africa, Asia and North and South America. Wilson (1932) described 31 species from North America. Eight species of *Talinum* have been reported for the southeastern United States (Bogle, 1969). *Talinum paniculatum* (Jacq.) Gaertn. and *T. triangulare* (Jacq.) Willd. are flat-leaved, horticultural escapes with worldwide distributions. Six species have terete leaves and inhabit shallow soils of rock outcrops. *Talinum parviflorum* Nutt., $2n = 48$ (Steiner, 1944) and $2n = 24$ (Hornberger & Smith, pers. comm.), and *T. calycinum* Engelm., $2n = 24$ (Steiner, 1944), range widely west of the Mississippi River with a few populations in southern Illinois (Mohlenbrock, 1975). Distribution ranges for the remaining four species are wholly east of the Mississippi River: *T. teretifolium* Pursh, $2n = 48$ (Steiner, 1944; Murdy, 1968; Murdy, Johnson, & Wright, 1970), occurs on granite, sandstone and serpentine from Georgia to Pennsylvania; *T. mengesii* Wolf, $2n = 24, 48$ (Steiner 1944; Murdy et al., 1970), occurs on sandstone and granite in Georgia, Alabama, and Tennessee; *T. appalachianum* Wolf, $2n = 24$ (Steiner, 1944), consists of a few populations within a one-mile radius on gneiss in central Alabama, and *T. calcaricum* Ware, $2n = 48$ (Krebs, 1971, Master's thesis, Emory Univ., GA), is restricted to limestone in central Tennessee and northwestern Alabama (Figure 1).

The six terete-leaved species have short stems bearing numerous succulent leaves and produce flowers on long, slender, cymosely-branched scapes. All produce ephemeral flowers which open in the afternoon between 1200 hours and 1800 hours EDT and close by 2000 hours EDT. The species are distinguished primarily by floral characteristics including length of petals, number of stamens, length of style relative to stamens, petal color, persistence of sepals, and seed color (Ware, 1967; Bogle, 1969; Black & Murdy, 1972).

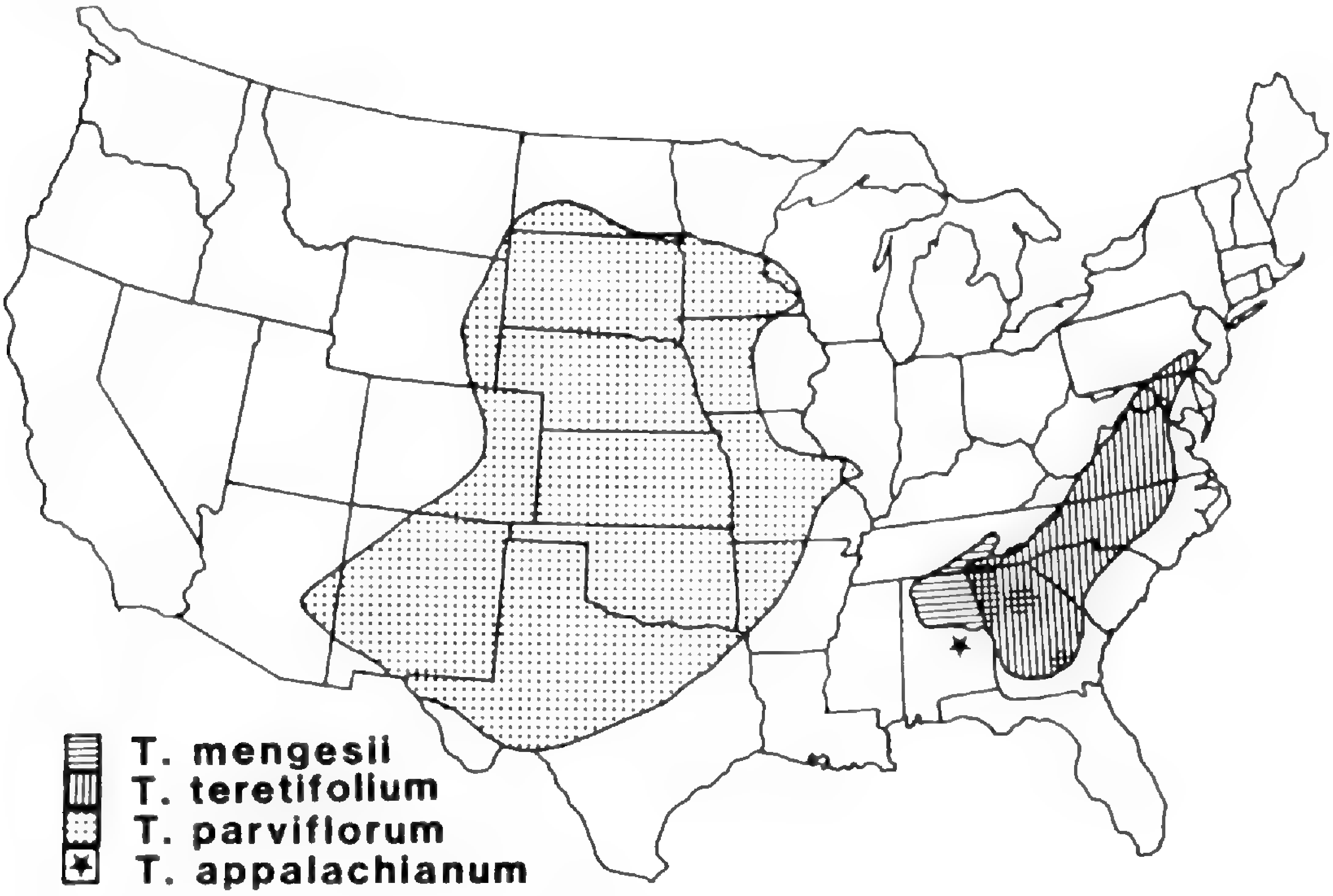


Figure 1. Distribution of *Talinum appalachianum*, *T. parviflorum*, *T. mengesii*, and *T. teretifolium*.

The research reported in this paper tested two hypotheses: 1) *Talinum appalachianum* is not a species distinct from *T. parviflorum* and 2) *T. teretifolium* is an allopolyploid derivative of *T. mengesii* and *T. parviflorum*.

In 1937, R. M. Harper discovered an isolated population of *Talinum* on rocks in central Alabama. Wolf (1939) noted a resemblance to *T. parviflorum* but named it *T. appalachianum*. The species, *T. appalachianum*, was not challenged by later investigators (Steiner, 1944; Bogle, 1969; Black & Murdy, 1972) in part because the nearest reported population of *T. parviflorum* occurred hundreds of miles west of this isolated population, and because Steiner (1944) had reported a chromosome number of $2n = 48$ for a population of *T. parviflorum* in Arkansas and $2n = 24$ for *T. appalachianum*. The species were thought to be at different ploidal levels until Hornberger and Smith (pers. comm.) reported $2n = 24$ for a *T. parviflorum* population from Washington County, Arkansas.

Based on the evidence from comparative morphology, distribution patterns and chromosome numbers, Murdy (1968) suggested that *Talinum teretifolium* was an allotetraploid and that *T. mengesii* had been one of its ancestral parents. Cytological analysis of interploidal hybrids between the two species supported the hypothesis, and the use of Anderson's method of extrapolated correlates (Anderson, 1949) suggested that a diploid species similar to *T. appalachianum* could have been the other ancestral parent (Black & Murdy, 1972).

MATERIALS AND METHODS

Talinum mengesii populations (1E5) were collected from one county in Alabama and four counties in eastern to central Georgia. *Talinum parviflorum* populations (6E8) were collected from single sites west of the Mississippi River in Arkansas, Kansas and Texas, and one population of *T. appalachianum* (9) was sampled from its only known station in Alabama. *Talinum teretifolium* populations (10E14) were sampled from five counties across Georgia. Locations for each population are given in Table 1.

Fourteen to twenty individuals were sampled in the field either from seed or rhizome. To minimize selection of the same genotype and yet provide a representative sample, one individual or capsule was collected per patch of plants. A patch was defined as a group of

Table 1. Sample site locations for populations of *Talinum*

Population Number	Location
T. mengesii	
1	Blake's Ferry, Randolph County, Alabama
2	Highway 34, Franklin, Heard County, Georgia
3	Powers Ferry Crossing, Coweeta County, Georgia
4	Costley Bridge Road, Rockdale County, Georgia
5	Highway 138, Walton County, Georgia
T. parviflorum	
6	Devil's Den State Park, Washington County, Arkansas
7	Sedan, Chautauqua County, Kansas
8	Inks Lake State Park, Burnet County, Texas
T. appalachianum	
9	Highway 22 and Coosa River, Coosa County, Alabama
T. teretifolium	
10	Carl, Barrow County, Georgia
11	Pendergrass, Jackson County, Georgia
12	Echols Mill, Oglethorpe County, Georgia
13	North High Shoals, Oconee County, Georgia
14	Kent Rock Road, Walton County, Georgia

plants separated from the next group by at least one meter. Plants subsequently grown from seed or transplants were potted in a mixture of granite outcrop soil, sand and peat (1:1:1) and were maintained in the greenhouse. One flower from each plant was collected and preserved in FAA for measurement of floral characters. Lengths of petals, pistils and styles were measured to the nearest 0.5 mm; number of stamens and number of ovules per ovary were recorded for each flower. Vouchers were deposited at GEO.

Chromosome counts were determined for three populations of *Talinum parviflorum* and one population of *T. appalachianum*. Plants were stripped of roots, and the rhizomes were placed in moist paper toweling. New roots that developed within 4 days were excised from the rhizome, placed in a 0.2% colchicine solution for 3 hours, and then transferred to Carnoy's fixative (3 absolute alcohol : 1 acetic acid) where they remained for at least 24 hours. Fixed root tips were hydrolyzed in 1 N HCl and acetocarmine squash preparations were made. Chromosomes were counted for a minimum of three plants to establish the chromosome number for a particular population.

Plants were destaminated in bud and subsequently hand pollinated in an isolation chamber. Mature seeds were collected and placed in dry storage for 5 weeks, refrigerated at 4OC in a moist petri-dish for a minimum of 6 weeks and germinated in sterilized granite outcrop soil amended with sand (1:1). Forty-nine crosses were made using 13 different *Talinum appalachianum* plants as female parents and pollen from several *T. parviflorum* individuals. Seeds from these crosses were pretreated and germinated. The resulting plants were grown to maturity and allowed to self-pollinate.

Crosses (107) were attempted using 17 different female parents of *Talinum appalachianum* and a mixture of pollen from several *T. mengesii* individuals. Seeds from these crosses were pretreated, germinated and grown to maturity in the greenhouse. Colchicine (1% in lanolin) was used to induce polyploidy in 15 of the sterile, interspecific hybrids. The branches that developed from treated nodes bore fertile flowers and were, therefore, assumed to be polyploid. Crosses were made between these flowers and those of the tetraploid, *Talinum teretifolium*. Five flowers from each hybrid plant were collected and preserved in FAA for floral character analysis. Pollen fertility was determined by staining the pollen with iodine and dividing the number of normal sized, starch-filled grains by the total number. Fruit set (percent of pollinations resulting in capsules) was determined from self and sib crosses of fertile flowers. Seed set (number of mature seeds per capsule) was recorded for successful crosses. Branches from hybrid plants are deposited at GEO.

RESULTS

One population of *Talinum appalachianum* from Alabama and three populations of *T. parviflorum* from Arkansas, Texas and Kansas had chromosome counts of $2n = 24$. The four populations could not be distinguished on the basis of vegetative habit and they were similar in floral morphology. *Talinum appalachianum* had slightly larger petals than *T. parviflorum*, but population means overlapped for number of stamens, style length and number of ovules (Table 2). In all four populations, anthesis occurred very late in the day between 1630 and 1800 hours EDT, and the flowers were self-pollinating at flower closure around 2000 hours EDT.

Table 2. Floral traits for *Talinum* populations[p]

Population	No. Plants	Petal Length	No. Stamens	Style Length	No. Ovules
T. mengesii					
1	20	8.48 (0.53)	52.30 (9.15)	4.04 (0.30)	35.05 (5.92)
2	20	8.96 (0.68)	61.55 (9.11)	4.64 (0.49)	35.80 (8.69)
3	20	8.61 (0.45)	60.20 (7.52)	4.23 (0.42)	39.90 (6.03)
4	20	10.78 (0.73)	67.35 (6.98)	6.20 (0.35)	46.75 (8.27)
5	20	10.00 (0.61)	71.20 (7.49)	5.81 (0.44)	59.50 (5.40)
Species Mean		9.37 (0.99)	62.52 (7.24)	4.98 (0.97)	43.40 (10.13)
T. parviflorum					
6	16	4.70 (0.49)	6.69 (1.57)	1.08 (0.19)	20.38 (5.69)
7	11	4.82 (0.48)	7.09 (1.88)	1.27 (0.23)	28.27 (6.88)
8	15	3.97 (0.31)	4.87 (0.34)	0.68 (0.17)	23.95 (3.40)
T. appalachianum					
9	18	5.17 (0.42)	5.72 (0.87)	1.12 (0.17)	24.78 (3.92)
Species Mean		4.66 (0.50)	6.09 (1.00)	1.04 (0.25)	24.35 (3.24)
T. teretifolium					
10	20	7.08 (0.59)	17.40 (3.44)	2.56 (0.26)	37.65 (5.67)
11	20	6.88 (0.65)	20.95 (4.74)	2.96 (0.19)	48.75 (6.16)
12	20	6.46 (0.53)	18.20 (2.86)	2.66 (0.23)	38.75 (6.10)
13	20	6.10 (0.45)	15.90 (1.21)	2.83 (0.23)	31.50 (4.16)
14	20	6.73 (0.44)	17.30 (2.81)	2.76 (0.21)	41.65 (6.28)
Species Mean		6.65 (0.38)	17.95 (1.87)	2.75 (0.15)	39.66 (6.29)
T. appalachianum × *T. mengesii* (synthetic hybrid)					
15	7	8.67 (0.29)	25.80 (2.42)	3.14 (0.14)	48.23 (1.77)
16	8	8.49 (0.21)	24.45 (3.02)	2.97 (0.28)	47.13 (7.82)

[p] Population means with standard deviations in parentheses.

Crosses between *Talinum appalachianum* and *T. parviflorum* resulted in 55% fruit set with mean seed set of 22.7 seeds per capsule (n = 49) as compared to 23.1 seeds per capsule from intrapopulation control pollinations of *T. appalachianum* (n = 10). Ten hybrid plants from crosses of *T. appalachianum* with *T. parviflorum*, Texas, and eight hybrid plants from crosses of *T. appalachianum* with *T. parviflorum*, Arkansas, were grown to maturity. All hybrid plants bore fertile flowers which ranged in pollen fertility from 68% to 85%, and which self-pollinated to produce fruit with mean seed set of 9 seeds per capsule. Ten *T. parviflorum* plants grown under the same environmental regime had 77% to 92% pollen fertility and produced fruit with an average of 11.0 seeds per capsule. Hybrids resulting from crosses with *T. parviflorum*, Kansas, did not flower during the first growing season.

An attempt to reconstruct the origin of the tetraploid species, *Talinum teretifolium*, using its presumed progenitors, *T. mengesii* and *T. appalachianum* (to be referred to hereafter as *T. parviflorum*, Alabama), was initiated in 1981. Only 6.5% of the 107 crosses attempted between *T. mengesii* and *T. parviflorum*, Alabama, resulted in fertile capsules with a mean of 4.5 seeds per capsule. Germination was attempted with 17 seeds; 15 germinated and survived. All 15 hybrid plants which were grown to maturity in the greenhouse were sterile; mean pollen fertility was less than 15% and fruit set was zero. Floral morphology and time of diurnal flower opening for the hybrids fell within the range of variability for *T. teretifolium*. They had a higher value for petal length, stamen number, style length and ovule number than most populations of *T. teretifolium* (Table 2, Figure 2). However, the *T. mengesii* plants used to make the crosses had high values for these quantitative traits (Table 2, Figure 2).

The 15 sterile F_1 hybrids were treated with colchicine. Nine of these produced a total of 15 branches with fertile flowers. Flowers from these branches had mean pollen fertility of 94.9% ($n = 24$), and produced mean fruit set of 50% ($n = 40$) when used in self and sib crosses.

Crosses between fertile flowers of the colchicine-treated F_1 hybrids and those of *Talinum teretifolium* plants yielded fertile progeny. Ten offspring from these crosses had a mean of 80% pollen fertility and produced an average of 31.2 (s.d., ± 7.5) seeds per capsule. Ten open-pollinated *T. teretifolium* plants had a mean of 85% pollen fertility and produced an average of 32.7 (s.d., ± 10.8) seeds per capsule.

DISCUSSION

The discovery that *Talinum parviflorum* and *T. appalachianum* are at the same ploidal level eliminated the major obstacle to considering these one species. The report of $2n = 48$ by Steiner (1944) for a single population of *T. parviflorum* from Springdale, Arkansas, may be a case of autopolyploidy. In addition to having the same chromosome number, *T. appalachianum* and *T. parviflorum* are

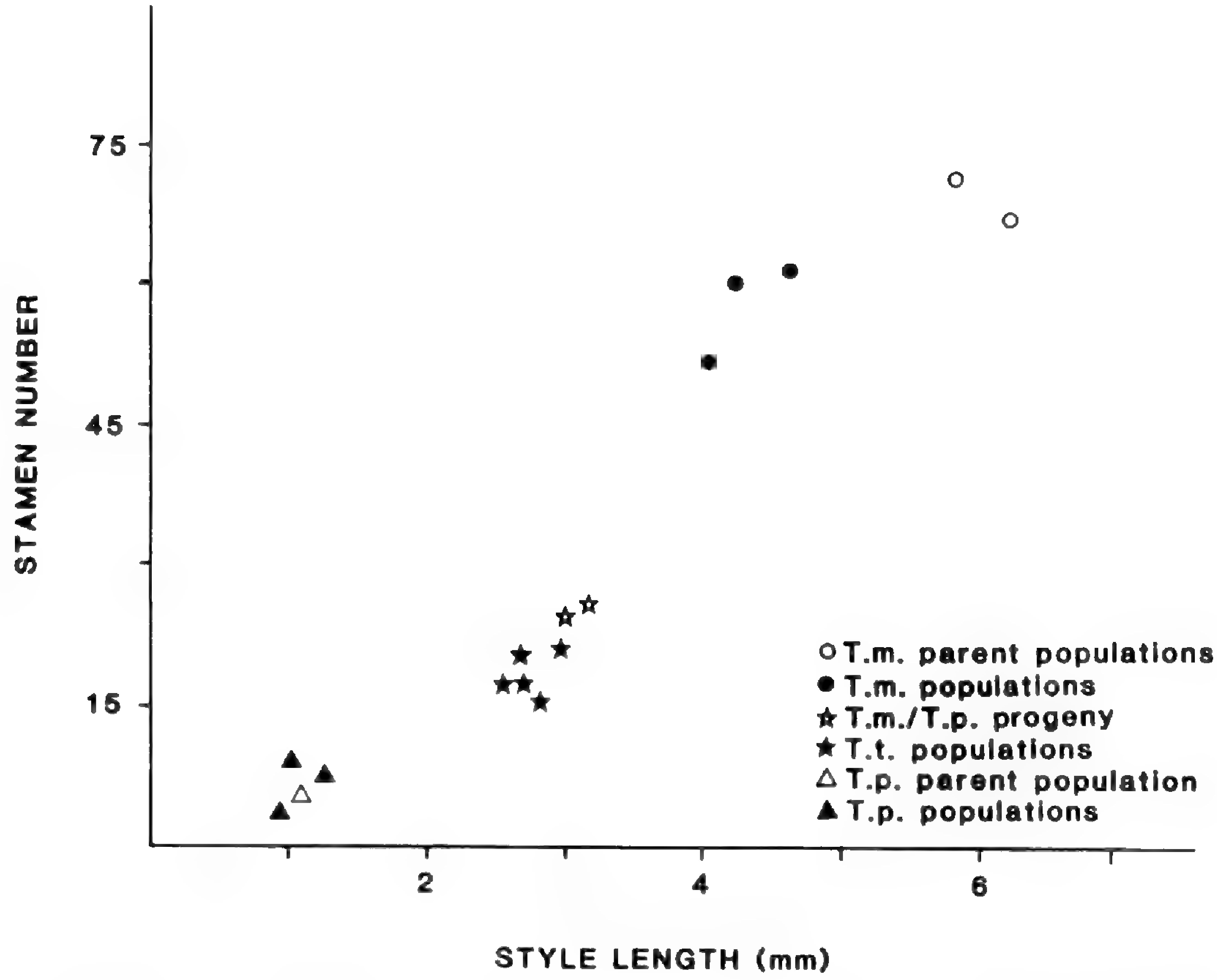


Figure 2. Comparison of synthetic hybrids (open stars) and *T. teretifolium* (solid stars) for two floral characters which are intermediate between the putative parent species, *T. mengesii* (circles) and *T. parviflorum* (triangles). Two *T. mengesii* populations (open circles) and one *T. parviflorum* population (open triangle) were used in the interspecific crosses. All symbols denote population means.

similar in habit, floral morphology, time of diurnal anthesis and breeding system. Furthermore, fertile hybrids resulted from crosses between the two taxa. These data support the hypothesis that the population which Wolf (1939) named *T. appalachianum* should be recognized as *T. parviflorum*.

Talinum appalachianum is currently listed in the Federal Register (U.S.D.I., 1983) as a proposed endangered species, but one in need of further biological research and field study. The evidence presented in this paper that *T. appalachianum* is not a distinct species should assist the Interior Department in deciding if this species is to be included in the permanent Endangered Species list and protected by law.

In attempting to reconstruct the evolutionary origin of an allotetraploid, the first consideration was the choice of diploid species to be used as the presumed ancestors. *Talinum mengesii* was chosen as one of the putative parents because a study of meiotic chromosome pairing in triploid and tetraploid hybrids between *T. teretifolium* ($2n$ = 48) and *T. mengesii* ($2n$ = 24, and $2n$ = 48) revealed that one-half of the chromosome complement of the tetraploid *T. teretifolium* was homologous with the entire chromosome complement of *T. mengesii* (Black & Murdy, 1972). Since interspecific hybrids between *Talinum* species are intermediate for all major traits that separate species (Murdy, et al., 1970; Krebs, 1971), the only species which could satisfy the extrapolated requirements for the other diploid ancestor was *T. parviflorum* (*T. appalachianum*, Alabama) which has small floral structures, few stamens and late anthesis. *Talinum calcaricum* was eliminated as a possibility because it is a tetraploid species. *Talinum calycinum* was eliminated from consideration because its range is far removed from that of *T. teretifolium* (Figure 1), and it has red flowers (Bogle, 1969) and sepals persistent in fruit (Wilson, 1932). *Talinum teretifolium, T. parviflorum* and *T. mengesii* have pink flowers and deciduous sepals.

It could be argued that the morphological similarity between the synthetic allopolyploid and *Talinum teretifolium* has more to do with the choice of parents than it does with genetic relatedness. However, the fact that crosses between the synthetic allotetraploid flowers and *T. teretifolium* produced fertile offspring is evidence that the genomes of the two entities are at the same ploidal level and are compatible. Fertile hybrids do not necessarily result when crosses are made between *Talinum* species at the same ploidal level. For example, only sterile hybrids were produced in crosses at the diploid level between *T. mengesii* and *T. parviflorum*. Sterile hybrids also were produced from interspecific crosses at the tetraploid level between *T. teretifolium* and *T. calcaricum* (Krebs, 1971, Master's thesis, Emory Univ., GA) and between *T. teretifolium* and an autopolyploid *T. mengesii* (Black & Murdy, 1972).

Talinum parviflorum populations in Alabama are separated from their nearest conspecific populations in Arkansas by hundreds of miles essentially devoid of rock outcrops. Do these Alabama populations represent a recent colonization from the west or the last remnant of a once more extensive distribution east of the Mississippi River? Evidence presented in this paper that *T. parviflorum* was one of the progenitors of *T. teretifolium*, which does not occur west of Georgia, supports the latter. Perhaps the demise of *T. parvi-*

florum in the east is related to the spread of its allotetraploid derivative, *T. teretifolium*.

CONCLUSION

Several lines of evidence support the conclusion that *Talinum appalachianum* is not a distinct species, but instead is conspecific with *T. parviflorum*. Artificial hybridization between *T. mengesii* and *T. parviflorum* produced sterile plants similar in all outward appearances to the alleged allotetraploid, *T. teretifolium*. Chromosome doubling produced fertile tetraploid flowers which, when crossed with *T. teretifolium*, produced fertile offspring. This result is evidence that the synthetic and natural allopolyploids have compatible genomes and supports the hypothesis that *T. teretifolium* originated as an allopolyploid derivative of *T. mengesii* and *T. parviflorum*.

LITERATURE CITED

Anderson, E. 1949. Introgressive Hybridization. John Wiley and Sons, New York.

Black, C. B., and W. H. Murdy. 1972. The evolutionary origin of *Talinum teretifolium*. Bot. Gaz. 133: 405E410.

Bogle, A. L. 1969. The genera of *Portulacaeae* and *Basellaceae* in the southeastern United States. J. Arnold Arb. 50: 566E598.

Mohlenbrock, R. H. 1975. Guide to the Vascular Flora of Illinois. Southern Illinois Univ. Press, Carbondale.

Murdy, W. H. 1968. Plant speciation associated with granite outcrop communities of the southeastern Piedmont. Rhodora 70: 394E407.

———, T. M. Johnson, and V. K. Wright. 1970. Competitive replacement of *Talinum mengesii* by *T. teretifolium* in granite outcrop communities of Georgia, U.S.A. Bot. Gaz. 131: 186E192.

Steiner, E. 1944. Cytogenetic studies on *Talinum* and *Portulaca*. Bot. Gaz. 105: 374E379.

U.S. Department of the Interior. 1983. Endangered and threatened wildlife and plants; supplement to review of plant taxa for listing as endangered or threatened species. Federal Register 48: 53640E53670.

Ware, S. 1967. A new *Talinum* (Portulacaceae) from the cedar glades of middle Tennessee. Rhodora 69: 466E475.

Wilson, P. 1932. *Talinum*. North American Flora 21: 280E289.

Wolf, W. 1939. The status of *Talinum* in Alabama. Amer. Midland Nat. 22: 315E332.

DEPARTMENT OF BIOLOGY
EMORY UNIVERSITY
ATLANTA, GA 30322

PANAX QUINQUEFOLIUM (ARALIACEAE) IN SOUTHEASTERN OKLAHOMA

WALTER H. LEWIS AND GARY A. THOMPSON

In the western ridges of the Ouachita Mountains a number of interesting range extensions of more northeastern vegetation are occasionally found. An example of such a find is *Panax quinquefolium* L. (American ginseng), a species rare in hilly, deciduous woods of two Oklahoma counties, Leflore and McCurtain. The following collections represent the most southwestern distribution of the species.

OKLAHOMA: Leflore Co.: 5 miles S of Big Cedar, 7 Oct 1973, *Bradley 283* (DUR, NLU, VDB); Page, 9 Sep 1913, *Stevens 2757* (NY); Rich Mt., ca. 7 miles from jct. US1 and US259, 25 Sep 1979, *Taylor 28244* (DUR, VDB); Rich Mt., 8.5 miles W of Arkansas-Oklahoma state line on Hwy. 1, 2 Aug 1984, *Lewis & Thompson 9805* (DUR, MO, OKL). McCurtain Co.: 8.4 miles NE of Smithsville, 11 Oct 1981, *Magrath 12349* (OCLA).

W. H. L.
DEPARTMENT OF BIOLOGY
WASHINGTON UNIVERSITY
ST. LOUIS, MO 63130

G. A. T.
DEPARTMENT OF HORTICULTURE
UNIVERSITY OF WISCONSIN
MADISON, WI 53706

IN MEMORIAM

Dr. James P. Poole, a member of the New England Botanical Club since 1945, died December 11, 1984, in Hanover, New Hampshire at the age of 95. A professor emeritus of botany at Dartmouth College, he had taught there for 35 years. He continued to serve after retirement in 1957 as the curator of the Jesup Herbarium. Born in Gloucester, Mass., he earned his BS in forestry from the University of Maine in 1912, his master's degree in 1918 and his doctorate in Botany in 1921 from Harvard University. Dr. Poole was recently voted by the Council to be an Honorary Member of the Club. He had written to the Club indicating that he could no longer read *Rhodora*, and because of that fact, felt he should be deleted from our rolls. The Council's action naming him an Honorary Member, to receive *Rhodora* for life, occurred less than a month before his death.

REDISCOVERY OF *MALAXIS PALUDOSA* (L.) SW. (ORCHIDACEAE) IN MINNESOTA

Timothy Reeves and Linda Reeves

ABSTRACT

The first documented field observation of *Malaxis paludosa* in Minnesota since 1938 is reported. Herbarium specimens confirm the occurrence of the species in five counties in the state; three represent newly published records. The species occurs in Alaska, Canada and Eurasia. Description of the habitat and list of associated species is provided. One site is reported where *M. paludosa* grows sympatrically with its congeners *M. unifolia* and *M. monophyllos*.

Key Words: Orchidaceae, *Malaxis paludosa*, bogs, Minnesota

Malaxis paludosa (L.) Sw. is a circumboreal orchid known in the continental United States only in Minnesota (Correll, 1950; Fernald, 1950; Gleason & Cronquist, 1963; Case, 1964; Luer, 1975; Petrie, 1981; Marquis & Voss, 1981). A survey of the literature and herbarium specimens (F, MICH, MIL, MIN, MSC, SDC, UWM, WIN, and WIS) revealed no Minnesota collections since 1938. The fact that two recent comprehensive photographic guides to North American Orchids (Luer, 1975; Petrie, 1981) have photographs of the species taken in Alaska and/or Canada, suggests that the Minnesota populations are infrequently seen. Our examination of specimens and field explorations since 1981 have added to the known distribution of the species in Minnesota. Other recently located sites found by Minnesota Department of Natural Resources personnel are also reported.

This inconspicuous orchid is known from scattered localities in Eurasia and North America. In Canada the species is known from British Columbia, Alberta, and Ontario. An excellent account of the Canadian localities is given by Baldwin (1961). We are aware of previously unreported collections from Manitoba (N of Gilbert Plains, 9 Aug 1970 and 18 Aug 1971, *Parker s.n.*, WIN, G. M. Keleher, pers. comm.).

The United States collections are from Alaska and Minnesota. The Alaska localities are listed by Baldwin (1961). Previous collections in Minnesota have come from the following counties: Otter Tail Co., Jul 1904, *Lyon s.n.* (MIN!); Clearwater Co., *Brayton 3165*

(MIN!), *Grant 3155* (MIN!, NY!), *Moyle 1266* (MIN!), *Rosendahl 352* (US!), *Rosendahl 4837, 5930, 5941* (MIN!); Hubbard Co., 11 Jul 1934, *Moyle s.n.* (MIN!), 29 Aug 1934, *Rosendahl 6957* (MIN!) [These Hubbard Co. locations are labelled "Clearwater Co." but cited localities are in Hubbard Co. Paul Rundell (pers. comm.) reported that the species was seen in the area in the 1970's.]; Becker Co., 11 Jul 1934, *Moyle 1450* (F!). This report is apparently the first published one of the Hubbard and Becker Co. collections. The species was reported from Itasca County by Correll (1950) but we cannot locate substantiating specimens.

On July 26, 1981, we located a population of *Malaxis paludosa* in Beltrami County, Minnesota (*T. & L. Reeves 7336* with A. Schmierer, MIN, NY, GH). This is the fifth county in which the species has been documented in the state. This site (which will not be identified precisely to protect the plants) is in a boggy conifer swamp. The dominant trees are *Picea mariana* (Mill.) BSP., *Abies balsamea* (L.) Mill., and *Larix laricina* (DuRoi) K. Koch. Common shrubs are *Alnus rugosa* (DuRoi) Spreng. and *Ledum groenlandicum* Oeder. *Betula pumila* L. occurs in the area.

Malaxis paludosa usually grows in semi-shaded sites which receive some sunlight during part of the day. The orchid flowers from late June to early August; fruiting plants persist into September. The orchid typically occurs on a mossy hummock, 15–30 cm above the water level in adjacent wet depressions. Plants have been found at the base of black spruce, balsam fir, and alder as well as on hummocks not near a trunk. *Sphagnum* carpets the forest floor but the plants of *M. paludosa* are most frequent on other mosses (but sometimes grow on *Sphagnum*). Commonly associated mosses are *Pleurozium schreberi* (Brid.) Mitt., *Thuidium delicatulum* (Hedw.) B.S.G., *Helodium blandowii* (Web. & Mohr) Warnst., *Callicladium haldanianum* (Grev.) Crum, *Pohlia nutans* (Hedw.) Lindb., *Plagiomnium ciliare* (C. Mull.) Kop., and *Sphagnum* sp. Commonly associated herbaceous species are: *Carex disperma* Dewey, *Rubus pubescens* Raf., *Viola canadensis* L., *Mitella nuda* L., *Fragaria vesca* L., *Pyrola secunda* L., *Linnaea borealis* L., and *Moneses uniflora* (L.) A. Gray. Other herbaceous species found near *M. paludosa* are *Malaxis unifolia* Michx., *Coptis trifolia* (L.) Salisb., *Aralia nudicaulis* L., *Platanthera obtusata* (Banks ex Pursh) Lindl., *Listera cordata* (L.) R. Br., *Goodyera repens* (L.) R. Br., *Circaea alpina* L., *Epilobium palustre* L, *Gaultheria hispidula* (L.) Muhl., *Trientalis borealis* Raf., *Galium aparine* L., *Galium obtusum* Bigel, *Thelypteris palustris* L, *Equisetum fluviatile* L., *Botrychium virginianum* (L.) Sw., and *Dryopteris cristata* (L.) A. Gray. The general area also has *Malaxis monophyllos* (L.) Sw., *Amerorchis rotundifolia* (Banks) Hultén, *Cypripedium reginae* Walt., *Cypripedium acaule* Ait., *Platanthera hyperborea* (L.) Lindl., *Pogonia ophioglossoides* (L.) Ker., *Calopogon tuberosus* (L.) BSP., *Corallorhiza trifida* Chat., *Sarracenia purpurea* L., *Drosera rotundifolia* L., *Caltha palustris* L., *Menyanthes trifoliata* L., *Ribes lacustre* (Pers.) Poir., *Eriophorum viridi-carinatum* (Engelm.) Fern., and *Aralia nudicaulis* L.

In addition to the Beltrami County locality discussed above we are aware of undocumented occurrences in Lake of the Woods (two sites) and Cass Counties, two other localities in Hubbard Co., one other site in Becker Co., and two additional Beltrami Co. localities (Paul Rundell, pers. comm.).

We have located only a few plants in three years of searching. In 1981 we located 15 plants in several hours of searching. In 1983 we found only 37 plants although we spent many hours throughout July looking for plants. Our field work in 1984 has increased the total number of plants seen to nearly 50. The total area searched at this site is about 65 ha and only a few scattered plants have been seen any distance from the main population. The diminutive plants of *Malaxis paludosa* commonly possess foliar embryos on leaf apices similar to those described and discussed by Taylor (1967). At one site three species *(M. paludosa, M. unifolia, M. monophyllos)* occur together. Our observations indicate that the flowering periods of the three species overlap considerably. This site is the only one of sympatry that we have seen and we are not aware of any other such site in North America. We are currently in the second year of a study of the pollination biology of *M. paludosa, M. unifolia*, and *M. monophyllos*. A report of our research on *M. paludosa* has been published in the American Orchid Society Bulletin (Reeves & Reeves, 1984).

ACKNOWLEDGMENTS

We thank William R. Buck for the moss determinations, Alan Schmierer for valuable field assistance and the entire Schmierer family for extensive support. We also thank Paul Rundell of the Minnesota Department of Natural Resources for his considerable support, information and advice, Russell Simmons and John Fylpaa for their interest, and the curators of the above-cited herbaria for their courtesy.

LITERATURE CITED

BALDWIN, W. K. W. 1961 *Malaxis paludosa* (L.) Sw. in the Hudson Bay lowlands. Canad. Field-Naturalist 75: 74-77.

CASE, FRED W., JR. 1964 Orchids of the Western Great Lakes Region. Cranbrook Inst. Sci., Bloomfield Hills, MI.

CORRELL, DONOVAN S. 1950. Native Orchids of North America North of Mexico. Chronica Botanica Company, Waltham, MA.

FERNALD, M. L. 1950 Gray's Manual of Botany. 8th ed. American Book Company, Boston.

GLEASON, HENRY A. and ARTHUR CRONQUIST. 1963 Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Van Nostrand Company, N.Y.

LUER, CARLYLE A. 1975. The Native Orchids of the United States and Canada Excluding Florida. N.Y. Bot. Garden, N.Y.

MARQUIS, ROBERT J. and EDWARD G. VOSS. 1981. Distributions of some western North American plants disjunct in the Great Lakes region. Michigan Bot. 20: 53-82.

PETRIE, WILLIAM. 1981. Guide to Orchids of North America. Hancock House, Blain, WA.

REEVES, LINDA M., and TIMOTHY REEVES. 1984. Life history and reproduction of *Malaxis paludosa* in Minnesota. Amer. Orchid Soc. Bull. 53(12): (in press).

TAYLOR, ROY L. 1967. The foliar embryos of *Malaxis paludosa*. Canad. J. Bot. 45: 1553-1556.

DIVISION OF SCIENCE AND MATHEMATICS
UNIVERSITY OF MINNESOTA, MORRIS
MORRIS, MN 56267

STUDIES IN THE *ARISTIDA* (GRAMINEAE) OF THE SOUTHEASTERN UNITED STATES. II. MORPHOMETRIC ANALYSIS OF *A. INTERMEDIA* AND *A. LONGESPICA*[1]

KELLY W. ALLRED

ABSTRACT

Morphologic features of the spikelets of *Aristida intermedia* Scribn. & Ball and *A. longespica* Poiret were compared using principal components and stepwise discriminant analyses. Major phenetic overlap existed between the two taxa. Central awn and lateral awn lengths were the best discriminators angle could not be used effectively. A single species with two varieties is proposed, var. *longespica* and var. *geniculata* (Raf.) Fern.

Key Words: *Aristida intermedia, A. longespica*, principal components, taxonomy, stepwise discriminant analysis

In an attempt to provide the treatment of *Aristida* for the Vascular Flora of the Southeastern United States project, several preliminary taxonomic surveys of this difficult genus were undertaken. The first (Allred, 1984) examined the morphologic relationships of *A. purpurescens* Poiret, *A. tenuispica* Hitchcock, and *A. virgata* Trinius. In this study, phenetic affinities of *A. intermedia* Scribner & Ball and *A. longespica* Poiret are examined. These surveys provide a justification for the taxonomic judgments that will be rendered in the floristic treatment, and are preliminary to more complete biosystematic investigations.

Aristida longespica was named from material collected in the Carolinas by Bosc. It is rather common throughout the eastern United States from New Hampshire to Florida and westward to Texas, Kansas, and Iowa. *Aristida intermedia* was named from a Mississippi collection made by Kearney, and is more common in the western range of *A. longespica*. Scribner and Ball drew the name *intermedia* from their belief that it was nearly intermediate between *A. longespica* and *A. purpurescens*. Both *A. longespica* and *A. intermedia* are erect annuals with often extensive vegetative branching and terminal, sometimes full, panicles. The two are usually

---

[1] Journal Article No. 1084 of the New Mexico Agricultural Experiment Station, Las Cruces, New Mexico.

separated using dimensions of the glumes, lemmas, and awns, with *A. intermedia* being larger. Gould (1975) regarded the two as only varietally distinct and applied the varietal name *geniculata* (Raf.) Fernald to the *A. intermedia* taxon.

The purposes of this study were to examine the morphologic variability of *Aristida intermedia* and *A. longespica*, particularly in the southeastern United States, and to determine the proper taxonomic status for any meaningful morphologic entities perceived.

MATERIALS AND METHODS

After careful study of the original descriptions and descriptions of the types in Henrard (1927), 172 specimens from throughout the presumed range of both taxa were selected for analysis, with about half thought to correspond to each taxon. However, no firm a priori identifications were made, and intermediate or problematic specimens were included. Three specimens of *Aristida dichotoma* Michaux were also included for reference to a closely related species. To develop OTUs (operational taxonomic units), each specimen was scored for the following characteristics: length of glumes, lemma, callus, and awns; and angle of deflection of the awns. These features are used to distinguish *A. intermedia* and *A. longespica*, but not necessarily *A. dichotoma*. Vegetative features were judged to be so similar as to be non-discriminatory and were not measured. A single mature spikelet from the upper third of the panicle was measured.

The data from each OTU were standardized so that each variable had a standard deviation of 1.0; they were subjected to principal components and stepwise discriminant analyses using the BMDP statistical package (Dixon, 1981).

RESULTS AND DISCUSSION

The principal components analysis (PCA) was based on a variable-by-variable correlation matrix. Variables with the highest correlations were central awn length and lateral awn length ($r = 0.868$), glume I length and glume II length ($r = 0.762$), and central awn length and lemma length ($r = 0.744$). These variables ought to be the most effective discriminators for these OTUs, if groups are to be discriminated. Central and lateral awn angle, considered diagnostic by many authors, had low correlation values; none was greater than ± 0.280.

The first and second components accounted for 55% and 14%, respectively, of the variation present in the study sample. Dispersion of OTUs along Component I was a function of size and reflected correlations with the length variables. Component II accounted for variability associated with awn angles (Table I).

The projection of OTUs onto the PCA grid showed no clear-cut separation into phenetic groups, with the exception of the three *dichotoma* OTUs located in the extreme "northwest" quadrant (Figure 1). Although spikelets of *dichotoma* and *longespica* appeared to be very similar (disregarding the coiled awn of *dichotoma*, which was not evaluated in this study), the PCA suggested that *dichotoma* was phenetically distinct from the *longespica* and *intermedia* entities.

Examination of specimens revealed that OTUs with longer awns, longer lemmas, and longer glumes (*intermedia*) tended to be located in the "eastern" portion of the PCA grid, and that OTUs with shorter awns, shorter lemmas, and shorter glumes (*longespica*) were placed in the "western" portion. Although the PCA demonstrated that size features of the spikelet, especially awn lengths, contributed to the dispersion of the OTUs along a size gradient of long to short, it is not an identification procedure and did not identify which OTUs belonged to *intermedia* and which to *longespica*, nor where the phenetic boundary between the two lay.

Table I. Factor loadings for components I and II in the PCA of *Aristida longespica* and *A. intermedia* OTUs. Loadings less than 0.250 are replaced by zero.

Variable	Component I	Component II
Central awn length	0.887	0.0
Lateral awn length	0.882	0.0
Glume I length	0.869	0.0
Glume II length	0.852	0.0
Lemma length	0.832	0.0
Callus length	0.763	0.0
Lateral awn angle	0.0	0.714
Central awn angle	0.0	0.597

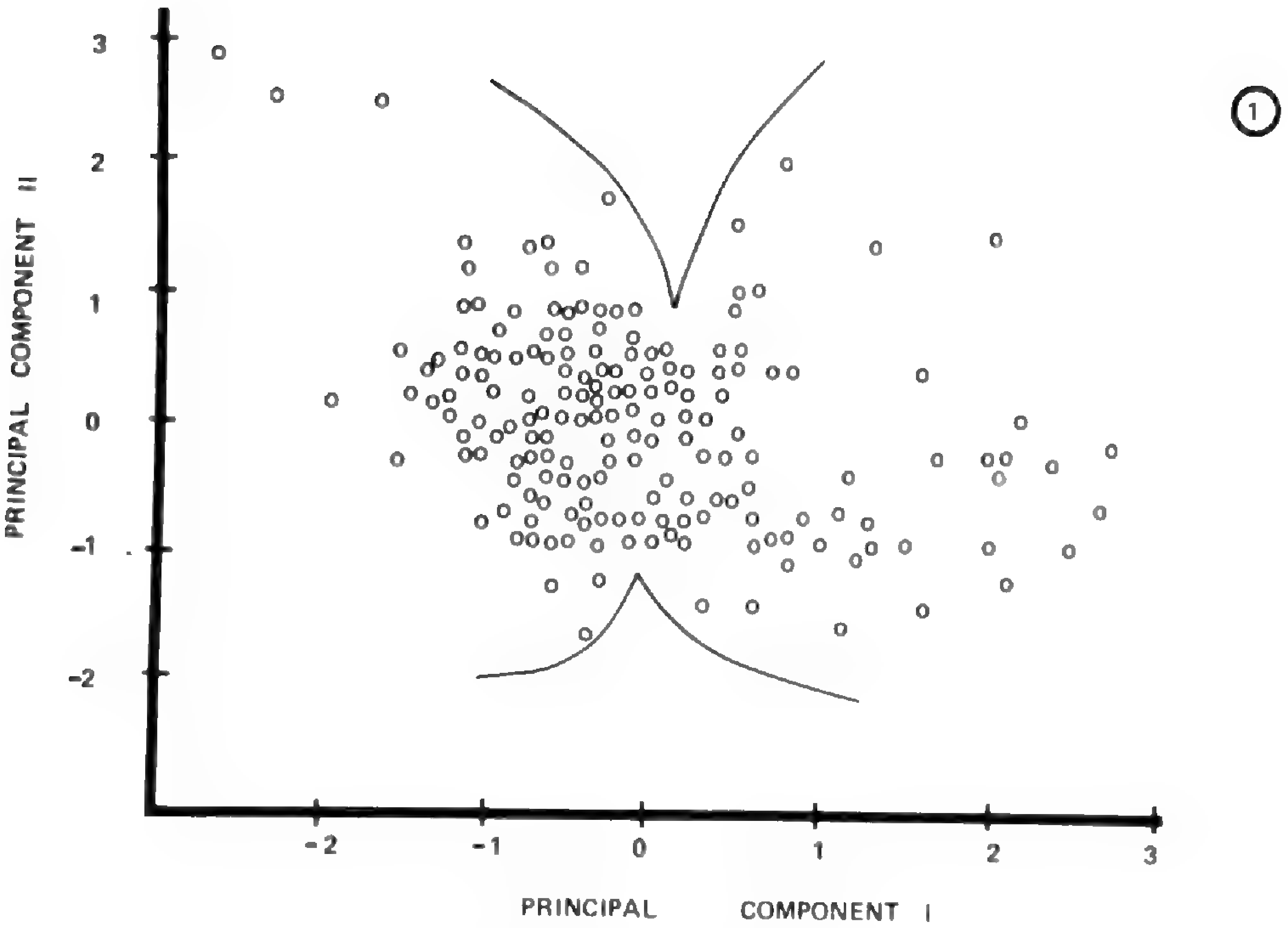


Figure 1. Principal components analysis of the *Aristida intermedia* and *A. longespica* complex. Projection of all OTUs against components I and II.

Stepwise discriminant analysis (SDA) can be used to test the validity of a priori classifications (for examples, *see* Baum, 1983a, b). One variable may be used as a marker, which places each OTU into a particular class, and then the SDA determines whether the remaining variables support this a priori classification. For example, the PCA factor loadings (Table I) suggested central awn length as a good discriminator along Component I. Using this variable as a marker, with a value of 10 mm as the cutpoint, all OTUs were classified as either *longespica* (central awn length less than 10 mm) or *intermedia* (central awn length of 10 mm or longer). The SDA then tested the validity of this a priori classification against that imposed by the correlation of the remaining variables one with another, and found that only 68% of the OTUs were "correctly" classified. The cutpoint value that gives the greatest percentage of correct classifications should be the value with the greatest discriminatory power for that variable. By testing numerous values for central awn length, it was found that the greatest percentage of "correct" classifications (95%) was achieved with a value of 15 mm. Likewise, a "best discriminator" value of 5 mm was selected for lateral awn length (86%). Henrard (1932), Fernald (1950), Gleason and Cronquist (1963), Small (1933), and Correll and Johnston (1970) each used the angle of the central awn as a main criterion for separating the two taxa, with *longespica* having a strongly divaricate or reflexed central awn and *intermedia* an erect or only slightly diverging central awn. A test of this feature by SDA gave only 65% correct classifications. Gould's (1975) two-thirds ratio of lateral awn to central awn length gave a 95% correct classification.

The SDA indicated that central awn length (15 mm, 95%), ratio of awn lengths (2/3, 95%), and lateral awn length (5 mm, 86%) can be used to identify the two taxa. However, the *composition* of the three classifications imposed by the SDA tests are dissimilar. That is, the OTUs classed in *longespica* using central awn length are not the same OTUs classed in *longespica* using the ratio of awn lengths. The compositions of each classification were compared, using a similarity index of $100 - 2c/(a+b)$, where "a" was the number of OTUs that both classifications placed in *longespica*, "b" the number of OTUs that both classifications placed in *intermedia*, and "c" the number of OTUs placed in different groups. The classifications by central awn length and by ratio of awn lengths were only 39% similar; those by lateral awn length and ratio of awn lengths only 21% similar. But, the classifications of central awn length and lateral awn length were 88% similar. A test by SDA of central and lateral awn lengths used together yielded 97% correct classifications. These two variables, then, which also have the greatest inter-variable correlation, offer the greatest discriminatory power in identifying *longespica* or *intermedia* OTUs.

The OTUs were then identified on the PCA grid according to the "best" classifications imposed by the SDA (Figure 2) and substantive phenetic overlap of the *longespica* and *intermedia* clusters was found. A summary of the variables (Table II) also illustrates this morphologic overlap. It may be noted that the means of central and lateral awn lengths were significantly different at the 0.01 probability level, indicating that even though the ranges overlapped, the values for the OTUs tended to be clustered about the mean, and extreme outliers were relatively infrequent.

Given the morphologic continuum from *longespica* to *intermedia* and the major phenetic coincidence of SDA-identified OTUs on the PCA grid, it seems reasonable to conclude that the recognition of two species, as proposed by Henrard (1932) and Hitchcock and Chase (1951), is not warranted. Recognizable phenetic units do

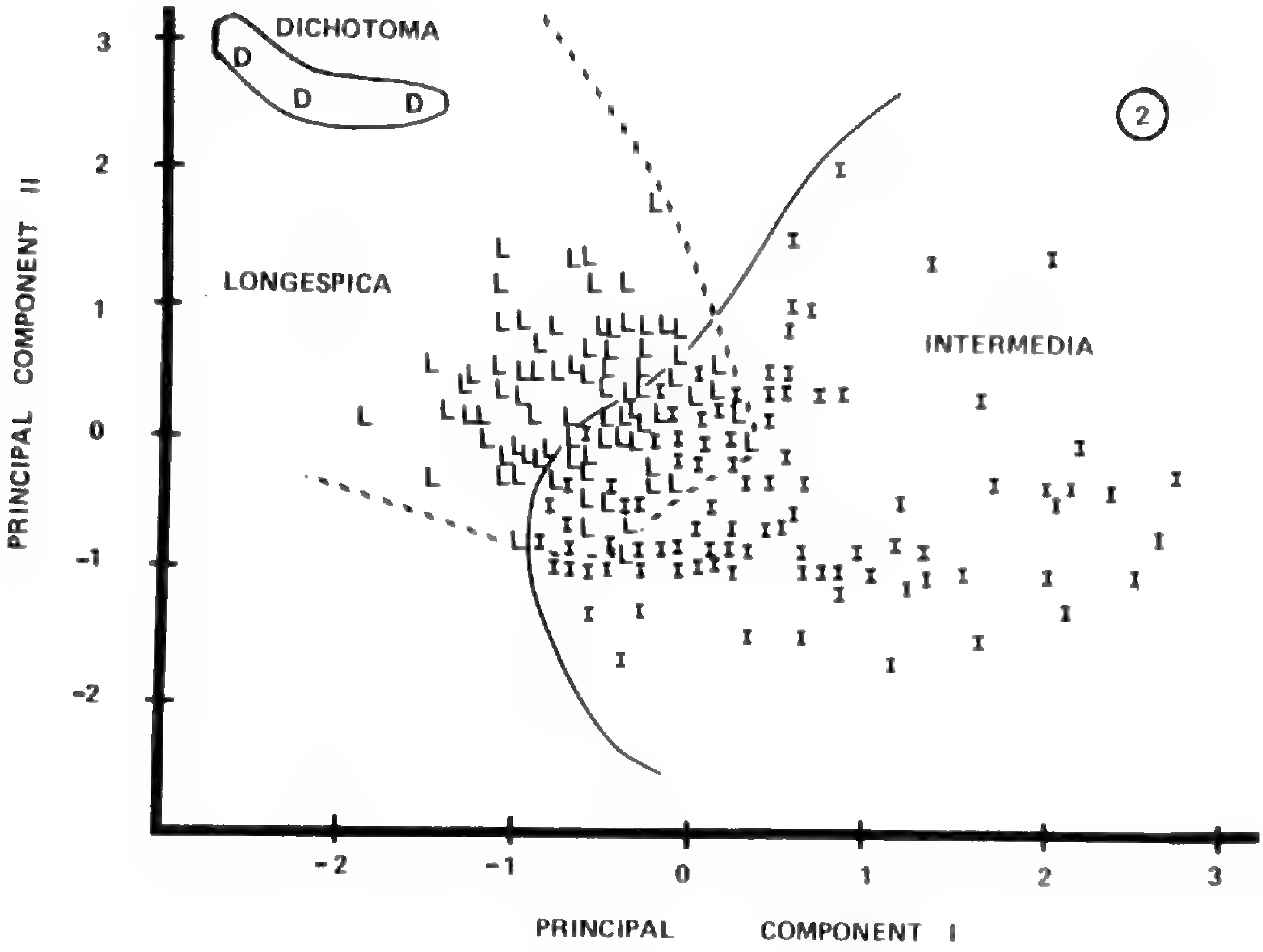


Figure 2. Principal components analysis of the *Aristida intermedia* and *A. longespica* complex. Projection of all OTUs against components I and II. The OTUs were identified according to the most accurate classification by the step-wise discriminant analysis.

exist, however, and taxonomic status for these units is appropriate. Gould (1975) treated the two taxa at the varietal level, and correctly applied the name *geniculata* (Raf.) Fernald to the variety that included *intermedia*. A fragment of the type of *Aristida geniculata* Raf. containing three spikelets was somewhat intermediate between *longespica* and the long-awned *intermedia*, but clearly within the range of variation of the *intermedia* phenetic cluster (Table II). The name *geniculata* is the only available name at the varietal level for this taxon, and thus is the correct name for the variety corresponding to the *intermedia* cluster in Figure 2. Shinners (1954) argued that *geniculata* was only a southern robust race of *A. longespica*, and that longer-awned plants of the upper Mississippi Valley belonged to a different species, which he named *A. necopina*. However, plants identical with the type of *A. necopina* are found in southeastern Texas, Louisiana, Arkansas, and Florida. In addition, the SDA tests showed that the "best" cut-points between the short-awned and long-awned forms were at 15 mm for central awns and at 5 mm for

Table II. Summary of variables for the *Aristida longespica* and *A. intermedia* OTUs.

Variable	*A. longespica*	*A. intermedia*	Fragment of type of *A. geniculata*
Central awn length (mm)	1–10(14)	(8)12–27	13–17
Lateral awn length (mm)	0–5(8)	(1)6–18	9–10
Glume I length (mm)	2.0–8.3	4.0–10	5–6.5
Glume II length (mm)	2.5–7	4.5–10.8	6.6–6.8
Lemma length (mm)	2.5–6.9	3.5–10	5.2–5.8
Callus length (mm)	0.2–0.5	0.2–0.7	0.3
Lateral awn angle	erect to ascending	erect to horizontal	erect
Central awn angle	erect to reflexed	erect to reflexed	divergent

lateral awns, and not at the 20 mm and 13 mm values that are required to separate *A. necopina*.

The correct nomenclature is as follows:

Aristida longespica Poir. var. *longespica* in Lam., Encycl. Sup. 1:452. 1810. *A. gracilis* Elliott, Bot. S.C. and Ga. 1:142. 1816.

Aristida longespica Poir. var. *geniculata* (Raf.) Fern., Rhodora 35:318. 1933. *A. geniculata* Raf., Amer. Monthly Mag. 2:119. 1817. *A. intermedia* Scribn. & Ball, USDA Div. Agrostol. Bull. 24:44. 1901. *A. necopina* Shinners, Rhodora 56:30. 1954.

The two varieties are best identified using awn lengths. All the variables are summarized in Table II.

ACKNOWLEDGMENTS

Many thanks to the curators of the following herbaria for their generous cooperation in loaning material for this study: APSC, ARK, AUA, DUKE, FLAS, FSU, KY, LAF, LSU, MARY, MO, NCSC, NCU, NLU, NO, SMU, TENN, UNA, URV, US, USCH, USF, VDB, VPI, WVA.

LITERATURE CITED

ALLRED, K. W. 1984. Studies in the *Aristida* (Gramineae) of the southeastern United States. I. Spikelet variation in *A. purpurescens*, *A. tenuispica*, and A. virgata. Rhodora 86: 73 77.

BAUM, B. R. 1983a. Morphometric relationships in *Hordeum vulgare* (Triticeae, Poaceae). I. *H. spontaneum*. Can. J. Bot. 61(7): 2015 2022.

———. 1983b. Morphometric relationships in *Hordeum vulgare* (Triticeae, Poacea). II. *Hordeum agriocrithon*, *H. distichum*, *H. laguncuIiforme*, *H. spontaneum*, and *H. vulgare*. Can. J. Bot. 61(7): 2023 2031.

CORRELL, D. S., and M. C. JOHNSTON. 1970. Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner.

DIXON, W. J. ed. 1981. BMDP Statistical Software. University of California Press, Berkeley.

FERNALD, M. L. 1950. Gray's Manual of Botany. 8th ed. American Book Co., New York.

GLEASON, H. A., and A. CRONQUIST. 1963. Manual of the Vascular Plants of Northeastern United States and Canada. Van Nostrand Reinhold Co., New York.

GOULD, F. W. 1975. The Grasses of Texas. Texas A & M University Press, College Station.

HENRARD, J. T. 1927. A critical revision of the genus *Aristida*. Meded. Rijks-Herb. Leiden No. 54A.

———. 1932. A Monograph of the Genus *Aristida*. Vol. II. Meded. Rijks-Herb. Leiden No. 58A.

Hitchcock, A. S., and A. Chase. 1951. Manual of the Grasses of the United States. Ed. 2. U.S.D.A. Misc. Publ. 200.

Shinners, L. 1954. Notes on north Texas grasses. Rhodora 56: 25–38.

Small, J. K. 1933. Manual of the Southeastern Flora. University of North Carolina Press, Chapel Hill.

DEPARTMENT OF ANIMAL AND RANGE SCIENCES
BOX 3-I
NEW MEXICO STATE UNIVERSITY
LAS CRUCES, NM 88003

STUDIES IN THE *ARISTIDA* (GRAMINEAE) OF THE SOUTHEASTERN UNITED STATES. III. NOMENCLATURE AND A TAXONOMIC COMPARISON OF *A. LANOSA* AND *A. PALUSTRIS*[1]

KELLY W. ALLRED

ABSTRACT

The correct name for the grass known as *Aristida affinis* (Schultes) Kunth in the United States is *A. palustris* (Chapman) Vasey, *A. affinis* being a synonym of *A. purpurescens* Poiret. The taxonomic relationship of *A. lanosa* Muhl. ex Elliott and *A. palustris* was assessed using principal components and stepwise discriminant analyses. The two taxa are clearly distinguished by a combination of several vegetative and spikelet structures and are not closely related phenetically.

Key Words: *Aristida affinis, A. lanosa, A. palustris*, taxonomy, principal components, discriminant analysis

This paper is the third in a series of preliminary surveys of the *Aristida* of the southeastern United States, preparatory to a floristic treatment of that region (*see* Allred 1984a, b).

Aristida lanosa was named in 1813 by Muhlenberg, but without a description, which he added in October 1817 in his "Descriptio uberior graminum." However, Elliott had picked up Muhlenberg's name *lanosa* and supplied the validating description in December 1816 (not February 1817 as stated in Henrard, 1927:286), and thus the correct author citation is *A. lanosa* Muhlenberg ex Elliott, or just *A. lanosa* Elliott. *Aristida lanosa* has been characterized by its lanose or floccose sheaths and tufts of hair at the panicle nodes, as well as the strikingly inverse glumes (first longer than second).

Aristida palustris (Chapman) Vasey is currently known in the United States as *A. affinis* (Schultes) Kunth, the basionym being *Chaetaria affinis* Schultes. *Chaetaria affinis* was based on *A. racemosa* Muhl., which was illegitimate because of the earlier *A. racemosa* Sprengel. Thus, *Aristida affinis* has as its type that of *A. racemosa* Muhl. An examination of the type of *A. racemosa* Muhl. (PH) showed this plant to belong to *A. purpurescens* Poiret. This state of affairs was accurately perceived and documented by

---

[1] Journal Article No. 1091 of the New Mexico Agricultural Experiment Station, Las Cruces, New Mexico.

Henrard (1926). Our plant in question is correctly known as *A. palustris*, the next available epithet, and is based on *A. virgata* Trin. var. *palustris* Chapman. Curiously, *A. palustris* was the name used by Hitchcock (1924) in his monograph of North American *Aristida* wherein he also correctly placed *A. racemosa* Muhl. in synonymy under *A. purpurescens*. However, he used *A. affinis* in the *Manual of the Grasses of the United States* (Hitchcock, 1935; Hitchcock and Chase, 1951) and this nomenclature has been adopted by all subsequent United States botanists.

Aristida lanosa and *A. palustris* are superficially similar. Both may be tall, robust grasses with rather stiff, elongate panicles and prominent awns. Allen (1980), Correll and Johnston (1970), Gleason and Cronquist (1963), and Gould (1975) treated the two as separate species but emphasized their similarity, suggesting that *A. palustris* was perhaps only a glabrous form of *A. lanosa*. Hall (1978; Ph.D. dissertation, Gainesville, FL) proposed recognizing *A. palustris* as *A. lanosa* var. *alabamensis* (not effectively published), and Wunderlin (1982) placed *A. palustris* in synonymy under *A. lanosa* with no infraspecific recognition at all. Fernald (1950) and Henrard (1927) suggested a similarity of *A. palustris* and *A. virgata*.

The purposes of this study were to compare the morphologic features of *Aristida lanosa* and *A. palustris* and to assess their taxonomic relationship.

MATERIALS AND METHODS

From throughout the southeastern ranges of the taxa, 172 specimens were examined, representing 86 specimens each of *Aristida lanosa* and *A. palustris*. To develop OTUs (operational taxonomic units), each specimen was scored for the following features: nodes exposed or hidden by the subtending sheaths (NODES), sheaths glabrous or lanose/floccose (SHPUB), panicle length (PANL), panicle nodes glabrous or pubescent (PANPUB), glume I length (GIL), glume II length (GIIL), number of nerves on glume I (GINERVE), lemma length (LEML), callus length (CALL), palea length (PALEAL), central awn length (CAWNL), and lateral awn length (LAWNL). The data were standardized so each variable had a standard deviation of 1.0, and then subjected to principal components analysis (PCA) based on a variable-by-variable correlation matrix. The classification of the OTUs suggested by the PCA was then tested by stepwise discriminant analysis. The BMDP statistical package was used in both analyses (Dixon, 1981).

RESULTS AND DISCUSSION

The first three components of the PCA accounted for 81% of the variability in the study sample (Table I), a situation derived in part from several high correlations among the variables (Table II). Noteworthy were high correlations involving pubescence features of the sheath and panicle, glume I nervation, and node exposure. These correlations reflect particularly the pubescence and covered nodes of *Aristida lanosa*, and the 2-keeled (2-nerved) first glume of *A. palustris*.

Dispersion of the OTUs along Component I was a function of awn lengths, pubescence (sheath and panicle), glume nervation, callus length, and node exposure. Component II revealed differences in lengths of spikelet structures, and Component III correlated with panicle length (Table I).

Projection of the OTUs along Components I and II resulted in two well-defined phenetic clusters separated along Factor I (Figure 1). To the "west" were OTUs with shorter awns, lanose sheaths and panicle nodes, 1-nerved first glumes, and shorter calluses. These

Table I. Factor (component) loadings for the principal components analysis of *Aristida lanosa* and *A. palustris* OTUs. Loadings less than ±0.250 have been replaced by zero.

Variable	Component I	Component II	Component III
Lateral awn length	.927	0.0	0.0
Panicle pubescence	.918	0.0	.277
Glume I nervation	.918	0.0	.277
Sheath pubescence	.916	0.0	.280
Callus length	.914	0.0	0.0
Node exposure	.893	0.0	.281
Central awn length	.855	0.0	0.0
Glume II length	0.0	.832	0.0
Glume I length	.566	.664	.279
Lemma length	.338	.654	0.0
Palea length	0.0	.607	.447
Panicle length	0.0	0.0	.822
Variance explained	56%	17%	8%

Table II. Variable by variable correlation matrix for principal components analysis of *Aristida lanosa* and *A. palustris* OTUs. Explanation for variable abbreviations is in the text.

	LAWNL	CAWNL	PALEAL	CALL	LEML
NODE	0.764	0.623	0.082	0.861	0.417
SHPUB	0.761	0.628	0.060	0.888	0.440
PANL	0.146	0.077	0.039	0.271	0.203
PANPUB	0.762	0.634	0.057	0.891	0.453
GIL	0.465	0.309	0.134	0.587	0.575
GIIL	0.172	0.269	0.287	0.129	0.361
GINERVE	0.762	0.634	0.057	0.891	0.453
LEML	0.268	0.148	0.168	0.298	1.000
CALL	0.786	0.685	0.108	1.000	
PALEAL	0.108	0.113	1.000		
CAWNL	0.918	1.000			
LAWNL	1.000				

OTUs were all referable to *Aristida lanosa*. To the "east" were OTUs characterized by the contrasting features of longer awns, glabrous sheaths and panicle nodes, 2-nerved first glumes, and longer calluses. These OTUs belong to *A. palustris*. Two OTUs (nos. 20 and 94) were placed in somewhat intervening positions between the two clusters; these OTUs were both widely separated along Component III and were not intermediate or transitional forms.

A test of the classification suggested by the PCA was performed using stepwise discriminant analysis (SDA). The SDA indicated 100% correct classification for all OTUs, from both *Aristida lanosa* and *A. palustris*.

Although generally glabrous, the sheaths of some *Aristida palustris* may be pubescent, but the hairs are of a different kind than in *A. lanosa*. Pubescence of *A. lanosa* is a true lanose or floccose type, the hairs being woolly or cottony, kinked, and usually intertwined (Figure 2). The illustration of *A. lanosa* in Hitchcock and Chase (1951, Fig. 699) is somewhat misleading. It appears in the drawing as if the internode, rather than the sheath, is covered with hair, and the hairs are almost of a dense velutinous nature. Typically, the pubescence of *A. lanosa* is rather patchy and shaggy. The specimen photographed in Figure 2 is the same one illustrated in Hitchcock and Chase (1951), *Canby s.n.*, Sussex Co., Delaware (US).

GINERVE	GIIL	GIL	PANPUB	PANL	SHPUB	NODE
0.933	0.032	0.648	0.933	0.368	0.938	1.000
0.994	0.022	0.705	0.994	0.364	1.000	
0.365	0.077	0.334	0.365	1.000		
1.000	0.015	0.713	1.000			
0.713	0.515	1.000				
0.015	1.000					
1.000						

The hairs of *Aristida palustris*, if present, are of a pilose type (Figure 3), often appressed, usually straight rather than kinked, and not at all woolly or cottony. They are similar to the hairs found on the sheaths of some plants of *A. purpurescens* and *A. condensata* Chapman.

The first glumes of *Aristida lanosa* and *A. palustris* are also very distinctive. In addition to being 1-nerved and markedly longer than the second, the first glume of *A. lanosa* curves slightly outward with a falcate shape (Figure 4). The first glume of *A. palustris*, conversely, is clearly 2-keeled because of the strong development of one lateral nerve, subequal to the second glume, and not falcate-curving (Figure 5).

Other features useful in distinguishing the two taxa are glabrous panicle nodes, longer callus and awns, and usually exposed lower nodes in *Aristida palustris*, versus woolly panicle nodes, shorter callus and awns, and covered lower nodes in *A. lanosa*. The features analyzed in this study are summarized in Table III.

Clearly, *Aristida lanosa* and *A. palustris* represent two very distinct taxa relative to each other. They are easily distinguished by a combination of vegetative and spikelet features; proposals to merge the two are not appropriate.

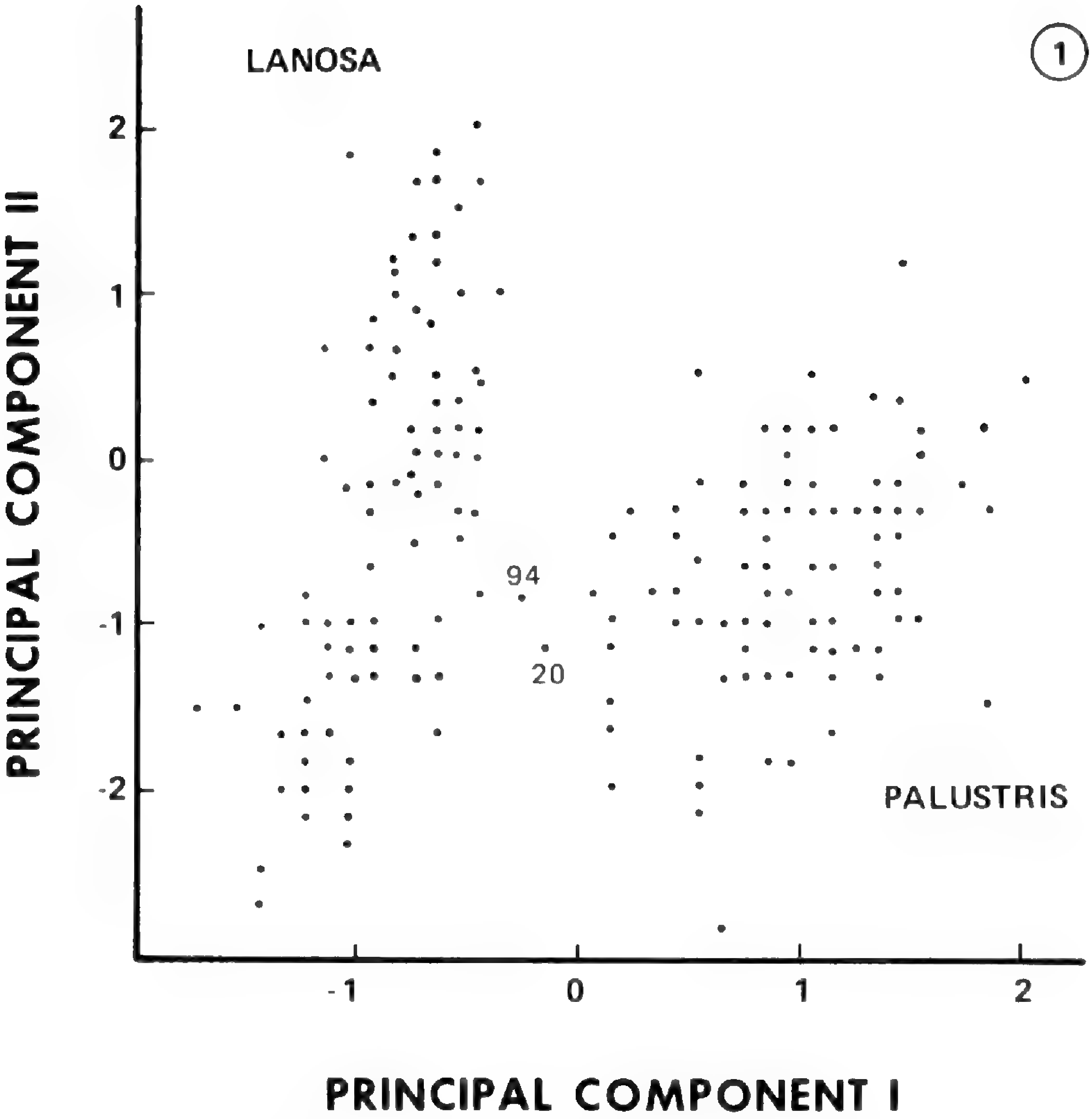
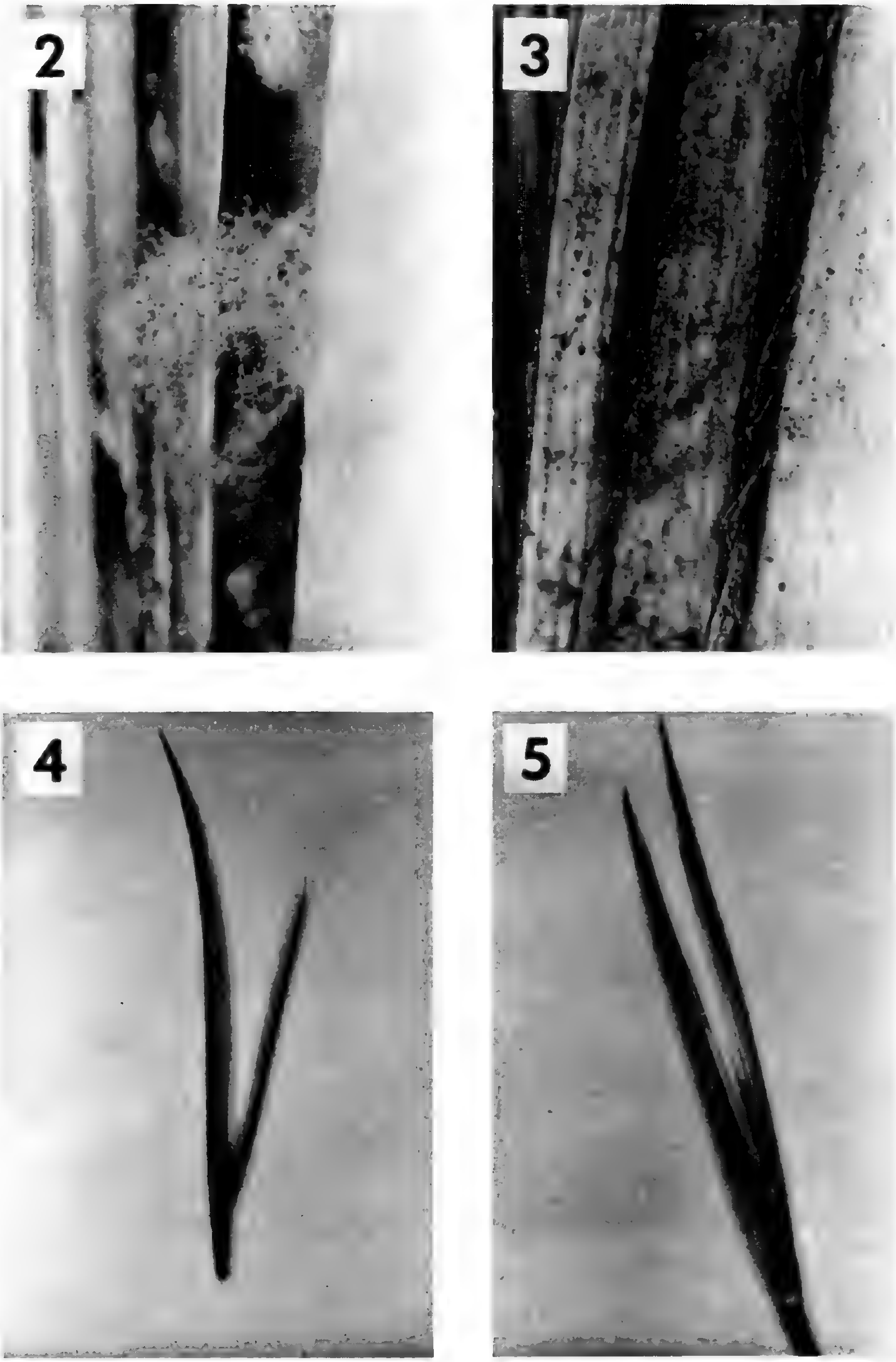


Figure 1. Distribution of OTUs along Components I and II of principal components analysis of *Aristida lanosa* and *A. palustris*.

ACKNOWLEDGMENTS

Many thanks to the curators of the following herbaria who loaned material for study: APSC, ARK, AUA, DUKE, FLAS, FSU, KY, LAF, LSU, MARY, MO, PH, NCSC, NCU, NLU, NO, SMU, TENN, UNA, URV, US, USCH, USF, VDB, VPI, WVA. Travis Columbus helped in data accumulation and analysis.



Figures 2-5. **2.** Sheath pubescence of *Aristida lanosa* (× ca. 15). **3.** Sheath pubescence of *Aristida palustris* (× ca. 15). **4.** Glumes of *Aristida lanosa* (× 4.6). **5.** Glumes of *Aristida palustris* (× 6).

Table III. Summary of morphologic features of *Aristida lanosa* and *A. palustris*.

Feature	*A. lanosa*	*A. palustris*
Lower nodes	covered by sheaths	mostly exposed
Sheaths	lanose or floccose	glabrous to pilose
Panicle length	26–74(82) cm	21–60(70) cm
Panicle nodes	with lanose tufts	glabrous
Glume I length	(8.7)9.5–18 mm	7.8–13.5 mm
Glume II length	8.4–15 mm	8.5–13 mm
Nerves glume I	1	2
Lemma length	6.5–14(17) mm	6–9.2 mm
Callus length	0.4–0.8 mm	0.7–1.4 mm
Palea length	1–1.9 mm	1–1.8 mm
Central awn length	1.2–2.8 cm	1.5–4.2 cm
Lateral awn length	0.7–1.7 cm	0.8–3(3.6) cm

LITERATURE CITED

Allen, C. M. 1980. Grasses of Louisiana. University of Southwestern Louisiana, Lafayette.

Allred, K. W. 1984a. Studies in the *Aristida* (Gramineae) of the southeastern United States. I. Spikelet variation in *A. purpurescens*, *A. tenuispica*, and A. virgata. Rhodora 86:73–77.

———. 1984b. Studies in the *Aristida* (Gramineae) of the southeastern United States. II. Morphometric analysis of *A. intermedia* and *A. longespica*. Rhodora 87:137–145.

Correll, D. S., and M. C. Johnston. 1970. Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner.

Dixon, W. J., ed. 1981. BMDP Statistical Software. University of California Press, Berkeley.

Fernald, M. L. 1950. Gray's Manual of Botany, ed. 8. American Book Co., New York.

Gleason, H. A., and A. Cronquist. 1963. Manual of the Vascular Plants of Northeastern United States and Canada. Van Nostrand Reinhold Co., New York.

Gould, F. W. 1975. The Grasses of Texas. Texas A & M University Press, College Station.

Henrard, J. T. 1926. A critical revision of the genus *Aristida*. Vol. I. Meded. Rijks-Herb. No. 54.

———. 1927. A critical revision of the genus *Aristida*. Vol. II. Meded. Rijks-Herb. No. 54A.

Hitchcock, A. S. 1924. The North American species of *Aristida*. Contr. U.S. Natl. Herb. 22(7):517–586.

———. 1935. Manual of the Grasses of the United States. Ed. 1. U.S.D.A. Misc. Publ. 200.

———, and A. Chase. 1951. Manual of the Grasses of the United States. Ed. 2. U.S.D.A. Misc. Publ. 200.

Wunderlin, R. P. 1982. Guide to the Vascular Plants of Central Florida. University Presses of Florida, Tampa.

DEPARTMENT OF ANIMAL AND RANGE SCIENCES
BOX 3 I
NEW MEXICO STATE UNIVERSITY
LAS CRUCES, NM 88003

TRILLIUM UNDULATUM FORMA *ENOTATUM*, A NEW PETAL COLOR FORM OF THE PAINTED TRILLIUM

THOMAS S. PATRICK

ABSTRACT

A white-flowered variant of painted trillium, *Trillium undulatum*, is described as forma *enotatum*. The new form is distinguished from forma *undulatum* by lack of a red blaze near the base of the petals. It is known from three populations in the southern Appalachian Mountains of Georgia and North Carolina.

Key Words: *Trillium*, southern Appalachian Mountains, petal color forms

Few trilliums are as distinctive as the eastern North American painted trillium, *Trillium undulatum* Willd. Major features of this species are: leaves ovate, acuminate, petiolate, coppery bluish-green; petals undulate, white with proximal red markings; anthers lavender with apiculate connectives and extrorse dehiscence; fruits baccate, bright red.

Individuals lacking red blazes on petals were recently found in three natural populations in association with typical painted trilliums. These peculiar specimens were not simply albinos; they generally displayed other anthocyanic trends (e.g., leaves off-green, major petal veins light red, both ovary apex and anthers lavender). As evident in treatments by Fernald (1950), Freeman (1975), Scoggan (1978), Soukup (1982), and many others, the genus is well endowed with a formal nomenclature for petal color variants. Authors, particularly Freeman (1975) and Patrick (1984), have inferred phylogenetic significance to petal color in trilliums and a practical resurgence of naming petal color forms has resulted. In accordance with provisions of the Sydney Code (Voss, 1983), a new petal color form is here described to accommodate the observed variation in *T. undulatum*.

Trillium undulatum Willd. f. **enotatum** Patrick, *f. nov.*, a f. undulato petalis albis non sigillatim prope basin rubrotinctis differt.

Petals white, with or without faint red veins, but lacking distinct red markings near their bases. The petals are thus unmarked, as signified by the new Latin epithet.

TYPE: UNITED STATES. North Carolina. Swain Co.: along Beech Flats Prong, Oconaluftee River, in secondary forest of sugar maple, tuliptree, and eastern hemlock, elev. 2900 ft, Great Smoky Mountains National Park, 1 May 1983, *Patrick 4831* (HOLOTYPE: TENN; ISOTYPE: GRSM).

ADDITIONAL SPECIMENS EXAMINED: Georgia. Murray Co.: headwaters of Mill Creek around Lake Conasauga beneath *Rhododendron* and *Kalmia*, elev. 3300 ft, Chattahoochee National Forest, 30 Apr 1984, *Patrick 5105* (TENN). North Carolina. Avery Co.: along Flat Rock Trail near Mile 308, Blue Ridge Parkway, elev. 4000 ft, 6 May 1974 et seq., *Selby s.n.* (TENN photos!).

The new petal color form is known from three isolated stations in the Blue Ridge Province of the southern Appalachian Mountains. At the type locality, sympatric trilliums are *Trillium grandiflorum* (Michx.) Salisb. and *T. erectum* L. In Georgia, painted trilliums grow with *T. catesbaei* Ell. No other *Trillium* species are found at the third site (J. Selby, pers. comm.). *Trillium undulatum* is not suspected to hybridize with any other species. Its closest ally may not be among the extant American taxa.

ACKNOWLEDGMENTS

I thank James I. Jones, Jack H. Selby, and William A. Wood for sharing their independent discoveries with me. Bretta E. Perkins and Grace and Al Foster assisted in locating plants. As always, John D. Freeman proffered advice and encouragement.

LITERATURE CITED

FERNALD, M. L. 1950. Gray's Manual of Botany. 8th ed. American Book Co., New York.

FREEMAN, J. D. 1975. Revision of *Trillium* subgenus *Phyllantherum* (Liliaceae). Brittonia 27: 1–67.

PATRICK, T. S. 1984. *Trillium sulcatum* (Liliaceae), a new species of the southern Appalachians. Brittonia 36: 26–36.

SCOGGAN, H. J. 1978. The Flora of Canada. Part 2. Natl. Mus. Can. Publ. Bot. 7. pp. 93–545.

SOUKUP, V. G. 1982. New yellow-flowered forms of *Trillium* (Liliaceae) from the northwestern United States. Phytologia 50: 290–291.

VOSS, E. G., chairman. 1983. International Code of Botanical Nomenclature. Regnum Veg. 111.

DEPARTMENT OF BOTANY
THE UNIVERSITY OF TENNESSEE
KNOXVILLE, TENNESSEE 37996-1100

A REVISION OF THE CENTRAL AMERICAN SPECIES OF *MONNINA* (POLYGALACEAE)

CHARLOTTE M. TAYLOR

ABSTRACT

Eight species of *Monnina* are known to occur in Central America: *M. costaricensis* Chod., *M. crepinii* Chod., *M. guatemalensis* Chod., *M. saprogena* Donn. Sm., *M. sylvatica* Schlecht. & Cham., *M. xalapensis* H. B. K., and two new species, *M. ferreyrae* Taylor and *M. parasylvatica* Taylor, described herein. *Monnina xalapensis* is treated here as a widely ranging and variable species that includes *M. pittieri* Chod. and *M. latisepala* Blake. Reports of the occurrence of *M. pterocarpa* DC. and *M. brachystachya* Griseb. in Central America have not been confirmed.

Key Words: *Monnina*, Polygalaceae, Central America

INTRODUCTION

Monnina, a New World genus of about 150 species, is one of the largest genera in the Polygalaceae. It is found from the southwestern United States southward to southern Chile and Argentina, with the greatest concentration of species in the mountains of Colombia, Ecuador, and Peru. The genus was established by Ruiz and Pavon (1798); the name commemorates Don Jose Moniño, Count of Floridablanca, a patron of scientific exploration. Ten years later, Bonpland independently published *Hebeandra* for those species of *Monnina* with unwinged drupaceous fruits. The genus was next investigated extensively by Chodat (1896, 1897), whose published studies are the only comprehensive treatments of the genus. Ferreyra treated the species of Peru (Ferreyra, 1946), Colombia (Ferreyra, 1953a), Ecuador (Ferreyra, 1953b), and Venezuela (Ferreyra, 1957) in excellent detail, and these papers cover most of the species in the genus.

Species of *Monnina* in the United States, Mexico and Central America were first treated together by Blake (1924). More recent accounts of the genus have been published for Costa Rica (Standley, 1937), Guatemala (Standley & Steyermark, 1949), and Panama (Lewis & Herrera-Macbryde, 1969). In the present treatment the species of Central American countries from Guatemala through Panama are revised. Only two additional species, *M. ciliolata* DC. and *M. wrightii* Gray, are found north of this area.

Three other genera of Polygalaceae are known from Central America. *Monnina* is distinguished by its one- or few-seeded, indehiscent, drupaceous fruits, that are either unwinged or winged along the entire margin. The fruits of *Polygala* L. are several-seeded, dehiscent capsules; those of *Securidaca* L. are one-seeded samaras, with a wing on one side only. Flowers of *Securidaca* are usually recognizable also by the tuft of hairs or the appendages at the apex of the keel, which are lacking in *Monnina*. *Securidaca* can usually be distinguished also by its vining habit. In *Moutabea* Aubl. the fruits are drupaceous, and the calyx and corolla are united into a tube. Flowers of *Moutabea* lack the winglike sepals characteristic of most polygalaceous flowers.

MORPHOLOGY

Plants of *Monnina* are generally erect small to medium-sized shrubs, although individuals of *M. sylvatica* and *M. parasylvatica* are sometimes herbaceous. Occasional individuals of *M. sylvatica* may be scandent. *Monnina saprogena* is the only epiphytic species in Central America.

The stems are rounded, with smooth bark. The leaves are estipulate, alternate, and entire. Those of *Monnina costaricensis* sometimes appear serrulate, but actually the margins are entire and finely crisped. The apices of the leaves are acute, often with a very short (0.5–1 mm long) cartilaginous or apiculate tip. The leaf shape is generally elliptic, ranging in the Central American species from broadly elliptic or ovate (*M. parasylvatica* and *M. guatemalensis*) to very narrowly elliptic (the montane Costa Rican form of *M. xalapensis*). The leaves are usually membranaceous but may be coriaceous (*M. guatemalensis*) or somewhat succulent (*M. saprogena*). Many of the species have blades with tapering bases, so that the petioles are difficult to delimit; in general, the petiole is more similar in texture and pubescence to the stem.

Young leaves and twigs are pubescent, but become glabrate with age. The young growth of most species is puberulous or strigillose with short, appressed, unicellular trichomes, and older growth is nearly glabrous. A few species (*Monnina guatemalensis, M. crepinii*, and *M. ferreyrae*) are pilosulous or tomentulose with spreading trichomes that are often yellowish or orangish, and older growth often retains its pubescence. Both conditions are found in *M. xala-*

pensis, which is characteristically puberulous or strigillose over most of its range but is densely spreading-pilosulous in its montane Costa Rican form. Glandular trichomes are found infrequently on the leaves of some individuals of *M. saprogena*.

The flowers are arranged in loose to dense racemes or panicles that are borne terminally and in upper leaf axils. In *Monnina guatemalensis* and sometimes in *M. crepinii* and *M. ferreyrae* the racemes are aggregated terminally; this arrangement is similar to that of some South American species. The peduncle length is included in the raceme measurements given here. The pubescence of the raceme axes is similar to that of the stem, though usually denser. The axes are often bright red or purple.

The flowers are borne on short pedicels that are similar in pubescence and color to the raceme axis, and subtended by one bract and two bracteoles. The bracts are ovate or lanceolate, ciliate, glabrous adaxially but usually at least slightly pubescent abaxially, and often tinged with purple. In some species the bracts are about the size of the young flower buds; in others they are much longer and often conspicuous in the silhouette of the raceme. Lengths given in the species descriptions are those of the longest bracts still adhering in the inflorescence. Bracteoles are similar to the bracts in shape, color, and pubescence, but smaller. Although in some individuals bracts and bracteoles may persist until the fruit starts to develop, they are usually deciduous before anthesis.

The flowers are zygomorphic; they superficially resemble papilionaceous flowers but are not homologous (Figure 1). Kunth's descriptions of the flower parts may be confusing, since he mistakenly considered polygonaceous flowers to be resupinate (Humboldt, Bonpland & Kunth, 1821) and thus described the upper sepal as the lower sepal, the lower sepals as the upper, and so forth.

The five sepals are strikingly dimorphic in two whorls. The outer whorl contains three similar, rather reduced sepals, the upper one usually noticeably larger than the lower two. The lower two sepals are usually free, but they are fused for part of their length in *Monnina saprogena* and *M. costaricensis*, as well as in many South American species. The three outer sepals are usually glabrous adaxially, pubescent abaxially, and ciliate. Each sepal generally has one to five longitudinal veins, or as many as nine in the broadly ovate sepals of the "latisepala" form of *M. xalapensis*. These outer sepals

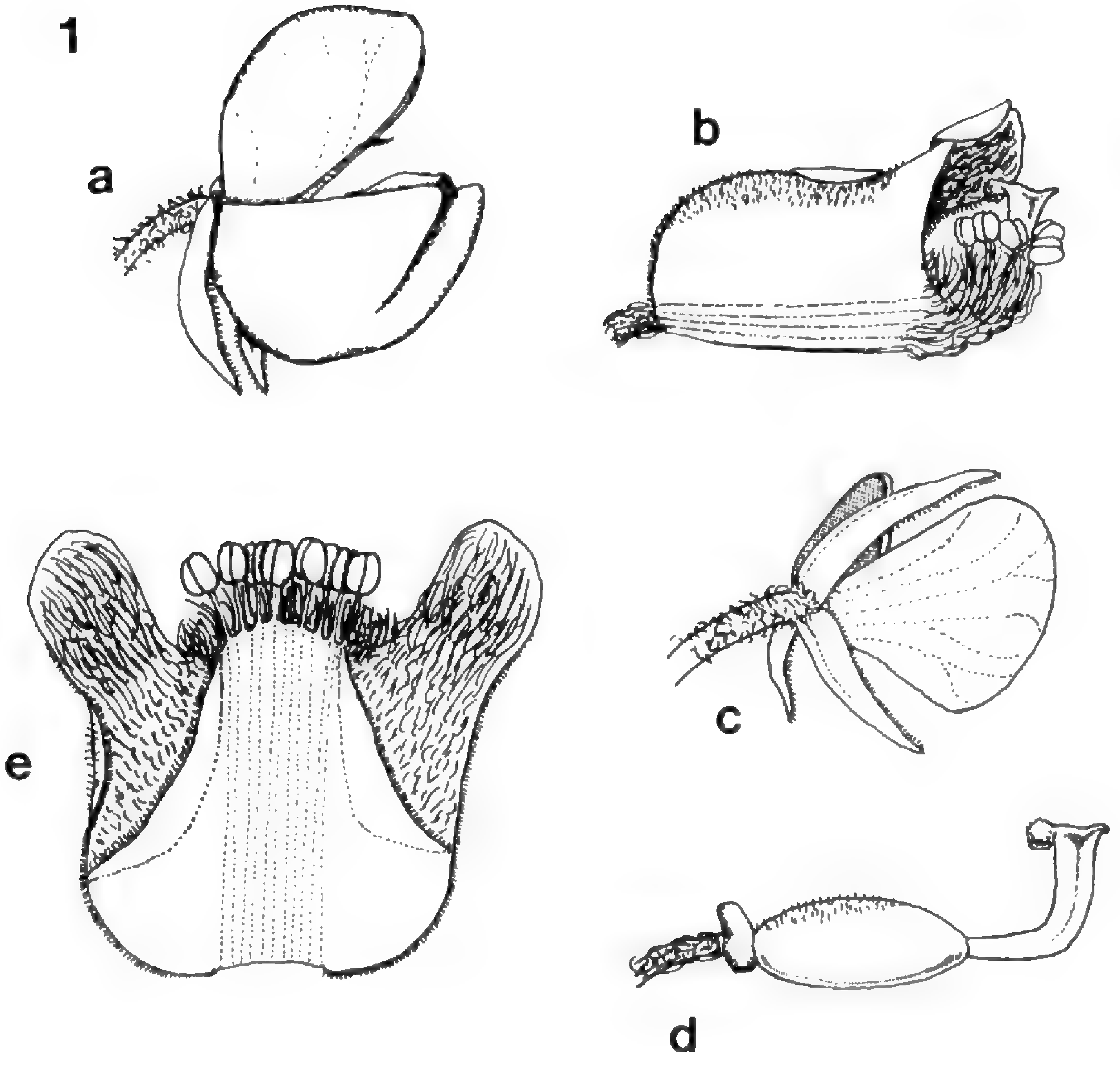


Figure 1. Floral morphology of *Monnina*; **a**, habit of flower; **b**, staminal sheath, showing habit in flower; **c**, sepals; **d**, gynoecium; **e**, staminal sheath unfolded, interior (adaxial) view.

vary in color from greenish to dark blue or purple. The inner two sepals are expanded as orbicular or obovate wings, which are borne laterally and are widely spreading when the flower is open. It is primarily these two inner sepals that enclose the rest of the flower in bud. The wings are virtually indistinguishable in shape, color, and size among species. They are blue or blue-violet, glabrate or minutely puberulent, and often ciliate.

The lower of the three petals is expanded into a broad boat-shaped keel that encloses the remaining parts of the flower. It is broadly and shallowly three-lobed at the apex and strongly pleated along either side of the central fold. The keel is glabrous or minutely puberulent, and ranges in color from greenish to bright yellow in newly opened flowers to blue or violet in older flowers.

The upper two petals are articulated near the apex of a staminal sheath as two bluish or purplish limbs; these are characteristically appressed-pubescent on both surfaces and are also densely pilose on the inner surfaces of the limbs. The staminal sheath is composed of fused filaments and is split longitudinally along the upper side, where the petals are attached. Ferreyra (1946) referred to this structure as a "staminal tube," but strictly speaking it is not a tube, but rather a folded laminar structure. When this staminal sheath is folded to enclose the gynoecium, the pilose tufts on the petal limbs interlock to cover the open top of the sheath. This structure is entirely enclosed by the keel.

The stamen-petal sheath measurement is the distance from the base of the sheath to the articulation of the filaments; the diagonal measurement is the distance from the center of the base of the unfolded sheath diagonally to the apex of one of the petal limbs. The diagonal measurement is included as some indication of the length of the petals and the shape of the sheath. In the Central American species the free portions of the filaments are pilose, and the pubescence often extends down the abaxial surface for as much as half the length of the staminal sheath.

In all Central American species of *Monnina* there are eight stamens in two fascicles of four stamens each. (In a few South American species there are only six stamens in two fascicles of three.) The free portions of the filaments are 0.8 1.4 mm long in most species, although they may be as long as 1.8 mm in *M. crepinii*. The anthers are held in a circle around the style. The filaments bend and vary slightly in length to acommodate this arrangement. The anthers are 0.3–0.6 mm long, subglobose, two-celled, and dehiscent by an apical pore.

The superior ovary is elliptical or cylindrical and often somewhat flattened. It may be glabrous or pubescent; the pattern of pubescence varies from a few scattered hairs along the upper margin to a dense sericeous covering over the entire surface. The ovary is usually about 1–2 mm long before fertilization. After fertilization, it rapidly enlarges to several times its former size. For this reason, measurements of ovary size are omitted. The ovary is subtended by a glandular disk, which is enlarged toward the adaxial side of the pedicel into a knoblike process about 0.6–1 mm long. As the fruit develops, this gland persists in shriveled form. The style is very strongly flattened and bent at a right angle to the axis of the ovary. The stigma is unequally bilobed, with the ventral lobe larger and glandular, and is exserted from the staminal tube but usually enclosed by the keel. The ovary is bilocular, and each locule is uniovulate (Chodat, 1897).

The fruits of *Monnina* are indehiscent with one to three seeds. The fruits may be dry and winged, or more commonly fleshy or "drupaceous" and unwinged. All Central American species of *Monnina* belong to subg. *Monnina*, which is characterized by drupaceous, unwinged fruits. This group has been treated incorrectly by many authors as subg. *Hebeandra* (Bonpland) Chodat. Although some drupaceous fruits have rather thin, fluted margins when dried, these are not the dry membranaceous wings of subg. *Pterocarya* (DC.) Chodat. The fresh mature fruits of subg. *Monnina* are lustrous purplish black and very succulent and sweet. Descriptions of fruits presented here apply to immature, dried fruits.

Leaf shape, pubescence, size and position of racemes, floral bracts, and outer sepals are the features primarily used in delimiting species. The outer sepals are the most variable of the floral parts, as well as the most conspicuous. Keel and staminal sheath sizes are presented as more exact measurements of flower size than the general overall length measurement used by some authors. There is almost no interspecific variation in flower size in the Central American species. The pitting and marginal ridge patterns of the dried fruits also provide characters that are often useful in identifying herbarium specimens.

DISTRIBUTION AND ECOLOGY

Plants of *Monnina* are generally found in moist to wet, middle to high elevations (500–3000 m). *Monnina parasylvatica* has been collected as low as 300 m, the lowest elevation of any Central American species. The shrubs are common in brushy areas, pasture edges, forests, and along roads.

Plants bloom throughout the year, and hence are almost perpetually in fruit. It is common to find racemes with both flowers and fruit. The months listed for each species are those for which flowering collections were seen. Pollination vectors are unreported. The keel of the flower is either entirely blue or suffused with pale to deep yellow distally. The yellow appears shortly before the flower opens and seems to be a signal that the flower is newly opened or receptive. The keel turns blue after the flower has been open for a time; a concomitant change in stigma color has been observed (Inouye, 1977). Flowers are rather faintly but very sweetly fragrant.

MATERIALS

In addition to the material at DUKE, specimens, including available type material, were very kindly loaned by the following herbaria: A, BH, BM, BR, CAS, CU, DS, F, FSU, GH, MO, NY, US, WIS. Many specimens at US, including type material, were unavailable.

SYSTEMATIC TREATMENT

Monnina Ruiz & Pavon, Syst. Veg. Peruv. Chil. 169. 1798. TYPE: *M. polystachya* Ruiz & Pavon.

Hebeandra Bonpland, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 2: 40. 1808. TYPE: *non design.*

Shrubs or rarely herbs or weakly clambering vines, terrestrial or sometimes epiphytic; stems terete (or striate)*, pubescent (or rarely glabrous), with smooth bark. Leaves simple, alternate, estipulate (or stipules reduced to glands or spines), entire (or denticulate), pubescent (or rarely glabrous), pinnately veined, petiolate or rarely subsessile. Inflorescences racemose or paniculate; raceme axes and pedicels pubescent (or rarely glabrous); bracts solitary (or rarely absent), membranaceous, caducous; bracteoles paired (or rarely absent), membranaceous or scarious, caducous. Flowers zygomorphic; sepals five in two whorls, the outer three sepals free or the lower two connate, the inner two sepals expanded into obovate to suborbicular petaloid wings; petals three, the lower one expanded as a boat-shaped keel enclosing the staminal sheath, the upper two fused to the filaments and articulated as limbs; stamens eight in two fascicles of four (or rarely six in two fascicles of three), filaments fused nearly to apex into a sheath split along its upper side, enclosing the gynoecium, sheath (glabrous or) pilose apically and abaxially; anthers basifixed, (one- or) two-celled (sometimes emarginate or mucronate), dehiscent by an apical pore; ovary superior, one- (or

---

*Descriptions in parentheses apply to species not known to occur in Central America.

two-) celled, glabrous or pubescent, bicarpellate, ovules solitary in each cell, pendulous; disk expanded to one side, glandular. Fruit indehiscent, fleshy (or samaroid, rarely intermediate), with 1(–2) seeds.

About 150 species, southwestern United States to Chile and Argentina, the greatest concentration in Colombia, Ecuador, and Peru.

KEY TO SPECIES

1. Lower sepals connate for 1/3 to 3/4 of their length . . . . (2)
  2. Leaves coriaceous, elliptic to narrowly elliptic; dried fruits smooth; outer sepals rounded; inflorescences paniculate; pedicels 1.5–2.5 mm long; usually epiphytic . . . . 1. *M. saprogena*
  2. Leaves membranaceous, narrowly elliptic to narrowly rhombic; dried fruits pitted; outer sepals acute; racemes usually one, up to three, always simple; pedicels 3.0–4.0 mm long; terrestrial . . . . 2. *M. costaricensis*
1. Lower sepals free . . . . (3)
  3. Racemes compound, or at least the terminal raceme usually branched twice or more; staminal tube 2.5 mm long or shorter . . . . 3. *M. parasylvatica*
  3. Racemes simple, or the terminal raceme occasionally with as many as two branches; staminal tube 2.5 mm or longer . . (4)
    4. Staminal tube 4.2–5.5 mm long; keel 6.5–8.0 mm long; sepals lanceolate to lance-ovate, the upper sepal often bent near the apex; young stems and petioles pilosulous, hairs spreading . . . . 4. *M. crepinii*
    4. Staminal tube 2.5–4.0(4.5) mm long; keel 3.2–6.5 mm long; sepals lance-ovate to very broadly ovate, the upper sepal never bent; young stems and petioles pilosulous or strigillose, hairs spreading or appressed . . . . (5)
      5. Terminal racemes 2 or more, aggregated without subtending leaves, simple; leaves coriaceous, upper surface usually lustrous; plants of western Guatemala and adjacent Mexico . . . . 5. *M. guatemalensis*
      5. Terminal racemes solitary, simple or sometimes with 1–2 short branches; leaves membranaceous, upper sur-

face dull; plants ranging throughout Central America . . . . (6)

6. Floral bracts ovate to very broadly ovate, acute to shortly apiculate, the longest 1.5–3.5 mm long . . . . 6. *M. xalapensis*
6. Floral bracts narrowly ovate to lanceolate, attenuate, the longest 3.5–7.0 mm long . . . . (7)
   7. Pubescence of young stems and petioles puberulous, strigillose or tomentulose, appressed or somewhat spreading; plants ranging throughout Central America . . . . 7. *M. sylvatica*
   7. Pubescence of young stems and petioles pilosulous and widely spreading; plants of Honduras and Nicaragua . . . . 8. *M. ferreyrae*

DESCRIPTIONS OF SPECIES

1. **Monnina saprogena** J. Donnell Smith, Bot. Gaz. (Crawfordsville) 31: 109. 1901. TYPE: COSTA RICA: San José: La Palma, *Tonduz 7406* (HOLOTYPE: US).

Erect to pendant, epiphytic or very rarely terrestrial shrubs 0.5–3 m tall; stems strigillose, hairs whitish. Leaves fleshy, elliptic to narrowly elliptic, (2.5)4–8.5 cm long, (1)1.5–4 cm wide, glabrate to moderately strigillose throughout, occasionally also sparsely glandular-pubescent on lower surfaces; petioles 2–7 mm long. Inflorescences paniculate, up to three times compound, 4.5–10 cm long, axes and pedicels moderately short-strigillose; bracts ovate to rounded, strongly concave, 1.5–3 mm long, glabrate to minutely puberulent, ciliate; bracteoles 1/3–1/2 as long as bracts, lanceolate to rounded. Flowers on pedicels (1.2)1.5–2.5 mm long; outer sepals ovate, apically rounded, somewhat concave, glabrate, ciliate, upper sepal 1.5–2.5 mm long, lower sepals (0.5)1–1.5 mm long, connate for 1/2–3/4 of their length; inner sepals (wings) 3.5–5 mm long, 3–4 mm wide, minutely puberulent, upper margins ciliate basally; keel 4.5–6 mm long, (2.5)3–4 mm high, minutely puberulent, ciliolate, greenish yellow; stamen-petal sheath 3.5–4.5 mm long, 4.5–6 mm diagonally, moderately pubescent, usually pilose abaxially; ovary glabrous; style (1.5)2–2.5 mm from curve to apex. Dried fruits elliptic, (4)5.5–6.5(7) mm long, 3–4.5 mm wide, smooth, upper margin and occasionally lower margin narrowly ridged; pedicels elongating only slightly as fruit develops.

DISTRIBUTION: Cloud forests, highlands of Costa Rica (Alajuela Guanacaste–Puntarenas border region, Cartago, Heredia, San José) south to Volcán Chiriquí in Panama (Chiriquí), 1500–3000 m. Flowering Jan.–Mar., May–Oct., Dec. Distribution map, Figure 5.

This taxon is the most distinctive of the Central American species of *Monnina.* It is distinguished by its epiphytic habit, spreading panicles, fleshy or leathery leaves, smooth dry fruits, rounded ovate bracts, and rounded and partially connate lower sepals. It is endemic to the mountains of Costa Rica and Panama. The only other *Monnina* in Central America with connate lower sepals is *M. costaricensis.* This species is easily distinguished from *M. saprogena* by its terrestrial habit, simple and usually solitary racemes, membranaceous leaves, pitted dry fruits, and sharply acute sepals. *Monnina guatemalensis*, endemic to Guatemala, may also have coriaceous elliptic leaves, but it is easily distinguished by its terrestrial habit, simple though sometimes aggregated racemes, pitted dry fruits, lanceolate bracts, free lower sepals, and brownish tomentulose pubescence.

Monnina saprogena was originally considered endemic to Volcan Irazu, but later collections have considerably broadened its known range. It is now known from the slopes of Volcan Barba and from the Monteverde area (at the junction of the provinces of Alajuela, Guanacaste, and Puntarenas) south to Volcan Chiriqui in Panama. This species was not included in the *Flora of Panama* (Lewis & Herrera-MacBryde, 1969).

The type collection was labelled by Tonduz as growing "in a rotted trunk." However, the habit of this species is epiphytic rather than saprogenic.

SELECTED SPECIMENS EXAMINED: **Costa Rica:** ALAJUELA-GUANACASTE-PUNTARENAS BORDER REGION: near and on Continental Divide, 25 km E and SE of Monteverde, *Burger & Gentry 8707* (F); CARTAGO: along road 23 miles NW of Pastora, *Primack & Luteyn 206* (DUKE); slopes of Volcán Turrialba, *Wilbur et al. 21954* (DUKE); along ICE road, 9 km W of Tapanti Dam, 9 km SE of Tapanti bridge over Río Grande de Orosí, *Wilbur 30758* (DUKE); CARTAGO-SAN JOSÉ BORDER REGION: near km 56 on Interamerican Highway, S of Cartago, *Raven 20940* (CR, F, MO, NY); HEREDIA: near Río Las Vueltas, about 12 km NE of Heredia, *Taylor & Taylor 17718* (MO, NY, US); SAN JOSÉ: Alto La Palma, about

16 km NE of Guadeloupe, *Wilbur et al. 22508* (DUKE); about 35 km NE of Cascajal, in vicinity of Río Cascajal, *Wilbur 24409* (DUKE); **Panamá**: CHIRIQUÍ: southern slopes of Cerro Horqueta, N of Boquete, *Wilbur et al. 13472* (DUKE).

2. **Monnina costaricensis** Chodat, Bull. Soc. Roy. Bot. Belgique 30(1): 304. 1891. LECTOTYPE: COSTA RICA: Heredia: forêts de Rancho Flores, *Pittier 2138* (LECTOTYPE: G; ISOLECTOTYPES: BR!, CR!).

Slender shrubs 0.5–2 m tall; stems moderately puberulent or tomentulose, hairs white or pale yellowish. Leaves membranaceous, narrowly elliptic to narrowly rhombic, (2.5)4–10 cm long, (0.5)1–3(3.5) cm wide, glabrate to puberulent or tomentulose, marginally often crisped; petioles 5–10(15) mm long. Inflorescences racemose; racemes simple, loose, solitary or rarely 2–3, 4–15(17) cm long, axes and pedicels slightly to moderately puberulent or tomentulose, usually dark blue; bracts ovate, 1.5–3 mm long, slightly to moderately puberulent, ciliate; bracteoles 1–1.5 mm long, narrowly lanceolate. Flowers on pedicels 3–4 mm long; outer sepals narrowly to rather broadly ovate, apically acute, sparsely puberulent, ciliate, upper sepal 2–3(3.2) mm long, lower sepals 1.8–2.5 mm long, connate for (1/10)2/5–3/4 of their length; inner sepals (wings) 4–5 mm long, 3.5–4.5(5.5) mm wide, glabrous or very minutely puberulent basally; keel 4–6(6.5) mm long, 2.5–3.5(4.5) mm high, glabrous or sometimes minutely puberulent within, yellow; stamen-petal sheath 3–4(4.2) mm long, 3.5–4.5(5.5) mm diagonally, moderately pubescent, usually glabrous abaxially or rarely sparsely pilose; ovary glabrous to sparsely strigillose; style (1.8)2–2.5 mm long from curve to apex. Dry fruits narrowly ovate, 7.5–9 mm long, 3.5–4.5 mm wide, upper and lower margins narrowly ridged; fruiting pedicels 3.5–5 mm long.

DISTRIBUTION: Wet montane forests to subparamo thickets, highlands of Costa Rica (Cartago, Heredia, San José), 1500–2500(3100) m. Flowering Feb., Mar., May-Aug., Nov. Distribution map, Figure 4.

Monnina costaricensis is characterized by its partially connate acute lower sepals, comparatively long petioles and pedicels, solitary loose racemes, and ovate dried fruits. It is endemic to the mountains of central Costa Rica.

In Central America only *Monnina saprogena* also has partially connate lower sepals. The differences between these species are discussed in the treatment of *M. saprogena. Monnina xalapensis* of montane Costa Rica also has narrowly elliptic leaves and simple, loose, often solitary racemes; however, its free lower sepals, short petioles and pedicels, elliptic-rounded dry fruits, and pilosulous pubescence easily separate it from *M. costaricensis.*

Chodat cited two type specimens, *Pittier 2138*, from Rancho Flores, and *Pittier 874*, from Turrialba. *Pittier 2138* must be considered the lectotype since Blake (1924) cited "Rancho Flores" as the type locality in his treatment of *M. costaricensis.*

SELECTED SPECIMENS EXAMINED: **Costa Rica:** HEREDIA: Río Las Vueltas (upper Río Patria), eastern slope of Volcán Barba, near Continental Divide, *Burger & Liesner 6392* (F); slopes of Volcán Barba above Sacramento, before Laguna, *Wilbur et al. 23517* (DUKE); CARTAGO: continuation of CR 224 on ICE property, about 13 km beyond bridge at Tapanti, *Almeda et al. 3023* (CAS); E of Irazú, *Stork 2036* (F); along Interamerican Highway, about 24 km W of Villa Mills, about km 73, *Wilbur & Stone 8794* (DUKE); slopes of Volcán Turrialba, *Wilbur et al. 21938* (DUKE).

3. **Monnina parasylvatica** Taylor, *sp. nov.*

Frutex vel raro herba 0.5–3 m altus, puberulus; folia membranacea, elliptica usque ovata, 6–14.5 cm longa, 2.5–6.5 cm lata, petiolis 2–6 mm longis; inflorescentiae paniculata, racemi 3–10, 5–17 cm longi; bracteae anguste lanceolatae, 1.5–4 mm longae, sepala externa libera, ovata 1.5–3.4 mm longa; carina 3.2–4.8 mm longa; lamina ex staminibus et petalis constata 2–2.5 mm longa; ovarium glabrum vel strigillosum.

TYPE: COSTA RICA: Cartago: slopes above Plantanillo, 3000 ft, *Wilbur & Stone 10604* (HOLOTYPE: DUKE; ISOTYPES: DS, F, MO, NY).

Terrestrial shrubs or rarely bushy herbs 0.5–3 m tall; stems slightly to moderately puberulent, hairs whitish. Leaves membranaceous, elliptic to ovate, (6)7.5–12(14.5) cm long, 2.5–6.5 cm wide, glabrate to moderately puberulent; petioles (2)3–6 mm long. Inflorescence paniculate; racemes 3–10, 5–15(17) cm long, simple or branched, at least the terminal one usually branched; axes and pedicels puberulent or tomentulose; bracts narrowly lanceolate, 1.5–3.2(4.0) mm long, sparsely puberulent, ciliate; bracteoles 1/3–1/2 as long as the bracts, rather scarious. Flowers borne on

2

3

Figure 2. Habit of *Monnina parasylvatica* (from *Wilbur & Stone 10604*, DUKE).

Figure 3. Habit of *M. ferreyrae* (from *Rubio 31*, MO).

pedicels 0.5–1.2 mm long; outer sepals ovate, somewhat concave, somewhat puberulent, ciliate, upper sepal 2.4–3.4 mm long, lower sepals 1.5–2 mm long, free; inner sepals (wings) (3)3.5–4(4.5) mm long, 2.5–3.5(4) mm wide, glabrous to very sparsely puberulent, ciliate basally; keel (3.2)3.5–4.8 mm long, 2–2.6 mm high, glabrous or sparsely puberulent within, yellow to yellow-green; stamen-petal sheath 2–2.5 mm long, (3.5)4.0–4.1 mm diagonally, sparsely pubescent, rarely pilose abaxially; ovary glabrous to sparsely strigillose; style 1.5–2(2.5) mm long from curve to apex. Dried fruits oblong to elliptic, 5.5–7 mm long, 3–4 mm wide, lower margin narrowly ridged; pedicels elongating only slightly as fruit develops.

DISTRIBUTION: Roadsides, thickets, and disturbed areas, Mexico to Panama, 300–1200(1500) m. (Guatemala: Baja Verapaz; Honduras: Copán; Nicaragua: Chontales, Matagalpa; Costa Rica: Alajuela, Cartago, Guanacaste, Limón; Panamá: Coclé, Veraguas). Flowering throughout the year. Habit, Figure 2. Distribution map, Figure 6.

This species is distinguished by its widely elliptic-ovate leaves, long lanceolate floral bracts, relatively small flowers, and paniculate inflorescences. Although most of the racemes may be simple, usually at least the terminal one is branched.

Monnina parasylvatica and *M. sylvatica* resemble each other strongly, but these species can be separated by several reliable characters. The flowers of *M. sylvatica* are generally larger and more loosely arranged than those of *M. parasylvatica* and are subtended by longer, more conspicuous floral bracts. Racemes of *M. sylvatica* are typically simple and axillary, although the terminal raceme may occasionally be branched once or twice. The terminal raceme of *M. parasylvatica* is typically branched twice or more, and the axillary racemes are usually branched as well. Additionally, *M. sylvatica* tends to be more densely puberulent than *M. parasylvatica*, and the young growth is often tomentulose rather than puberulent. This last difference is not a clear distinction, although it can be a useful character. These distinctions are summarized in Table 1.

SELECTED SPECIMENS EXAMINED: **Guatemala:** BAJA VERAPAZ: Pauzal, *von Tuerckheim II.1735* (BM, BR, F, GH, NY); **Honduras:** COPÁN: near Tierra Blanca, *Williams et al. 24921* (F, US); **Nicaragua:** CHONTALES: near Santo Domingo, *Bunting & Licht 1168* (DUKE, F, NY, US); MATAGALPA: road to Aranjuez, Cordillera Central, *Williams & Molina 20151* (F, NY, US, WIS); **Costa Rica:** ALAJUELA: near Artezelea and Methodist Rural Center, NE of Quesada, *Molina et al.*

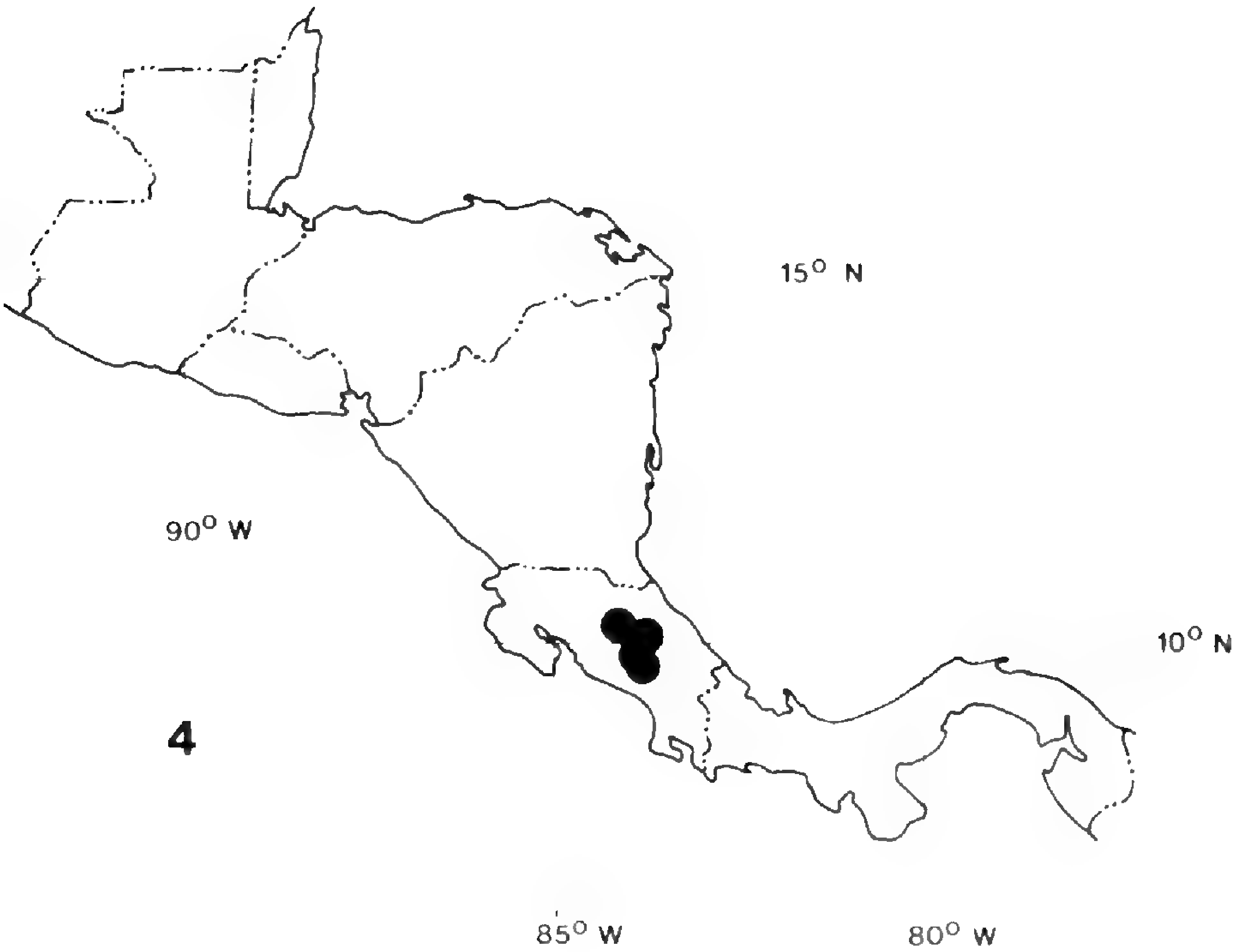


Figure 4. Distribution of *Monnina costaricensis* in Central America.

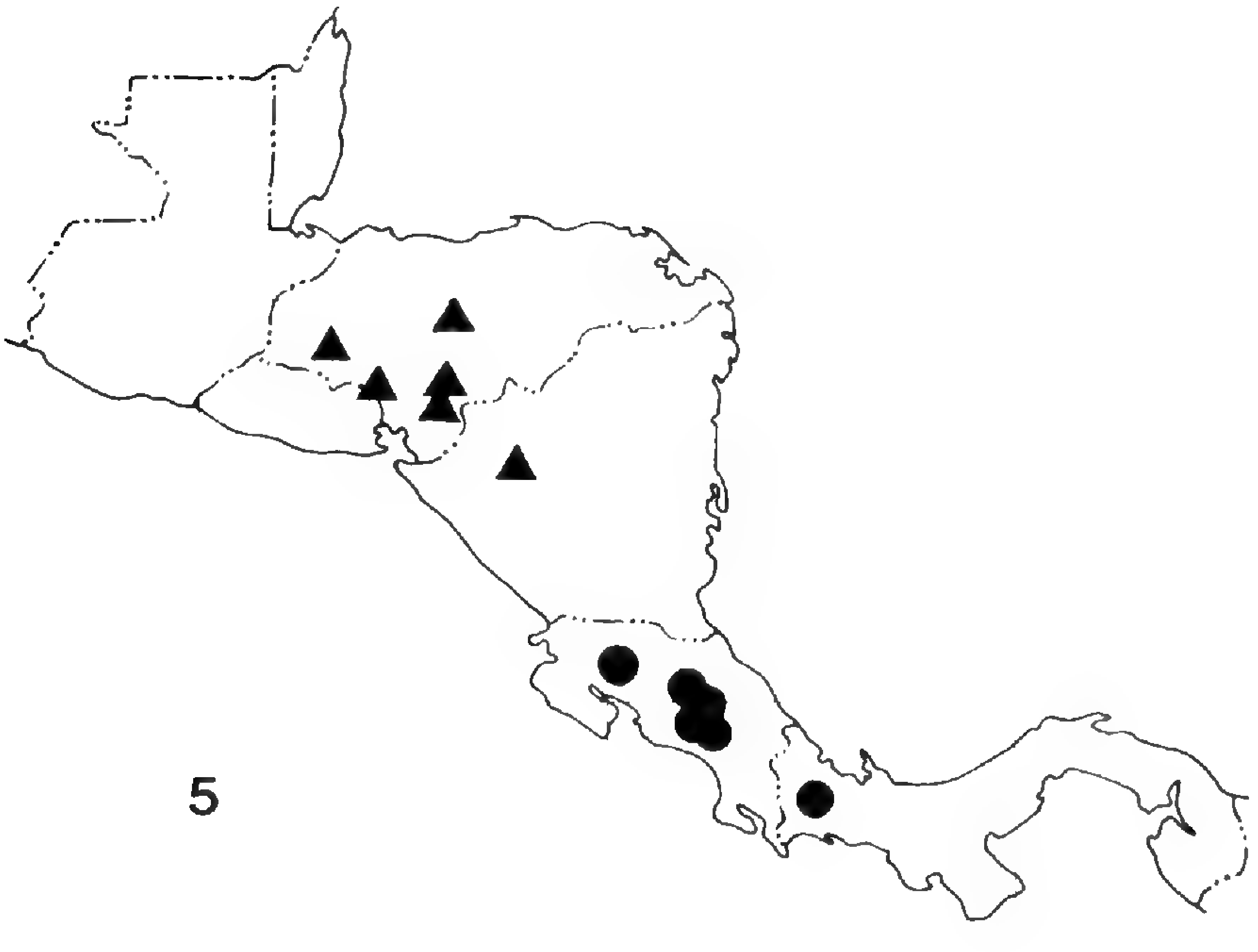


Figure 5. Distribution of *Monnina saprogena* (circles) and *M. ferreyrae* (triangles) in Central America.

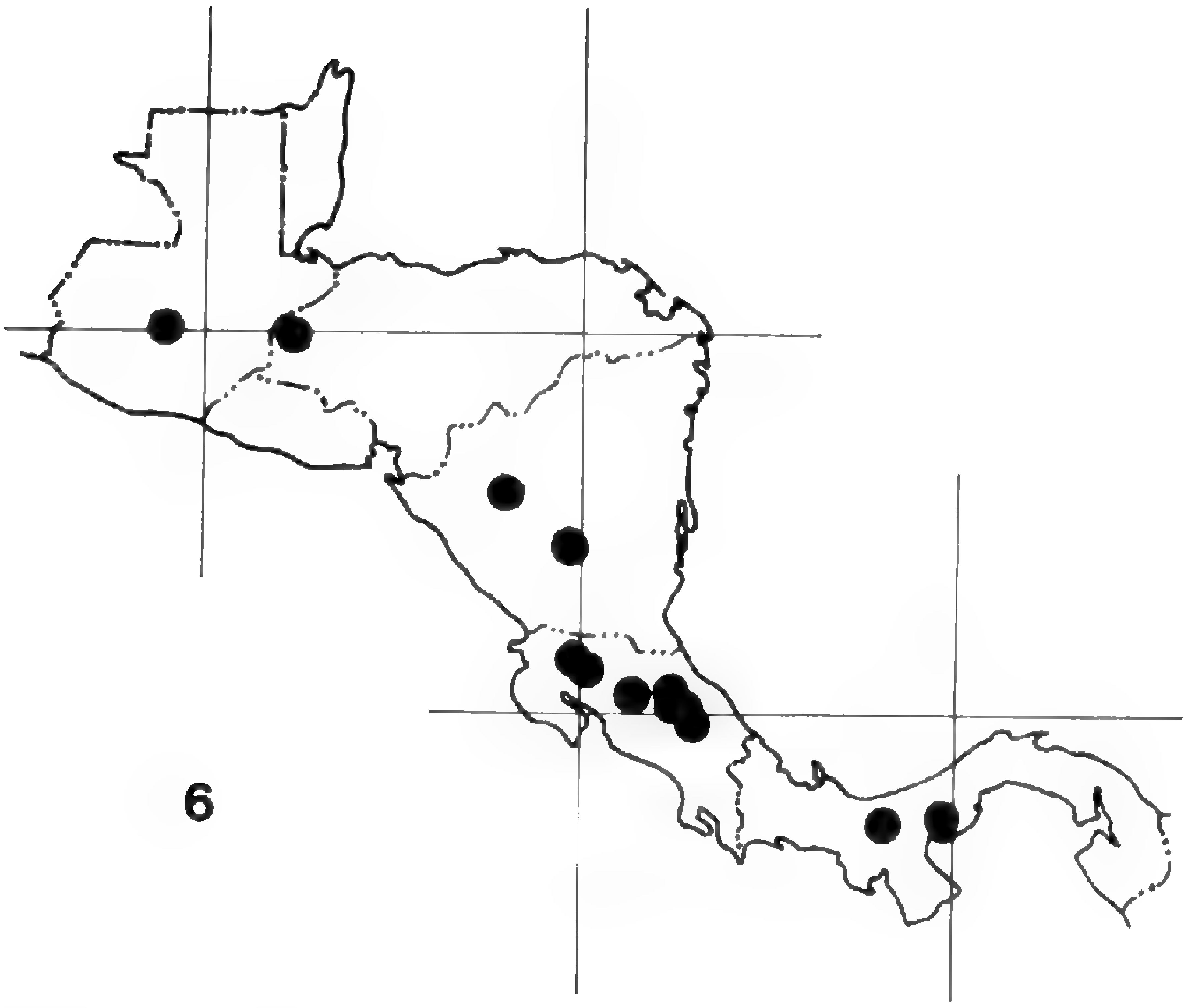


Figure 6. Distribution of *Monnina parasylvatica* in Central America.

17229 (F, NY, US); GUANACASTE: Laguna del Arenal, Tilarán-Arenal road, *Jimenez M. 2705* (F, MO, NY); LIMÓN: ca. 16 km SW of Siquirres, *Wilbur 30460* (DUKE); **Panama:** COCLÉ: slopes of Cerro Pajita, crater of El Valle de Antón, *Wilbur et al. 11125* (DS, DUKE, F, GH, MO, NY); VERAGUAS: slopes N of Escuela Agrícola, *Wilbur & Luteyn 19101* (DUKE).

4. **Monnina crepinii** Chodat, Bull. Soc. Roy. Bot. Belgique 30(1): 302. 1891. TYPE: COSTA RICA: Paramos de Buena Vista, dans la règion super sylvatique, 5000 m, *Pittier 3495* (HOLOTYPE: G; ISTOYPES: BR! CR!).

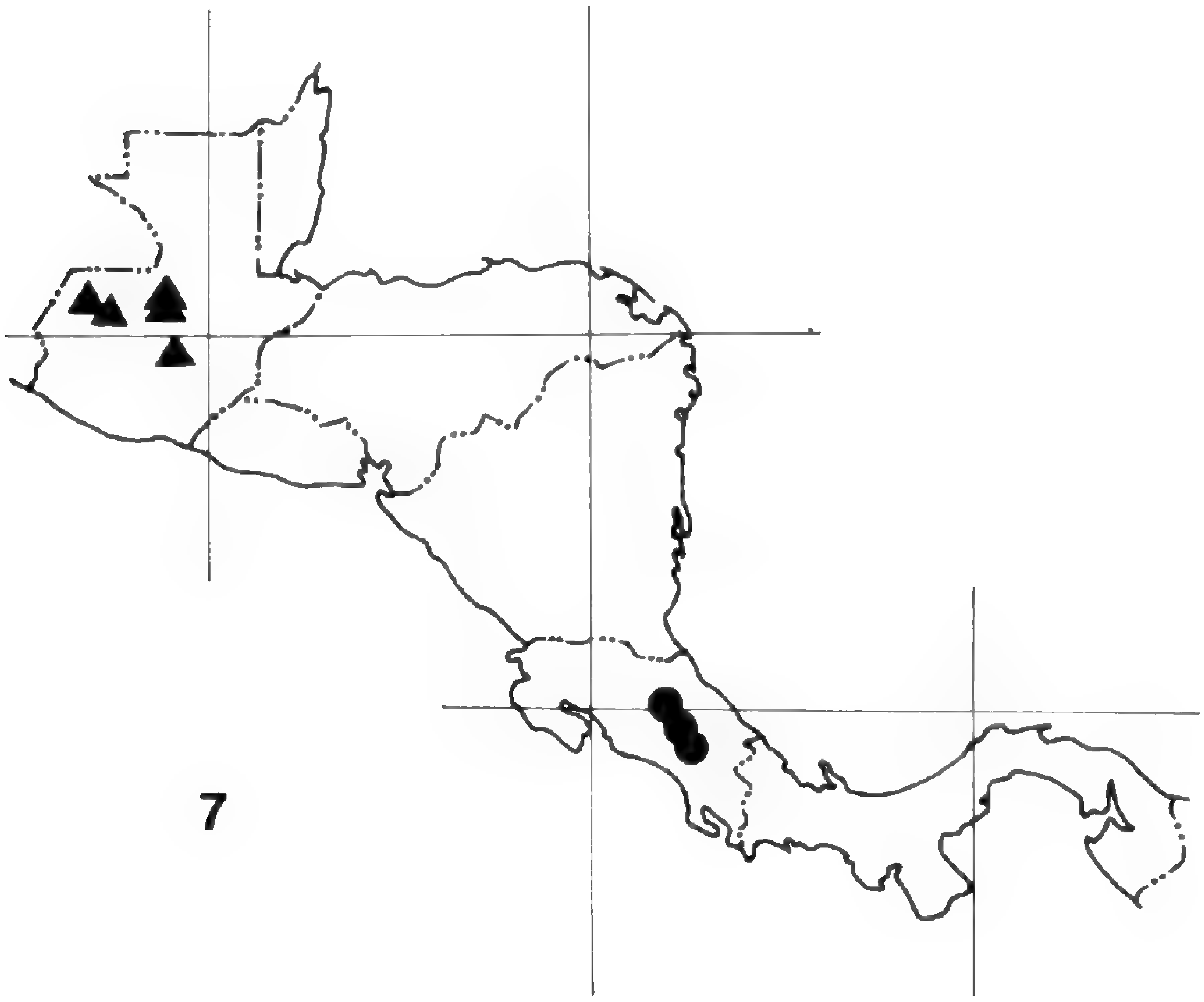
Terrestrial shrubs 1–6 m tall; stems densely to sparsely pilosulous, hairs spreading, whitish-yellow to yellowish-orange. Leaves membranaceous, elliptic to oblanceolate, (5.3)5.5–14(14.5) cm long, 1.5–5.5 cm wide, pilosulous; petioles 0–10 mm long. Inflorescences racemose or somewhat paniculate; racemes 1–6, simple, dense, sometimes aggregated terminally, 6–15(17) cm long; axes and pedicels pilosulous; bracts lance-ovate, 3–4(7.5) mm long, moderately puberulent, ciliate; bracteoles 1/3–1/2 the length of the bracts. Flowers borne on pedicels (1.8)2–3 mm long; outer sepals lanceolate

Table 1. Summary of the distinctions between *Monnina sylvatica* and *M. parasylvatica.*

CHARACTER	*M. sylvatica*	*M. parasylvatica*
Pubescence	puberulent to tomentulose	puberulent
Terminal raceme	usually simple, rarely with 1–2 branches	usually compound, with 3 or more branches
Floral bracts	narrowly lanceolate, (2.0)2.5–5.0(6.5) mm long	lanceolate, 1.5–3.2(4.0) mm long
Staminal sheath	2.5–4.0(4.5) mm long	2.0–2.5 mm long
Keel	(3.2)4.0–6.0 mm long, 2.5–3.2 mm high	(3.2)3.5–4.0(4.5) mm long, 2.0–2.6 mm high

to lance-ovate, glabrate, ciliate; upper sepal often bent to about 90 degrees near the apex, 4–5.5(7) mm long, lower sepals (3.4)4–5(5.5) mm long, free; inner sepals (wings) (5.5)6–7 mm long, 4.5–5.5 mm wide, glabrous to minutely puberulent within, ciliate basally; keel (6.5)6.8–8(8.8) mm long, 3.5–4.5(5) mm high, glabrous or sometimes puberulent within, ciliate basally, dull greenish to yellow; stamen-petal sheath 4.2–5.5 mm long, (5.2)6.2–8 mm diagonally, moderately pubescent, slightly to strongly pilose abaxially; filaments 0.8–1.8 mm long; ovary glabrous or pilosulous basally and sometimes along upper margin; style (2.4)2.6–3.2 mm long from curve to apex. Dried fruits oblong, 7–8.5(9.5) mm long, (3.5)4–4.5 mm wide, pitted, narrowly ridged marginally; pedicels elongating only slightly as fruit develops.

DISTRIBUTION: Cordillera Talamanca and Volcán Irazú, Costa Rica (Cartago, San José), 2000–3000 m. Flowering Jan.-Sept., Dec. Distribution map, Figure 7.



7

Figure 7. Distribution of *Monnina crepinii* (circles) and *M. guatemalensis* (triangles) in Central America.

Monnina crepinii has the largest flowers of the genus (Chodat, 1897). It is easily recognized by its large flowers, simple dense racemes that are sometimes aggregated terminally, lanceolate or very narrowly ovate sepals, and spreading, often yellowish, pilosulous pubescence. This species is presently known only from Volcán Irazú and the northern portion of the Cordillera Talamanca of Costa Rica. Only one specimen (*Wilbur 25456*, DUKE) was seen from Volcán Irazú.

The differences between *Monnina crepinii* and the other pilosulous or tomentulose species of Central American *Monnina* are discussed in the treatment of *M. guatemalensis.*

Blake (1924) apparently did not examine any specimens of *Monnina crepinii* and considered it a doubtful species. Standley included it in his treatment for Costa Rica (1937) with the notation that he had seen no specimens. However, it appears to be abundant within a rather restricted range.

SELECTED SPECIMENS EXAMINED: **Costa Rica:** CARTAGO: km 75, about 21 km NW of Villa Mills along Interamerican Highway, *Wilbur & Stone 8787* (DUKE, F, GH); NE flank of Volcán Irazú in saddle between Irazú and Cerro Alto Grande, near Lechería San Gerardo, *Wilbur 25456* (DUKE); near El Cañon, 40 km S of Cartago, *Williams et al. 28229* (BM, F, NY); SAN JOSÉ: Cerro region, on CR 2, 2.2 km N of La Georgina, *Davidson 7242* (CAS, F, MO, NY, US).

5. **Monnina guatemalensis** Chodat, Bull. Herb. Boissier 4: 249. 1896. TYPE: GUATEMALA: Alta Verapaz: Cobán, *von Tuerckheim s. n.* (HOLOTYPE: K).

Terrestrial shrubs 1–3 m tall; stems pilosulous, hairs widely spreading, often golden to orange-yellow. Leaves somewhat coriaceous, elliptic to obovate, (5)5.5–11.5(12) cm long, (2)2.5–5(8) cm wide, sparsely pilosulous; petioles 2–7 mm long. Inflorescences racemose; racemes 2–8 or rarely more, simple, aggregated terminally, 7–17 cm long; axes and pedicels pilosulous; bracts lanceolate to narrowly lance-ovate, acuminate, 4–6.5 mm long, glabrous or sparsely puberulent, ciliate; bracteoles 1/2–1/3 as long as the bracts, often scarious. Flowers on pedicels 1–1.5 mm long; outer sepals lance-ovate to ovate, usually strongly conduplicate, glabrous to sparsely puberulent, ciliate, upper sepal 3.2–4 mm long, lower sepals 2.5–4 mm long, free, often a little asymmetric with the midvein slightly below the center; inner sepals (wings) 4–4.8 mm long, 3.2–3.6 mm wide, glabrous, ciliate; keel 4–4.6 mm long, 2.5–3.5 mm high, glabrous or rarely sparsely puberulent within, ciliate; stamen-petal sheath 2.5–3(3.2) mm long, 3.8–4.8 mm diagonally, moderately pubescent, marginally pilosulous, moderately pilose abaxially; ovary glabrous, style 1.5–2 mm long from curve to apex. Dried fruits elliptic, (6)6.5–8 mm long, (3.5)4–4.5(5) mm wide, pitted, lower margin narrowly ridged; pedicels elongating only slightly as fruit develops.

DISTRIBUTION: Moist to wet forests and thickets, Mexico (Chiapas) and Guatemala (Alta Verapaz, Baja Verapaz, El Quiché, Huehuetenango), 1200–1500 m. Flowering Jan.–May, July–Aug., Nov. Distribution map, Figure 7.

Monnina guatemalensis is characterized by its golden-brown to orangish-yellow pilosulous pubescence, long lanceolate floral bracts that considerably exceed the flower buds which they subtend, broadly elliptic coriaceous leaves, and simple racemes that are often aggregated terminally. The flowers on dried specimens are usually rosy rather than bluish, although labels describe them as purplish to blue-violet. The species is known only from Guatemala and adjacent Mexico.

Species that might be confused with *Monnina guatemalensis* are the other densely pilosulous or tomentulose species of *Monnina* in Central America: *M. crepinii* and the montane form of *M. xalapensis*, both of Costa Rica and Panama; *M. ciliolata* of Mexico; and *M. ferreyrae* of Honduras and Nicaragua. The Costa Rican form of *M. xalapensis* is distinguished by its narrowly elliptic leaves, ovate or lance-ovate bracts that are about equal in length to the flower buds, and generally few, axillary, loose racemes. *Monnina crepinii* usually has oblanceolate leaves, lance-ovate bracts about equal in length to the flower buds, long lanceolate sepals, and large flowers in rather congested racemes. *Monnina ciliolata* DC., known only from central Mexico, is characterized by stems that are loosely tomentulose or pilosulous with whitish or whitish-yellow hairs, lanceolate to lance-obovate leaves, short ovate bracts, very short rounded sepals, and few simple racemes. *Monnina ferreyrae* is similar to *M. guatemalensis* in its long lanceolate floral bracts and yellowish pilosulous pubescence, but *M. ferreyrae* has narrower and generally smaller leaves, inflorescences composed of a few simple racemes, inner sepals (wings) that are often puberulent on the outer surface, and pedicels with appressed rather than spreading pubescence.

Comparatively few specimens of *Monnina guatemalensis* were seen. Most of these date from the explorations of the 1930's and 1940's, which is surprising considering the extensive recent collecting in Guatemala and Chiapas.

Selected specimens examined: **Mexico:** CHIAPAS: near Rancho Buena Vista near Pantelho, *Ton 3664* (F); **Guatemala:** ALTA VERAPAZ: Cobán, *von Tuerckheim 11.674* (BR, CAS, F, GH, NY); BAJA VERAPAZ: mountainside N of Divide, N of Santa Rosa, *Standley 69880* (F); EL QUICHÉ: Valley, Nebaj, *Skutch 1773* (A, F, NY); HUEHUETENANGO: between Yulhuitz and Maxbal, Sierra de los Cuchumatanes, *Steyermark 48674* (F).

6. **Monnina xalapensis** Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 5: 414. 1821. Type: mexico: Xalapa, *Humboldt & Bonpland s.n.* (holotype: p). *Monnina aestuans* ε. *xalapensis* Kuntze, Revis. Gen. Pl. 48. 1891.

Hebeandra euonymoides Bonpland, Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 2: 42. 1808. Type locality: Xalapa, Mexico. *Non M. euonymoides* Schlechtendal, Linnaea 14: 380. 1840.

?*Monnina bifurcata* DC., Prodr. 1: 339. 1824. Type locality: Mexico.

?*Monnina obscura* G. Don, Gen. Hist. 1: 367. 1831. Type locality: Mexico.

Monnina euonymoides Schlechtendal, Linnaea 14: 379. 1840. Type: Mexico: Chiconquiaco, 29 Sept., *Schiede s.n.* (holotype: hal).

Monnina pittieri Chodat, Bull. Soc. Roy. Bot. Belgique 30: 303. 1891. Lectotype: Costa Rica: Cartago: near Esmeralda, *Pittier 1885* (lectotype: g; isolectotype: br!).

Monnina latisepala Blake, N. Amer. Fl. 25: 376. 1924. Type: Panama: Chiriquí: Alto de Cuesta, around Camp Aguacatal, eastern slope of Volcán Chiriquí, *Pittier 3119* (holotype: us).

Monnina blakeana Standley, Fieldiana, Bot. 28: 593. 1937. Type: Costa Rica: Cartago: Dulce Nombre, *Standley 35810* (holotype: us, photographs f!, gh!; isotype: f!).

Terrestrial, slender, bushy-topped shrubs or suffrutescent herbs 1–7 m tall; stems strigillose or puberulous, hairs whitish, appressed or widely spreading. Leaves membranaceous, elliptic to oblanceolate, (2.5)4–11(15) cm long, 0.5–6 cm wide, strigillose to puberulent or pilosulous; petioles 1–5 mm long. Inflorescences racemose; racemes simple, 1–4, 3–15 cm long, strigillose or puberulous or occasionally pilosulous; bracts lance-ovate to very widely ovate, (1.2)1.5–3.5 mm long, glabrate to moderately puberulent, cilioliate; bracteoles narrowly ovate to lanceolate, usually 1/2 or more as long as the bracts. Flowers on pedicels 0.8–2.5(3) mm long; outer sepals lance-ovate to very broadly ovate, glabrate to puberulent, ciliate, commonly 3–5 veined but up to 9–11 veins in very broadly ovate forms, upper sepal (1.2)1.5–4(4.2) mm long, lower sepals (1.2)1.5–3.5(4) mm long, free; inner sepals (wings) (3.5)4–6(6.5) mm long, 3–5(5.5) mm wide, glabrous or puberulent within, ciliate basally or more commonly throughout; keel (3.8)4.5–6.5(7) mm long, (2)2.5–3.8(4) mm high, glabrous or sparsely puberulent within, ciliate basally, suffused with yellow apically; stamen-petal sheath 2.5–4(4.5) mm long, (3.6)4–6.5 mm diagonally, moderately pubescent, often slightly pilose abaxially; ovary glabrous or sparsely strigillose; style 2–2.5(3) mm long from curve to apex. Dried fruits elliptical to globose, (5.5)6.5–8 mm long, 3.5–4 mm wide, pitted, lower margin rounded or slightly ridged; pedicels elongating only slightly as fruit develops.

DISTRIBUTION: Second growth forests, dry montane and cloud forest areas, southern Mexico to Panama, (1000)1300–3300 m. (Guatemala: Alta Verapaz, Baja Verapaz, Chimaltenango, El Quiché, Guatemala, Huehuetenango, Quezaltenango, Sacatepequez, San Marcos, Sololá, Totonicapán; Honduras: Ocotepeque, El Sonsonante; Nicaragua: Granada, Jinotega, Matagalpa; Costa Rica: Alajuela, Cartago, Heredia, San José; Panamá: Chiriquí). Flowering throughout the year. Distribution map, Figure 8.

Monnina xalapensis is treated here as a wide-ranging, variable species with several well-marked but not completely distinct geographic forms. It is generally characterized by elliptic leaves, few simple racemes, lance-ovate to very broadly ovate sepals, and lance-ovate bracts equal to or only a little longer than the flower buds they subtend. Amount and nature of pubescence, leaf size, flower size, sepal shape, and raceme number vary widely.

Typical *Monnina xalapensis* has lance-elliptic to oblanceolate leaves, strigillose pubescence, ovate to lance-ovate bracts about 1.5–2 mm in length with rounded or sometimes acute apices, pedicels about 0.8–1.5 mm long, ovate outer sepals about 1.5–2.5 mm long, and glabrous or sparsely strigillose ovaries and fruits. This form is found throughout the range of the species.

The plants described as *Monnina pittieri* by Chodat appear to be an extreme form that is not clearly separable from *M. xalapensis.*

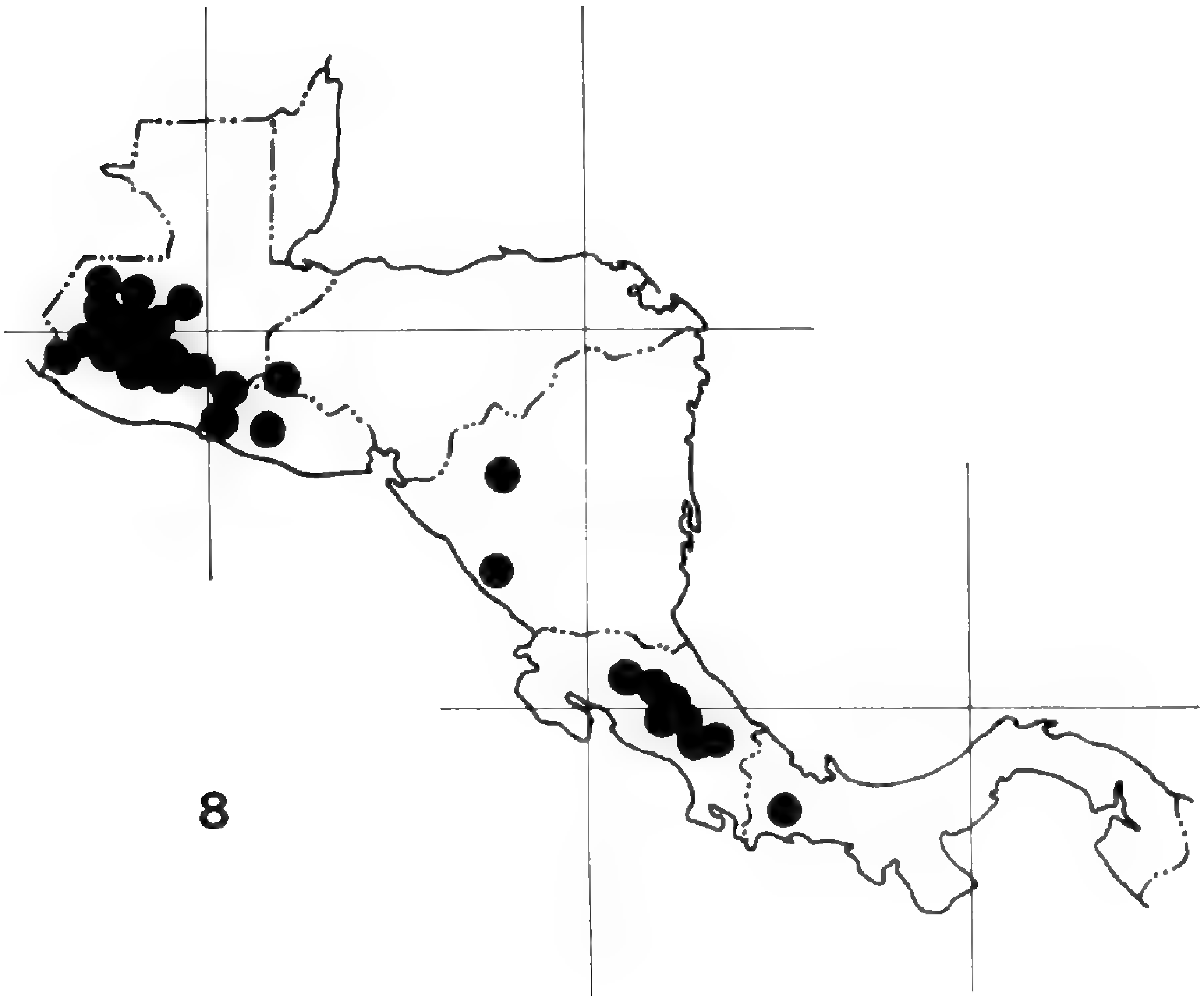


Figure 8. Distribution of *Monnina xalapensis* in Central America.

This form is found in the mountains of Costa Rica and northern Panama and is most strongly expressed by plants from thickets near or above treeline. It is distinguished by very slender supple branches, short, very narrowly elliptic leaves (typically 2.5–4.5 cm long and 0.5–1.5 cm wide), whitish pilosulous pubescence, carmine red leaf margins and petioles, and short, usually solitary, loose racemes with pedicels about 1.5–3 mm long. The montane form and the typical form overlap widely in pubescence, leaf size, inflorescence arrangement, flower size, and other characters that have been used to separate these species. There appears to be no reliable way to distinguish between these taxa. The characters are strongly correlated only at comparatively high and low elevations, and intermediates are common at middle elevations. It seems likely that there is some ecotypic adaptation correlated with pubescence and leaf size, because comparatively glabrous and large-leaved individuals are occasionally encountered in sheltered areas at higher elevations. There is no consistent "suite" of characters that distinguishes this ecotype, however, and it is not recognized taxonomically here. The three specimens cited by Chodat in his original description of *M.*

pittieri demonstrate this problem, since each shows only some of the characters he used to delimit the species. Chodat considered each of these specimens a different variant of *M. pittieri.* Both Blake (1924) and Standley (1937) treated *M. pittieri* as a separate species. Blake cited "woods near Esmeralda, Costa Rica" as the type locality for this species; only one of Chodat's syntypes, *Pittier 1885*, was collected at this locale, and thus this specimen must be regarded as the lectotype.

The apically rounded or obtuse leaves of *Monnina blakeana* were thought by Standley to distinguish it as a separate species. However, obtuse or emarginate leaves are found occasionally on many specimens of *M. xalapensis*, and perhaps result from damage during development. Although Standley's specimen has only obtuse leaves, it does not appear to represent a new taxon.

In Panama, *Monnina xalapensis* has been collected only in the western province of Chiriquí. Most specimens fall into what Blake called *M. latisepala*, which is characterized by very broadly ovate outer sepals with 5–11 veins. These wide sepals are usually slightly imbricate in contrast to the narrower, usually 1–5-veined outer sepals of the more typical form of *M. xalapensis.* Additionally, the ovary and mature fruits of the *M. latisepala* form are moderately to densely strigillose and the leaves are usually elliptic-obovate. However, as with the *M. pittieri* form, separation of this from the typical *M. xalapensis* is difficult. Again, many specimens from Panama and southern Costa Rica show intermediate conditions and various combinations of the characters used to distinguish *M. latisepala.* This form is not well delimited and is not recognized taxonomically here.

The intermediate condition of several specimens (from Honduras, *Molina et al 31374*, F; from El Salvador, *Molina & Molina 12612*, F; from Costa Rica, *Jimenez M. 1188*, F, and *Wilbur 14204*, DUKE) suggests that *Monnina xalapensis* hybridizes with *M. sylvatica* or *M. parasylvatica.* These plants have long lance-elliptic, somewhat obovate leaves, simple racemose inflorescences, fruits that are nearly globose but slightly ridged marginally when dry, and short lanceolate bracts.

SELECTED SPECIMENS EXAMINED: **Guatemala:** ALTA VERAPAZ: Tactic, *von Tuerckheim 8447* (F, GH, MO); BAJA VERAPAZ: Chilasco, *Contreras 10961* (MO, US); CHIMALTENANGO: ruins of Ixinche, 3–4 km from Tecpán, *Molina & Molina 12443* (F, NY); EL QUICHÉ: Pacula Abaj, W of Chichicastenango, *Molina et al.*

16308 (F, NY); GUATEMALA: hills S of Mixco, *Williams & Molina 11763* (GH, MO); HUEHUETENANGO: Sierra de los Cuchumatanes, road to San Juan Ixcoy, *Molina et al. 16440* (F, NY, MO); QUEZALTENANGO: Cantón La Esperanza, about 6 km from San Juan Ostuncalco, *Molina et al. 16616* (F, NY, US); SACATEPEQUEZ: along road between San Lucas and Antigua, *Molina et al. 15957* (F, NY); SAN MARCOS: El Boquerón, near border of Dept. Quezaltenango, *Standley 66307* (F, NY); SOLOLÁ: mountain slopes above Lake Atitlán, *Williams et al. 25351* (F, NY, US); TOTONICAPÁN: Cerro María Tecum, Sierra Madre Mountains, 10–20 km E of Totonic, *Williams et al. 23135* (F, NY); **Honduras:** OCOTEPEQUE: Cordillera Merendón, *Williams et al. 31320* (F); **El Salvador:** CHALATENANGO: E slope of Las Esemiles, *Tucker 1003* (F, GH, NY); LA LIBERTAD: rim of Volcán San Salvador, *Williams & Molina 10621* (F, MO); SAN SALVADOR: Volcán San Salvador, road from Finca Florencia to S rim of crater, *Carlson 375* (A, F); SANTA ANA: cloud forest of Montecristo, *Molina et al. 16735* (F, NY, US); SONSONANTE: near top of Cerro Verde, *Croat 42224* (MO); **Nicaragua:** GRANADA: Volcán Mombacho, *Molina & Williams 20033* (F, NY, US, WIS); JINOTEGA: about 6 miles N of Santa María de Ostuma, beyond Hacienda La Fundador, *Wilbur & Almeda 16504* (DUKE); MATAGALPA: Cordillera Central between Aranjuez and Peor es Nada, *Molina 22980* (F, NY); **Costa Rica:** ALAJUELA: slopes of Volcán Poas, W of Vara Blanca, *Wilbur & Stone 8695* (DUKE); CARTAGO: upper slopes of Volcán Irazú, *Wilbur & Teeri 13742* (DS, DUKE, F, GH, MO, NY); Cartago-Irazú road, at road to Tierra Blanca, *Wilbur 26495* (DUKE); HEREDIA: pastures above Cerro La Cruz, 8 km NW of Heredia, *Lent 1916* (F, MO, NY, US); SAN JOSÉ: SE of Higuito along Altos de Tablazo, *Wilbur 24603* (DUKE); SW slopes along trail from Canaan to summit of Cerro Chirripo, *Evans et al. 117* (F); **Panama:** CHIRIQUÍ: about halfway between Cerro Punta and Bambito, *Wilbur et al. 10889* (DS, DUKE, F, GH, MO); Palo Alto, just E of Boquete, *Stern et al. 1085* (GH, MO, US).

7. **Monnina sylvatica** Schlechtendal & Chamisso, Linnaea 5: 231. 1830. TYPE: MEXICO: Xalapa, Oct., *Schiede s.n.* (HOLOTYPE: HAL). *Monnina aestuans β. silvatica* Kuntze, Revis. Gen. Pl. 48. 1891. Orth. var.

?*Monnina deppei* G. Don, Gen. Hist. 1: 367. 1831. TYPE LOCALITY: Mexico.

Monnina sylvicola Chodat, Bull. Soc. Roy. Bot. Belgique 30(1): 303. 1891. SYNTYPES: COSTA RICA: San José: plantations près d'Asserí, *Tonduz 1272* (G, BM!, BR!, photographs US!); bois superior du Rodeo, *Pittier 1641* (G, CR!).

?*Monnina crispata* Blake, N. Amer. Fl. 25(5): 377. 1924. TYPE: PANAMA: Chiriquí: Río Ladrilla and vicinity, above Boquete, *Pittier 3289* (HOLOTYPE: US).

Erect or occasionally clambering terrestrial shrubs or rarely bushy herbs 1–6 m tall; stems moderately to densely puberulent or tomentulose, hairs whitish or yellowish. Leaves membranaceous, elliptic to elliptic-ovate, 6.5–14(16) cm long, (1.8)2–5(6) cm wide, sparsely to moderately puberulent; petioles 3–5 mm long. Inflorescences racemose; racemes 3–10, (6)7.5–15(27) cm long, simple or occasionally the terminal raceme branched once or twice; axes and pedicels densely puberulous or tomentulose, often reddish to carmine; bracts very narrowly lanceolate, (2)2.5–5(6.5) mm long, moderately puberulent, ciliate; bracteoles 0.5–1 mm long, scarious. Flowers on pedicels 0.8–1.5 mm long; outer sepals ovate, hooded, moderately puberulent, ciliate, upper sepal 1.8–2.8(3.2) mm long, lower sepals 1–2(2.5) mm long, free; inner sepals (wings) 3–5 mm long, 3–4.2 mm wide, glabrous to very sparsely puberulent, ciliate basally; keel (3.2)4–6 mm long, 2.5–3.2(4) mm high, glabrous or moderately puberulent within, yellow-green; stamen-petal sheath 2.5–4(4.5) mm long, (3.5)4–5(6) mm diagonally, moderately pubescent, sometimes pilose abaxially; ovary glabrous; style 1.5–2(2.5) mm long from curve to apex. Dried fruits elliptic to ovate, 6.5–8 mm long, 3–5(6) mm wide, pitted, margins narrowly ridged; pedicels elongating only slightly as fruit develops.

DISTRIBUTION: Roadsides, thickets, hedgerows, and disturbed areas, central Mexico to western Panama (600)700–2000(2400) m. (Guatemala: Chiquimula, El Quiché, Quezaltenango, San Marcos, Suchitepequez; Honduras: Ocotepeque, Olancho; El Salvador: Santa Ana; Nicaragua: Chontales, Matagalpa; Costa Rica: Alajuela, Cartago, Heredia, Puntarenas, San José; Panamá: Chiriquí.) Flowering throughout the year. Ill. Ann. Missouri Bot. Gard. 56(1): 26, fig. 2. 1969. Distribution map, Figure 9.

Monnina sylvatica is a widespread and rather common species of comparatively low elevations. The characters that distinguish it are discussed in the treatment of *M. parasylvatica*.

Chodat (1896, 1897) separated *Monnina sylvicola* from *M. sylvatica* on the basis of its connate lower sepals. This is inaccurate because the type specimen has free lower sepals.

It is possible that *Monnina sylvatica* hybridizes with *Monnina xalapensis*, as was suggested by Lewis & Herrera-MacBryde (1969). While the one speciment they cite as a hybrid (*Dwyer et al. 435*, MO) is within the range of variation seen in Panamanian *M. xalapensis*, several other specimens are intermediate. These are listed in the treatment of *M. xalapensis*.

SELECTED SPECIMENS EXAMINED: **Guatemala:** CHIQUIMULA: Montaña Norte to El Justal, Cerro Brujo, SE of Concepción de Las Minas, *Steyermark 31070* (F); EL QUICHÉ: Nebaj, *Skutch 1773* (F); QUEZALTENANGO: along Quezaltenango-Colomba road, *Skutch 1975* (A); SAN MARCOS: outer slopes of Volcán Taju-

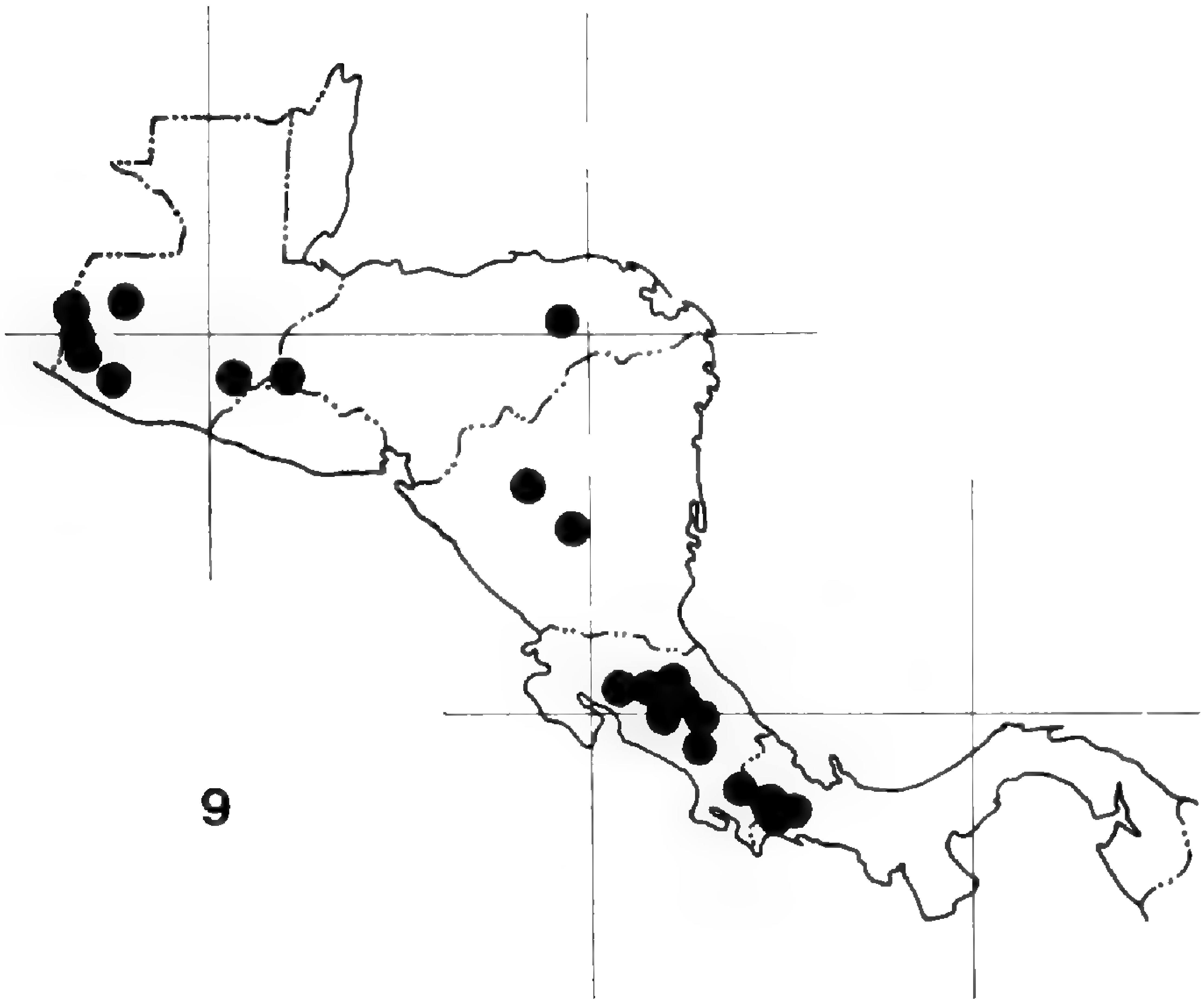


Figure 9. Distribution of *Monnina sylvatica* in Central America.

mulco, Sierra Madre mountains, *Williams et al. 26857* (NY); SUCHITEPÉQUEZ: Finca Moca, *Skutch 2105* (F); **Honduras:** OCOTEPEQUE: El Portillo, Cordillera Merendón, *Molina 22355* (F); OLANCHO: 85°25′ W, 15°15′ N, Río Wampu, *Nelson & Clewell 525* (MO); **El Salvador:** SANTA ANA: cloud forest of Montecristo, *Molina & Molina 12612* (F); **Nicaragua:** CHONTALES: Santo Domingo, *Narvaez et al. 3399* (F, GH, NY); MATAGALPA: La Fundadora, Cordillera Dariense, *Hall & Bockus 7939* (GH, MO); **Costa Rica:** ALAJUELA: La Palma de San Ramón, *Brenes 4055* (F, MO, NY); CARTAGO: vicinity of Bonilla Arriba, about 13 km by road NE of Santa Cruz, *Wilbur 25534* (DUKE); HEREDIA: between San Rafael and Río San Rafael, *Utley & Utley 4170* (DUKE); PUNTARENAS: near Finca Las Cruces, S of San Vito de Java, *Raven 21870* (DS, F); SAN JOSÉ: between Río Alhambre and Río Conejo, vicinity of San Gabriel and Frailes, *Jimenez M. 2591* (DS, F, MO, WIS); **Panama:** CHIRIQUÍ: road to volcano, N of Concepción, *Skog et al. 4012* (GH, MO).

8. **Monnina ferreyrae** Taylor, *sp. nov.*

Frutex vel suffrutex 0.5–2 m altus, pilosulus, pilis patulis; folia membranacea, elliptica usque obovata, 5.5–11.5 cm longa, 2–4 cm lata, petiolis 1–5 mm longis; racemi simplices, solitarii vel interdum dua usque quator, 6–15 cm longi; bracteae anguste ovatae, apice acuminatae, 4–7.5 mm longae, pubescentia patula; sepala externa libera, triangularia usque ovata, 3–4 mm longa; carina 4.5–5.5 mm longa; lamina 2.5–3.5 mm longa ex staminibus et petalis constata; ovarium glabrum.

TYPE: HONDURAS: Morazán: mixed dense and wet cloud forest on mountain La Tigra, SW of San Juancito, 1800–2100 m, *Molina et al. 16995* (Holotype: NY; Isotypes: F, NY, US).

Terrestrial shrubs or suffrutescent herbs 0.5–2 m tall; stems densely pilosulous, hairs widely spreading, usually golden to orangish-brown. Leaves membranaceous, elliptic to obovate, (5.5)6-11.5 cm long, 2–4 cm wide, moderately to sparsely pilosulous; petioles 1–5 mm long. Inflorescences racemose; racemes 1–2, simple, 6–11(15) cm long; axes and pedicels densely pilosulous; bracts lanceolate to narrowly lance-ovate, attenuate, 4–7.5 mm long, rather densely pilosulous, ciliate; bracteoles narrowly lanceolate, 1.5–2 mm long, scarious. Flowers on pedicels 0.8–1.2 mm long; outer sepals triangular-ovate, sparsely to moderately puberulent, ciliate; upper sepal 3.5–5 mm long, lower sepals 3–4 mm long, free; inner sepals (wings) 4.5–5 mm long, 3–4 mm wide, glabrous or moderately puberulent, ciliate; keel 4.5–5.5 mm long, 3–3.5 mm high, glabrous to sparsely puberulent within, occasionally ciliate basally; stamen-petal sheath 2.5–3.5 mm long, 3–4.5 mm diagonally, moderately pubescent, glabrous to sparsely pilose abaxially; ovary glabrous; style 2–2.5 mm long from curve to apex. Dried fruits oblong to obovate, 6–8 mm long, 4–4.5 mm wide, pitted, lower margin and occasionally upper also ridged; pedicels elongating only slightly as fruit develops.

DISTRIBUTION: Cloud forests, moist open forests, and thickets; Honduras (Cortes, El Paraiso, La Paz, Lempira, Morazán) and Nicaragua (Matagalpa), 1500–2000 m. Flowering Feb.–Nov. Habit, Figure 3. Distribution map, Figure 5.

This previously undescribed species is characterized by elliptic to obovate membranaceous leaves, pilosulous pubescence, few simple racemes, and attenuate lanceolate floral bracts. It is presently known only from Honduras and Nicaragua. The specific epithet honors Professor Ramon Ferreyra, who has studied the numerous South American species of this genus.

Monnina ferreyrae is distinguished from most of the other species of *Monnina* in Central America by its dense, often orangish, pilosulous pubescence and its lanceolate floral bracts. The distinctions among the pilosulous Central American species of *Monnina* are discussed in the treatment of *M. guatemalensis.*

SELECTED SPECIMENS EXAMINED: **Honduras:** CORTES: Montaña de Cusuco, Cordillera Idalfonso, *Molina 7235* (F, GH, US); EL PARAISO: Mt. Yuscarán, *Molina 626* (F, GH); LA PAZ: Montaña Verde, Cordillera Guajiquiro, *Molina & Molina 24382* (F); LEMPIRA: Montaña Puca, between Guatan and Cuabano, *Molina 12909* (F): MORAZÁN: Cerro de Uyuca, near Zamorano, *Webster et al. 11874* (F, GH, MO); slopes of La Montañita, *Williams & Molina 10424* (DS, F, MO); **Nicaragua:** MATAGALPA: road to La Fundadora, N of Santa María de Ostuma, Cordillera Central, *Williams et al. 23432* (F).

EXCLUDED SPECIES

Monnina pterocarpa Ruiz & Pavon, Syst. Fl. Peruv. Chil. 174. 1798. Blake (1924) cited as doubtful Hemsley's record of this Peruvian species from Panama. No specimens or further records of this species have been seen; the report is possibly of a chance introduction or else a mistake.

Monnina brachystachya Grisebach, Abh. Koenigl. Ges. Wiss. Gottingen 19: 75. 1874. This species was originally described from Argentina. Larsen (1967) gives its range as "from Mexico to Argentina," but presents no documentation. No specimens from Central America were seen, nor is it reported in Ferreya's treatments for northern South America (1946; 1953a; 1953b; 1957).

ACKNOWLEDGMENTS

I thank the curators of the herbaria listed above, who promptly and courteously made specimens available. I am greatly indebted to a number of people for their help, including John MacDougal, Sherri Herndon, Mitsu Suyemoto, Gordon Tucker, Melvin Turner, Tom Wendt, and Mark Wetter. Special thanks go to Dr. Robert Wilbur, who suggested this problem, for his patient, invaluable help.

LITERATURE CITED

BLAKE, S. F. 1924. Polygalaceae. N. Amer. Fl. 25: 374–379.

CHODAT, R. H. 1896. Conspectus systemicus generis Monninae. Bull. Herb. Boissier 4: 243 253.

______. 1897. Polygalaceae. *In*: A. Engler & K. Prantl, eds. Die Naturlichen Pflanzenfamilien III(4): 323–345.

Ferreyra, R. 1946. A revision of the Peruvian species of *Monnina*. J. Arnold Arbor. 27: 123–168.

———. 1953a. A revision of the Ecuadorian species of *Monnina* (Polygalaceae). Lloydia 16: 193–226.

———. 1953b. A revision of the Colombian species of *Monnina*. Smithsonian Misc. Collect. 121: 1–5.

———. 1957. A revision of the Venezuelan species of *Monnina*. Brittonia 9: 9–17.

Humboldt, A. von, A. Bonpland & C. S. Kunth. 1821. Polygalaceae. Nova genera et species plantarum, vol. 5: 392–423.

Inouye, R. 1977. I've got them *Monnina* blues (and yellows). *In*: Tropical Biology 77-4. Organization for Tropical Studies, Durham, N.C.

Larsen, K. 1967. Cytological studies on *Monnina*. Feddes Repert. 75: 43–46.

Lewis, W. H. and O. Herrera-MacBryde. 1969. Polygalaceae. *In*: Flora of Panama Pt. VI. Ann. Missouri Bot. Gard. 56: 9–28.

Ruiz, H. and J. Pavon. 1798. Systema vegetabilium florae peruvianae et chilensis.

Standley, P. C. 1937 Polygalaceae. *In:* Flora of Costa Rica. Fieldiana, Bot. 18: 592–596.

———, and J. A. Steyermark. 1949. Polygalaceae. *In:* Flora of Guatemala Pt. VI. Fieldiana, Bot. 24: 5–22.

DEPARTMENT OF BOTANY
DUKE UNIVERSITY
DURHAM, N.C. 27706

A REVISION OF *RIBES* L. SUBG. *GROSSULARIA* (MILL.) PERS. SECT. *GROSSULARIA* (MILL.) NUTT. (GROSSULARIACEAE) IN NORTH AMERICA[1]

QUINN P. SINNOTT[2]

ABSTRACT

The genus *Ribes* has not been monographed on a worldwide basis since 1907, and this revision of sect. *Grossularia* is the first in a series of studies on this economically important genus. In the present study over 11,000 herbarium specimens were examined and extensive fieldwork conducted. Herbarium specimens examined provided detailed information about variation on a broad geographic scale in addition to allowing the distribution of each species to be plotted. Herbarium based studies were supplemented with field studies that provided an understanding of the variation within the section at the population level. Ability to contrast the intrapopulational variation indicated by field studies with broad interpopulational variation found from herbarium specimens allowed the assignment of taxonomic rank with confidence. Field studies were conducted through most of the range of the section in North America. A sample of herbarium specimens representing most of the variance within the section was analyzed by multivariate numerical taxonomic methods.

The seventeen species recognized in sect. *Grossularia* in North America by Berger in 1924 are reduced to nine species, one having five subspecies, one with two varieties, and one with three varieties. The subspecies represent new combinations and one of the varieties has been re-established.

Key Words: *Ribes*, *Grossularia*, gooseberry, currant, revision, North America

INTRODUCTION

Ribes L. (Grossulariaceae) is a cosmopolitan genus of about 150 species native to the temperate zones of North America and Eurasia, the northwestern part of Africa and the Andes in South America. Several authors divide the genus into two genera, *Ribes* L. (the currants) and *Grossularia* Mill. (the gooseberries). Most recent authors generally accept only the one genus, *Ribes*, with several subgenera.

---

[1] Scientific Article No. A-3518, contribution No. 6591 of the Maryland Agricultural Experiment Station.

[2] Present address: Database Management Unit, Germplasm Resource Information Network, Plant Genetics and Germplasm Institute, Bldg. 001, BARC-WEST, USDA, ARS Beltsville, MD 20705.

The last worldwide monograph of *Ribes* was that by Janczewski (1907) who divided the genus into six subgenera with 133 species and 19 hybrids. In the 70-plus years since this monograph, enough new information about the genus has accumulated that Spongberg (1972) concluded that *Ribes* "is in need of a thorough taxonomic revision, including typification, with the application of current rules of nomenclature."

This project involves a revision of one of the sections in *Ribes* along with historical and nomenclatural discussions of the entire genus.

HISTORY OF THE GENUS

The earliest literature reference to the currants and gooseberries is apparently the "Spina Ceanothus" of Theophrastus (Dodoens, 1578). In his herbal, Dodoens discussed two types of gooseberries and their medicinal value, gooseberries that had "whitish branches, set full of sharpe prickles" and red gooseberries, whose flowers were in racemes or "a great many hanging downeward by small strings or stems." This was an early recognition of the fundamental division between the gooseberries with spiny stems and few flowers, and the currants with smooth stems and racemose flowers. This distinction eventually led many authors to recognize two genera, *Grossularia* (the gooseberries) and *Ribes* (the currants).

Just how the generic name *Grossularia* became associated with the gooseberries is uncertain, but both Dodoens (1578) and Parkinson (1640) noted the French colloquialism for currants and gooseberries was "groseille" or "groseiller." Parkinson indicated that the French word came from the resemblance of gooseberries to "*Grossus* small greene figges", while Miller (1731) and Don (1834) believed that *Grossularia* was derived from the Latin "*grossus*", meaning thick, due to the characteristic thick skin of the fruit in some species.

The generic name *Ribes*, for the currants, apparently has a clearer derivation. Parkinson (1640) noted that "the name of *Ribes* and *Ribesius frutex* is generally given to these plants for some likeness. . .to the *Ribes* of Serapio". He qualified this by stating it was probably an incorrect reference to the *Ribes* of Serapio. Coville (1935) believed *Ribes* was derived from the Arabic "ribas" (reebahs), a name for a species of rhubarb used in preparation of a syrup by mixing sugar with the juice of the stems. This medicinal concoction was imbibed as a general tonic. Coville speculated that after the Arabic conquest of Spain in the Eighth Century A.D. the conquerors were unable to find the species of rhubarb they called ribes or "robb ribas". Instead, they substituted the juice from the fruit of a red currant which produced a similarly tart concoction. In Europe, at least, "ribas" became associated with the currants and persisted as the common name.

Tournefort (1700), the "father of the genus concept" (Jones and Luchsinger, 1979), chose *Grossularia* as the generic name for both currants and gooseberries. Undoubtedly his French background influenced his choice of that name over *Ribes.* Miller (1731) used both generic names in the first edition of *The Gardener's Dictionary.* Dillenius (1732) also recognized two genera, using an alternate spelling of *Ribes, Ribesium,* for the currants. Linnaeus (1737, 1738) concurred with Tournefort and placed currants and gooseberries in a single genus although he chose *Ribes* rather than *Grossularia.* In 1753, Linnaeus continued his usage of *Ribes,* making it the valid generic name according to the modern rules of nomenclature (Stafleu et al., 1978). It is of interest to note that Linnaeus gave the Arabic species of rhubarb used in the syrupy concoction the name *Rheum ribes* in recognition of the long association of this common name with that plant (Coville, 1935). Linnaeus recognized the natural subdivision within *Ribes,* listing the currants under "Ribesia inermia" and the gooseberries under "Grossularia aculeata", although neither category carried nomenclatural rank (Brizicky, 1969). A total of eight species was listed in *Species Plantarum* (Linnaeus, 1753), three of which were found in North America, *Ribes rubrum, R. oxyacanthoides* and *R. cynosbati.* Some of these species were known long before 1753 as both Plukenet (1705) and Dillenius (1732) had American material in hand and had proposed polynomials for *R. oxyacanthoides.* Philip Miller (1754) retained both genera in his fourth abridged version of *The Gardener's Dictionary,* validating *Grossularia* as a generic name.

The currants and gooseberries were variously treated during the 18th and 19th centuries. Adanson (1763) accepted only *Grossularia* and referred it to the family Portulacaceae. Scopoli (1772) also accepted the sole genus *Grossularia,* without family placement, as did Gaertner (1789). Medikus (1789) differed by recognizing two genera, *Grossularia* and *Ribesium.* Jussieu (1789), like Linnaeus, accepted only *Ribes,* placing the genus in Cactaceae. Ventenant (1799) was the first to refer *Ribes* to Saxifragaceae, the family where most recent workers have placed the genus. Lamarck and De Candolle (1805) moved *Ribes* to the newly segregated family Grossulariaceae, a name now conserved (Stafleu et al., 1978). They recognized the basic subdivision within the genus between the currants and gooseberries, but failed to propose taxonomic categories. Persoon (1805) finally established two subgenera (cf. Table 1), *Ribesia* (= *Ribes*) and *Grossularia* (Brizicky, 1969; Spongberg, 1972).

In North America, new species were being described as a result of numerous botanical explorations in the 19th century. Michaux (1803) recognized nine species of *Ribes,* seven of which were new, with five of the nine belonging to sect. *Grossularia.* Pursh (1814), a decade later, described 17 species, including three new species from western America collected by Lewis and Clark. Nuttall (1818) proposed two sectional names in *Ribes,* sect. *Ribesia* (= sect. *Ribes*) and sect. *Grossularia,* with ten species in the former and seven in the latter. Hooker (1832) distinguished 22 species of *Ribes* in the boreal regions of North America.

Much as knowledge of *Ribes* was increasing in North America, so too was information on the genus increasing elsewhere. Richard (1823), in a discussion of medicinally important species, established the new sectional name *Botrycarpum.* Berlandier (1826) monographed the genus *Ribes* while a student of De Candolle; his efforts were later used by De Candolle (1828) in reviewing Grossulariaceae in the *Prodromus.* In Berlandier's work, four sectional names were recognized: *Robsonia* and *Symphocalyx* were newly proposed and *Ribes* and *Grossularia* were earlier sections proposed by Nuttall. A total of 53 species was recognized, 16 of which were new. Reichenbach (1828) divided *Ribes* into four subgenera (Brizicky, 1969), raising the Berlandier sections *Robsonia* and *Symphocalyx* and retaining the two Persoon subgenera *Ribes* and *Grossularia.* Don (1834) recognized 66 species of *Ribes* distributed in four sections, *Grossularia, Botrycarpum, Ribesia* and *Symphocalyx.*

Spach (1835, 1838) presented two revisions of Grossulariaceae, and in doing so created a number of complex nomenclatural problems. In his first review he published four supraspecific entities which appear to be new genera. In his second review, he clearly established those entities as genera with the statement, "Cette famille se compose des genres suivants," followed by a list of eight

Table 1. Summary of nomenclatural information for genera, subgenera, and sections of *Ribes*. Asterisks denote the first author to validly publish the basionym. Columns with more than one entry under a given rank indicate alternate combinations. In combinations, R = *Ribes*, and G = *Grossularia* as genera. Lectotypes designated here are indicated by (!), previously designated lectotypes have author citations. Types designated by author of basionym are indicated by ^{1}, and types designated by inclusion of a single species or Art. 22.4 are indicated by ^{2}. # indicates a combination cited without basionym or included taxa and therefore invalid.

BASIONYM	GENUS	SUBGENUS	SECTION	TYPE
Andina			*R*. subg. *Parilla* sect. *A*. Jancz., 1905*	*R. andicola*^{2}
Berisia		*R*. subg. *B*. (Spach) Jancz. 1903	*R*. sect. *B*. Spach, 1838* *R*. subg. *B*. sect. *B*. *(Spach)* Jancz., 1906b nom. superfl.	*R. alpinum* L. (!)
Botrycarpum	*B*. (A. Rich.) Reichb. 1837		*R*. *sect*. *B*. A. Rich., 1823*	*R. nigrum* L.^{2}
Calobotrya	*C*. Spach, 1835*	*R*. subg. *C*. (Spach) Jancz., 1903	*R*. subg. *Coreosma* sect. *C*. (Spach) Jancz., 1906a	*R. sanguineum* Pursh^{2}
Cerophyllum	*C*. Spach, 1838*	*R*. subg. *C*. (Spach) Keep, 1962#	*R*. subg. *Coreosma* sect. *C*. (Spach) Jancz., 1906a	*R. cereum* Dougl. (!)
Chrysobotrya	*C*. Spach, 1835*			*R. aureum* Pursh (!)
Conostylium			*R*. sect. *C*. Spach, 1838*	*R. petraem* Wulfen in Jacq. (!)
Coreosma	*C*. Spach, 1835*	*R*. subg. *C*. *(Spach)* Jancz., 1903	*R*. subg. *Coreosma* sect. *C*. (Spach) Jancz. 1906a	*R. floridum* L'Hér. (!)

Table 1. (Continued)

BASIONYM	GENUS	SUBGENUS	SECTION	TYPE
Cylindrostylium			*R.* sect. *C.* Spach, 1838*	*R. prostratum* L'Hér. (!)
Cynosbatium			*G.* sect. *C.* Spach, 1838*	*R. cynosbati* L.[2]
Davidia			*R.* subg. *Berisia* sect. *D.* Jancz., 1906b*	*R. davidii* Franchet[2]
Diacantha			*R.* subg. *Berisia* sect. *D.* Jancz., 1906b*	*R. diacantha* Pallas[2]
Distylium			*G.* sect. *D.* Spach, 1838*	*R. oxyacanthoides* L. (!)
Fargesia			*R.* subg. *Coreosma* sect. *F.* Jancz., 1906a*	*R. fargesii* Franchet[2]
Grossularia	*G.* Mill., 1754*	*R.* subg. *G.* (Mill.) Pers., 1805	*R.* sect. *G.* (Mill.) Nutt. 1818	*R. grossularia* L. Coville & Britton (1908)
Grossularioides		*R.* subg. *G.* Jancz., 1903*	*R.* subg. *Grossularioides* sect. *G.* (Jancz.) Rehd., 1940	*R. montigenum* McClatchie (!)
Hemibotrya			*R.* subg. *Parilla* sect. *H.* Jancz., 1905*	*R. fasiculatum* Sieb. & Zucc. (!)
Heritiera		*R.* subg. *H.* (Jancz.) A. Berger, 1924	*R.* subg. *Coreosma* sect. *H.* Jancz., 1906a*	*R. laxiflorum* Pursh (!)
Hesperia		*G.* subg. *H.* A. Berger, 1924*		*R. hesperium* McClatchie[2]
Limnobotrya	*L.* Rydb., 1922*			*R. lacustre* (Pers.) Poir.[1]
Lobbia		*G.* subg. *L.* A. Berger 1924		*R. lobbii* A. Gray[2]

Microsperma		*R.* subg. *M.* (Jancz.) Keep, 1962#	*R.* subg. *Coreosma* sect. *M.* Jancz., 1906a*	*R. ambiguum* Maxim.[2]
Parilla		*R.* subg. *P.* Jancz., 1905*	*R.* subg. *Parilla* sect. *P.* Jancz., 1905*	*R. parviflorum* Phillippi (!)
Rebis	*R.* Spach, 1835*			*R. albifolium* Ruiz & Pavón (!)
Ribes	*R.* L., 1753*	*R.* subg. *R.*	*R.* sect. *R.*	*R. rubrum* L. — Coville & Britton (1908)
Robsonia	*R.* (Berland.) Reichb., 1837	*R.* subg. *R.* (Berland.) Reichb., 1828 *G.* subg. *R. (Berland)* A. Berger, 1924	*R.* sect. *R.* Berland., 1826*	*R. fuchsioides* Sessé & Mociño[2] ex Berland. = *R. speciosum* Pursh
Symphocalyx		*R.* subg. *S.* (Berland) Reichb., 1828	*R.* sect. *S.* Berland., 1826*	*R. flavum* Berland. (!)

names: *Chrysobotrya, Cerophyllum, Coreosma, Rebis, Botryocarpium* (based on Richard's section), *Robsonia* (based on Berlandier's section), *Ribes,* and *Grossularia.* The first entity was a new name found only in the second revision. The next three names appeared in the first revision, therefore their date of publication was probably 1835, although there is some question of the intended ranks in the first paper (the fourth name in the first paper, *Calobotrya,* was put into synonymy under *Coreosma* in the second paper).

The fifth and sixth names in the second paper represented new combinations and the last two names were pre-existing generic names. In some genera Spach did not place any species, in others he placed species in different genera in the two versions of his paper. Although he recognized that *Ribes cynosbati, R. divaricatum* and *R. oxyacanthoides* belonged to the genus *Grossularia,* he failed to make the new combinations.

Endlicher (1839) accepted two genera in his Ribesiaceae, *Ribes* and *Robsonia,* the latter one of Spach's new combinations. *Ribes* was divided into three groups, "Grossularia, Bibesia, and Siphocalyx" which have no nomenclatural rank (Brizicky, 1969). Of the two misspelled groups, only the latter was repeated in subsequent publications by Torrey and Gray (1840) and Engler and Prantl (1891). Torrey and Gray (1840) capped the early efforts on the North American members of *Ribes,* dividing the genus into four subgenera (Brizicky, 1969), with a total of 28 species. Many of the new species were based on descriptions supplied to them by Nuttall from his collections in the American west.

Engler and Prantl (1891) reviewed *Ribes* recognizing three sections, placing the genus in the family Saxifragaceae. Section *Ribesia* (= *Ribes*) was further subdivided into three subsections, sect. *Grossularia* was subdivided into two subsections and sect. *Siphocalyx* (= *Symphocalyx* of Berlandier) was not subdivided. Dippel (1893) accepted the subgeneric concept of Torrey and Gray rather than the sectional concept used by Engler and Prantl.

Janczewski (1903, 1906a, 1906b, 1907) provided the most comprehensive review of the genus, and the last world-wide monograph of the currants and gooseberries. He recognized only the genus *Ribes,* dividing it into six subgenera: *Grossularioides, Parilla, Berisia, Coreosma, Ribesia* (= *Ribes*) and *Grossularia.* The first three subgenera were newly proposed, the third and fourth names were new combinations, and the last two names were extant subgeneric taxa. In addition to recognizing subgenera, Janczewski produced numerous sectional names. A total of 133 species was included in the monograph (Janczewski, 1907), 46 of which were native to North America. Shortly after Janczewski's monograph, Coville and Britton (1908) reviewed the North American species of currants and gooseberries for the *North American Flora* series published by the New York Botanical Garden. They departed from the conservative trend adopted by previous workers and reinstated *Grossularia* as a genus. Included were 43 species of currants (*Ribes*) and 40 species of gooseberry (*Grossularia*), nearly twice the number of American species outlined by Janczewski. Also proposed were a number of infrageneric names without designation of rank, some of which were later given a rank by Berger (1924). These names along with their subsequent ranks are listed in Table 2.

Berger (1924) examined the economically important species of currants and gooseberries. Two of Janczewski's subgenera were excluded from this work, the Eurasian subg. *Berisia* and subg. *Parilla* from the Andes Mountains. Following Coville and Britton (1908), Berger accepted both *Grossularia* and *Ribes* as genera. *Ribes* was divided into eight subgenera, some of which were based on Janczewski's sectional names. *Grossularia* was divided into four subgenera, *Hesperia, Lobbia, Robsonia,* and *Eugrossularia*

Table 2. List of valid names published in Coville and Britton (1908) without designation of rank. Type species for each name is indicated; most are typified by Article 22.4 (Stafleu et al., 1978), a few by the inclusion of a single species. Starred names were given series rank by Berger (1924).

Ribes		*Grossularia*	
NAME	TYPE	NAME	TYPE
americana	*R. americanum* Mill.	cynosbati*	*R. cynosbati* L.
aurea	*R. aureum* Pursh	divaricatae*	*R. divaricatum* Dougl.
hudsoniana	*R. hudsonianum* Richards.	lobbii*	*R. lobbii* A. Gray
lacustria	*R. lacustre* (Pers.) Poir	madrenses*	*R. madrense* Cov. & Rose
nigra	*R. nigrum* L.	menziesii*	*R. menziesii* Pursh
prostrata	*R. glandulosum* Grauer	microphyllae*	*R. microphyllum* HBK
rubra	*R. vulgare* Lam.	niveae*	*R. niveum* Lindl.
sanguinea*	*R. sanguineum* Pursh	pinetorum*	*R. pinetorum* Greene
tortuosa*	*R. tortuosum* Benth.	reclinatae*	*R. reclinata* L.
viburnifolia	*R. viburnifolium* A. Gray	setosae*	*R. setosum* Lindl.
viscosissima	*R. viscosissimum* Pursh	speciosae*	*R. speciosum* Pursh
		watsonianae*	*R. watsonianum* Koehne

(= *Grossularia*). The first two were newly proposed subgenera; the second was based on an unranked Coville and Britton name. The third subgenus, subg. *Robsonia,* represented a new combination under *Grossularia* and the last subgenus represented an autonym if *Grossularia* is accepted at the generic rank.

Many floristic treatments of the currants and gooseberries in the mid-20th century followed Berger, at least at the specific level (Abrams, 1944; Munz and Keck, 1959). Keep (1962) suggested that interspecific breeding patterns indicate *Ribes* should be divided into nine subgenera, two of which would be new combinations. As these nine subgenera were only suggested, the new combinations are not being considered validly published. A list of generic, subgeneric and sectional names and combinations along with their types is presented in Table 1. Some of the lectotypes are here designated.

It is evident from the preceding discussion that a consensus regarding the number of genera of currants and gooseberries has not been reached. The anatomical studies by Stern et al. (1970) indicated that no features of the wood or leaves warrant the recognition of two genera. In addition, the existence of the spiny currants (*R. lacustre* and *R. montigenum*) indicates the currants and gooseberries are less distinct than once thought. These spiny currants were unknown until the exploration of the New World. In this study the sole genus *Ribes* is recognized with several subgenera. Although all the subgenera have not been investigated, it appears that Janczewski (1907) presented a good subgeneric classification, dividing *Ribes* into six subgenera.

The family affinities of the currants and gooseberries have varied through time. As discussed above they have been variously placed in a separate family (Grossulariaceae or Ribesiaceae) or included in the Saifragaceae. Within the Englerian classification system (Engler and Prantl, 1891) *Ribes* was placed in Saxifragaceae where it remained for some time. Recent classification schemes remove the currants and gooseberries into the segregate family Grossulariaceae (Airy-Shaw, 1973; Cronquist, 1981). For the present, the trend toward segregating Grossulariaceae is favored by this author, although the genera other than *Ribes* included by Cronquist (1981) need further study. Evidence for segregation includes the wholly inferior ovary, totally syncarpous gynoecium and fleshy fruit.

RIBES SUBG. *GROSSULARIA* SECT. *GROSSULARIA*

Ribes consists of shrubby species with alternate or clustered simple exstipulate, usually palmately lobed and veined leaves (a good generic description is provided in Spongberg, 1972). Subgenus *Grossularia* is characterized by those species of *Ribes* with nodal spines (and often internodal bristles) and one to four (five) flowers in axillary clusters. In colloquial terms and in the fruit breeding industry, subg. *Grossularia* represents the gooseberries. Numerous authors have accepted *Grossularia* as a genus, including Tournefort (1700), Coville and Britton (1908), and Berger (1924). Section *Grossularia* is characterized by those species of subg. *Grossularia* that typically have pubescent styles and a receptacular cup that is pubescent near the base of the stamens. The section is primarily North American, with nine species. Several European species were included with the American species by Berger (1924), but it appears that some of them are only distantly related to the North American species and probably belong to either a different section or a different subsection.

The existence of a group of hairy-styled species of gooseberries was first noted by Janczewski (1907). In his monograph, subg. *Grossularia* is divided into two sections, *Eugrossularia* and *Robsonia*. Within sect. *Eugrossularia* (= *Grossularia*), a major key division involves style pubescence, with nine species included in the hairy-styled group. Coville and Britton (1908) also used style pubescence to divide the genus *Grossularia* into two large subsets. Like Janczewski, they proposed no taxonomic rank for the hairy-styled group. Berger (1924) formally recognized the hairy-styled group of previous authors as *Grossularia* subg. *Eugrossularia* (= subg. *Grossularia*). Berger included 25 species in the subgenus, including seven European species that were primarily glabrous-styled. The species of sect. *Grossularia* treated in this revision are Berger's 17 hairy-styled North American species (here reduced to nine species). The largely glabrous-styled Eurasian species have been excluded, creating a cohesive study group of North American species. The only other North American species Berger (1924) included in subg. *Grossularia*, *R. echinellum* (Coville) Rehd., is related to the Pacific Coast species *R. lobbii* A. Gray, and is included in Appendix 1. This species lacks the style pubescence typical of sect. *Grossularia* and has the tubular petals and spiny fruits of some of the western species.

CYTOLOGY, REPRODUCTIVE BIOLOGY AND EVOLUTIONARY PROCESSES

The chromosome complement within sect. *Grossularia*, as with the genus *Ribes* in general, is very uniform. Chromosome counts of about two-thirds of the 150 species of *Ribes* all indicate that $n = 8$ (Tischler, 1927; Muerman, 1928; Zielinski, 1952; Spongberg, 1972). The only known naturally-occurring polyploid reported was a garden specimen of *R. gayanum* (Spach) Steudl. with $n = 16$ (Hamel, 1955). The evidence for the spontaneous polyploid nature of this garden plant was based on the uniformity of chromosome number within different tissues of the tetraploid plant. The uniformity of tetraploidy within this plant was in contrast to the variation found in tissues of colchicine-induced polyploids (Nilsson, 1944; Vaarama, 1947, 1948, 1949). In addition to regularity in chromosome number, the spontaneous tetraploid did not have the mitotic irregularities often found in the colchicine-induced polyploids.

Löve and Löve (1967) and Grant (1981) noted that montane plants generally have a higher frequency of polyploids than their low-elevation relatives. Many species of *Ribes* are montane, and the lack of polyploidy in the genus is interesting. In other papers, Stebbins (1950) and Bayer and Stebbins (1981) found a tendency for increased frequency of polyploidy in plants distributed in glaciated areas. Many species of *Ribes* were exposed to glaciation in North America and Europe, apparently adjusting to the conditions without an increase in polyploidy. The lack of polyploidy in the genus is consistent with observations by Stebbins (1938, 1947) that polyploidy is infrequent in woody plants as a general rule. Notable exceptions occur in the apomictic woody Rosaceae (Sinnott & Phipps, 1983). Grant (1971) outlined three major factors which influence the likelihood of a plant becoming polyploid: a) long-lived with a tendency for vegetative reproduction, b) primary speciation accompanied by chromosome repatterning, and c) interspecific hybridization between the primary species. The first and last criteria are met in *Ribes*, but there appears to have been little or no chromosome restructuring accompanying speciation in the genus. As a result, species can hybridize and the hybrid genomes are compatible and capable of pairing during mitosis and meiosis. Harlan and

De Wet (1975) indicated increases in chromsome number following the combining of incompatible genomes is the result of production and subsequent fusion of unreduced gametes in successive generations. They noted that unreduced gametes can also occur as a normal feature of meiosis. Muerman (1928) reported unreduced gametes in *Ribes*, but later workers did not report them (Zielinski, 1952). It would appear from the lack of polyploids in *Ribes* that unreduced gamete production is either infrequent or the unreduced gametes are non-functional.

The karotype of sect. *Grossularia*, as with the entire genus, is relatively uniform also. The chromosome complement in *Ribes* consists of relatively small chromosomes which, except for a pair of chromosomes with a satellite, cannot be distinguished from one another (Zielinski, 1952). Early reports by Tischler (1927) that chromosome size differences between species were significant and could be used to trace pairing in hybrids have been refuted by Darlington (1929) and Zielinski (1952). Darlington noted the chromosomes of *Ribes* are generally small (1.5–2.5μ) and vary little between species. Muerman (1928) indicated that apparent differences between species exist, but because of their small size and difficulty in quantification, the differences were often insignificant. Zielinski (1952) also found that the differences in chromosome size between species were insignificant.

The process of division, both mitotic and meiotic, is also relatively uniform in sect. *Grossularia*, as well as the entire genus. Descriptions of mitosis can be found in Zielinski (1952), descriptions of meiosis in Muerman (1928) and Zielinski (1952).

The base chromosome number for *Ribes* is $x = 8$, according to the majority of authors (Zielinski, 1952; Keep, 1962), although Vaarama (1947, 1948, 1949) stated the base number is $x = 4$, while Schoenagel (1931) and Goldschmidt (1964) suggested a base number of $x = 7$. Vaarama's conclusions would imply the genus is of a derived polyploid origin and all the modern species are tetraploids. In his examination of meristematic cells in root tips of colchicine induced polyploids, he noted marked variation in chromosome numbers. The frequency distribution of various chromosome numbers displayed two major peaks (at 16 and 32 chromosomes) and several minor peaks at 4, 8, 12 and 20 chromosomes. He reasoned that the base number of the genus must be 4, as physiologically active cells with four chromosomes were present, and the frequency peaks occurred at chromosome numbers divisible by 4. Stebbins (1938, 1947) noted that only woody plants with gametic chromosome numbers greater than $n = 11$ are probably derived from ancient stock with lower base numbers, and in conjunction with the beliefs of other cytologists (Zielinski, 1952), it is concluded here that the most likely base number is $x = 8$.

Because of uniformity in chromosome number and structure, many fertile hybrids have been formed between species of *Ribes*. Experimental hybrids have been formed between a number of wild species, both within sections and subgenera and between sections and subgenera. Keep (1962) summarized the results of many crossing experiments by noting that barriers to crossing within a section are usually weak and fertile hybrids are typically produced. Crosses between species in different sections or different subgenera typically result in inviable embryos or the hybrid plants are sterile. Nilsson (1955) reported that many of these sterile hybrids between distant species can become fertile with induced polyploidy. In Table 3, the results of crossing experiments within sect. *Grossularia* are presented. Although incomplete, they indicate that fertile hybrids can probably be formed between most of the species in sect. *Grossularia*. The occurrence of these interspecific hybrids in nature where distributional ranges overlap creates taxonomic difficulties.

The breeding barriers between sect. *Grossularia* and other sections have not been fully investigated. It appears that major chromosomal structural differences are not involved, although Goldschmidt

Table 3. Summary of infrasectional crosses within *Ribes* subg. *Grossularia* sect. *Grossularia*, with at least one parent a North American native. J. = Janczewski (1907), K = Keep (1962).

cynosbati	*cynosbati*										
divaricatum	–	*divaricatum*									
"gracile"	–	–	*"gracile"*								
grossularia	J	J	K	*grossularia*							
hirtellum	–	–	–	K	*hirtellum*						
inermis	–	–	–	–	–	*inermis*					
irriguum	–	–	–	K	–	–	*irriguum*				
missouriense	–	–	–	K	K	–	–	*missouriense*			
niveum	–	J	–	K	–	K	–	–	*niveum*		
oxyacanthoides	–	K	–	J	–	–	–	–	J	*oxyacanthoides*	
rotundifolium	–	–	J	–	–	–	–	–	K	–	*rotundifolium*

(1964) noted that certain instances of hybrid sterility appear to be based on structural incompatabilities. Differences in style lengths and the presence of potential lethal genes were considered important factors by Keep (1962). The interactions of incompatability genes in the section have not been investigated.

The pollinators of sect. *Grossularia* plants were reported to be long- and short-tongued bees, Diptera and Lepidoptera (Robertson, 1929). Observations by the present author indicate small butterflies and bees visit the flowers of some species, although it is not known if pollen is transferred by these vectors.

From the systematic and evolutionary biology viewpoint, *Ribes* represents an example of geographically determined speciation. Grant (1971) put *Ribes* into the "*Ceanothus* pattern" of speciation along with *Pinus, Quercus* and *Eucalyptus.* This pattern is characterized by uniform chromosome numbers and a lack of cross-breeding barriers between related species. Breeding barriers exist only between widely separated species (e.g., species of different sections or subgenera). Species within section *Grossularia* exhibit the classical sympatric speciation model as defined by Mayr (1963, 1976) and Grant (1981). Adaptation to differing geographic regions appears to have been the major evolutionary force. In an investigation of the distributions of the species in sect. *Grossularia* (Figure 1), it is apparent that most of the species are allopatric or have relatively large parts of their distribution distinct from other species. In some cases, such as *R. niveum,* the overall distribution of one species falsely appears to be included within the distribution of another. *Ribes niveum* and *R. inerme* were never found growing together; *R. inerme* typically is found at higher elevations than the former. It is this geographical isolation that regulates the speciation processes in the section. If the distributions of these species were to become more sympatric, intergradation would occur and many of the species would lose their identity.

Species of different sections or subgenera which display marked fertility barriers and are well differentiated morphologically have presumably been isolated for long periods of time or have been exposed to greater selection pressures to establish breeding barriers. Widely separated species such as these grow sympatrically with one another without apparent hybridization. This situation is commonly found with species of currants and gooseberries (different subgenera) growing at a given site.

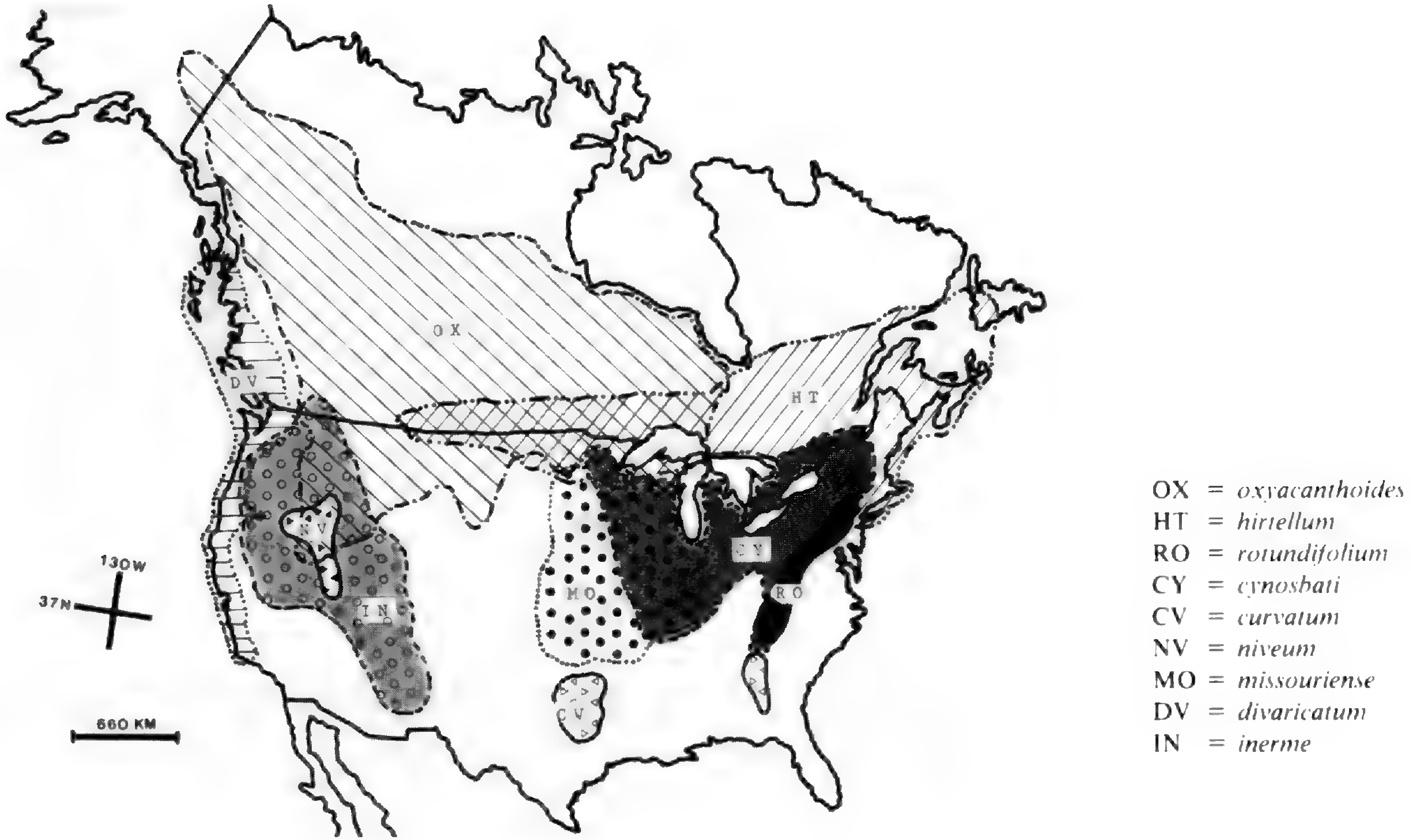


Figure 1. Composite map of the nine *Ribes* species in sect. *Grossularia* from North America. Most of the species have a relatively large part of their range distinct from other species (by elevational differences only in some cases).

Closely related species within sections, however, presumably have diverged more recently or have been exposed to less rigid selection pressures to establish isolation barriers. In such cases, these plants might be regarded as "incipient biological species." It appears that many species of sect. *Grossularia* currently recognized in various regional or local floras in North America are such "incipient biological species" and are therefore exceedingly difficult to recognize consistently throughout their range. In this treatment, species limits often could not be firmly established, as many species have regions of sympatry and show apparent hybrid swarms. The extent of the allopatric part of a taxon's distribution appeared to be a key element in the rank it would receive.

In order to classify the species within sect. *Grossularia* a divergence from the biological species concept had to take place and a modified species concept substituted. The taxonomic species concept chosen contained three elements: reproductive isolation, geographical isolation and morphological distinctiveness. An ideal species would meet all three criteria. The rank of species was applied to morphological entities that met the geographical isolation criterion to a large extent. If this criterion were met, the reproductive isolation criterion was thus met for most of the members of that entity. The rank of subspecies was applied to entities which appeared somewhat morphologically distinct and had only a small part of their distribution distinct from other taxa. Variety was used for entities which had a lesser degree of morphological distinctiveness, geographical isolation and reproductive isolation.

The taxonomic level concept employed is thus one of degree, with subspecies and varieties having a lesser degree of fulfillment of the three criteria of a species.

ENDANGERED SPECIES STATUS

At the present time, no species of *Ribes* is afforded legal protection as a listed Endangered or Threatened species under the auspices of the U. S. Endangered Species Act of 1973, as amended. Two species of *Ribes* were included in the review of endangered and threatened plants (U. S. Fish and Wildlife Service, 1980), although neither has become listed. One of these two species, *R. echinellum* (Coville) Rehd. was in 1976 proposed as an Endangered species, and is presently under review for listing. A discussion of this species can be found in the Appendix. The second species, *R. canthari-*

forme Wiggins, is considered a candidate for listing by the U. S. Fish and Wildlife Service (1980). No species within sect. *Grossularia* appeared in the review.

In the course of this revision of sect. *Grossularia,* several taxa were found to be likely candidates for federal concern as threatened plants. These candidates include species as well as subspecies and varieties. The three categories used in assessing the danger to each taxon follow MacBryde (1981). Category one, the most critical, represents taxa that are in immediate danger of going extinct. Their habitats have been heavily disturbed and the remaining habitat is extremely limited and not presently being managed with that plant in mind. This category is the "Endangered" status in the Endangered Species Act (Smith, 1980). Category two includes taxa that are relatively limited in distribution, or have been exposed to range destruction resulting in the loss of significant amounts of habitat, and are in danger of extinction in the future if present trends continue. This group is comparable to "Threatened" status under the Act. The third category represents taxa that bear watching, and could in the future become members of category one or two.

The two plants considered in category one are below the specific rank. It is hoped that the appropriate agencies will consider the threat to these taxa as significant, although infraspecific taxa have lower priority for listing (MacBryde, pers. comm., 1983). The two taxa are *Ribes oxyacanthoides* ssp. *cognatum* and *R. divaricatum* var. *parishii.* A more detailed discussion of the distribution and dangers to these taxa can be found in the taxonomic treatment below. Both entities are extremely rare, probably represented by three or less populations. In the case of *R. oxyacanthoides* ssp. *cognatum,* the author investigated many sites where herbarium records were available, and only one population consisting of three plants was found. In the case of *R. divaricatum* var. *parishii,* only two locations have ever been reported, and the most recent herbarium record seen for this study was 1963. It is possible that this taxon is now extinct, although the author was unable to investigate the two reported localities.

Three plants are considered to be within category two or "Threatened." Two are species, *Ribes niveum* and *R. curvatum,* and one is a variety, *R. divaricatum* var. *pubiflorum.* Both *R. niveum* and *R. divaricatum* var. *pubiflorum* are considered threatened due to encroachment and habitat destruction. Both were once relatively common and now have been drastically reduced in a major part of their range. *Ribes curvatum* represents a species which was never common, and is threatened because the few known populations are near metropolitan areas or are not presently protected. Further discussions of the threatened status of these three taxa can be found in the taxonomic treatement below.

Three plants are in the third or watch category, *Ribes oxyacanthoides* ssp. *irriguum, R. oxyacanthoides* ssp. *setosum* and *R. divaricatum* var. *divaricatum.* The two subspecies of *R. oxyacanthoides* have relatively small distributions, and significant disturbance could readily move them to the more threatened categories. *Ribes oxyacanthoides* ssp. *setosum* has a portion of its range in Yellowstone National Park, therefore is protected in that part of its range by federal regulations already. *Ribes oxyacanthoides* ssp. *irriguum* is found in several state parks in Washington and Oregon, and is minimally protected at the federal level in the Clearwater and Lolo National Forests. *Ribes divaricatum* var. *divaricatum* is partially protected in North America since a significant portion of its range is in the lightly inhabited portions of British Columbia. However, in the United States, the plants are rapidly becoming infrequent and the variety bears watching.

Of the remaining entities in sect. *Grossularia,* the majority appear to be in no immediate danger of becoming extinct in North America, although only *Ribes missouriense* appears to respond positively to repeated habitat disturbances. A discussion of each species endangerment can be found in the taxonomic treatment below. The maps have been prepared with the Endangered Species Act in mind, and have recent (post-1965) herbarium records separate from the older records. The lack of recent confirmation for a given county or state does not assure that that location has been disrupted, but does serve as a guideline for the endangered status of each species. In some cases, the lack of recent herbarium records indicates a lack of recent collectors or failure of this study to access all the pertinent herbaria.

TAXONOMIC TREATMENT

Ribes L. subg. **Grossularia** (Mill.) Pers. sect. **Grossularia** (Mill.) Nutt.

Grossularia Mill., Gard. Dict. abr. ed. 4, unpaged. 1754. *Ribes* L. subg. *Grossularia* (Mill.) Pers., Syn. Plant. 252. 1805. *Ribes* L. sect. *Grossularia* (Mill.) Nutt., Gen. N. Amer. pl. 1: 140. 1818. LECTOTYPE: *Ribes grossularia* L., designated by Coville and Britton (1908).

Grossularia Mill. sect. *Cynosbatium* Spach, Hist. nat. veg. 6: 178. 1838. TYPE: *Ribes cynosbati* L.

Grossularia Mill. sect. *Distylium* Spach, Hist. nat. veg. 6: 173. 1838. LECTOTYPE (here designated): *Ribes oxyacanthoides* L.

Plants small to medium shrubs 0.25–2 (3) m tall; *stems* multiple from the base, typically recurving and rooting at the nodes, occasionally remaining erect, the bark exfoliating, straw-colored to dark brown or grey, with internodal bristles of varying length and number present or absent; *wood* (cf. Stern et al., 1970) diffuse or ring porous, the vessels small and with scalariform perforation plates, the intervascular pits scaliform to opposite, circular to elongate, the rays homocellular and heterocellular; *nodal spines* normally present, 1–3 (7) (Figure 2a), eventually exfoliating with the bark or occasionally lacking shortly after secondary growth begins; *leaves* deciduous, alternate, exstipulate, the blade plicate in bud, isodiametric, oblong or broader than long, palmately lobed into 3–5 lobes, these coarsely toothed, the venation palmate, with hydathodes at teeth apices, the upper surface glabrous to pubescent and glandular, the lower surface glabrous to pubescent and glandular, the base deeply cordate to cuneate, the petiole often with a dilated base, the nodes trilacunar; *inflorescence* of 1–4 (5) flowers in axillary racemes (Figure 2b), occasionally with two inflorescences per node, each flower stubtended by a 1.5–2.5 mm long, typically glandular-ciliate bract; *flowers* with a campanulate to cylindric calyx tube (Figure 2c), the tube pilose within near base of style and filaments, the calyx lobes 5, shorter or longer than the tube, typically reflexed or diverging at right angles at anthesis, glabrous or pilose, the petals 5, white or tinged pink in age, obovate to rhombic, entire or rarely apically toothed or erose, inserted alternate to the sepals on the hypanthium rim, the stamens 5, inserted below and alternate to the petals (opposite the sepals) on the hypanthium, glabrous or ciliate, on filaments as long as the petals or 3–6 times longer, with anthers creme-colored to pale pink, glabrous to pilose, dehiscing by longitudinal slits, the pollen spheroidal, 8–9 aperturate, two-celled at anthesis; *pistil* with a style bifid to about midway to base, the style elongating during anthesis and usually exserting

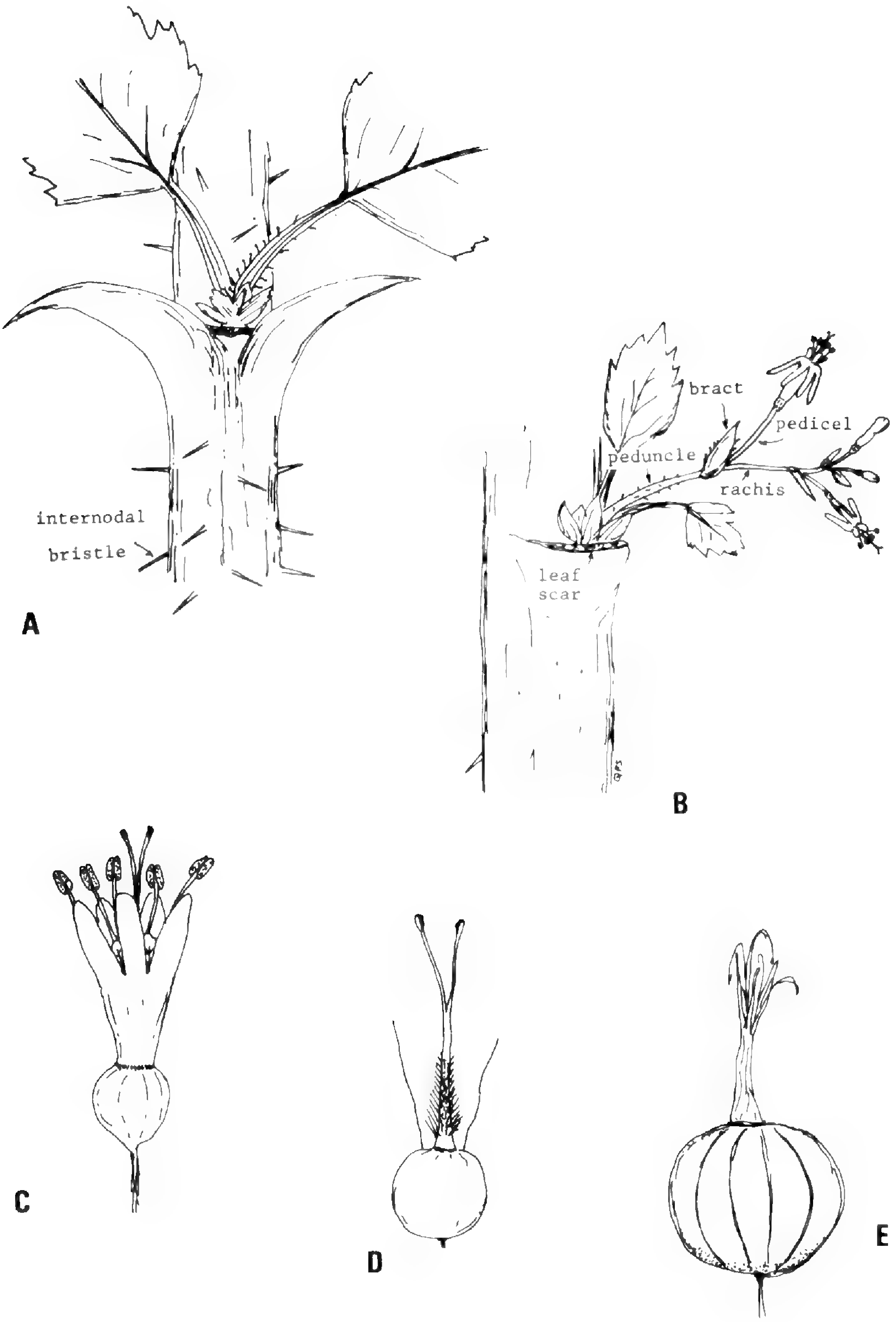


Figure 2. General morphology of sect. Grossularia, a) nodal spine, b) raceme, c) calyx tube, d) style pubescence, e) fruit.

the small stigmas above the anther level, the fused portion and lower free parts of the style hirtellous, the pubescence typically not continuous to the base of the style (Figure 2d), the style branches typically diverging, occasionally coherent, the ovary wholly inferior and fused to the hypanthium, glabrous, glandular, or glandular-bristly in one species, bicarpellate, syncarpous and without interior partitions, therefore unilocular, with many anatropous, bitegmic, crassinucellate ovules on two parietal placentae; *fruit* a spheroidal berry, smooth or rarely spiny, typically with the veins appearing as stripes on the ripe fruit (Figure 2e), the seeds small, 20–40, with a hard seed coat, enclosing an embryo embedded in endosperm; $x = n = 8$. Flowering in the spring before or as the leaves expand, fruiting soon after while late flowers are still opening. The fruit in some species persists through the winter until the following spring, although more typically they are rapidly eaten by birds and deer.

DISTRIBUTION. Section *Grossularia* is distributed throughout the temperate regions of North America north of Mexico (Figure 1). The species are typically woodland inhabitants, found primarily in deciduous tree associations in the eastern part of the continent and coniferous forest associations in the western part.

DISCUSSION. The 17 hairy-styled species that Berger (1924) discusses in North America in sect. *Grossularia* have been here reduced to 9 species, 4 subspecies, and 3 varieties. The composite ranges of the nine species are superimposed in Figure 1; individual detailed county maps (where applicable) are found in the individual treatments. The distributional information presented as county dot maps came from about 12,000 herbarium specimens borrowed from numerous herbaria (see acknowledgments) and field studies completed by the author. The field studies were undertaken throughout much of the range of the section in North America.

The taxa within sect. *Grossularia* (except for *Ribes inerme* var. *klamathense*) were analyzed numerically in the following manner. Seventy populations representing the 15 entities being analyzed were selected and scored for thirteen characters (Table 4). Each entity was represented by two or more of the seventy populations, except for *R. divaricatum* var. *parishii*, which is known only from two populations of which only one was represented in adequate detail for analysis. The seventy populations along with their identities are presented in Table 5. The populations were compared using

Table 4. List of characters used in the numerical analyses. Characters 1–13 were used in the 13-character analyses. For the 11-character analyses, characters 7, 11, 12 and 13 were excluded and characters 14 and 15 were added.

1. Calyx tube length
2. Sepal length
3. Petal length
4. Pedicel length
5. Stamen length
6. Style length
7. Petiole/leaf length ratio
8. Peduncle length
9. Calyx tube width
10. Angle leaf base
11. Length top lobe/leaf length
12. Widest point of leaf
13. # spines/node
14. Fruit surface
15. Stamen pubescence

the range overlap similarity coefficient (Sinnott, 1981) and the similarities were clustered using an unweighted average linkage procedure (Sneath & Sokal, 1973). The resulting dendrogram (Figure 3) generally indicates that the 15 entities are indeed morphologically intact groups, although *R. oxyacanthoides* ssp. *oxyacanthoides* and ssp. *setosum* are poorly resolved. The lack of clear distinction between the two subspecies represents the morphological intermediacy of the South Dakota populations, which I have put into the typical subspecies. In order to investigate the nearest neighbor relationships among the seventy populations, a phenetic network was constructed using single linkage (comparable to a minimum spanning tree or Prim network). The network (Figure 4) likewise indicates relatively good resolution of the species, with the primary exception remaining the subspecies of *R. oxyacanthoides.* Both representations of the 70 × 13 matrix indicate similar between-group relationships, with the long-stamened, cuneate-to-rounded-leaved species *R. curvatum, R. niveum,* and *R. missouriense* forming a group, and most of the subspecies of *R. oxyacanthoides* linking together. The apparent outcast position of *R. oxyacanthoides* ssp. *hendersonii* is largely the result of size differences playing a major role, as the initial data set included a number of size criteria. Size was found to be useful in distinguishing between most of the taxa in

Table 5. Identity and origin of the seventy populations of *Ribes* subg. *Grossularia* sect. *Grossularia* used in the numerical analyses.

R. cynosbati	1) Minnesota, 2) Indiana, 3) Ontario, 4) Vermont, 5) New York, 6) North Carolina, 7) Georgia, 8) Ohio, 9) Missouri, 10) Quebec
R. curvatum	11) Alabama, 12) Louisiana, 13) Oklahoma, 14) Tennessee, 15) Texas, 16) Georgia
R. niveum	17) Idaho, 18) Nevada, 19) Oregon, 20) Washington
R. missouriense	21) Kansas, 22) Illinois, 23) Iowa, 24) Minnesota, 25) Missouri, 26) Nebraska, 27) Wisconsin
R. rotundifolium	28) Maryland, 29) New York, 30) North Carolina, 31) Pennsylvania, 32) Tennessee, 33) Virginia
R. divaricatum var. *divaricatum*	34) British Columbia, 35) Washington, 36) Oregon
R. divaricatum var. *pubiflorum*	California: 37) Humboldt Co., 38) Alameda Co., 39) Marin Co., 40) San Luis Obispo Co., 41) Monterey Co.,
R. divaricatum var. *parishii*	42) Los Angeles Co., California
R. oxyacanthoides ssp. *setosum*	43) Wyoming, 44) Wyoming, 45) Wyoming, 46) Montana
R. oxyacanthoides ssp. *oxyacanthoides*	47) Yukon, 48) Northwest Territories, 49) Alberta, 50) South Dakota, 51) Saskatchewan, 52) Manitoba
R. oxyacanthoides ssp. *irriguum*	53) Idaho, 54) Washington, 55) Oregon
R. oxyacanthoides ssp. *hendersonii*	56) Idaho, 57) Montana
R. inerme	58) Montana, 59) Sierra Nevada (California), 60) Sierra Nevada (Nevada), 61) Oregon, 62) Washington, 63) Utah
R. hirtellum	64) Quebec, 65) Ontario, 66) Nova Scotia, 67) Maine, 68) Massachusetts
R. oxyacanthoides ssp. *cognatum*	69) Washington, 70) Oregon

the section and the difficulty in distinguishing ssp. *hendersonii* was not critical.

After character evaluation, 4 of the 13 characters were shown to vary little among the seventy populations and a second data set was prepared consisting of 11 characters, 9 from the original data set and 2 new characters (Table 4). This 70 × 11 matrix was analyzed using the procedures outlined for the first data set. As in the previous analyses, the 15 entities are generally well established (Figures 5 and 6). In addition, the resolution of inter-group relationships

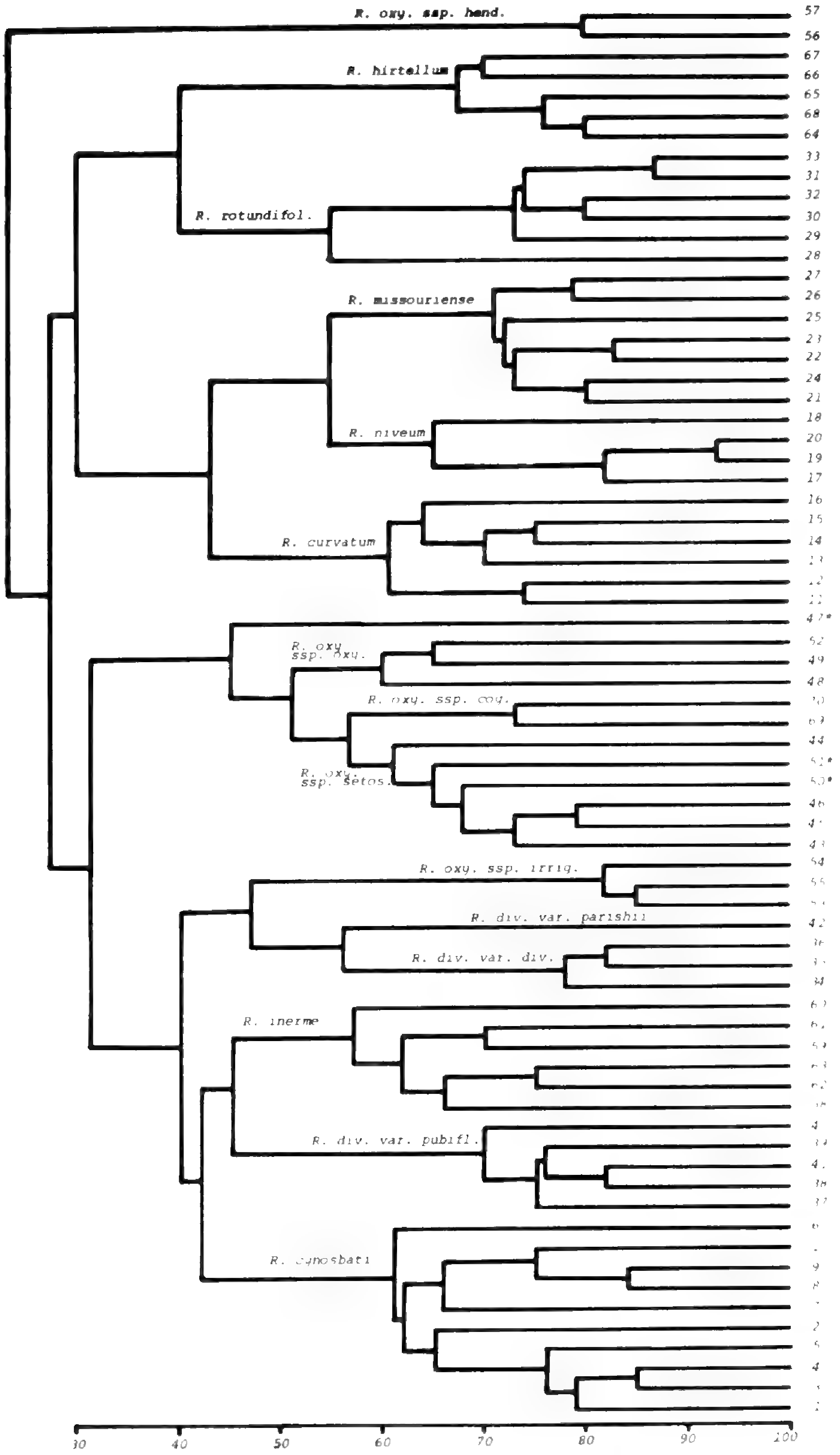


Figure 3. Dendrogram of 70 populations of sect. *Grossularia* generated by average linkage clustering of range-overlap similarities, based on 13 characters. Populations (x-axis) are listed in Table 5. Populations of *Ribes oxyacanthoides* ssp. *oxyacanthoides* indicated by an asterisk are clustered with other taxa. The y-axis equals percent similarity.

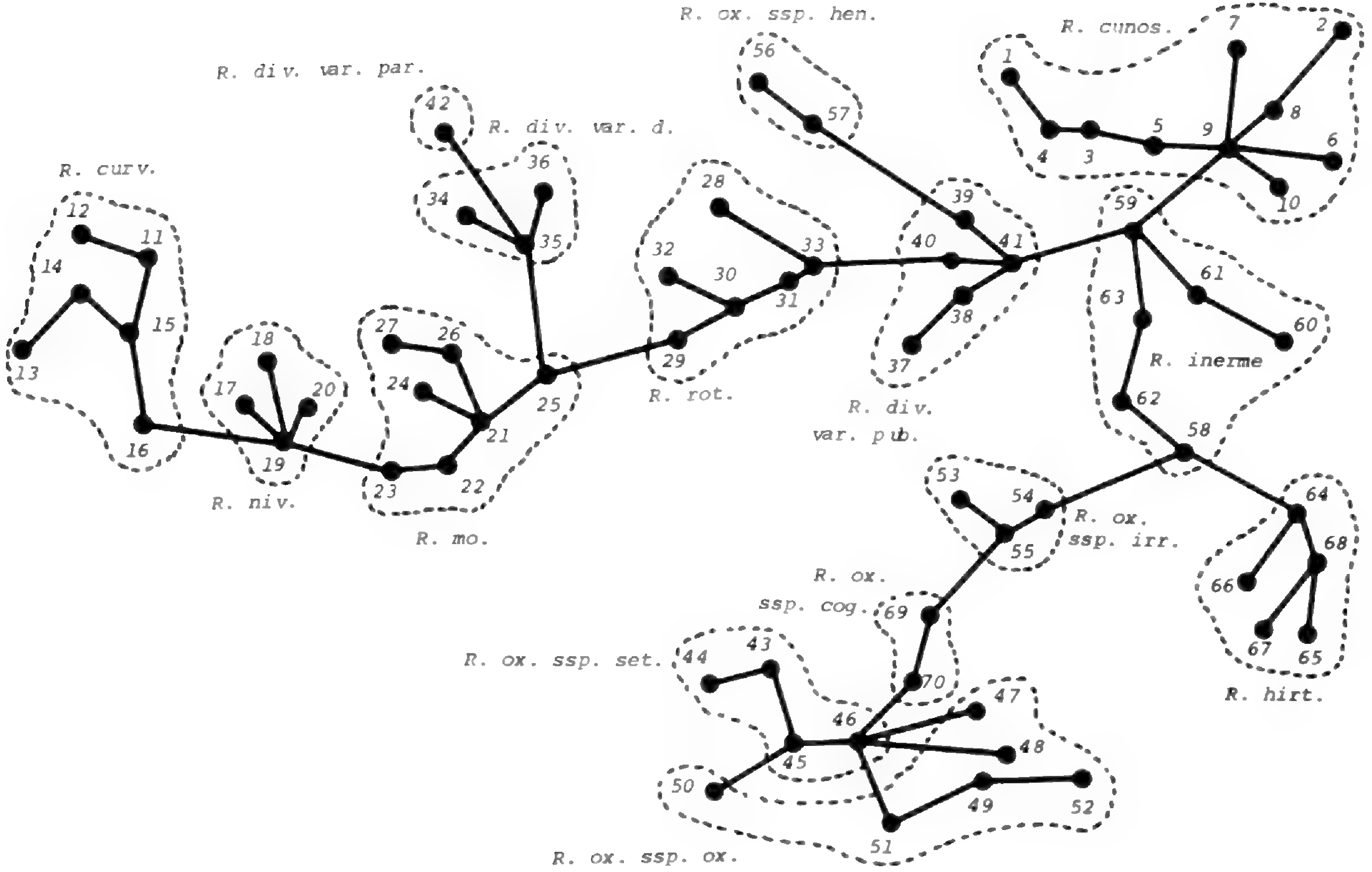


Figure 4. Single linkage network of 70 populations of sect. *Grossularia based on 13 characters. Populations are identified in Table 5. Network internodes are proportional to distance.*

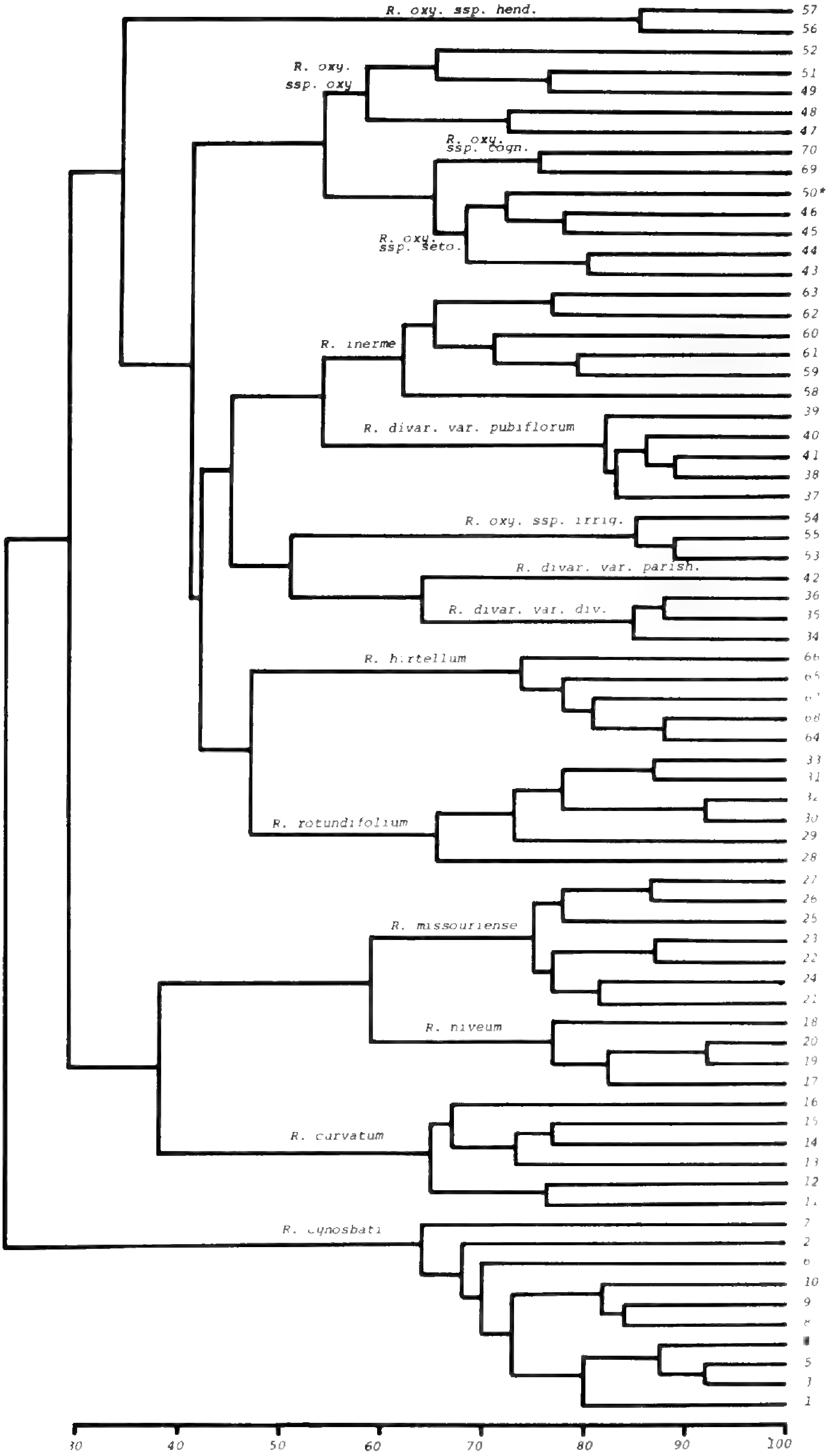


Figure 5. Dendrogram of 70 populations of sect. Grossularia generated by average linkage clustering, based on 11 characters. Populations are identified in Table 5. The population of *Ribes oxyacanthoides* ssp. *oxyacanthoides* marked by an asterisk is clustered with another species. The y-axis is percent similarity.

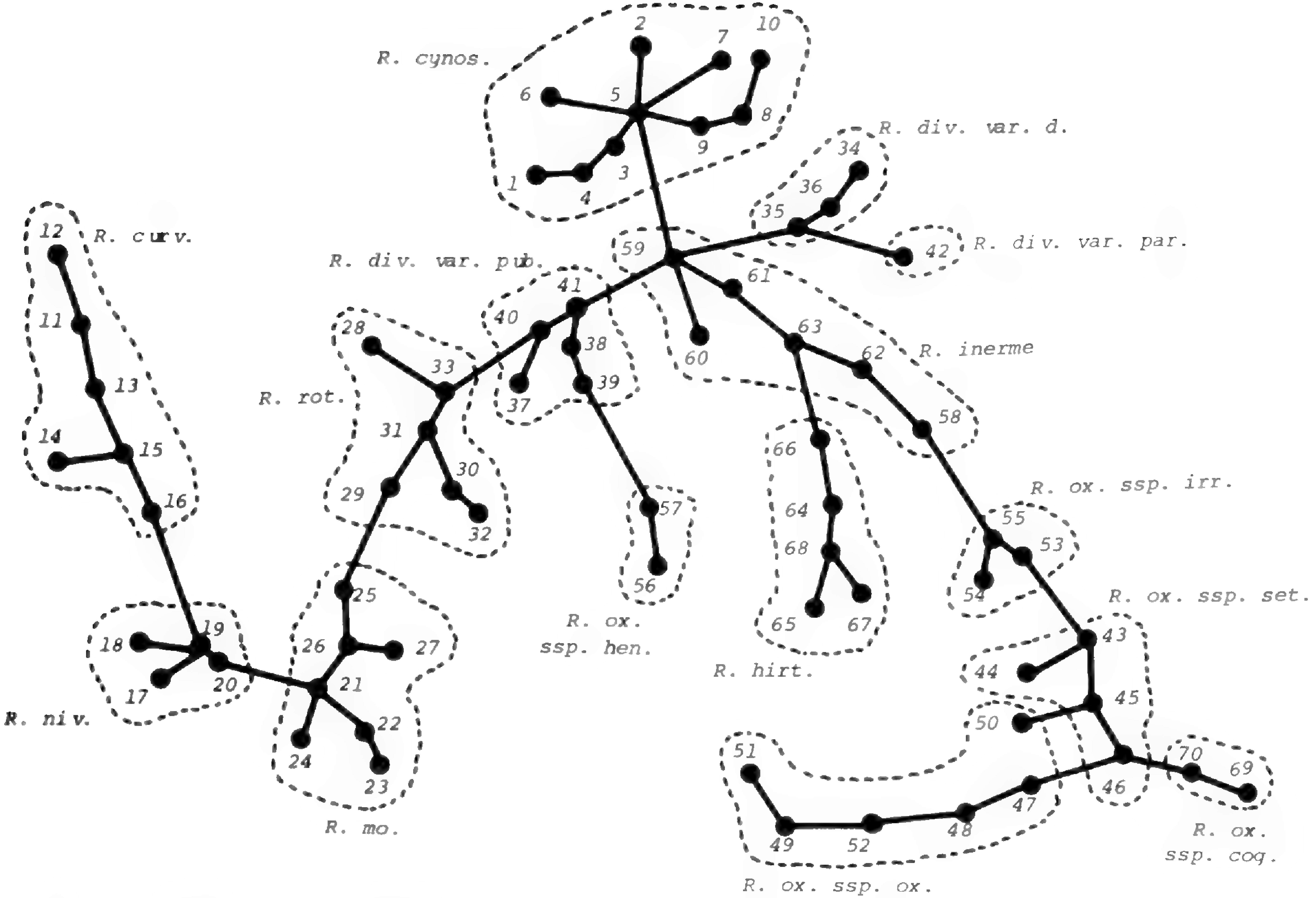


Figure 6. Single linkage network of 70 populations of sect. *Grossularia* based on 11 characters. For identity of populations, refer to Table 5. Network lengths are proportional to distance.

improves somewhat. *Ribes oxyacanthoides* ssp. *irriguum* is oriented near the other subspecies of *R. oxyacanthoides* in the networks. In order to further investigate the inter-group relationships, another phenetic network was generated using a double linkage criteria (an unassigned entity is placed on the developing network between its two nearest neighbors). This procedure is comparable to the Wagner Network procedure of Farris (1970) and uses the median state criteria for linkage nodes (linkage nodes are equivalent of the hypothetical ancestor of Farris, 1970). The seventy populations were first reduced to the 15 entities, and this grouped data was recoded into ordered multistate characters. Some of the resulting clear resolution of this network was due to this recoding, as some taxa were adjusted to fit into a single state (Figure 7).

The results of the numerical analyses, combined with intuitive evaluations, indicate that the 15 taxa in sect. *Grossularia* are generally distinct and can be divided into 5 assemblages. The first assemblage contains the rather unique species *Ribes cynosbati*, the only member of the section with spiny fruits (although numerous western species of other sections have spiny fruits). The basic flower structure of this species is similar to *R. oxyacanthoides* ssp. *irriguum* and to *R. inerme*. The second group within the section contains *R. niveum*, *R. curvatum* and *R. missouriense*. All three of these species are characterized by the long stamen filaments, short flower tube, long sepals, long styles and cuneate to rounded leaves. *Ribes niveum* and *R. missouriense* represent sister species, distinguished by minor morphological characteristics and distribution, while *R. curvatum* has several features not represented in the other two species. The third group within the section consists of species with medium length stamens and purplish calyces; it includes *R. rotundifolium* and *R. divaricatum*. The fourth group contains *R. inerme* and *R. hirtellum*, two species with intermediate length stamens and relatively small floral parts. The last group consists of *R. oxyacanthoides* and its subspecies. These entities are characterized by the short filaments which position the anthers about at the level of the petals.

Cladistic interpretations were not drawn from any of the numerical procedures due to the relatively small size of this section in relation to the entire genus and because *Ribes* does not appear to be a suitable genus for cladistic analysis. Cladistic analysis assumes a

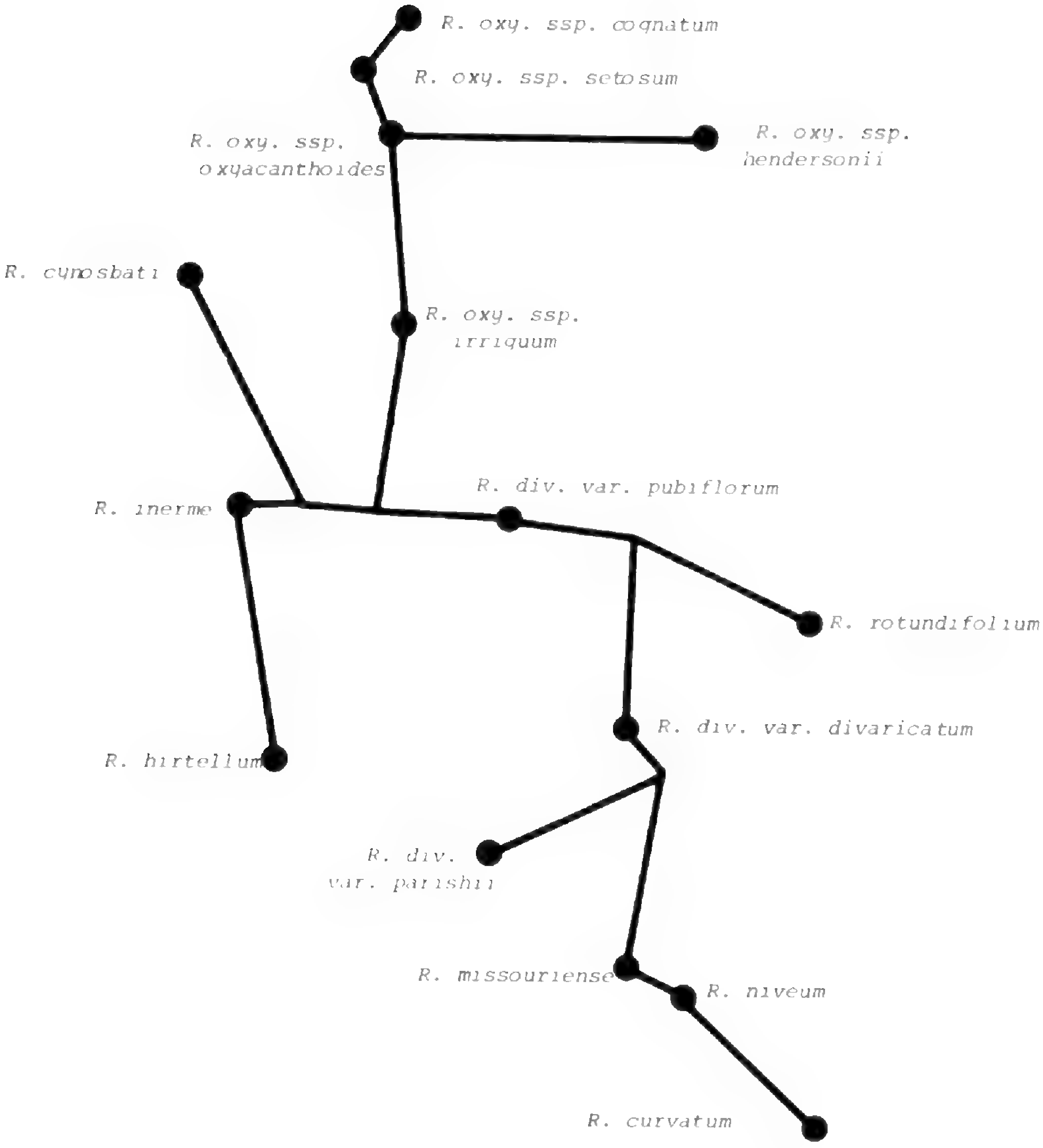


Figure 7. Double linkage network of 15 taxa of sect. *Grossularia*. Network internode lengths are proportional to character state differences based on 11 characters.

monophyletic lineage and it is clear that hybridization and reticulate evolution dominate the genus at the species level. No single character is capable of distinguishing a given species, as each species is characterized only by a unique suite of character states.

Definitive evolutionary relationships among these taxa and those in other sections of *Ribes* were not resolved at this point in the study of the genus. It appears at this stage that sect. *Grossularia* approaches the spiny-fruited western species through *R. cynosbati* and a link between *R. oxyacanthoides* and members of the smooth-styled species *R. velutinum* Greene, *R. lasianthum* Greene and *R. leptanthum* A. Gray seems likely.

KEY TO SPECIES OF SECT. GROSSULARIA IN NORTH AMERICA

A. Ovary with stalked glands which become stiff spines on the mature fruit; distributed throughout the eastern deciduous forest region of the United States and Canada .... 1. *R. cynosbati*

AA. Ovary and fruit smooth

  B. Filaments to as long as the petals, positioning anthers about level to petal apices; distributed from James Bay to Alaska .... 2. *R. oxyacanthoides*

  BB. Filaments 2–5 times longer than petals, positioning anthers 1.5–10 mm beyond the petal apices

    C. Style less than 8 mm long; sepals less than 5 mm long; filaments less than 5 mm long

      D. Leaves typically cuneate; northeastern United States and adjacent Canada .... 3. *R. hirtellum*

      DD. Leaves typically cordate; western North America

        E. Calyx greenish-white, glabrous to short pilose; leaves often glabrous; Rocky Mountains south of Canada, Intermountain Region and Sierra Nevada .... 4. *R. inerme*

        EE. Calyx purple-green, pilose; leaves hairy; southern British Columbia to California...5. *R. divaricatum*

    CC. Style greater than 8 mm long; sepals 5–9 mm long; filaments 5–12 mm long

      F. Calyx tube typically purplish or purple-green

        G. Leaves deeply cordate; Pacific Coast from southern British Columbia to California .... 5. *R. divaricatum*

        GG. Leaves rounded to truncate; Appalachian Mountains from New York to Tennessee .... 6. *R. rotundifolium*

      FF. Calyx tube white or creme-colored

        H. Petals entire; leaves not punctate

I. Filaments and anthers glabrous; Great Plains and adjacent eastern deciduous forest west of the Appalachian Mountains ..... 7. *R. missouriense*

II. Filaments or anthers hairy; Snake River and Humboldt River watersheds .... 8. *R. niveum*

HH. Petals often toothed; leaves glandular-punctate below; southeastern United States ....9. *R. curvatum*

1. **Ribes cynosbati** L. (Figure 8)

Ribes cynosbati L., Sp. Pl. 202. 1753. *Grossularia cynosbati* (L.) Mill., Gard. Dict., unpaged, 1768. TYPE: CANADA, *Kalm s.n.* (HOLOTYPE: LINN, 278.9, as IDC microfiche!).

Ribes gracile Michx., Fl. bor.-amer. 111. 1803. TYPE: UNITED STATES, in montibus Tennessee, *Michaux s.n.* (HOLOTYPE: P, as IDC microfiche!, and observations by H. G. Bedell).

Ribes huronense Rydb. in Britton, Man. Fl. N. States 487. 1901. TYPE: Lake Huron, *Todd s.n.* (HOLOTYPE: K, not seen).

Ribes cynosbati L. var. *glabratum* Fernald, Rhodora 7: 156. 1905. *Grossularia cynosbati* (L.) Mill. var. *glabrata* (Fernald) A. Berger, New York Agric. Exp. Sta. Techn. Bull. 109: 92. 1924. LECTOTYPE (here designated): UNITED STATES, Virginia, Smythe Co., northeast slope of Whitetop Mountain, 28–29 May 1892, *Small s.n.* (GH!; ISOLECTOTYPES: A!, MO!, WIS!, WS!).

Ribes cynosbati L. forma *inerme* Rehder, Mitt. Deutsch. Dendrol. Ges. 19: 250. 1910. *Ribes cynosbati* L. var. *inerme* (Rehder) L. H. Bailey, Stand. Cycl. Hort. 2962. 1916. *Grossularia cynosbati* (L.) Mill. forma *inermis* (Rehder) A. Berger, New York Agric. Exp. Sta. Techn. Bull. 109: 92. 1924. LECTOTYPE (here designated): UNITED STATES, Vermont, Chittenden Co., near Charlotte, 4 Aug 1902, *Rehder s.n.* (A!).

Grossularia cynosbati (L.) Mill. var. *villosa* A. Berger, New York Agric. Exp. Sta. Techn. Bull. 109: 92. 1924. LECTOTYPE (here designated): UNITED STATES, Vermont, Chittenden Co., near Burlington, 1 Jul 1896, *Waugh 957* (BH!).

Ribes cynosbati L. var. *atrox* Fernald, Rhodora 37: 261. 1935. *Ribes cynosbati* L. forma *atrox* (Fernald) B. Boivin, Naturaliste Canad. 93: 435. 1966. TYPE: CANADA, Ontario, Manitoulin Co., south of Little Current, Manitoulin Island, 29 Jun 1934, *Fernald & Pease 3358* (HOLOTYPE: GH!; ISOTYPE: US!).

Plant a small to medium shrub 0.5–1.5 m tall; *stems* erect to spreading and rooting at the tips, the bark green to brownish or purplish when young, glabrous or pubescent when young, glabrous in age, occasionally with internodal bristles especially when young and on vigorous vegetative shoots; *nodal spines* purplish to grey, (0) 1–2 (3), 5–15 mm long, straight or slightly curved; *leaves* isodiametric to slightly wider than long, the blade 17–50 mm long, 20–50 mm

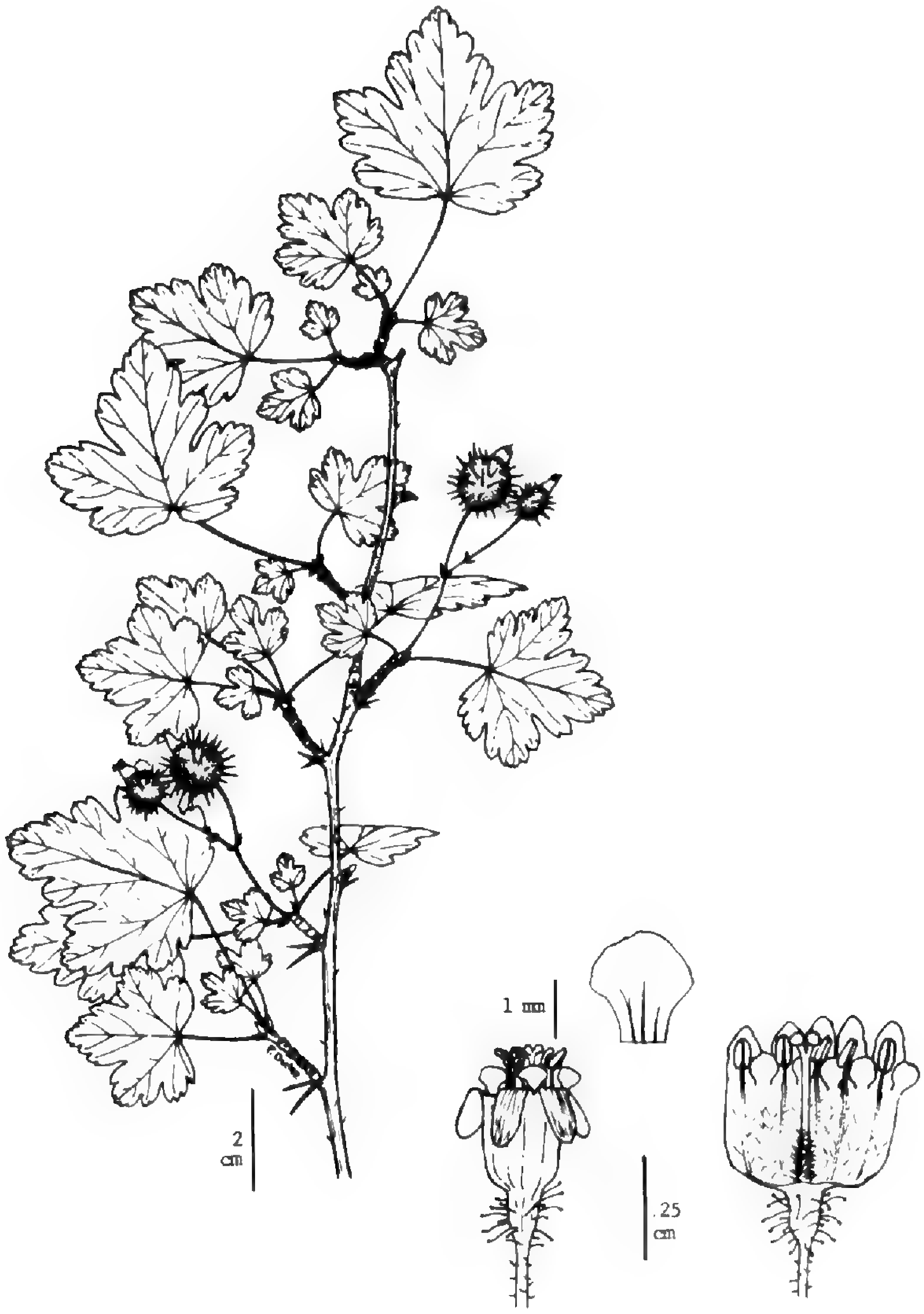


Figure 8. Illustration of *Ribes cynosbati*: habit, flower, open flower and petal. Note the characteristic spiny fruit and short filaments.

wide, deeply 3–5-lobed, the lobes with rounded teeth, pubescence variable, the upper surface from glabrous or pilose to nearly hirsute, with glandular hairs sparsely intermixed, the lower surface normally pilose to nearly velutinous, rarely subglabrous and only occasionally with intermixed glandular hairs, the apex acute (about 90°), the base usually cordate to deeply cordate (190–230°), the petiole 10–30 mm long, pilose and with both eglandular hairs and glandular hairs of varying lengths, those nearest the base longer and more often plumose; *inflorescence* of 1–3 (4) flowers on pilose to glandular, 7–25 mm long, peduncles; *flowers* on 5–16 mm long, glabrous or pilose and glandular pedicels, subtended by bracts 1.5–2.5 mm long, these hairy and glandular on the margins; *hypanthium* cylindrical, greenish-white, the tube 3–4.5 mm long, 3.5–4 mm wide, glabrous to scattered hairy, the calyx lobes 2.5–4 mm long, erect to recurved in age, glabrous or sparsely hairy, the petals obovate, 1–2 mm long, white, the filaments 1–2 mm long, glabrous, exserting the greenish-yellow, glabrous anthers just above the petals; *pistil* with a style divided about halfway, 4.5–7 mm long, usually villous on the lower half or glabrous throughout, the ovary glandular when young with the hairs becoming stiff eglandular prickles on the fruit; *fruits* armed, greenish to pale red at maturity, 7–15 mm in diameter, usually prickly with stiff, broad-based bristles 3–5 mm long varying in number from few to many or rarely none; $n = 8$ (Sax, 1931). Flowering from May–Jun, fruiting from May–Aug.

DISTRIBUTION. Widely distributed in the past throughout the eastern deciduous forest from Ontario and Quebec southward to Oklahoma and Georgia. Due to extensive agricultural and other uses of the land in this region, *Ribes cynosbati* is often restricted to patches of woods alongside roads, woodlots that are not heavily grazed, and in federal, state, and local parks and natural areas. Large populations are now rare and only scattered individuals are found (Figure 9).

PLANT ASSOCIATIONS. In the northern part of the range in Canada, *Ribes cynosbati* typically inhabits mesic *Thuja, Betula* and *Populus* swamps or poorly drained areas. In the United States, and in some parts of Canada, it forms a major shrub component in deciduous forests mainly in the *Acer-Ulmus-Fraxinus* association. In other locations as in the higher Appalachian chain and in the northern regions of Canada and the United States, *R. cynosbati* is also found with coniferous species such as *Picea, Pinus* and *Tsuga.* The larger extant populations of *R. cynosbati* appear to be found in deciduous woodlands rich in *Ulmus.*

DISCUSSION. *Ribes cynosbati* is a widely distributed species and as a result it is rather variable in all aspects from pubescence to spininess of stems and fruits. This has led to the recognition of several infraspecific entities, and the confusion and misapplication of some names. Among the latter is *R. gracile,* a synonym of *R. cynosbati,* which is discussed in detail under *R. missouriense.* As with other species in sect. *Grossularia,* minor pubescence differences are not considered to be systematically significant. Lectotypes

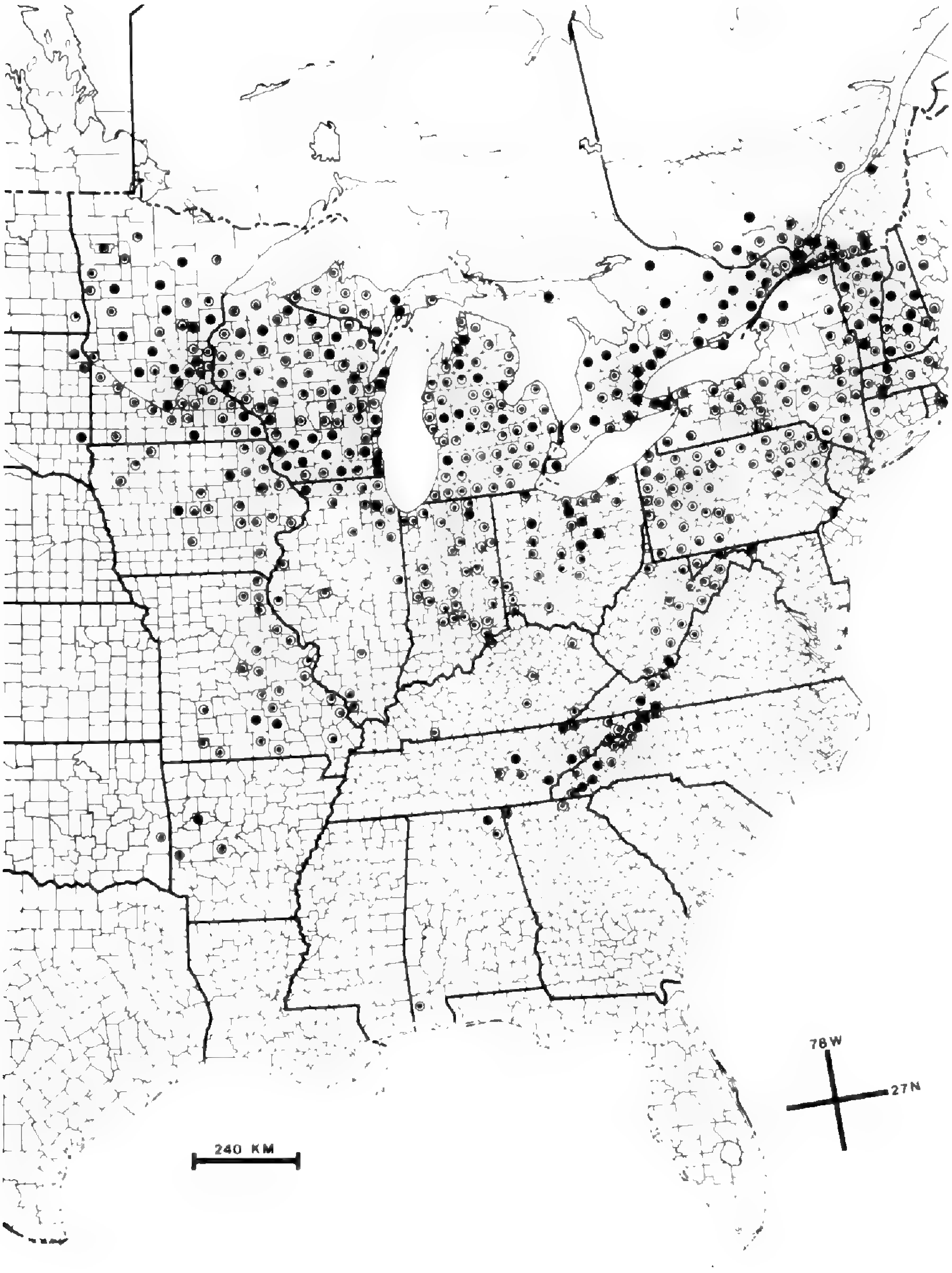


Figure 9. County dot distribution map of *Ribes cynosbati.* Solid circles represent post-1965 collections.

are selected for two of these variants. Fernald (1905) cited four syntypes for his var. *glabratum*, two from Ohio and one each from Virginia and North Carolina. The specimen from Virginia is hereby selected as the lectotype as it clearly displays the critical characters given by Fernald. Berger's (1924) var. *villosa* is represented by two specimens annotated by him currently found at BH (Hyypio, 1981, personal communication). The lectotype is a "wild" specimen having been collected in the field, while the other is a cultivated plant grown at the Experiment Station in Geneva, New York, prepared by S. A. Beach in 1899.

Fernald's (1935) var. *atrox* has frequent internodal bristles indicative of young vegetative or recently grazed shoots. Internodal bristles are typically lost with the excising of the epidermal layers associated with the development of secondary growth so that reproductive shoots generally have few or no such bristles. The type collection retained the internodal bristles into reproductive age, although most of the fertile side-shoots are smooth and only the main branch is excessively bristly.

Although Rehder (1910) proposed forma *inerme* for the smooth-fruited extremes in *Ribes cynosbati,* the epithet became quickly confused and misapplied to the smooth-stemmed variants of the species (Seymour, 1969; Scoggan, 1978). Seymour, unaware of this, proposed forma *invitans* for the smooth-fruited specimens of *R. cynosbati,* but the type (a Pringle collection from Vermont) is actually a specimen of the smooth-fruited species, *R. hirtellum.* Rehder was unable to clearly distinguish between the smooth-fruited forms of *R. cynosbati* and *R. hirtellum* insofar as one of his syntypes was the same Pringle collection selected by Seymour as the holotype for his forma *invitans.*

Some of the smooth-fruited specimens of *Ribes cynosbati* appear to represent interbreeding between that species and several others. These can be distinguished by other unusual or intermediate characters in addition to the smooth fruits. Specimens from Monroe County, Tennessee, and from several counties in Michigan and Wisconsin, show intermediate features that suggest interbreeding with *R. rotundifolium* or *R. missouriense* in Tennessee, and with *R. hirtellum* or *R. missouriense* in the Great Lakes region. Such smooth-fruited specimens of *R. cynosbati,* no matter their origin, are of horticultural importance.

REPRESENTATIVE SPECIMENS. **Canada.** ONTARIO: Bruce Co., Stokes Bay, *Krotkov 9117* (TRT, US), Carleton Co., Prescott, *Sinnott 1507* (MARY), Essex Co., Point Pelee, *Maycock & Maryniak 2882* (DAO, MIMG), Muskoka Co., Gravenhurst, *Soper & Dale 3427* (TRT); QUEBEC: Argenteuil Co., Riviere Outaouais, *Boivin & Rens 14243* (DAO, MTMG, WIS), Gatineau Co., Gatineau Park, *Gillette & Crompton 13394* (CAN, DAO, TRT), Jacques-Cartier Co., Montreal, *Boivin 731* (DAO, GH, MO), Missisquoi Co., Phillipsburg, *Maycock 7070* (MTMG). **United States.** ALABAMA: Jackson Co., Pisgah Gorge, *Kral 34396* (NY, TENN); ARKANSAS: Logan Co., Magazine Mtn., *Palmer 26927* (A, KSC, MIN); CONNECTICUT: Litchfield Co., Canaan, *Graves 6241* (PH); GEORGIA: Union Co., Wolfpen Gap, *Duncan 21598* (GA); ILLINOIS: Cook Co., Palos Park, *Umbach 2982* (WIS), Jo Daviess Co., Portage, *Lansing 4108* (F, PH), Lake Co., Waukegan, *Gates 3055* (F, MICH); INDIANA: Brown Co., Treulac, *Freisner 3864* (BRY, PH), Montgomery Co., Sugar Cr., *Deam 17611* (A), Porter Co., Woodville Jct., *Steyermark 63557* (F); IOWA: Boone Co., Bluff Cr., *Pammel & Rosen 101* (MO), Johnson Co., McBride State Park, *Ives & Bugbee 62* (UC), Winneshiek Co., Bluffton, *Tolstead s.n.* (MIN); KENTUCKY: Madison Co., West Lake, *Pittillo 77* (LL); MAINE: Franklin Co., Strong, *Furbish s.n.* (GH); MARYLAND: Washington Co., Potomac R., *Hill 10275* (MARY); MASSACHUSETTS: Berkshire Co., Deerfield R., *Fernald & Long 9591* (PH), *Franklin Co., Buckland, Seymour 3848* (AC, GA, UTC); MICHIGAN: Cheyboygan Co., Douglas L., *Ehlers 1588* (DS, WIS), Ingham Co., Onondaga, *Voss 5407* (MICH), Mackinac Co., Mackinac Isl., *Churchill 451* (GH, MO), St. Clair Co., Port Huron, *Dodge s.n.* (MICH, NCU); MINNESOTA: Blue Earth Co., Madison L., *Moore 24465* (MIN), Hennepin Co., Ft. Snelling, *Beach 49* (GH, MIN), Houston Co., La Crescent, *Sinnott 1594* (MARY), Winona Co., Whitewater State Park, *Sinnott 1619* (MARY); MISSOURI: Clark Co., Dumas, *Bush 5913* (GH, MO, NY, US, VT), Texas Co., Current R., *Steyermark 14570* (MO); NEW HAMPSHIRE: Cheshire Co., Walpole, *Boufford 5498* (MO, NCU, SMU); NEW YORK: Greene Co., New Baltimore, *Brown 714* (MICH), Jefferson Co., Waterton, *Sinnott 1510* (MARY), Tompkins Co., Ithaca, *Weigand 4247* (A, MIN, TEX); NORTH CAROLINA: Haywood Co., Pigeon R., *Boufford 13620* (MO), Jackson Co., Beech Flat Cr., *Pittillo s.n.* (AC, ARIZ, BRY, COLO, DS, MICH, MONTU, MTMG, NHA, RSA, TRT, UTC, WIS, WTU); NORTH DAKOTA: Richland Co., Leonard, *Stevens 1345* (CAN, MIN, NCU, UC, US, WIS); OHIO: Cuyahoga Co., Cleveland, *Beardslee* s.n. (MO, NY), Ashland Co., Mifflin, *Sinnott 1525* (MARY); PENNSYLVANIA: Bradford Co., Troy, *Bartram s.n.* (NY, PH); SOUTH DAKOTA: Minnehaha Co., Palisades State Park, *Sinnott 1640* (MARY), Roberts Co., Sisseton, *Stephens & Brooks 31862* (NY); TENNESSEE: Sevier Co., Great Smoky Mts., *Underwood 651* (NY, RM); VERMONT: Bennington Co., Manchester, *Day 70* (AC, GH, US, VT), Chittenden Co., Lake Champlain, *Seymour 23438* (MO, SMU); VIRGINIA: Giles Co., Beanfield Mtn., *Fogg 14595* (PENN), Whitetop Mtn., *Sinnott 1451* (MARY); WEST VIRGINIA: Pendleton Co., Seneca R., *Core 3214* (GH, NY); WISCONSIN: Brown Co., DePere, *Keefe et al. s.n.* (DAO, NY, WIS), Dane Co., Blue Mounds, *Anderson 23* (WIS), Sauk Co., Devil's L., *Sinnott 1588* (MARY).

2. **Ribes oxyacanthoides** L. (Figure 10)

Plant a small to large shrub 0.3–1.5 m tall; *stems* erect to sprawling, intricately branched to openly branched, the bark grey, straw-colored or red-brown, pubescent when young, becoming glabrate, typically with internodal bristles frequent; *nodal spines* red-brown or gray, 2–3 (6), 5–13 mm long, curved or straight; *leaves* isodiametric to often broader than long, the blade 7–35 mm long, 8–40 mm wide, deeply 3–5 lobed, the lobes with rounded teeth, the upper

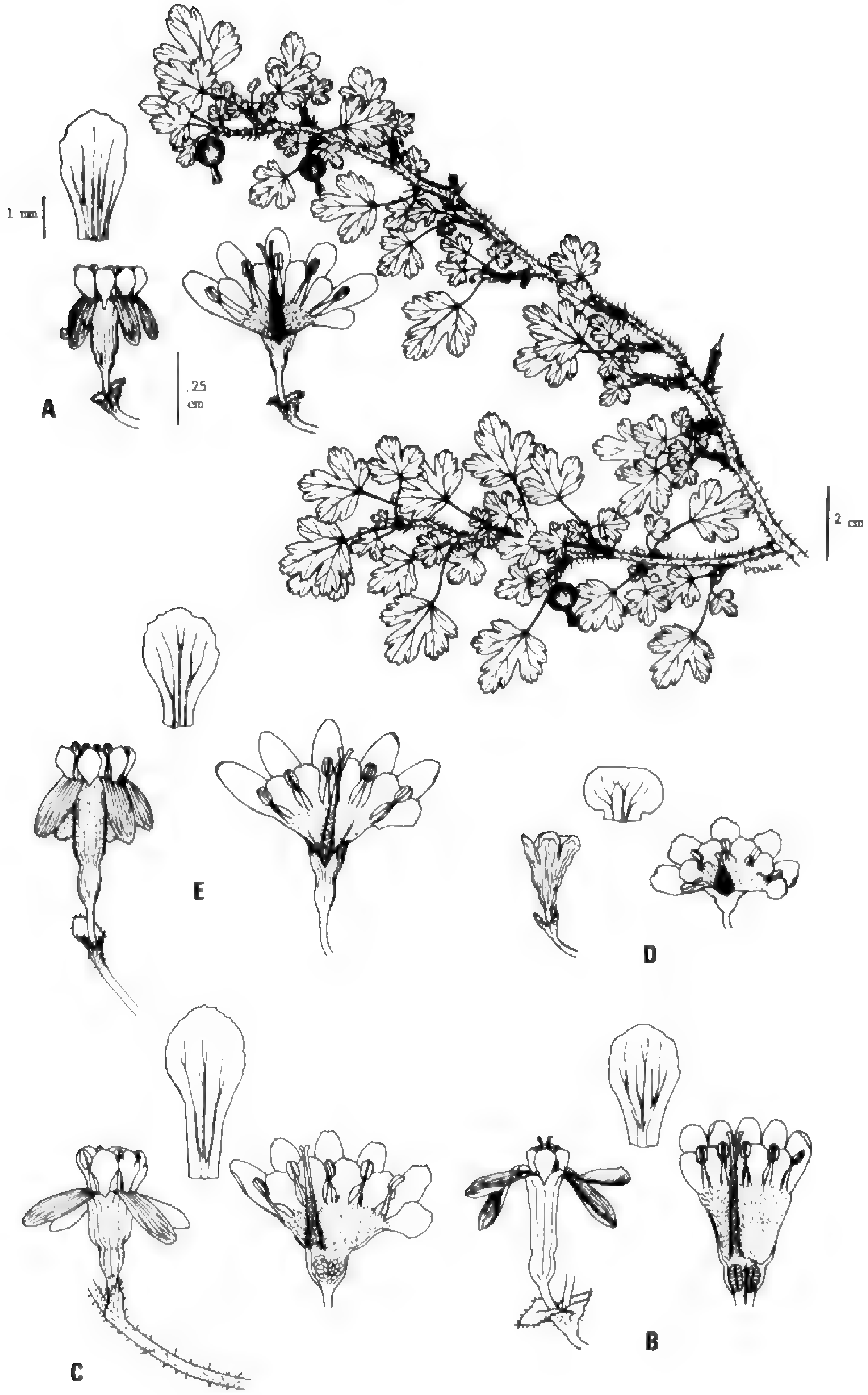


Figure 10. Illustration of *Ribes oxyacanthoides* and subspecies: a) ssp. *oxyacanthoides*, habit, flower and petal, b) ssp. *setosum*, flower and petal, c) ssp. *irriguum*, flower and petal, d) ssp. *hendersonii*, flower and petal, e) ssp. *cognatum*, flower and petal.

surface pilose and glandular, the lower surface usually pilose to villous, rarely glabrate, glandular with stalked and sessile glands, the apex 90–100°, the base truncate to deeply cordate (170–230°), the petiole 5–25 mm long, pilose or glabrous, often with scattered glands, some of these fringed; *inflorescence* of 1–3 (4) flowers on glandular to glabrous 1–15 mm long peduncles; *flowers* on 2–7 mm long, glabrous or occasionally glandular pedicels, subtended by bracts 1–2 mm long, these glandular ciliate; *hypanthium* tubular, campanulate or cylindric, greenish-white to white, the tube 1.5–5.5 mm long, 2–4 mm wide, glabrous to pilose, the calyx lobes glabrous to pilose, diverging at right angles at anthesis, the petals white, 1–3.5 mm long, narrowly spatulate, the filaments 0.5–3.5 mm long, glabrous, positioning the glabrous anthers at the level of the petal apices; *pistil* with a style divided to one third, 2.5–8 mm long, the ovary glabrous; *fruit* smooth, 7–16 mm in diameter, greenish-purple at maturity.

DISTRIBUTION. *Ribes oxyacanthoides* has the largest range of all the species in sect. *Grossularia* extending across the boreal region of Canada from the Hudson Bay west into Alaska. Southern extensions of the species in the United States occur in the northern Rocky Mountains, northern Great Lake states, the Black Hills of the Dakotas and the Palouse region of Oregon and Washington (Figure 11).

DISCUSSION. *Ribes oxyacanthoides* is divided into five subspecies, each of which is localized and generally allopatric. The subspecies rank is being used in *Ribes* systematics to denote entities which differ in regard to many features, but the degree of difference is less than that which would denote species. This is obviously a subjective hierarchy to a great extent, and in the case with *R. oxyacanthoides* subspecies are denoted by incomplete geographical and morphological disjunctions. All five subspecies share short filaments, glandular leaves, spininess and general pubescence. In terms of geography, the five subspecies appear to represent local radiations in the glaciated regions of the northwestern and north-central United States. The ssp. *oxyacanthoides* has the largest range, extending across the boreal regions of North America from the Hudson Bay to Alaska, with southern extensions into the Great Lake states and the Dakotas. In the Rocky Mountains of Wyoming, Idaho, and Montana, ssp. *setosum* replaces ssp. *oxyacanthoides*. In the subalpine and alpine part of the range of ssp. *setosum*, it is replaced by ssp. *hendersonii*. To the west, ssp. *irriguum* replaces ssp. *setosum* at elevations below 1500 m, and is the characteristic gooseberry of the Blue Mountains of Oregon and Washington. In the lower and drier Palouse prairie country, ssp. *cognatum* occurs.

Key to the subspecies of *Ribes oxyacanthoides*

A. Calyx tube narrowly tubular, 3.75–5.5 mm long, 1–2 mm wide
  B. Calyx tube glabrous; twigs red-brown; Rocky Mountains of Montana, Idaho and Wyoming ....2b. ssp. *setosum*
  BB. Calyx tube pilose; twigs grey to staw-colored; Palouse prairie region of Washington and Oregon .... 2e. ssp. *cognatum*
AA. Calyx tube campanulate to short cylindric, 1.5–3.75 mm long, 2–5 mm wide
  C. Peduncles 7–15 mm long; petals 3–3.5 mm; calyx lobes 4.5–5.5 mm long; Blue Mountains of Oregon and Washington and adjacent Idaho ...... 2c. ssp. *irriguum*
  CC. Peduncles 1–5 mm long; petals 1–3 mm long; calyx lobes 2.5–4 mm long
    D. Calyx tube cylindric, 2–4 mm long; leaves truncate; boreal North America, primarily in Canada, with isolated populations in the Black Hills .... 2a. ssp. *oxyacanthoides*
    DD. Calyx tube campanulate to rotate, 1.5–2 mm long; leaves deeply cordate; subalpine and alpine Rocky Mountains of Idaho, Montana and Nevada............... ....2d. ssp. *hendersonii*

2a. **Ribes oxyacanthoides** L. ssp. **oxyacanthoides** (Figure 10a)

Ribes oxyacanthoides L., Sp. pl. 201. 1753. *Grossularia oxyacanthoides* (L.) Mill., Gard. Dict., unpaged, 1768. LECTOTYPE: figure 166, in Dillenius, 1732, Hort. elth., designated by Gray (1876).

Plant a medium shrub 0.75–1.5 m; *twigs* straw-colored to grey; *internodal bristles* typically frequent; *nodal spines* 2–3; *leaves* subcuneate to truncate (rarely subcordate), the blade 15–30 mm long, 20–35 mm wide, the lower surface pilose and evenly glandular; *peduncles* 2–6 mm, glabrous or with scattered glands; *pedicels* 2–5 mm, glabrous; *calyx tube* 2.5–4 mm long, 2–3 mm wide, glabrous, the calyx lobes 2.5–4 mm long, glabrous; *petals* 2–3 mm; *filaments*

1.75–2.5 mm; *style* 5.5 8 mm; $n = 8$ (Taylor & Brockman, 1966). Flowering from May–Jun, fruiting from Jun–Aug.

DISTRIBUTION. The ssp. *oxyacanthoides* is primarily a Canadian entity distributed from the Hudson Bay lowlands west to the Yukon Territories and in the United States west to Alaska. Southern extensions into the United States occur in the northern Great Lakes states and the Black Hills of South Dakota (Figure 11). In the Rocky Mountains ssp. *oxyacanthoides* is replaced with ssp. *setosum*.

PLANT ASSOCIATIONS. In the boreal region of Canada and Alaska, ssp. *oxyacanthoides* typically inhabits limestone and Precambrian rock outcrops or gravelly river and lakeshores (Thieret, 1963; Porsild & Cody, 1980). Associated species are *Pinus banksiana* Lamb., *Picea glauca* (Moench) Voss, and species of *Betula* and *Populus*. In the southern part of the range in North and South Dakota, it is often associated with *Pinus ponderosa* Dougl. near rock outcrops.

DISCUSSION. This subspecies is the sole member of subg. *Grossularia* in the boreal region of North America, and is relatively homogeneous. Some minor confusion surrounded the proper epithet for the northern gooseberry, until Gray (1876) lectotypified *Ribes oxyacanthoides* on the Dillenius figure. Previously, the Hudson Bay gooseberry was believed to be *R. hirtellum* Michx.

In the contact zone between ssp. *oxyacanthoides* and *Ribes hirtellum*, intermediates are found with varying combinations of the two entities. These apparent hybrids are common along the southern coast of James Bay in Ontario and Quebec.

REPRESENTATIVE SPECIMENS. **Canada.** ALBERTA: Cameron Cr., *Breitung 16142* (JEPS, NY), Lake Minnewauca, *Malte & Watson 749* (CAN, UC), Kimball, *Shaw 1418* (BRY), 27 mi. W. Swan Hills, *Musselman 3624* (WIS), Lake Aththabaska, *Preble 185* (US), Waterways *Raup 2531* (CAN); BRITISH COLUMBIA: Kamloops, *Calder & Saville 8557* (DAO, UC), Guichon Cr., *Hitchcock & Martin 7415* (A, COLO, DS, NY, RM, UC, WS), Radium Hot Springs, *McCabe 6201* (UC), Prophet R., *Calder & Gillette 24529* (COLO), Dawson Cr., *Raup & Abbe 3517* (CAN); MANITOBA: Clear L., *Baldwin 10925* (CAN), Lake Winnepegosis, *Scoggan 4451* (CAN), Churchill R., *Cody 1041* (CAN, WIS), York Factory, *Scoggan 6015* (CAN, GH); NORTHWEST TERRITORIES: Keewatin District, Loon Point, *Baldwin et al. 757* (CAN), Mackenzie District, Yellowknife, *Cody & McCanse 2109* (COLO, US), Great Bear L., *Porsild & Porsild 3682* (CAN, US), Wood Buffalo Park, *Raup 2538* (CAN, GH), Lady Evelyn Falls, *Thieret & Reich 4782* (CAN, NY); ONTARIO: Cochrane District, Moose R., *Johansen 53* (CAN), Kenora District, Minnitaki L., *Baldwin 9031* (CAN), Thunder Bay District, Pigeon Bay, *Garton 1936* (GH, NY, RM, UC); SASKATCHEWAN: Douglas Provincial Park, *Gray & Brown 1815* (CAN), Matador Field, *Skoglund 17* (CAN, GH).

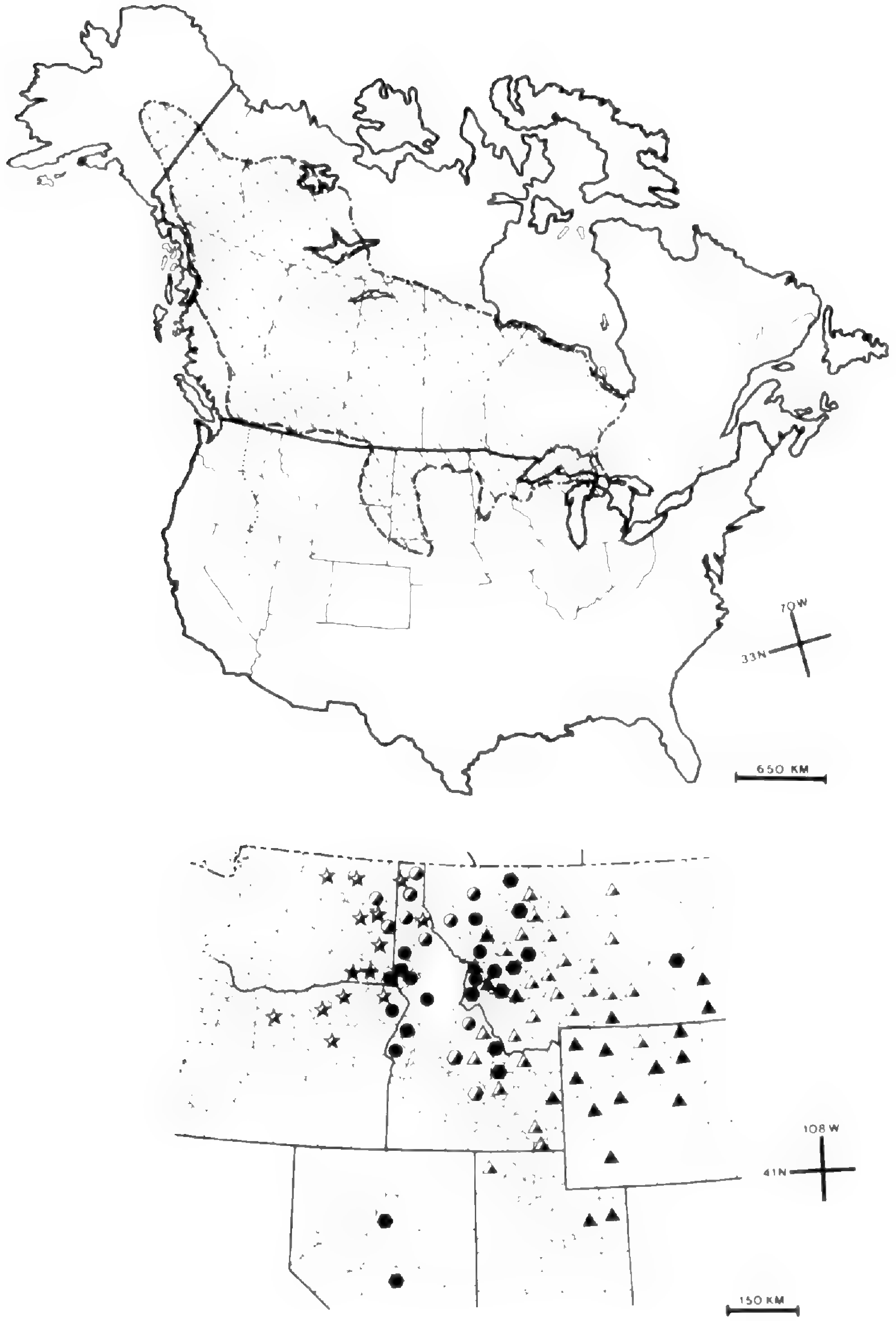


Figure 11. Distribution map of *Ribes oxyacanthoides*. Top, distribution of ssp. *oxyacanthoides* (hatched area) and the combined range of the other four subsp. (dotted line). Bottom, county dot distribution map of the four atypical subsp.: circles = ssp. *irriguum*, triangles = ssp. *setosum*, stars = ssp. *cognatum* and hexagons = ssp. *hendersonii*. Solid symbols indicate post-1965 records.

Lake Athabaska, *Tyrrell 8687* (CAN); YUKON: Whitehorse, *Anderson 9574* (CAN, GH), Pine Cr., *Raup & Raup 12078* (A, CAN), Little Atlin L., *Youngman & Tessier 309* (CAN). **United States.** MICHIGAN: Emmett Co., Cecil Bay, *Gates 12085* (DS), Keweenaw Co., Isle Royal, *McFarlin 2113* (CAN), Marquette Co., Ishpeming, *Rydberg s.n.* (NY), Ontonagon Co., Porcupine Mtns., *Fassett 19640* (GH, WIS); MINNESOTA: Cook Co., Gooseberry R., *Fassett & Curtis 19966* (WIS), Yellow Medicene Co., Granite Falls, *Moore 13100* (A); MONTANA: Roosevelt Co., Little Muddy Cr., *Bartlett & Grayson 386,* (US) Sheridan Co., Medicene L., *Hotchkiss 6880* (WTU); NEBRASKA: Sioux Co., Cottonwood Cr., *Tolstead 41903* (TEX, UC); NORTH DAKOTA: Ramsey Co., Devil's L., *Palmer 36871* (A, NY, US), Slope Co., Little Missouri R., *Stevens 889* (A, DAO, MIN, SMU, UC, WIS); SOUTH DAKOTA: Custer Co., Wind Caves National Park, *Rutter 36* (UC), Custer State Park, *Sinnott 1664* (MARY), Lawrence Co., Tilford, *Palmer 37333* (A, NY, US); WISCONSIN: Barron Co., Barron Hills, *Fassett & Schmidt 15565* (GH); WYOMING: Crook Co, Green Mtn., *Nelson 2223* (RM).

2b. **Ribes oxyacanthoides** L. ssp. **setosum** (Lindl.) Sinnott, *comb. nov.* (Figure 10b)

Ribes setosum Lindl., Trans. Hort. Soc. London 7: 243. 1830. *Grossularia setosa* (Lindl.) Coville & Britton, N. Amer. Fl. 22: 222. 1908. TYPE: a cultivated specimen of unknown origin, presented to the Horticultural Society by Loddige, (HOLOTYPE: CGE!).

Ribes saximontanum E. E. Nels., Bot. Gaz. (Crawfordsville) 30: 119. 1900. TYPE: UNITED STATES, Wyoming, Park Co., Golden Gate in Yellowstone Park, 28 June 1899, *Nelson & Nelson 5542* (HOLOTYPE: RM!; ISOTYPES: A!, MO!, RM!, US!).

Ribes camporum Blank., Montana Coll. Agric. Sci. Stud. Bot. 1: 63. 1905. LECTOTYPE (here designated): UNITED STATES, Montana, Custer Co., 7 mi. south of Custer Station, 3 May 1890. *Blankinship 9* (MONT!).

Plant a medium to tall shrub 0.5–1.5 m; *twigs* tan to reddish-brown; *internodal bristles* usually present on young wood; *nodal spines* occasionally with a few additional smaller spines; *leaves* deeply cordate, the blade 20–35 mm long, 20–40 mm wide, the lower surface pilose and evenly glandular or glabrate; *peduncles* 3–6 mm, scattered glandular and pilose or glabrous; *pedicels* 2–5 mm, glabrous to scattered glandular; *calyx tube* 3.5–5 (5.5) mm long, 1–2.5 mm wide, glabrous, the calyx lobes 3.5–5 mm long, glabrous; *petals* 2–3 mm; *filaments* 2–3 mm; *style* 6.5–8.5 mm; $n = 8$ (Zielinski, 1952). Flowering from May–Jun, fruiting from Jun–Aug.

DISTRIBUTION. The ssp. *setosum* is localized to the Rocky Mountains of central and southern Montana, eastern Idaho, northern Utah and the mountains of Wyoming from 1500–2700 m (Figure 11). Subspecies *setosum* and ssp. *oxyacanthoides* intergrade in eastern Montana and Wyoming, and frequent intermediates are found. Populations from South Dakota and eastern Wyoming appear somewhat intermediate, and have been assigned to ssp. *oxyacanthoides*. No specimen from Canada seen by me is referable to ssp. *setosum* although the two subspecies are similiar, differing primarily by the length and width of the calyx tube, leaf base and twig color.

PLANT ASSOCIATIONS. *Ribes oxyacanthoides* ssp. *setosum* inhabits high elevation river banks and rocky slopes. Along rivers, typical associates are species of *Populus, Prunus, Acer* and *Salix*. In drier rocky places, typical associates are *Artemisia* and *Rhus trilobata* Nutt.

DISCUSSION. Considered a species in most regional floras, this entity replaces the more northern ssp. *oxyacanthoides* in the mountains of Montana, Wyoming and Idaho. The ssp. *oxyacanthoides* is typically not a montane species, and is found at low elevations in the boreal forest.

The specimens collected by Douglas in 1826–1827, from the Saskatchewan River in Canada are representative of ssp. *oxyacanthoides,* not ssp. *setosum.* Lindley (1830a) did not cite the Douglas material in the type description, but later the same year he included the Douglas material when the species was illustrated in the *Botanical Register* (Lindley, 1830b). A Douglas collection from this region is mounted with the type at CGE; other Douglas collections of ssp. *oxyacanthoides* are at K.

REPRESENTATIVE SPECIMENS. **United States.** IDAHO: Bannock Co., Mink Cr., *Beard s.n.* (RM), Custer Co., Morgan Cr., *Hitchcock & Muhlick 9358* (NY, UC, UTC, WTU), Lemhi Co., Gibbonsville, *Christ & Ward 14686* (NY); MONTANA: Beaverhead Co., Red Rock Cr., *Breitung 17793* (DAO), Broadwater Co., Townsend, *Booth 56338* (GH, RM), Carbon Co., Red Lodge, *Hitchcock & Muhlick 13562* (CAS, DS, MO, NY, PH, RM, UC, UTC, WS, WTU), Cascade Co., Hardy, *E. Palmer 36958* (A, NY), Custer Co., Cow Cr. Camp, *Lackschewitz 5598* (MONTU), Gallatin Co., Bozeman, *M. E. Jones s.n.* (A, ARIZ, CAS, GH, MO, UC, US), Granite Co., Phillipsburg, *Sinnott 1871* (MARY), Madison Co., Madison National Forest, *Coville s.n.* (US), Meagher Co., Little Belt Mts., *Hitchcock & Muhlick 12362* (CAN, CAS, DS, GH, MO, NY, PH, RM, UC, UTC, WTU), Missoula Co., Missoula, *M. E. Jones s.n.* (CAS, MO, POM), Park Co., Suksdorf Gulch, *Suksdorf 163* (UTC, WTU), Powell Co., Helmville, *Hitchcock & Muhlick 11694* (NY, PH, WS, WTU), Ravalli Co., Darby, *Calder & Saville 20610* (DAO), Stillwater Co., Absarokee, *Renner 398* (DAO); UTAH: Box Elder Co, Rosvere, *Cottam 2962* (BRY), Duchesne Co., Lower Stillwater, *Brothers 1598* (BRY), Uintah Co., Mosby Narrows, *Goodrich 299* (UT); WYOMING: Campbell Co., White Trail Butte, *Hortman & Dueholm 6204* (NY), Big Horn Co., Big Horn Mts., *Worthley 74* (RM, US), Crook Co., Hulett, *Ownbey 645* (COLO, GH, MO, MONTU, UC, UTC), Fremont Co., Popo Agie R., *Goodrich 13701* (BRY), Garfield Co., Blackfoot Divide, *Holmgren 2066* (UTC), Natrona Co., Platte Canyon, *Gooding 133* (A, MO, RM), Park Co., Mammoth Hot Springs, *Mearns 2371* (DS, NY, US), Shoshone R., *Sinnott 1881* (MARY), Sheridan Co., Wolf, *Cary 734* (US), Sublette Co., Pole Cr., *Dunwiddie 18* (WIS), Teton Co., Hogback Canyon, *Williams & Pierson 712* (CAS, GH, MO, NY, POM, RM, UTC), Washakie Co., Tensleep, *Sinnott 1888* (MARY).

2c. **Ribes oxyacanthoides** L. ssp. **irriguum** (Douglas) Sinnott, *comb. nov.* (Figure 10c)

Ribes irriguum Douglas, Trans. Hort. Soc. London 7: 516. 1830. *Ribes divaricatum* Douglas var. *irriguum* (Douglas) A. Gray, Amer. Naturalist 10: 273. 1876. *Ribes oxyacanthoides* L. var. *irriguum* (Douglas) Jancz., Mém. Soc. Phys. Genève 35: 1907. *Grossularia irrigua* (Douglas) Coville & Britton, N. Amer. Fl. 22: 222. 1908. TYPE: UNITED STATES, Washington, Asotin Co., Munro's Fountain, Blue Mountains, 28 Jul 1826, *Douglas 220* (HOLOTYPE: K, as a photograph!; ISOTYPE: BM!).

Ribes leucoderme A. Heller, Bull. Torrey Bot. Club 24: 93. 1897. *Ribes oxyacanthoides* L. var. *leucoderme* (A. Heller) Jancz., Mém Soc. Phys. Genève 35: 388. 1907. TYPE: UNITED STATES, Idaho, Nez Perces Co., Lake Waha, Craig Mountains, 2 Jun 1896, *Heller & Heller 3175* (HOLOTYPE: BKL!; ISOTYPES: A!, DAO!, DS!, F!, MICH!, MIN!, NY!, PH!, UC!, WS!).

Grossularia non-scripta A. Berger, New York Agric. Exp. Sta. Techn. Bull. 109: 107. 1924. *Ribes non-scriptum* (A. Berger) Standley, Field Mus. Nat. Hist., Bot. Ser. 8: 139. 1930. LECTOTYPE (here designated): a cultivated specimen raised at Geneva, New York, (source perhaps Colorado, according to Berger), collected and pressed 15 May 1924, *Berger s.n.* (BH! ISOLECTOTYPE: BH!).

Plant a medium shrub 0.75–1.5 m; *twigs* grey to straw-colored; *internodal bristles* absent or few; *nodal spines* 0–2 (3); *leaves* cordate to truncate (rounded), the blade 20–30 mm long, 25–40 mm wide, the lower surface pilose to felty, glandular; *peduncles* 6–15 mm, pilose with glandular and eglandular hairs; *pedicels* 3–6 mm, glabrous; *calyx tube* 2.5–4 mm long, 2.5–4 mm wide, glabrous, the calyx lobes 4.5–5.5 mm long, glabrous (pilose); *petals* 3–3.5 mm; *filaments* 2.5–3.5 mm; *style* 6.5–8 mm; $n = 8$ (Zielinski, 1952). Flowering from May–Jun, fruiting from Jun–Jul.

DISTRIBUTION. The ssp. *irriguum* is restricted in distribution to north-central Idaho, western Montana, Oregon, and southwestern Washington at elevations from 900–1500 m (Figure 11). This entity is the most common gooseberry in the Blue Mountains of Oregon and Washington, an area below the elevational range of ssp. *setosum* and above that of the more western ssp. *cognatum*. This subspecies is listed as a sensitive plant (as *Ribes irriguum*) in the state of

Washington (Washington Natural Heritage Program, 1981, 1982). In Oregon, *R. irriguum* is listed as "Rare and Endangered" in the state, but more abundant elsewhere (Siddall et al., 1979). As discussed under the chapter on endangered species, *R. oxyacanthoides* ssp. *irriguum* is not in immediate danger of becoming extinct. In the Blue Mountain region of Washington and adjacent parts of Oregon and Idaho, the subsp. is relatively frequent, although its overall range is still relatively small. As a result, major disturbances in this region would rapidly affect the plant.

PLANT ASSOCIATIONS. This subspecies is associated with *Pinus monticola* Dougl. ex D. Don, *P. ponderosa* Dougl. ex Laws, *Populus* sp., and *Crataegus* sp. Unlike many members of sect. *Grossularia*, ssp. *irriguum* is typically associated with conifers.

DISCUSSION. Subspecies *irriguum* is a relatively distinct gooseberry which differs from the other subspecies of *Ribes oxyacanthoides* by a broad calyx tube with lobes that are longer than the tube. Another characteristic feature is the long glandular peduncle. Some difficulty in designating isotypes of *R. leucoderme* was encountered. The published holotype is accession number 3175, collected 2 Jun 1896, yet several apparent isotypes have the correct accession number but are dated 3–4 Jun 1896, while others have the proper date but are accession number 2175. Some of the latter specimens have been changed to #3175. All of these flowering specimens from Lake Waha are considered isotypes.

Specimens appearing to be ssp. *irriguum* from central Montana and the mountains of Wyoming represent probable hybrid swarms between *Ribes inerme* and *R. oxyacanthoides* ssp. *setosum*. These intermediates have the relatively broad calyx tube and long peduncles of *R. inerme* combined with the nodal spines, twig color and short stamens of the latter. In some specimens from these hybrid swarms, the filaments are slightly longer than the petals, as is characteristic of *R. inerme*. Two such hybrid swarms were analyzed in the field, one near Phillipsburg, Granite Co., Montana, the other 15 miles west of Buffalo, Johnson Co., Wyoming. At both sites, plants of *R. inerme* and *R. oxyacanthoides* ssp. *setosum* were present in addition to the intermediates. These putative hybrids are not the relatively distinct *R. oxyacanthoides* ssp. *irriguum* found west of the range of ssp. *setosum*. The subspecies *irriguum* is distinguished from these apparent hybrids by the characteristic glandular peduncle and general pubescence. The distribution of ssp. *irriguum* is west of the range of ssp. *setosum* therefore hybridization cannot be producing the plants of ssp. *irriguum*. It is possible to speculate that hybridization between ssp. *setosum* and *R. inerme* could have been the origin of ssp. *irriguum* at some past time, but the modern elements of this subsp. are totally capable of independent reproduction and have developed a distinct geographical distribution.

REPRESENTATIVE SPECIMENS. **United States.** IDAHO: Adams Co., Indian Valley, *M. E. Jones s.n.* (NY, POM, RM), Meadows, *Sinnott 1747* (MARY), Bonner Co., Hope, *Dunkle 376* (MIN, NY, RM), Idaho Co., French Cr., *Cronquist 6180* (GA, MIN, NY, ORE, OSC, RSA, SMU, UTC, WIS, WTU), Selway Falls, *Sinnott 1830* (MARY), Kootenai Co., Lake Couer d'Alene, *Epling & Hauck 10114* (MO), Latah Co., Potlatch Cr., *Ownbey & Ownbey 2014* (ARIZ, ORE, WIS, WS, WTU), Lewis Co., Craigmont, *Daubenmire 37159* (WS, WTU), Winchester Lake, *Sinnott 1825* (MARY), Nez Perces Co., Forest, *Brown 17* (MIN, MO, NY, UC), Shoshone Co., Calder, *Christ 10959* (NY), Washington Co., Payette National Forest, *Lewis 2261* (UTC); MONTANA: Flathead Co., Columbia Falls, *Williams s.n.* (A, DS, GH, MO, NY, RM, UC), Lake Co., Bison Range, *Thomas 11925* (DS, MONTU), Missoula Co., Stark, *Kirkwood 1380* (CAS, DS, NY, ORE, UC), 19 mi E Lolo Pass, *Sinnott 1859* (MARY), Ravalli Co., Stevensville, *Stickney 1186* (MONTU), Sanders Co., Paradise, *C. L. Hitchcock 1539* (CAS, MONTU, POM); OREGON: Wallowa Co., Hurricane Cr., *Mason 1082*, Wallowa L., *M. E. Jones 25453* (DS, MO, UTC, WTU); WASHINGTON: Asotin Co., Anatone, *Baker 5969* (NY, WTU), Field's Spring State Park, *Sinnott 1785* (MARY), Stevens Co., no loc. *Beattie & Chapman 2153* (WS).

2d. **Ribes oxyacanthoides** L. ssp. **hendersonii** (C. Hitchc.) Sinnott, *comb. nov.* (Figure 10d)

Grossularia neglecta A. Berger, New York Agric. Exp. Sta. Techn. Bull. 109: 106. 1924, non *R. neglecta* Rose (1905). *Ribes hendersonii* C. Hitchc., Univ. Wash. Publ. Biol. 17(3): 73. 1961. TYPE: UNITED STATES, Idaho, Butte or Custer Co., Lost River Mountains, 8000 ft., 14 Aug 1895, *Henderson 4048* (HOLOTYPE: US!).

Plant a low intricately branched shrub 0.3–0.5 m; *twigs* straw-colored to tan; *internodal bristles* occasionally present; *nodal spines* (1) 2–3, often with additional spines smaller than the primary spines; *leaves* deeply cordate, the blade 7–11 mm long, 8–11 mm wide, the lower surface finely dense pilose and glandular; *peduncles* 1–3 mm, glabrous to glandular; *pedicels* 1–3 (4) mm, glabrous; *calyx tube* 1.5–2 mm long, 2–2.5 mm wide, glabrous, the calyx lobes 2.5 mm long, glabrous (scattered hairy); *petals* 1–1.5 mm; *filaments* 0.5–1 mm; *style* 2.5–3 mm; chromosome number not reported. Flowering from Jun–Jul, fruiting from Jul–Aug.

DISTRIBUTION. The ssp. *hendersonii* is found in rocky places above the treeline in Idaho, Montana, and scattered stations in

Nevada (Figure 11). This relatively diffuse distribution is probably in part due to the lack of extensive alpine and subalpine collections rather than rarity of this subspecies. Plants collected by the author from 3000 m in the Bighorn Mountains appear to have the habit of ssp. *hendersonii* but were not yet in flower in mid-June.

DISCUSSION. This subalpine entity was first described by Berger (1924) as *Grossularia neglecta,* a name unavailable under the genus *Ribes* due to a previous *R. neglectum* Rose. The distribution of ssp. *hendersonii* is probably more continuous, consisting of a series of high elevation populations in the northern Rocky Mountains of the United States.

REPRESENTATIVE SPECIMENS. **United States.** IDAHO: Blaine Co., Smokey Mts., *Macbride & Payson 3745* (DS, GH, POM, US), Butte Co., Pass Cr. Gorge, *Hitchcock & Muhlick 8842* (CAS, UC, WTU), Custer Co., *Hitchcock et al., 3785* (CAS, WTU), Lemhi, Co., Gilmore, *Hitchcock & Muhlick 9309* (NY, WS, WTU); MONTANA: Deerlodge Co., Upper Seymour L., *Lackschewitz 4594* (MONTU, MTMG), Glacier Co., St. Mary, *Shaw 3075a* (BRY), Granite Co., Racetrack Peak, *Lackschewitz 6312* (MONTU, NY, WTU), Lewis and Clark Co., Haystack Butte, *Lackschewitz 4274* (MONTU, WTU), Powell Co., Mt. Baldy, *Lackschewitz 5590* (MONTU, WTU), Ravalli Co., Mine Cr. Road near border, *Cory 1676* (MONTU, WTU), Rosebud Co., Northern Cheyenne Indian Reservation, *Lackschewitz 5978* (MONTU), Teton Co., Choteau Mtn., *Lackschewitz 4473* (MONTU); NEVADA: Lander Co., Bunker Hill, *Goodrich 13342* (BRY), Nye Co., Ophir Pass, *Goodrich 11671* (BRY).

2e. **Ribes oxyacanthoides** L. ssp. **cognatum** (Greene) Sinnott, *comb. nov.* (Figure 10e)

Ribes cognatum Greene, Pittonia 3: 115. 1896. *Grossularia cognata* (Greene) Coville & Britton, N. Amer. Fl. 22: 222. 1908. TYPE: UNITED STATES, Oregon, Umatilla Co., Umatilla River at Pendleton, 17 May 1896, *Howell 1929* (HOLOTYPE: NDG! ISOTYPE: ORE!).

Plant a medium to tall shrub 0.75–1.5 m; *twigs* reddish-tan to greyish; *internodal bristles* occasionally present; *nodal spines* (1) 2–3; *leaves* deeply cordate, the blade 25–35 (40) mm long, 30–45 mm wide, the lower surface short pilose and evenly glandular; *peduncles* 3–7 mm, glandular pilose; *pedicels* 3–5 mm, glabrous or glandular pilose; *calyx tube* 3.75–5 mm long, 1.5–2.5 mm wide, pilose with long hairs, the calyx lobes 4–5 mm long, pilose; *petals* 2.25–3 mm; *filaments* 1.75–2.5 mm; *style* 7–8.5 mm; $n = 8$ (Zielinski, 1952). Flowering from Apr–May, fruiting from May–Jul.

DISTRIBUTION. Once found along many of the rivers in the Palouse prairie region of southeastern Washington and northeastern Oregon, ssp. *cognatum* is nearly extinct in the United States. Field work in the Palouse region, including the type locality along the Umatilla River near Pendleton, Oregon resulted in the location of only a single population. This location consisted of three plants found at Lewis and Clark Trail State Park, Columbia Co., Washington. Most of the rivers and their tributaries where populations of ssp. *cognatum* once grew have been highly modified and fenced for grazing. Presently considered on the Washington state "Endangered" list as an endangered species (Denton et al., 1977; Washington Natural Heritage Program, 1981, 1982), it is clear that reduction to subspecific status should not affect the priority in conserving this endangered entity, the rarest taxon in sect. *Grossularia*. Two collections from southern British Columbia have been seen, one as recently as 1979.

PLANT ASSOCIATIONS. The ssp. *cognatum* inhabits moist canyons and river and creek banks with species of *Populus, Betula, Salix* and *Crataegus douglasii* Lindl.

DISCUSSION. Subspecies *cognatum* resembles ssp. *setosum* in floral characteristics, sharing the long tubular calyx, although the two subspecies are totally allopatric. In eastern Washington, ssp. *cognatum* is slightly sympatric with ssp. *irriguum* and a few intermediate specimens were found in the herbarium from the vicinity of Spokane.

REPRESENTATIVE SPECIMENS. **Canada.** BRITISH COLUMBIA: Similkameen District, Grand Forks, *A. A. Rose 7953* (UBC), Mt. Anarchist, Osoyoos, *Krajina 645-33* (UBC). **United States.** OREGON: Grant Co., Canyon Cr., *Henderson 5174* (CAS, GH, MO, ORE), Morrow Co., Lexington, *Leiberg 30* (A, F, MO, ORE, POM), Umatilla Co., Pendleton, *Cusick 3410* (F, GH, ORE, RM, WS, WTU), Wallowa Co., Imaha, *M. E. Peck 17659* (NY, WILLU), Wasco, Co., Tygh Cr., *M. E. Peck 17377* (WILLU); WASHINGTON: Columbia Co., Tallow Flat, *Darlington 219* (RM, WS), Lewis and Clark Trail State Park, *Sinnott 1787* (MARY), Ferry Co., below Republic, *Sprague 324* (WS), Lincoln Co., Sprague, *Sandberg & Leiberg 150* (CAS, GH, MO, NY, ORE), Okanogan Co., 45 mi SE Oroville, *Young & Rockie s.n.* (OSC), Spokane Co., Spokane, *Gooding & Bach s.n.* (WTU), Walla Walla Co., Walla Walla, *Booth s.n.* (WS), Whitman Co., Union Flat, *Piper 1810* (A, GH, NY, PH, POM, VT, WTU).

3. **Ribes hirtellum** Michx. (Figure 12)

Ribes hirtellum Michx., Fl. bor.-amer. 111. 1803. *Grossularia hirtella* (Michx.) Spach, Hist. Nat. Veget. 180. 1838. *Ribes oxyacanthoides* L. var. *hirtellum* (Michx.) Scoggan, Fl. Canada 51. 1978. TYPE: CANADA, Quebec, ad amnem Sagney (HOLOTYPE: P, as IDC microfiche!, and observations by H. G. Bedell).

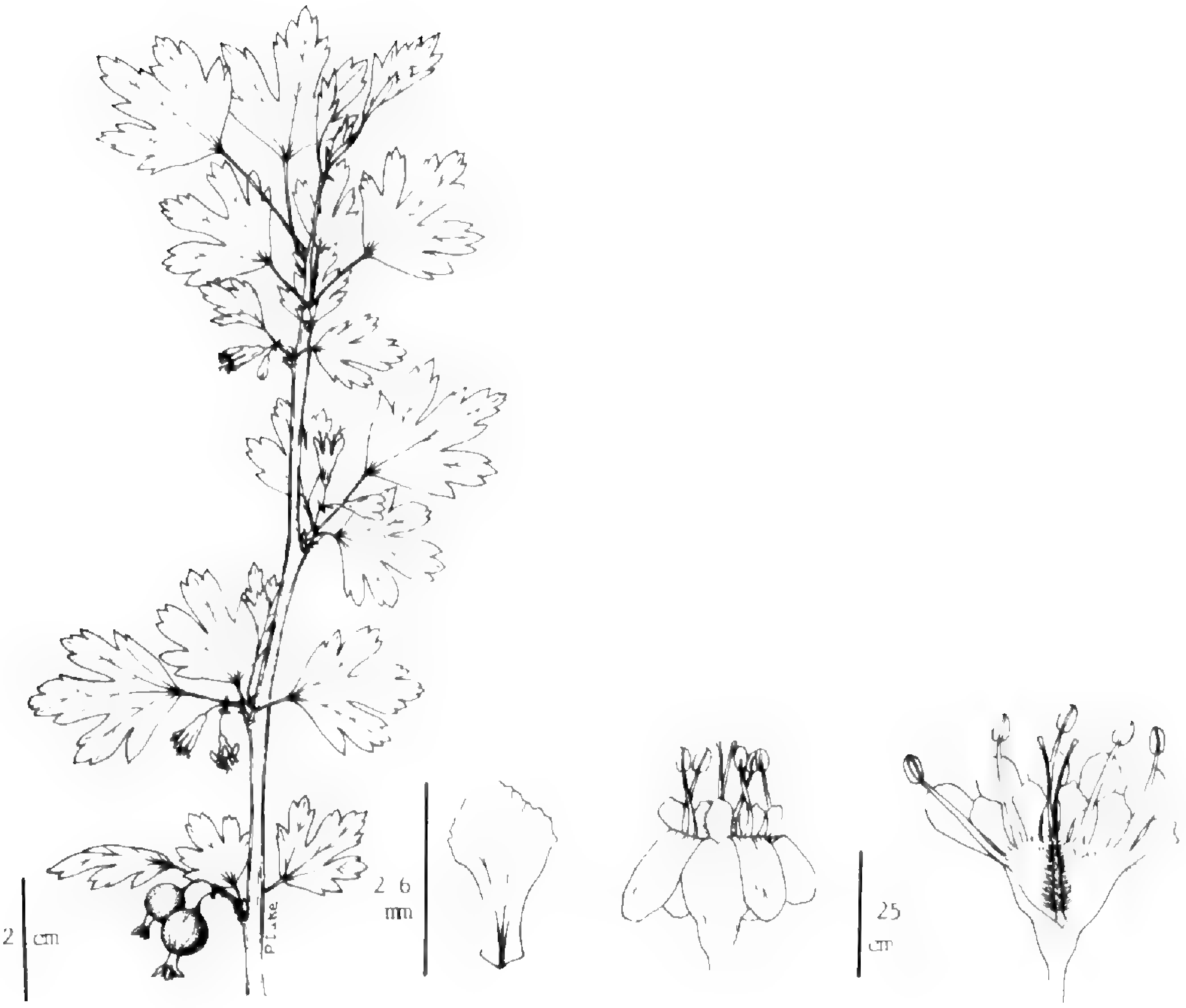


Figure 12. Illustration of *Ribes hirtellum:* habit, flower, open flower and petal.

Ribes saxosum Hook., Fl. bor.-amer. 231. 1832. *Ribes oxyacanthoides* L. var. *saxosum* (Hook.) Coville, Contr. U.S. Natl. Herb. 4: 100. 1893. *Ribes hirtellum* Michx. var. *saxosum* (Hook.) Fernald, Rhodora 13: 76. 1911. *Grossularia saxosa* (Hook.) Lunell, Amer. Midl. Naturalist 4: 414. 1916. TYPE: CANADA, undulating grounds of the interior, *Douglas s.n.* (HOLOTYPE: K, as a photograph!).

Ribes oxyacanthoides L. var. *calcicola* Fernald, Rhodora 7: 155. 1905. *Ribes hirtellum* Michx. var. *calcicola* (Fernald) Fernald, Rhodora 13: 76. 1911. LECTOTYPE (here designated): CANADA, Quebec, Bonaventure Co., Arborvitae swamps at the mouth of the Bonaventure River, 2 Aug 1904, *Collins et al. s.n.* (GH! ISOLECTOTYPES: GH!, MICH!, NY!, UC!, US!, VT!).

Ribes cynosbati L. forma *invitans* Seymour, Fl. New England 303. 1969. TYPE: UNITED STATES, Vermont, Chittenden Co., near Charlotte, 22 Jul 1879, *Pringle s.n.* (HOLOTYPE: VT!; ISOTYPES: A!, VT!).

Plant a medium shrub 0.5–1.5 m tall; *stems* erect to often sprawling and rooting at the nodes, the bark grey to tan, glabrous or sometimes pubescent when young, glabrous in age, occasionally with internodal bristles; *nodal spines* grey to tan, 0–2 (3), 3–8 mm long, primarily straight, occasionally slightly curved; *leaves* as broad as long to broader than long, the blade 10–25 mm long, 15–30 mm wide, trilobed above the midpoint, the lobes toothed, occasionally appearing 5-lobed, the upper surface scattered pilose to evenly pilose, eglandular, the lower surface pilose to densely hirsute, typically eglandular, the apex acute (about 90°) and the base cuneate to nearly truncate or rarely subcordate (130–170°), the petiole 7–15 (20) mm long, pilose with eglandular hairs, matted near the apex with longer often plumose glands scattered near the base, short non-plumose glands absent; *inflorescence* of 1–3 flowers on glabrous to scattered pilose 2–6 mm long peduncles; *flowers* on 2–5 mm long, glabrous pedicels, subtended by bracts 1–2 mm long, these pilose and occasionally glandular on the margins; *hypanthium* campanulate, tapering to a rounded to subcuneate base, greenish-white to pale white, the tube 2–2.7 mm long, 2.5–3.5 mm wide, glabrous or pilose to densely pilose, the calyx lobes 3–4 mm long, recurved in age, glabrous or pilose to densely pilose, the petals white to tinged with purple, 1.7–2.5 mm long, obovate, the filaments 3–4.5 mm long, glabrous, exserting the cream-colored glabrous anthers beyond the petals; *pistil* with a style divided to about halfway, 6–7 mm long, villous on the lower half, the ovary glabrous; *fruit* smooth and glabrous, 7–11 mm in diameter, greenish to purplish at maturity; $n = 8$ (Taylor & Brockman, 1966). Flowering from May–Jul, fruiting from Jun–Sep.

DISTRIBUTION. Widely distributed in the southeastern part of Canada and adjacent northeastern United States, extending south to scattered localities in Pennsylvania, Michigan, New York, Indiana and South Dakota. In the western part of its range it is distributed along the southern part of the prairie provinces and is occasional in the southern part of British Columbia (Figure 13).

PLANT ASSOCIATIONS. *Ribes hirtellum* is typically found in bogs, swampy areas along rivers, margins of poorly drained soils or in rocky drier habitats along rivers. In the United States, most of the southern range extensions are located in tamarack (*Larix*) bogs remaining intact from Pleistocene glaciation. In Canada. *R. hirtellum* is characteristic of *Thuja* swamps, *Populus-Salix* lowland regions, and drier regions among rocks along rivers and lake margins.

Figure 13. County dot distribution map of *Ribes hirtellum*. Solid circles indicate post-1965 records.

DISCUSSION. *Ribes hirtellum* occurs in a wide range of habitats from swamps to dry rocky places in a relatively broad geographic region. As a result, this species varies in pubescence, stem armature and leaf size, and to some extent in leaf shape. In addition, it is sympatric with both *R. cynosbati* and *R. oxyacanthoides* in portions of its range, and the presence of apparent hybridization further complicates the morphology of the species. A relatively extensive area of sympatry and potential interbreeding occurs with *R. oxyacanthoides* in the James Bay region of Ontario and Quebec. Morphological evidence indicates that the two species are crossing and plants can be found with various combinations of leaf and floral features. One combination, with the truncate to subcordate leaves of *R. oxyacanthoides* and the longer-stamened flowers of *R. hirtellum*, is particularly frequent. Several specimens labeled *R. saxosum* appear to be hybrid plants based on their intermediate morphology, but the type specimen of *R. saxosum* appears to be primarily *R. hirtellum*. Hooker (1832) based this species on Douglas material but substituted *R. saxosum* for the Douglas manuscript name "*R. saxatile*" as that epithet had already been used in the genus. From Douglas' journal (Douglas, 1914) the most probable collection date for the holotype was the spring or summer of 1827. At this time Douglas left the West Coast of North America, crossed the Rocky Mountains in southern Canada, and headed eastward via the Athabaska and Saskatchewan rivers to Lake Winnipeg. Along the Saskatchewan River both *R. hirtellum* and *R. oxyacanthoides* are found and morphological intermediates between the two are likely. It is probable that Douglas encountered his specimen of atypical *R. hirtellum* in this area of Canada.

Recent authors, and in particular Fernald (1950), have segregated the truncate- to subcordate-leaved specimens of *Ribes hirtellum* as var. *saxosum*. Some of the plants assigned to this taxon are probably intermediates between *R. hirtellum* and *R. oxyacanthoides* as they occur in regions of sympatry. Other specimens identified as var. *saxosum* appear to be intermediates between *R. hirtellum* and *R. cynosbati*. Such specimens are found where these two species have overlapping ranges in the northeastern United States and southern Ontario and Quebec. Some collections identified as var. *saxosum*, however, appear to be atypical specimens of *R. hirtellum*, and are not influenced by recent or past hybridization. Such specimens appear to be uncorrelated with other morphological or distributional patterns. The leaf character is not consistent enough with regard to habitat preference and morphology to warrant recognition at any taxonomic level.

Ribes hirtellum var. *calcicola* was proposed by Fernald (1905, 1911) to accommodate specimens of *R. hirtellum* that have densely hairy leaves and pilose calyces. These specimens occur in various places throughout the range of *R. hirtellum*, often with some degree of habitat or site correlation. Hairy specimens appear typical on Manitoulin Island and in certain regions of the Gaspé Peninsula. Despite some indications of site specificity, the variation from pilose to densely hairy plants is continuous, and in general the distribution pattern of the form is inconsistent.

Ribes huronense was considered to be a synonym of *R. hirtellum* by Coville and Britton (1908) and by Berger (1924), although it is a synonym of *R. cynosbati.*

Ribes hirtellum forms part of the species group characterized by stamens about twice the length of the petals. The other member of this group is the Rocky Mountain and Sierra Nevada species, *R. inerme.* The two are similar in flower structure and stamen length, but differ in flower size, peduncle length, leaf shape and pubescence of the leaves. Some authors (Smiley, 1921) have considered the two species to be variants of a single species (see *R. inerme*). The presence of apparent sister species, differing in a number of characters and separated geographically, is frequent in sect. *Grossularia.* In the case of *R. hirtellum* and *R. inerme,* the two species are entirely allopatric with the possible exception of parts of southern Alberta. This distributional discontinuity combined with morphological differences argues for the specific status of the two entities.

REPRESENTATIVE SPECIMENS. **Canada.** ALBERTA: Edmonton, *Moss 4779* (CAN); BRITISH COLUMBIA: Copper Cr., *Calder & Saville 8291* (CAN, NY, WTU); MANITOBA: Otterburne, *Macoun s.n.* (CAN, US), Gull Lake, *Sinnott 1184* (MARY); NEW BRUNSWICK: Bass R., *Fowler 1762* (CAN), Wolf Isl., *Hogdon et al. s.n.* (NHA); NEWFOUNDLAND: Pointe Riche, *Fernald et al. 1782* (NY, US, WIS), Knob L., *Powell & Maycock s.n.* (MTMG); NOVA SCOTIA: Grand Narrows, *Fernald & St. John 11075* (GH), Barton, *Jack 3726* (A, UC); ONTARIO: Blind R., *Fassett 14766* (GH, WIS), Cochrane, *Pease & Wells 38826* (GH), Dinorwic, *Sinnott 1158* (MARY), Manitoulin Isl., *Soper & Bell 9897* (CAN); PRINCE EDWARD ISLAND: St. Peter's Bay, *Fernald & St. John 11074* (CAN, NY); QUEBEC: Black L., *Blais et al. s.n.* (COLO), Maria, *Marie-Victorin et al. 33306* (CAS), Perce, *Scoggan 986* (CAN); SASKATCHEWAN: McKauge, *Breitung 963* (CAN, GH, UC). **United States.** CONNEC-

TICUT: Litchfield Co., Litchfield, *Britton s.n.* (NY); ILLINOIS: McHenry Co., *Vasey s.n.* (GH); INDIANA: Steuben Co., Pokagon State Park, *E. Palmer 40371* (A); MAINE: Aroostock Co., Sawyer's Pond, *Seymour 26417* (CAS, SMU), Lincoln Co., Ocean Point, *Fassett 13490* (US); MASSACHUSETTS: Dukes Co., Martha's Vineyard, *Seymour 1219* (GH, NY, US), Norfolk Co., Westwood, *Moore 1629* (A); MICHIGAN: Cheyboygan Co., Cheyboygan, *Yuncker 10327* (GH, SMU), Mackinac Co., Bois Blanc Isl., *Dodge 65* (DS, GH); MINNESOTA: Clearwater Co., L. Itasca, *Thorne 31357* (RSA), St. Louis Co., Duluth, *Gilbert 139* (GH, US); NEBRASKA: Cherry Co., Merriman, *Bates s.n.* (NY); NEW HAMPSHIRE: Rockingham Co., Hampton Falls, *Hogdon & Steele 11842* (NHA), Strafford Co., Durham, *Hogdon 5327* (NHA); NEW JERSEY: Warren Co., Green Pond, *Mackenzie 7736* (NY); NEW YORK: St. Lawrence Co., Canton, *Phelps 553* (GH, NY), Tompkins Co., Michigan Hollow, *Eames & Weigand 2448* (A, GH, TEX); NORTH DAKOTA: Pembina Co., Akra, *Stevens 1327* (CAN, NY, US); OHIO: Portage Co., Streetsboro, *Cusick 10041* (RSA); PENNSYLVANIA: Lancaster Co., Lancaster, *Small s.n.* (NY, US); RHODE ISLAND: Providence Co., E. Providence, *Stanford s.n.* (DS); SOUTH DAKOTA: Custer Co., Sylvan L., *E. Palmer 37351* (US), Lawrence Co., Whitewood, *Hayward 1240* (F, RM); VERMONT: Addison Co., Middlebury, *Brainerd s.n.* (VT), Rutland Co., Rutland, *Eggleston s.n.* (GH, NY, US, VT, WIS); WEST VIRGINIA: Upshur Co., Bucklin, *Pollock s.n.* (US); WISCONSIN: Door Co., L. Michigan, *Fassett 18155* (GH, NY, WIS), Lincoln Co., Corning, *Seymour 14639* (WIS).

4. **Ribes inerme** Rydb. (Figure 14)

Plant a medium shrub 0.75–1.5 m tall; *stems* erect to sprawling and rooting at the tips, the outer bark straw-colored to pale brown, becoming grey in age, glabrous to pubescent when young, glabrous in age, usually without internodal bristles; *nodal spines* straw-colored to brown, 0–3, often only 1, 3–8 mm long, thin to relatively thick and curved slightly; *leaves* isodiametric to broader than long, the blade 20–30 mm long and wide, deeply 3–5 lobed, the lobes extending halfway to the midvein, toothed with rounded dentations, the upper surface glabrous to pubescent, eglandular, the lower surface glabrous to pilose with eglandular hairs, the apex 80–100°, the base cordate to rarely truncate (180–230°), the petiole 15–25 mm, glabrous to pilose with eglandular hairs; *inflorescence* of 1–4 flowers on glabrous 5–15 mm long peduncles; *flowers* on 3–9 mm long glabrous pedicels with 1.5–2 mm long subtending bracts, these glabrous to pilose and minutely glandular; *hypanthium* cup-shaped to campanulate, widest near apex, yellowish-white to white, the tube 2–2.75 mm long, 2.5–3.5 mm wide, the calyx lobes glabrous to pilose, 3–4 mm, diverging at right angles to reflexed at anthesis, the petals white, 1.5–2 mm long, obovate-spatulate, the filaments 2.5–3.5 mm, glabrous, exserting the glabrous creme-colored anthers

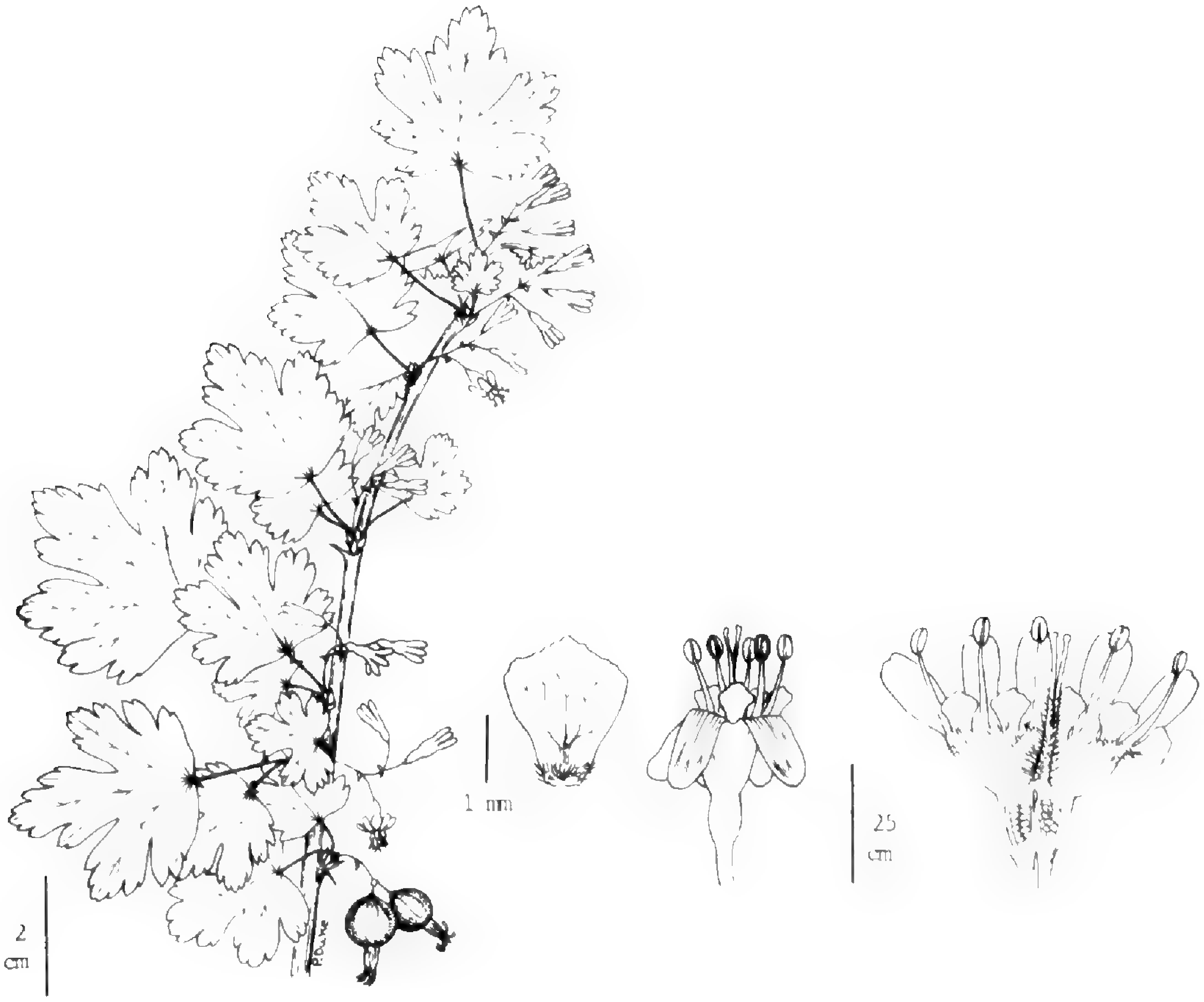


Figure 14. Illustration of *Ribes inerme:* habit, flower, open flower and petal.

1.5–2 mm above the petals; *pistil* with a style divided to one third, 5–6.5 mm long, the ovary glabrous; *fruit* smooth, 7–11 mm in diameter, greenish-purple.

DISTRIBUTION. *Ribes inerme* is found throughout the Rocky Mountains, the Sierra Nevada, and eastern Cascade Mountain axis in western North America, from 1200 to 3000 m (Figure 15).

DISCUSSION. *Ribes inerme* can be divided into two varieties based on a correlation of morphological and geographical features. One variety, var. *klamathense,* represents a potential series of hybrid populations between *R. divaricatum* var. *pubiflorum* and *R. inerme* var. *inerme.* Figure 16 represents a three character scatter diagram which indicates the intermediacy of var. *klamathense* on this subsample of characters. Owing to lack of experimental proof of hybridization and the uniqueness of the geographic region, this potential hybrid swarm is retained at the varietal rank (see discus-

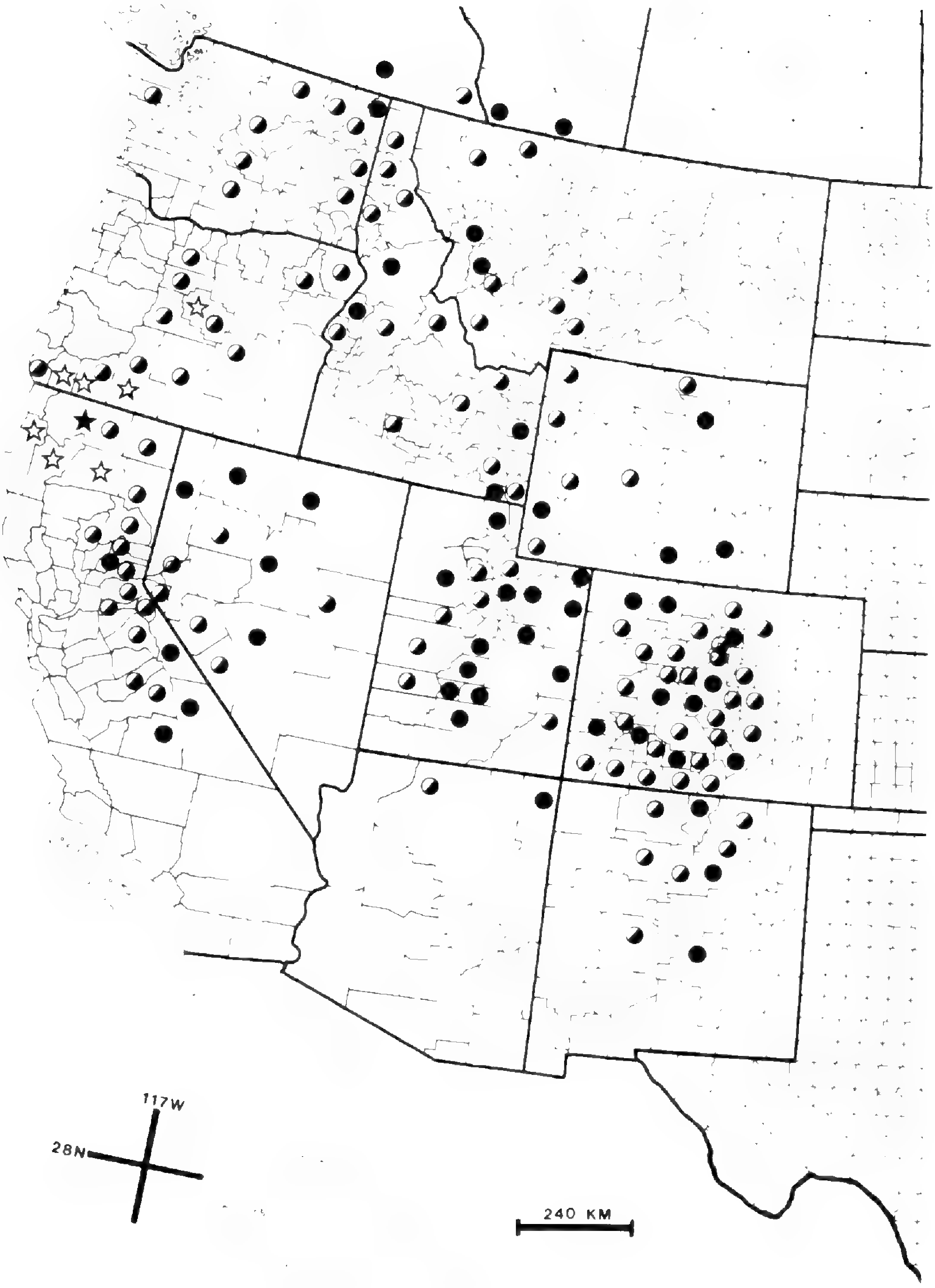


Figure 15. County dot distribution map of *Ribes inerme*. Solid circles represent post-1965 collections; stars represent var. *klamathense*.

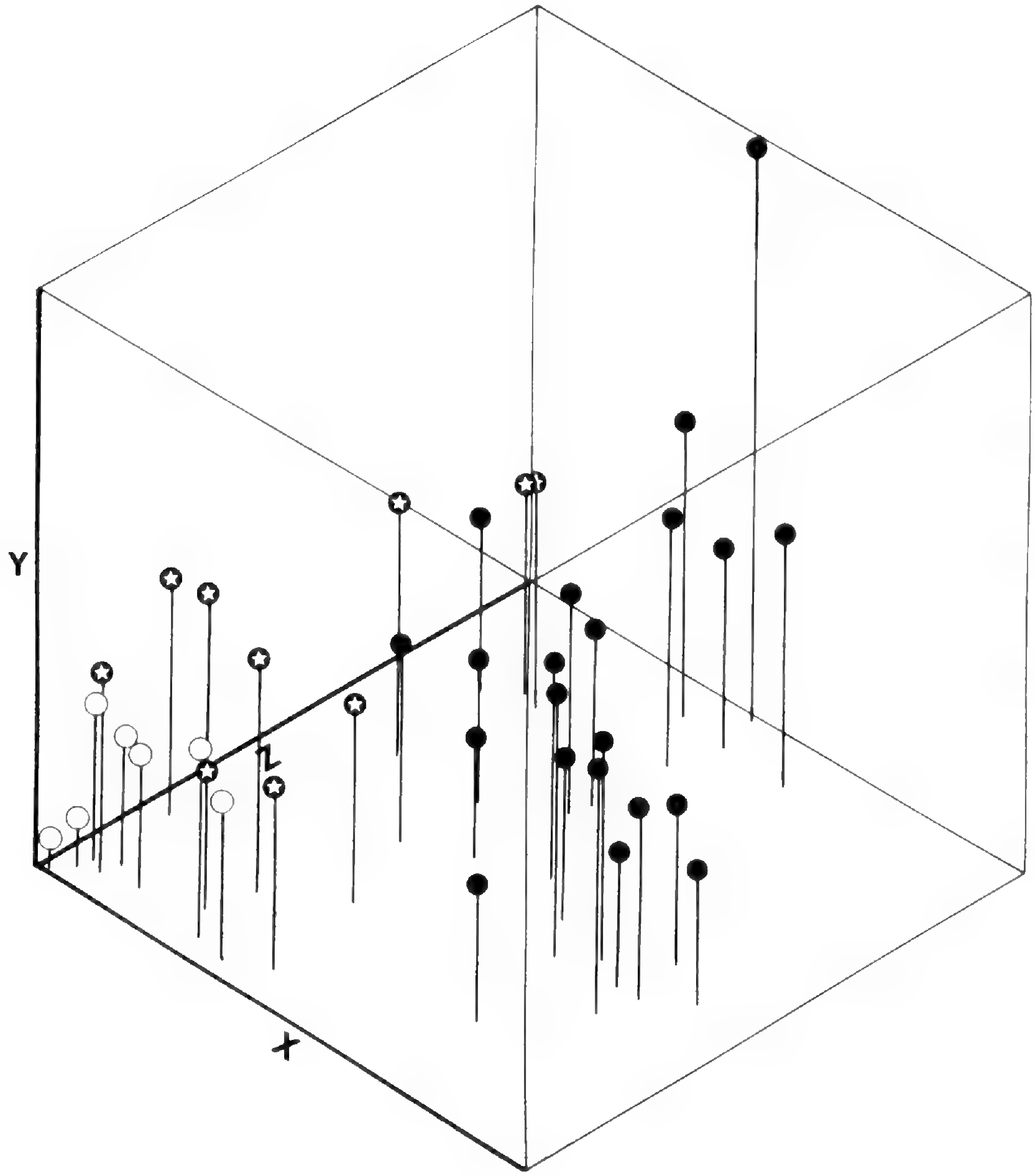


Figure 16. Three dimensional scatter diagram of 38 individuals of the putative hybrid complex *Ribes inerme* var. *klamathense* (stars) and its probable parent species *R. inerme* var. *inerme* (open circles) and *R. divaricatum* (solid circles). The x-axis equals stamen length/petal length, y-axis equals pedicel length, z-axis is degree of thorniness.

sion under that variety). The following key to varieties is to be used only for collections originating in the Klamath Mountain region in northern California and southern Oregon. Specimens of var. *inerme* from Colorada south in the Rocky Mountains often have pubescent twigs and leaves, but presumably do not represent potential hybridization betwen *R. divaricatum*, a coastal species, and *R. inerme*.

Key to the varieties of *Ribes inerme*

A. Calyx tube and lobes glabrous; leaves glabrous or with a few hairs; peduncles 5–12 mm .... 4a. var. *inerme*

AA. Calyx tube and lobes pilose; leaves pilose; peduncles 10–15 mm .... 4b. var. *klamathense*

4a. **Ribes inerme** Rydb. var. **inerme**

Ribes inerme Rydb., Mem New York Bot. Gard. 1: 202. 1900. *Grossularia inermis* (Rydb.) Coville & Britton, N. Amer. fl. 22: 224. 1908. *Ribes hirtellum* Michx. var. *inerme* (Rydb.) Smiley, Univ. Calif. Publ. Bot. 9: 227. 1921. *Ribes divaricatum* Douglas var. *inerme* (Rydb.) McMinn, Ill. man. Calif. shrubs 156. 1939. TYPE: USA, Wyoming, Park Co., along cold brooks, Yellowstone Park, June 1885, *Tweedy 830* (HOLOTYPE: NY!).

Ribes purpusi Koehne ex Blank., Montana Coll. Agric. Sci. Stud. Bot. 1: 64. 1905. *Ribes oxyacanthoides* L. var. *purpusii* (Koehne ex Blank). Jancz., Mém. Soc. Phys. Genève 35: 388. 1907. *Grossularia purpusi* (Koehne ex Blank.) Rydb., Fl. Rocky Mts. 396. 1917. LECTOTYPE (here designated): USA, Montana, Stillwater Co., Limekiln Cañon, 18 Jun 1900, *Blankinship s.n.* (MONT!).

Ribes valicola Greene ex Rydb., Fl. Colorado 177. 1906. TYPE: USA, Colorado, Conejos Co., Los Piños (Bayfield), 27 May 1899, *Greene 372* (HOLOTYPE: NDG!; ISOTYPES: MO!, NDG!, NY!, POM!).

Ribes oxyacanthoides L. var. *nevadense* Jancz., Mem. Soc. Phys. Genéve 35: 387. 1907. TYPE: USA, California, Tulare Co., Moses Mts., Sierra Nevada, cultivated at Cracow, Poland, collected from garden plant 27 June 1904, *Janczewski s.n.* (HOLOTYPE: KRAM!)

Ribes oxyacanthoides L. var. *vagum* Jancz., Mem. Soc. Phys. Genéve 35: 388. 1907. TYPE: USA, Colorado, Delta Co., Surface Creek, collector unknown (HOLOTYPE: KRAM).

Grossularia inermis (Rydb.) Coville & Britton var. *pubescens* A. Berger, New York Agric. Exp. Sta. Techn. Bull. 109: 105. 1924. LECTOTYPE (here designated): USA, Colorado, Beaver Cr., 1896, collector unknown (BH!).

Grossularia inermis (Rydb.) Coville & Britton forma *puberula* A. Berger, New York Agric. Exp. Sta. Techn. Bull. 109: 105. 1924. *Ribes inerme* Rydb. forma *puberulum* (A. Berger) St. John, Fl. SE Washington 187. 1937.

Lectotype (here designated): USA, Wyoming, Albany Co., stream banks, Centennial, 28 May 1909, *A. Nelson 9319* (BH!; ISOLECTOTYPES: GH!, MICH!, MIN!, MO!, POM!, RM!).

Ribes inerme Rydb. var. *subarmatum* M. Peck, Leafl. W. Bot. 7: 183. 1954. Type: USA, Oregon, Jackson Co., moist bank along Dead Indian Road, 12 miles NE of Ashland, 7 July 1931, *M. E. Peck 16729* (HOLOTYPE: WILLU!).

Ribes inerme Rydb. forma *incisum* W. A. Weber, Univ. Colorado Stud., Ser. D., Phys. Sci. 23: 2. 1966. Type: USA, Colorado, Boulder Co., summit of Sugarloaf Mountain, foothills of the Front Range W. of Boulder, ca. 8000 ft, 18 July 1965, *Weber & Jones 12916a* (HOLOTYPE: COLO!; ISOTYPES: DAO!, GH!, NY!, RM!, UC!).

Leaves glabrous to short-pilose in the southern portion of the range, the petioles usually without plumose glands; *peduncles* 5–12 mm long; *pedicels* 2–6 mm, glabrous; *hypanthium* glabrous, the calyx lobes glabrous or scattered hairy in the southern part of the range; $n = 8$ (Zielinski, 1952). Flowering from May–Jun, fruiting from Jun–Aug.

Distribution. *Ribes inerme* var. *inerme* can be found above 1000 m in the Rocky Mountains, Sierra Nevada, and Cascade Range (Figure 15). This variety typically inhabits wet places and streams among rocks. In the northern part of the range in Montana and Wyoming, field studies by the author indicate this variety to be relatively sporadic. Herbarium records indicate that the primary range of var. *inerme* is in the central Rocky Mountains, the mountains of Nevada and Utah, and the Sierra Nevada. As the variety is relatively montane, much of the original range is probably intact and the low frequency of post-1965 collections in this case apparently is due to infrequent collecting rather than rarity of the variety.

Plant associations. This variety is associated with a number of tree species, depending on the location. In the Sierra Nevada, Munz and Keck (1959) reported the associated species to be *Abies magnifica* A. Murr., *Pinus murrayana* Grev. & Balf., *P. monticola* Douglas and *P. ponderosa* Douglas. In the northern part of the range, var. *inerme* is associated with species of *Pinus, Picea* and *Salix* along rivers.

Discussion. *Ribes inerme* var. *inerme* is morphologically related to the eastern species *R. hirtellum,* as noted by Smiley (1921) and others. The similarities include the generally short or lacking nodal spines and above all, the filaments which are about twice the length of the petals. This variety is rather variable throughout its range in leaf and twig pubescence, and number and length of nodal spines. In the Sierra Nevada, Cascade Range and mountains of the Great Basin in Nevada, the plants are almost uniformly glabrous, relatively non-spiny and have filaments slightly less than twice as long as the petals. In this area var. *inerme* typically represents the only member of sect. *Grossularia* present and is therefore easily recognized. In the northern part of the range, var. *inerme* is sympatric with *R. oxyacanthoides* ssp. *oxyacanthoides,* ssp. *cognatum,* ssp. *irriguum,* and ssp. *setosum.* The variation pattern becomes particularly complex in Montana and Wyoming, where var. *inerme* interacts with *R. oxyacanthoides* ssp. *setosum.* Populations have been studied where the two entities occur together with apparent hybrids. These hybrids combine the features of both entities, and resemble the more western *R. oxyacanthoides* ssp. *irriguum* (see discussion under ssp. *irriguum*). South of Montana and Wyoming, the var. *inerme* becomes more pubescent. In Utah, the majority of specimens correspond to the glabrous individuals found in the Sierra Nevada and Great Basin mountain ranges in Nevada, although occasional pubescent individuals occur. From Colorado southward in the Rocky Mountains and associated mountain ranges, the frequency of pubescent plants rapidly increases so that in Arizona and New Mexico the typical specimen has pubescent twigs and often pubescent leaves. Berger (1924) published a pubescent variety and form from among the pubescent specimens of var. *inerme,* but the pattern of variation appears too sporadic and continuous to warrant taxonomic recognition. Variation in twig and leaf pubescence is common in sect. *Grossularia.*

An interesting variant, var. *subarmatum,* has berries which are covered with short spines, a feature found only in one species of North American sect. *Grossularia.* Other than the type, no specimens were found in any herbarium investigated, and the holotype likely represents a freak mutant or a possible hybridization with a spiny-fruited species such as *R. watsonianum* Koehne.

REPRESENTATIVE SPECIMENS. **Canada.** ALBERTA: Mt. Crandell, *Breitung 15662* (DAO, MO), Waterton L. Park, *Malte 215* (CAN); BRITISH COLUMBIA: Alexander Cr. Bridge, *Taylor & Sherk 4851* (DAO). **United States.** ARIZONA: Apache Co., Hawley L., *Watt & Lehto s.n.* (ASU), Coconino Co., Kaibab Plateau, *Goodding 153-49* (ARIZ); CALIFORNIA: Butte Co., Jonesville, *A. Heller 12044* (A, CAS, COLO, DS, F, GH, MO, OSC, PENN, WIS, WTU), Inyo Co., Big Pine Cr., *J. T. Howell 23687* (CAS), Nevada Co., Sagehen Cr., *True & Howell 3891* (CAS), Tulare Co., Ground Hog Meadow, *Ferris & Lorraine 10762* (DS, OSC, SMU, UC, WTU); COLORADO: Boulder

Co., Nederland, *W. A. Weber 5516* (CAS, DAO, SMU, TEX), Mineral Co., Creede, *Stewart 1125* (COLO), Routt Co., Steamboat Springs, *Goodding 1613* (COLO, GH, MO, RM); IDAHO: Bear Lake Co., St. Charles Cr., *Christ & Christ 18654* (NY), Shoshone Co., Prichard, *Epling & Hauk 10187* (MO, OSC); MONTANA: Flathead Co., Avalanche L. *V. Bailey 61* (UC), Gallatin Co., Bridger Mts., *Floodman 533* (MIN, NY), Glacier Co., Lake Sherburne, *Harvey 4783* (MONTU, NCU); NEVADA: Elko Co., Lamoille Canyon, *Holmgren 1712* (NY, UTC), Washoe Co., Peavine Mtn., *Howell et al. 50399* (CAS, RENO), White Pine Co., Berry Cr., *Detling 9052* (ORE); NEW MEXICO: Rio Arriba Co., Tierra Amarilla, *Eggleston 6490* (GH), San Miguel Co., Willow Cr., *Hill & Cress 11724* (GH, MARY, MO, NY, VT), Taos Co., *Iltis & Iltis 4323* (SMU, WIS); OREGON: Crook Co., Pauline L., *M. E. Peck 9666* (DS, MIN, MO, PH), Deschutes Co., Deschutes R., *E. Nelson 789* (GH, MIN, NY, RM, UC, WTU), Lake Co., Lakeview, *Applegate 3051* (DS); UTAH: Cache Co., Logan Canyon, *Muenscher & Maguire 2355* (UC, UTC), Daggett Co., Crouse Canyon, *Neese 4552* (BRY), Salt Lake Co., City Cr. Canyon, *M. E. Jones 1754* (A, DS, NY, ORE, POM, RM, UTC), Sevier Co., Fish L. Plateau, *J. A. Harris 28729* (MIN, MO, UC); WASHINGTON: Ferry Co., Toroda Cr., *Sprague 322* (OSC, WIS), Stevens Co., Kettle Falls, *Piper s.n.* (WS), Whitman Co., Pullman, *Elmer 1256* (A, MICH, MO, VT); WYOMING: Albany Co., Sand Cr., *A. Nelson 7005* (GH, MIN, MO, NY), Sheridan Co., Big Horn Mts., *Smith 1942* (RM), Teton Co., Treasure Mtn., *L. C. Anderson 260* (UTC).

4b. **Ribes inerme** Rydb. var. **klamathense** (Coville in Coville & Britton) Jepson.

Grossularia klamathensis Coville in Coville & Britton, N. Amer. fl. 22: 225. 1908. *Ribes klamathense* (Coville in Coville & Britton) Fedde, Just's Bot. Jahresber. 36: 519. 1910. *Ribes inerme* Rydb. var. *klamathense* (Coville in Coville & Britton) Jepson, Man. fl. pl. Calif. 472. 1925. *Ribes divaricatum* Douglas var. *klamathense* (Coville in Coville & Britton) McMinn, Ill. man. Calif. shrubs 156. 1939. TYPE: UNITED STATES, Oregon, Klamath Co., Keno, 10 May 1898, *Applegate 2008* (HOLOTYPE: US!).

Leaves pilose to hirsute, the petioles often with plumose glandular hairs; *peduncles* 10–15 mm long; *pedicels* 6–12 mm, glabrous to pilose; *hypanthium* subglabrous to pilose with long hairs, the calyx lobes usually pilose with long hairs; $n = 8$ (Zielinski, 1952). Flowering from Apr–May, fruiting from May–Jul.

DISTRIBUTION. This variety is restricted to the overlap region of *Ribes inerme* and *R. divaricatum* in the Klamath and Siskiyou mountains of northern California and adjacent Oregon (Figure 15).

PLANT ASSOCIATIONS. The var. *klamathense* is reported with *Pinus ponderosa* Douglas, *P. lambertiana* Douglas, *Abies magnifica* A. Murr., *Pseudotsuga menziesii* (Mirb.) Franco and *Salix*.

DISCUSSION. It appears that on a morphological and geographical basis, var. *klamathense* represents hybridization between

Ribes inerme and *R. divaricatum*. Microspore development, as indicated by pollen stainability, is normal, but reports of fertile interspecific hybrids in sect. *Grossularia* are numerous (Janczewski, 1907; Keep, 1962). As both putative parental species are $n = 8$ (as are all species of *Ribes* counted), chromosome counts do not help resolve the question of putative hybrid origin of var. *klamathense*. Even if the variety is of hybrid origin, taxonomic rank can still be justified if the entity has become stabilized and capable of reproducing without extensive sorting of parental features in the offspring. According to Grant (1971, 1981), the origin of plant species by hybridization could very well be a significant speciation mechanism. The var. *klamathense* could represent an evolving species that can at present be recognized at the varietal level.

An alternative hypothesis is that *Ribes divaricatum* and *R. inerme* have not fully diverged and var. *klamathense* represents an ancestral gene pool. The Klamath Mountain region contains a high number of endemic and relictual species (Whittaker, 1960, 1961; Stebbins & Major, 1965; Denton, 1979), with 64 of the 211 endemics representing relicts. An ancestral species hypothesis such as this was presented by Bennett et al. (1982) for *Abies*. Until breeding studies indicate the inability of var. *klamathense* to reproduce without extensive character sorting, it appears best to continue recognition at the varietal level.

REPRESENTATIVE SPECIMENS. **United States.** CALIFORNIA: Humboldt Co., Lack Pond, *Tracy 16281* (DS, MIN, UC, UTC, WTU), *Tracy 16813* (ARIZ, DAO, JEPS, NCU, RM, RSA, UC, WS, WTU), Shasta Co., Twin Valleys, *M. S. Baker 295* (JEPS, UC), Goose Valley, *Baker & Nutting s.n.* (RM, UC), Hat Cr., *C. L. Hitchcock 6559* (DS, NY, POM, RSA, UC, UTC, WTU), Siskiyou Co., Mt. Shasta, *M. E. Brown 376* (F, MIN, MO, NY) Yreka Cr., *Butler 1362* (DS, JEPS, MIN, POM, RM, UC), Sisson, *Heller 8042* (A, DS, F, GH, KSC, MIN, NY, PH, WIS), Trinity Co., Trinity R., *Bacigalupi et al. 3374* (JEPS, MIN, UC), Corral Bottom, *Sawyer & Buck 2884* (BRY); OREGON: Crook Co., Deschutes R. near Madras, *M. E. Peck 13159* (OSC), Jackson Co., Applegate R., *Abrams & Benson 10269* (DS, RM), Jacksonville Cr., *Applegate 4593* (DS, WTU), Josephine Co., Takilma, *Abrams & Benson 10344* (DS), Applegate Valley, *Thompson 2208* (DS, WTU), Klamath Co., Klamath L., *Applegate 4043* (DS, F, UC), Keno, *M. E. Peck 9425* (DS, GH, MO, NY, PH).

5. **Ribes divaricatum** Douglas (Figure 17)

Plant a medium to large shrub 1–1.5 (2) m tall; *stems* erect to sprawling and rooting at the tips, the bark grey, pubescent when young and usually for several years, eventually becoming glabrate,

Figure 17. Illustration of *Ribes divaricatum* sens. lat.: habit, flower, open flower and petal.

usually with internodal bristles; *nodal spines* brown or grey, 1–3, often only 1 except on new growth, 7–20 mm long, usually stout and often curved; *leaves* isodiametric to broader than long, the blade 20–35 mm long, 20–40 mm wide, deeply 3–5-lobed, the lobes extending halfway to midvein, the lobes toothed, the upper surface pilose with eglandular hairs, the lower surface usually pilose to villous or rarely glabrate, the apex about 90°, the base truncate to cordate (170–220°), occasionally cuneate, the petiole 10–25 mm long, pilose with eglandular hairs occasionally intermixed with glandular ones with a few plumose near the base; *inflorescence* of 1–4 flowers on glabrous to pilose, 5–15 mm long peduncles; *flowers* on 4–10 mm long, glabrous or pilose pedicels, subtended by bracts 1.5–2 mm long, these pilose with stiff hairs and intermixed glands; *hypanthium* obconic, narrowed at the base, reddish to purplish-green, the tube 1.5–3.5 mm long, 1.7–4 mm wide, glabrous or villous, the calyx lobes glabrate to villous, spreading to reflexed at anthesis, the petals white or pink to red, 1.2–3 mm long, broadly spatulate, the filaments 3.5–7 mm long, glabrous, exserting the glabrous anthers; *pistil* with a style divided to about halfway, 4.5–11 mm long, villous on the lower half, the ovary glabrous; *fruit* smooth, 7–12 mm in diameter, bluish-black at maturity.

DISTRIBUTION. Along the Pacific coast of western North America from the Queen Charlotte Islands, British Columbia, southward to southern California (Figure 18).

DISCUSSION. *Ribes divaricatum* is divided into three varieties based on several morphological characters which are correlated with geographical distribution. Principal components analysis of 100 OTUs representing the three variants based on six characters is shown in Figure 19. The figure representing a three dimensional scatter diagram of the first three component axes shows reasonably good separation of var. *divaricatum* and var. *pubiflorum*, but var. *parishii* is only partially isolated. This analysis indicates that the two most geographically distant entities are the most alike morphologically. In previous treatments (McMinn, 1939; Munz & Keck, 1959; Munz, 1974), only var. *parishii* is segregated.

Key to the varieties of *Ribes divaricatum*

A. Filaments 3.5–4.7 (5) mm long; petals 1.2–1.8 mm long, white; style 5.5–7.5 mm long; coast ranges of southern Oregon southward to Santa Barbara Co., California .... 5b. var. *pubiflorum*

AA. Filaments more than 5 mm long; petals 2–3 mm long, white or red-pink; style 8–11 mm long

  B. Calyx tube 1.7–2.7 mm long; petals white; coastal areas from Queen Charlotte Islands southward to southern Oregon .... 5a. var. *divaricatum*

  BB. Calyx tube 2.8–3.5 mm long; petals pink or red; foothills of the San Gabriel and San Bernardino Mts., southern California .... 5c. var. *parishii*

Figure 18. County dot distribution (left) and outline (right) map of *Ribes divaricatum*. Square symbols represent var. *divaricatum* (DV), circles denote var. *pubiflorum* (PU) and triangles var. *parishii* (PA). Solid symbols represent post-1965 records.

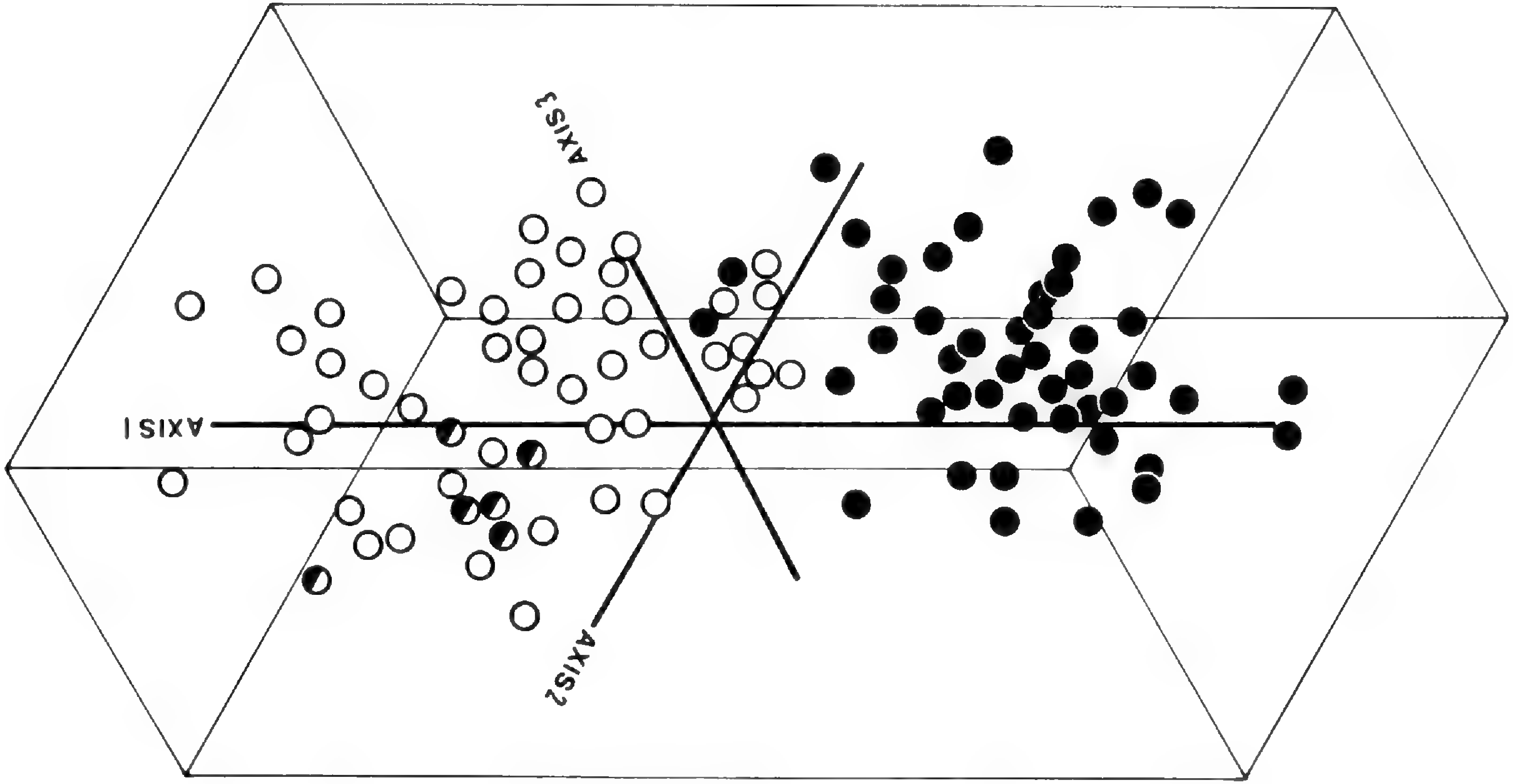


Figure 19. Three-dimensional ordination of 100 individuals of the *Ribes divaricatum* complex. Closed circles = var. *pubiflorum*, open circles = var. *divaricatum* and half cirlces = var. *parishii*. Note how var. *parishii* clusters near var. *divaricatum* despite great geographical separation.

5a. **Ribes divaricatum** Douglas var. **divaricatum**

Ribes divaricatum Douglas, Trans. Hort. Soc. London 7: 515. 1830. *Ribes divaricatum* Douglas var. *douglasii* Jancz., Mém. Soc. Phys. Genève 35: 391. 1907, nom. superfl. *Grossularia divaricata* (Douglas) Coville & Britton, N. Amer. fl. 22: 224. 1908. LECTOTYPE (here designated): UNITED STATES, Washington, near Indian villages on the northwest coast from 45° to 52° N latitude (from near the mouth of the Columbia River), 1825, *Douglas s.n.* (K, as a photograph!; ISOLECTOTYPE: BM!).

Ribes divaricatum Douglas var. *glabriflorum* Koehne, Deut. Dendrol. 200. 1893. NEOTYPE (here designated): a cultivated garden specimen grown at Berlin Botanical Garden, 1 May, 8 Jul 1895, *Koehne s.n.* (B!; duplicates of the neotype: GH!, OXF!).

Ribes suksdorfii A. Heller, Muhlenbergia 3: 11. 1907. TYPE: UNITED STATES, Washington, Klickitat Co., near Bingen, 17 Apr 1897, *Suksdorf s.n.* (HOLOTYPE: BKL!; ISOTYPES: A!, DS!, F!, GH!, MO!, NY! — probable, RM!, TEX!, UC!, WS!).

Ribes divaricatum Douglas var. *rigidum* M. Peck, Leafl. W. Bot. 7: 182. 1954. TYPE: UNITED STATES, Oregon, Curry Co., near Goldbeach, 24 Jul 1945, *M. E. Peck 23968* (HOLOTYPE: WILLU!).

Hypanthium obconic, the tube 1.7–2.5 mm long, 2.5–3 mm wide, glabrous to scattered pubescent, the calyx lobes 4–6 mm long, glabrous to sparsely pubescent; *petals* white, 2–3 mm long; *filaments* 5–7 mm long; *style* 8–11 mm long; $n = 8$ (Goldschmidt, 1964). Flowering from Apr–May, fruiting from May–Jul.

DISTRIBUTION. The var. *divaricatum* inhabits coastal forests from the Rogue River region of southern Oregon northward along the Pacific Coast to the Queen Charlotte Islands of southern British Columbia. Near the southern boundary of var. *divaricatum*, where it meets var. *publiflorum*, intermediates are found. Jepson (1957) noted that "the Rogue River is one of the greatest importance as defining by a mainly physiological barrier the botanical boundary of the California province. . ." He further noted that there are more species that meet their northern or southern boundaries in that region than those that traverse the region. In Munz and Keck (1959), the Rogue River area of Oregon denotes the northern extension of the Redwood Forest Community.

From the lack of recent collections of var. *divaricatum* in the United States portion of its range, and the difficulties encountered in 1982 when attempting to locate sizable populations, it is likely that the plants are becoming scarce in the southern part of its range. In British Columbia the range is relatively intact and the variety is not as rare as in the United States (Figure 18).

PLANT ASSOCIATIONS. The var. *divaricatum* is basically a plant of riparian habitats, commonly found in association with *Pseudotsuga menziesii, Acer macrophyllum* Pursh, and various species of *Salix* and *Populus.*

DISCUSSION. Two elements are listed in the original description of *Ribes divaricatum,* a wild collection gathered by Douglas and a cultivated specimen grown by the Horticultural Society in London. The Douglas specimen is hereby selected as the lectotype. It was gathered near the mouth of the Columbia River in 1825, and is likely the twelfth specimen collected by Douglas upon his arrival at the mouth of the Columbia River in April of 1825 (Douglas, 1914). The cultivated specimens were most likely raised from seeds gathered by him taken later in the year.

Ribes divaricatum var. *glabriflorum* has been neotypified, as type material of this variant dated prior to 1893 when the name was published has not been located at Berlin. Specimens used in the preparation of the type description presumably have been destroyed. The neotype represents the sole Koehne collection at B with this name associated with it.

REPRESENTATIVE SPECIMENS. **Canada.** BRITISH COLUMBIA: Sooke, *Calder & Mackay 29967* (CAS, DAO, MIN), Nanaimo, *Calder et al. 16230* (DAO, WIS), Queen Charlotte Sound, *McCabe 1784* (UC), Port Alberni, *Rosendahl & Butters 1967* (GH, MIN, MO, NY). **United States.** OREGON: Benton Co., McDonald Forest, *Dennis 2955* (DAO, DS, NCU, OSC), Clackamas Co., Springwater, *Goodding s.n.* (OSC, TEX), Clatsop Co., Columbia Beach, *Abrams 8943* (DS, POM), Coos Co., Coquille R., *Abrams & Benson 10542* (DS, RM), Curry Co., Cape Blanche, *Abrams & Benson 10630* (DS, RM), Douglas Co., Reedsport, *Benson 170* (DS), Hood River Co., Mt. Hood N.F., *Goodding & Evinger s.n.* (OSC), Linn Co., Monument Peak, *Gilkey s.n.* (OSC), Multnomah Co., Sandy R., *Thompson 4028* (A, DS, GH, MIN, MO, PH, POM), Wasco Co., The Dalles, *Hitchcock & Muhlick 21517* (DS, NY, RM, RSA, WS, WTU); WASHINGTON: Clallam Co., Olympic Mts., *Elmer 2653* (A, MIN, MO, NY), Gray's Harbor Co., Montesano, *Heller & Heller 3921* (A, DS, GH, MO, NY, PH, RM, UC, WIS, WS), Island Co., Whidby Isl., *Thompson 8932* (A, MO, NY, UC), Jefferson Co., Brinnon, *Sinnott 1803* (MARY), King Co., Redmond, *M. E. Jones 6391* (PH, WTU), Klickitat Co., Bingen, *M. E. Jones 6313* (UC, WTU), San Juan Co., Friday Harbor, *Zeller & Zeller 973* (A, GH, MIN, MO), Skagit Co., Anacortes, *C. L. Hitchcock 3445* (CAS, COLO, DS, POM, RM, UTC, WS, WTU), Snohomish Co., Sylvanus, *Benson 1165* (DS, WTU).

5b. **Ribes divaricatum** Douglas var. **pubiflorum** Koehne

Ribes villosum Nutt. In Torr. & Gray, Fl. N. Amer. 1: 547. 1840, non Wallich (1824). *Ribes tomentosum* K. Koch, Wochenschr. Gartnerei Pflanzenk. 2: 138. 1859. *Ribes rotundifolium* Michx. var. *villosum* (Nutt. in Torr. &

Gray) Dippel, Handb. Laubhjolzk. 3: 288. Nov. 1893. *Ribes divaricatum* Douglas var. *villosum* (Nutt. in Torr. & Gray) Zabel, Handb. Laubh. Deutche Dendrol. Ges. 137. 1903. TYPE: UNITED STATES, California, Santa Barbara Co., common on the plains near Santa Barbara, Apr 1836, *Nuttall s.n.* (HOLOTYPE: BM!; ISOTYPES: NY!, PH!).

Ribes divaricatum Douglas. var. *pubiflorum* Koehne, Deut. Dendrol. 200. May 1893. NEOTYPE (here designated): a cultivated garden specimen grown at Berlin Botanical Garden, 8 May 1897, 16 May 1899, *Koehne s.n.* (MO!; duplicate of the neotype: OXF!).

Ribes divaricatum Douglas var. *montanum* Jancz., Mém. Soc. Phys. Genève 35: 391. 1907. TYPE: UNITED STATES, California, Lake or Colusa Co., Snow Mtn., no date or collector (HOLOTYPE: KRAM!).

Hypanthium obconic, the tube 1.5–2 mm long, 1.7–2.5 mm wide, pilose to villous, the calyx lobes 3.5–4.5 mm long, pilose to villous; *petals* white, 1.2–1.7 mm long; *filaments* 3.5–4.7 (5) mm long; *styles* 5–7 mm long. Flowering from Apr–May, fruiting from May–Jul.

DISTRIBUTION. The var. *pubiflorum* occurs from the Rogue River area of southern Oregon southward along the Pacific coast to Santa Barbara Co., California. The low frequency of recent collections could indicate that the variety is now uncommon to rare. Unlike the typical variety, var. *pubiflorum* does not have large sections of undisturbed habitat. In numerous field trips in Mendocino, Marin, Contra Costa, Alameda and Santa Cruz counties during 1972–1976, this variety was not observed. Two detailed local studies within the range of this variety in north-central California failed to locate populations of var. *pubiflorum* (Wetzl, 1972; Sinnott et al., 1980).

PLANT ASSOCIATIONS. In the northern part of its range, var. *pubiflorum* is found in forests dominated by *Sequoia sempervirens* (D. Dons) Endl., *Lithocarpus densiflorus* (Hook. & Arn.) Rehd. and *Pseudotsuga menziesii*. In the southern part of its range, the typical associates are *Umbellularia, Aesculus, Quercus agrifolia* Nees and various species of *Salix* along rivers.

DISCUSSION. *Ribes divaricatum* var. *pubiflorum* is neotypified because no Koehne collections of this taxon dating prior to 1893 can be found at B. The neotype (at MO) consists of a flowering and fruiting branch, and the flowering branch is considered the type. The label indicates that the flowers were observed (collected?) on 8 May 1897 and 16 May 1899. The foliage material is dated 23 Aug 1897 and 18 Jul 1899.

In the northern part of its range in northern California and southern Oregon, specimens of *Ribes divaricatum* are sometimes difficult to assign to var. *divaricatum* or var. *pubiflorum*. This region denotes the zone of overlap of these two varieties and is also the location of *R. inerme* var. *klamathense*. As discussed under that variety, var. *klamathense* could represent a hybrid or introgressive swarm of intermediates between *R. inerme* and *R. divaricatum* var. *pubiflorum*.

REPRESENTATIVE SPECIMENS. **United States.** CALIFORNIA: Alameda Co., Strawberry Canyon, *Jepson 9598* (JEPS), Colusa Co., Fouts Spr., *Hoffman 2526* (UT), Contra Costa Co., Lafayette, *Davy 997* (MIN, UC), Del Norte Co., Elk Valley, *Tracy 12037* (A, UC), Humboldt Co., Eureka, *Tracy 17507* (UC, UTC), Lake Co., Snow Mtn, *Ackley s.n.* (CAS), Marin Co., Mt. Tamalpais, *J. T. Howell 16357* (CAS, UC), Mendocino Co., Longvale, *Tracy 16831* (JEPS, UC, UTC, WIS, WTU), Monterey Co., Carmel R., *Heller 6523* (COLO, DS; F, GH, MIN, NY, PH, POM, RM, TEX, UC, US), San Francisco Co., Lake Merced, *Rubtzoff 3016* (CAS, RSA), San Luis Obispo Co., Morro Bay, *Hoover 6648* (CAS, DS), San Mateo Co., Searsville L., *Rose 65008* (COLO, DS, RSA), Santa Barbara Co., La Purisima Mission, *Breedlove 4154* (CAS, DS, SMU), Santa Clara Co., Pleasant Valley, *Etienne s.n.* (CAS), Santa Cruz Co., Felton, *J. T. Howell 19593* (A, CAS), Sonoma Co., Laguna de Santa Rosa, *Rose 62018* (ARIZ, COLO, GA, GH, MICH, MIN, RSA, RM, SMU, TEX, WS).

5c. **Ribes divaricatum** Douglas var. **parishii** (A. Heller) Jepson

Ribes parishii A. Heller, Muhlenbergia 1: 134. 1906. *Grossularia parishii* (A. Heller) Coville & Britton, N. Amer. fl. 22: 224. 1908. *Ribes divaricatum* Douglas var. *parishii* (A. Heller) Jepson, Fl. Calif. 2: 151. 1936. *Ribes divaricatum* Douglas ssp. *parishii* (A. Heller) E. Murray, Kalmia 12: 22. 1982. TYPE: UNITED STATES, California, San Bernardino Co., San Bernardino Valley, 1000 ft elev., 15 Mar 1905, *Parish 5364* (HOLOTYPE: BKL!; ISOTYPE: NY!).

Hypanthium broadly obconic, the tube 2.8–3.5 mm long, 3.2–4.5 mm wide, villous, the calyx lobes 4.7–6 mm long, villous; petals pink to red, 2–2.5 mm long; *filaments* 4.5–5.5 mm long; *style* 9–10 mm long. Flowering from Feb–Mar, fruiting from Mar–Jun.

DISTRIBUTION. Known only from a few scattered locations along the San Gabriel River Canyon near El Monte and Pasadena, Los Angeles Co., and along Warren Creek in the San Bernardino Valley of San Bernardino Co. The only recent collection observed during this study was one made from Pico Rivera, Los Angeles Co., (9 Mar 1963, *Miller s.n.*). No specimens have been gathered in the type area since 1920. It would appear that this variety is now rare and perhaps a candidate for federal protection under provisions of the Endangered Species Act.

Plant associations. From label data and floristic notes, var. *parishii* is restricted to *Salix* swales in riparian habitats.

Discussion. Jepson (1936) and McMinn (1939) reported that some specimens of *Ribes divaricatum* from Santa Barbara and San Luis Obispo counties approach var. *parishii*. In this study only one such specimen was seen. This seeming intermediate between var. *parishii* and var. *pubiflorum* is from Carpenteria, Santa Barbara Co., (*Brewer 252* at UC, GH, MO).

Representative specimens. **United States.** CALIFORNIA: Los Angeles Co., Lexington Wash, *Coville 171* (A, CAS, DS, NY, POM, UC), El Monte, *Davidson s.n.* (DAO, DS), San Gabriel R., *Wheeler 2452* (CAS, COLO, DS, MICH, MO, UC), San Bernardino Co., San Bernardino Valley, *Parish s.n.* (A, DS, F, GH, MO, UC), Warren Cr., *Parish 11190* (ARIZ, DS, GH, POM, UC), San Bernardino, *Parry s.n.* (MO), *Vasey s.n.* (F).

6. **Ribes rotundifolium** Michx. (Figure 20)

Ribes rotundifolium Michx., Fl. bor.-amer., 1: 110. 1803. *Grossularia rotundifolia* (Michx.) Coville & Britton, N. Amer. fl. 22: 223. 1908. Type: UNITED STATES, in montibus excelsis Carolinae, *Michaux s.n.* (HOLOTYPE: P, as IDC microfiche!, and observations by H. G. Bedell).

Ribes triflorum Willd., Hort. berol. 61. 1806 *Grossularia triflora* (Willd.) Spach, Hist. nat. veg. 6: 176. 1838. Type: UNITED STATES, America boreali (HOLOTYPE: B, as IDC michrofiche!).

Ribes stamineum Hornem., Hort. bot. hafn. 237. 1813. Lectotype (here designated): UNITED STATES, America boreali, collector and date unknown (C!).

Plant a medium shrub 0.75–1.5 m; *stems* erect to recurving and rooting at the tips, the bark purple to grey in age, glabrous, rarely with internodal bristles; *nodal spines* purple to grey, 0–1 (2), 3–11 mm long, normally straight; *leaves* as broad as long, the blade 15–35 mm long, and wide, trilobed above the midpoint, the lobes with rounded teeth, the upper surface finely short pilose when young, becoming glabrate and often lustrous in age, the lower surface with axillary hairs to glabrous, the apex rounded to acute (80–90°), the base typically rounded to cuneate, rarely subcordate, (130–170°), the petiole 8–20 mm long, glabrous to short pilose and with scattered longer glands near base; *inflorescence* of 1–3 flowers on glabrous, 5–10 mm long peduncles; *flowers* on 4–7 mm long, glabrous pedicels, subtended by bracts 1.5–2 mm long, these glabrous or with a few short glands; *hypanthium* narrowly campanulate, purplish-green, the tube 1.5–2 mm long, 2–3 mm wide,

Figure 20. Illustration of *Ribes rotundifolium:* habit, flower, open flower and petal.

glabrous, the calyx lobes 4–4.5 mm long, spreading, glabrous, the petals 2–2.5 mm long, obovate, white, the filaments 5.5–7 mm long, glabrous, exserting the cream-colored glabrous anthers above the petals; *pistil* with a style divided to halfway, 7–9 mm long, villous in the lower half, the ovary glabrous; *fruits* smooth and glabrous, pale purple when ripe, 7–12 mm in diameter; chromosome number not reported. Flowering from May–Jun, fruiting from Jun–Jul.

Distribution. *Ribes rotundifolium* is an Appalachian and associated mountain species, distributed from New York south to North Carolina and Tennessee. Reports from New England usually represent misidentified specimens of *R. hirtellum,* although a Patton collection from Mount Meriden, New Haven Co., Connecticut is *R. rotundifolium.* This species typically inhabits shaded or partially shaded rock outcrop regions in the mountains, above 1000 m in the southern part of the range, but at lower elevations in the north (Figure 21).

PLANT ASSOCIATIONS. Depending on the elevation and latitude, *Ribes rotundifolium* is associated with species of *Quercus, Picea, Tsuga, Tilia, Hamamelis virginiana* L. and *Acer spicatum* Lam.

DISCUSSION. *Ribes rotundifolium* is relatively invariate in floral features, but variable in foliage characters in some parts of the range. The typical plant has rounded-cuneate leaves while certain populations in the southern part of the range appear to have subcordate leaves. The frequency of subcordate leaves is high in the Great Smokey Mountains of Tennessee and North Carolina, a region of sympatry with *R. cynosbati*, a species with cordate leaves. As the floral features and other characters do not indicate gene flow, the appearance of subcordate leaves in *R. rotundifolium* in this region of sympatry is apparently due to some factor other than hybridization and gene flow.

Two specimens are mounted on the type sheet of *Ribes stamineum,* one is *R. rotundifolium,* the other *R. cynosbati.* The lectotype is here designated as the specimen of *R. rotundifolium.*

REPRESENTATIVE SPECIMENS. **United States.** CONNECTICUT: New Haven Co., Mount Meriden, *Patton s.n.* (GH); MARYLAND: Allegany Co., Rocky Gap Gorge, *Hill & Riefner 9919* (MARY), Frederick Co., Cunningham Falls, *Baltars 1112* (DS, GA, LL, NY, SMU, TENN, US), Garrett Co., Oakland, *E. Palmer 39554* (A, PH, MO, NY, US), Washington Co., Blue Mtn., *Canby s.n.* (ARIZ, MICH, WS); NEW JERSEY: Hunterdon Co., Warren Glen, *Benner 8648* (PH), Passaic Co., Greenwood, *Mackenzie 2562* (MO, NY, US), Sussex Co., Newton, *Britton s.n.* (NY), Warren Co., Brass Castle, *Schaeffer 39062* (PH), NEW YORK: Delaware Co., Arkville, *Wilson s.n.* (NY), Essex Co., Wallface Cliff, *Smith 4594* (GA), Greene Co., Catskill Mountains, *Dodd s.n.* (NY), Orange Co., Black Rock Forest, *Raup 7217* (GH, NY); NORTH CAROLINA: Avery Co., Roan Mtn., *Redfield 11725* (MO), *Sinnott 1470* (MARY), Haywood Co., Pigeon R., *Wilbur 7115* (GA, MICH, SMU, TEX, UC), Mitchell Co., Roan Mt., *Radford & Pence 44999* (ASU, COLO, MASS, MICH, MIN, RSA, SMU, TENN, TEX, WIS, WTC), Swain Co., Clingman's Dome, *Jennison 2761* (TENN), Yancey Co., Mt. Mitchell, *Greenlee 246* (ASU, COLO, MICH, MIN, RSA, SMU, TENN, UC, WTC); PENNSYLVANIA: Bedford Co., Sulphur Springs, *Bright 6107* (MIN, SMU, WIS), Berks Co., *Bethel 10054* (PH), Bucks Co., Haycock Mtn., *Benner 4103* (F, MICH, MO, PENN, PH, POM), Carbon Co., Blue Mountains, *Fogg 11953* (GH, PENN), Centre Co., Poe Paddy State Forest, *Fogg 16761* (NY, PENN), Franklin Co., Fort Loudon, *E. Palmer 43592* (MIN, MO), Fulton Co., Sideling Hill, *Sinnott 1409* (MARY), Lehigh Co., Lehigh R., *Pretz 1903* (KSC, PH), Monroe Co., Pocono Plateau, *Harshberger s.n.* (A, F, GH, MIN,

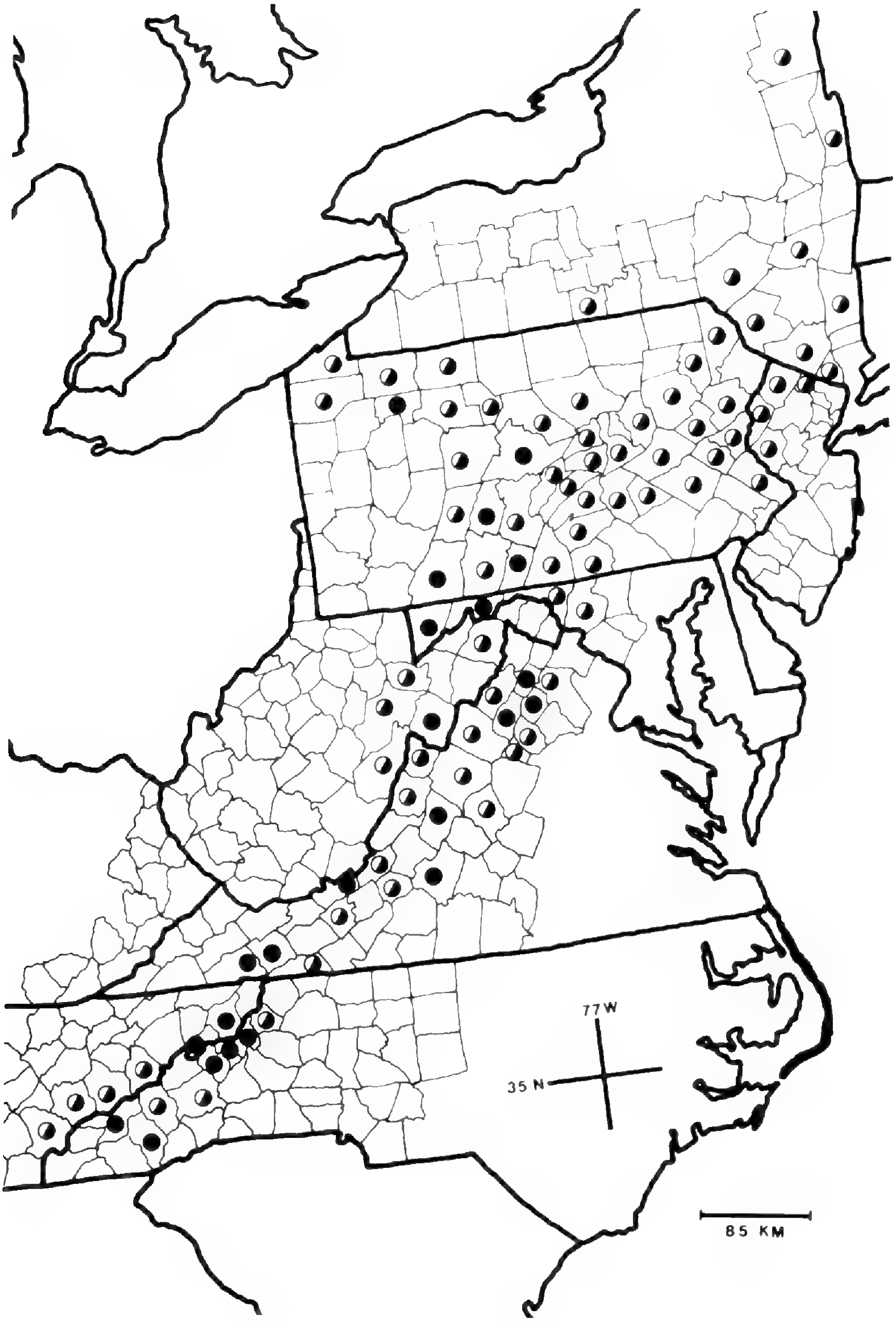


Figure 21. County dot distribution map of *Ribes rotundifolium*. Solid circles represent post-1965 records.

MO, RM), Northampton Co., Riverton, *Schaeffer 25577* (PH), Schuylkill Co., Zion's Grove, *Wagner 3163* (PENN), Somerset Co., Allegheny Mtn., *Sinnott 1517* (MARY); TENNESSEE: Blount Co., Thunderhead Mtn., *Jennison 384* (TENN), Carter Co., Roan Mtn., *Rydberg 9334* (NY), *Sinnott 1465* (MARY), Cocke Co., Inadu Knob, *Jennison 3276* (TENN), Sevier Co., Mount LeConte, *Iltis 1374* (SMU), Unicoi Co., Beauty Spot Gap, *Busing 80-119* (TENN); VIRGINIA: Augusta Co., Mount Rogers, *Heller 802* (F, PH, US), Bedford Co., Peaks of Otter, *Freer 7003* (GH, SMU), Fauquier Co., Rattlesnake Mtn., *Allard 2874* (US), Giles Co., Mountain L., *Fogg 14748* (GH, PENN), Grayson Co., Whitetop Mtn., *Leeds 1929* (PH), Madison Co., Marksville, *Fosberg 33419* (GH), Page Co., Stony Man Mtn., *Steele & Steele 160* (GH, MIN, MO, NY, US), Rappahannock Co., Hogback Overlook, *Sinnott 1942* (MARY), Rockbridge Co., Elk Pond Mtn., *Freer 8474* (SMU), Shenandoah Co., Masnutten Mtn., *Allard 4497* (GH, NY, US), Smythe Co., Whitetop Mtn., *Sinnott 1459* (MARY); WEST VIRGINIA: Hampshire Co., Capon Springs, *Hunnewell 18064* (GH), Pendleton Co., Panther Mtn., *Rydberg 9160* (CAS, NY, PH), Pocahontas Co., Cass, *Clarkson 1684* (SMU), Tucker Co., Little Blackwater R., *Allard 10140* (GH, US).

7. **Ribes missouriense** Nutt. in Torr. & Gray (Figure 22)

Ribes missouriense Nutt. in Torr. & Gray, Fl. N. Amer. 1: 548. 1840. *Grossularia missouriensis* (Nutt. in Torr. & Gray) Coville & Britton, N. Amer. fl. 22: 221. 1908. TYPE: UNITED STATES, Missouri, Independence Co., near Independence, Apr 1834, *Nuttall s.n.* (HOLOTYPE: BM as photograph!; ISOTYPES: GH!, NY!, PH!).

Ribes missouriense Nutt. in Torr. & Gray var. *ozarkanum* Fassett, Rhodora 39: 377. 1937. TYPE: UNITED STATES, Arkansas, Washington Co., sandstone cliffs near White R., Goshen, 20 Apr 1936, *Fassett 18020* (HOLOTYPE: WIS!; ISOTYPES: NY!, US!).

Plants a medium to large shrub 1.5–2 m tall; *stems* erect to sprawling and rooting at the tips, the bark greyish to straw colored, glabrous to puberulent, rarely with internodal bristles; *nodal spines* purple to greyish or sometimes purplish-brown, 1–3, 7–18 mm long, stout and straight; *leaves* isodiametric, the blade 17–30 mm long, 18–35 mm wide, trilobed or occasionally appearing 5-lobed, the lobes toothed, the upper surface thinly puberulent to hirsute or glabrous when young, becoming glabrate and somewhat lustrous with age, primarily eglandular, the lower surface villose-tomentose to puberulent when young, becoming hirsute to occasionally glabrade with age, eglandular, the apex rounded (about 90°), the base generally broadly cuneate to rounded (130–170°), sometimes subcordate when sympatric with *R. cynosbati,* the petiole 7–20 mm long, puberulent, with longer and often plumose hairs and elongated glands near the base, short glands absent; *inflorescence* of 1–4 flowers on puberulent, glandular or nearly glabrous, 8–20 mm long

Figure 22. Illustration of *Ribes missouriense:* habit, flower, open flower and petal.

peduncles, occasionally with 2 inflorescences arising from a single bud; *flowers* on 5–13 mm long, glabrous pedicels, subtended by bracts 2–2.5 mm long, these ciliate with glandular and eglandular hairs; *hypanthium* short cylindric, white, the tube 1.5–2.5 mm long and wide, glabrous or puberulent, the calyx lobes 5–7.5 mm long, reflexed at anthesis, glabrous or sparsely pubescent, the petals white to occasionally pinkish-tinged in age, 2–3 mm long, narrowly obovate-spatulate, the filaments 8.5–11 mm long, glabrous, exserting the glabrous cream to pale pink anthers beyond the petals; *pistil* with a deeply divided style 11–14 mm long, the ovary glabrous; *fruit* smooth, 7–12 mm in diameter, red to purple at maturity; $n = 8$ (Sax, 1931). Flowering from Apr–Jun, fruiting from May–Jul.

DISTRIBUTION. The historical distribution of *Ribes missouriense* was apparently throughout the tall grass prairie and adjacent deciduous forests in the midwestern portion of the United States. Over the last century, heavy agricultural use has extirpated many populations. Nonetheless, *R. missouriense* is unusual for the sect. *Grossularia* in that it will recover from human disturbances if a suitable habitat exists for recovery.

In a portion of its distribution, *Ribes missouriense* is sympatric with *R. cynosbati;* the former is always more abundant than the latter in disturbed sites. The abundance of flowers, edible fruit and hardiness of *R. missouriense* is noteworthy, for at times it becomes aggressive in invading abandoned pastureland in a fashion analagous to *Rubus* or *Crataegus.* The beauty and hardiness of the species might explain the unusual disjunct locations found in the northeastern part of its range. It is likely that many of these individuals represent cultivated plants or plants which have escaped from cultivation; the majority were collected in or near cities (Figure 23).

PLANT ASSOCIATIONS. In the eastern part of its range *Ribes missouriense* is typically found in rich deciduous forests composed of varying combinations of *Quercus, Tilia, Ostrya, Acer, Ulmus, Prunus, Populus, Carya, Juglans* and *Pinus strobus.* To the west, where the trees are restricted to waterways, *R. missouriense* is typically associated with *Quercus, Populus* and *Salix* along river and stream banks, often among rocks.

DISCUSSION. This species is relatively homogeneous throughout its range and therefore few segregates have been proposed within it. The var. *ozarkanum* is here reduced to synonymy as it represents only a minor variant in the Ozark Plateau, where the plants are somewhat less pubescent. Plants from adjacent Kansas, for example, show a complete range of variation from subglabrous to villous, as can be found in most species in sect. *Grossularia.*

Despite the relative lack of published names associated with *Ribes missouriense,* it has had a confused and complicated taxonomic history. Most of the confusion revolves around its association with the name *R. gracile.* In this treatment, *R. gracile* is considered to be a taxonomic synonym of *R. cynosbati,* as the holotype of Michaux's *R. gracile* clearly has the long peduncle, cordate leaf base, campanulate calyx tube and bristly ovary characteristic of that species. As the type is in flower, Michaux's description of *R. gracile* gave no mention of fruit surface features, a key

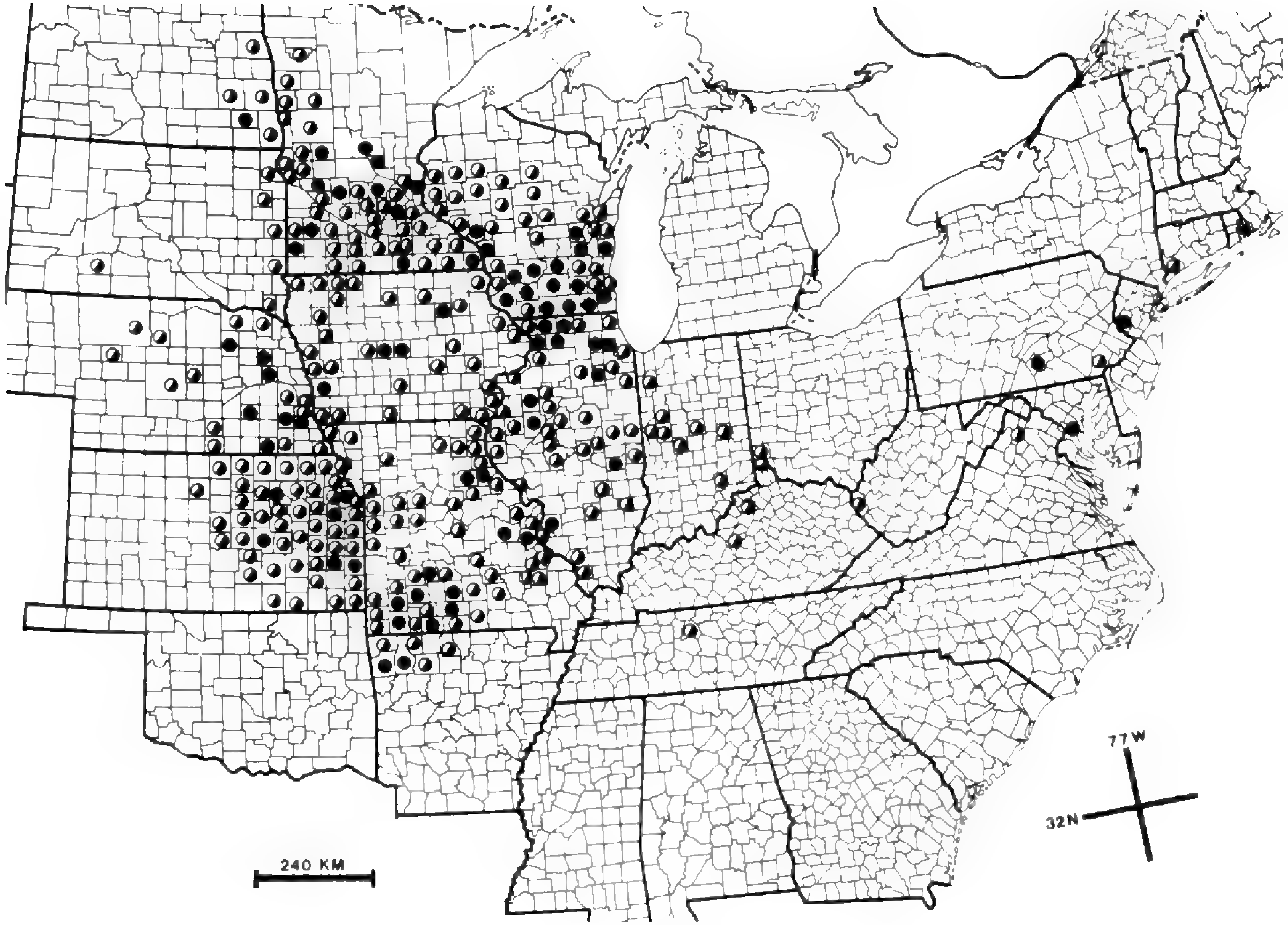


Figure 23. County dot distribution map of *Ribes missouriense*. Solid circles indicate post-1965 collections. Note the probable cultivated or weedy escapes in the eastern states.

feature in the recognition of *R. cynosbati.* In the type region given for *R. gracile* (mountains of Tennessee) are three species: *R. cynosbati, R. rotundifolium* and *R. curvatum.* The first two were included in Michaux's flora, with *R. rotundifolium* described as a new species therein. It is reasonable to assume that *R. rotundifolium* was well known to Michaux and not likely to be confused with his *R. gracile. Ribes cynosbati* is included in his Flora, thus the question arises whether or not Michaux had another species in mind when he proposed *R. gracile. Ribes missouriense* is unlikely because it occurs primarily on the plains west of the mountains, yet Pursh (1814) and others associated it with Michaux's *R. gracile. Ribes curvatum* is found in the mountains of Tennessee (Figure 27) and it is possible that this was the species Michaux was attempting to describe. The type specimen of *R. gracile* is not a specimen of *R. curvatum* though; it appears that Michaux confused an unusual flowering specimen of *R. cynosbati* and published it as a new species.

Torrey and Gray (1840) apparently believed that *Ribes curvatum* was what Michaux had in mind for *R. gracile* as their description of that species fits *R. curvatum* perfectly. *Ribes gracile* is a synonym of *R. cynosbati,* thus Torrey and Gray should have proposed a new epithet for the southeastern plants. It was not until 1896 that *R. curvatum* finally received a legitimate name. Gray (1876) later decided (as had Pursh, 1814) that *R. gracile* was the correct name for the Great Plains gooseberry (*R. missouriense*).

Coville and Britton (1908) came to the same conclusions arrived at here, placed *R. gracile* in synonymy under *R. cynosbati* and recognized both *R. curvatum* and *R. missouriense.* At the same time, unfortunately, Janczewski (1907) referred the name *R. gracile* to the Appalachian mountain species *R. rotundifolium* and applied *R. rotundifolium* to plants here placed in *R. missouriense.* Berger (1924) followed Coville and Britton.

Since its origin in 1803, *Ribes gracile* has been misapplied to *R. missouriense* (Pursh, 1814), *R. curvatum* (Torrey & Gray, 1840) and *R. rotundifolium* (Janczewski, 1907). As a result, some herbarium material has been badly confused.

REPRESENTATIVE SPECIMENS. **United States.** ARKANSAS: Benton Co., Osage R., *Demaree 4772* (A, MO, TEX), Washington Co., Fayetteville, *Fassett 19871* (GH, MO, NY, UC, WIS); CONNECTICUT: Fairfield Co., Norwalk, *Eames & Godfrey s.n.* (NY, PH, VT); ILLINOIS: Cook Co., Desplaines R., *Bennett 492* (F, SMU), Jo Daviess

Co., Stockton, *Hermann 890* (A, F, NY); INDIANA: Marion Co., Indianapolis, *Deam 5613* (MICH), Tippecanoe Co., Lafayette, *Deam 54757A* (SMU); IOWA: Boone Co., Ledges State Park, *W. A. Weber 637* (COLO), Storey Co., Ames, *Pammel 348* (F, GH, MIN, RM, US); KANSAS: Douglas Co., Lawrence, *Marsh 1536* (NCU, NY, SMU), Riley Co., without location, *J. B. Norton 148* (GH, KSC, MO, NY, RM, US); KENTUCKY: Henry Co., Rt. 153 & 322, *Gentry 896* (NY), Nelson Co., without location, *Agnes 1472* (RM); MARYLAND: Prince Georges Co., College Park, *Sinnott 1945* (MARY); MINNESOTA: Faribault Co., Blue Earth R., *Sinnott 1621* (MARY), Hennepin Co., Minneapolis, *Heller s.n.* (A, MO, NY, RM, UC, US), Winona Co., Whitewater State Park, *Sinnott 1597* (MARY); MISSOURI: Boone Co., Columbia, *Dunn 12769* (NY, RSA), Stone Co., James R., *E. J. Palmer 5837* (A, MICH, MO, US); NEBRASKA: Jeffereson Co., Alexandria L., *Koch 8076* (MASS, UT), Lancaster Co., Lincoln, *Churchill 487* (MO); NEW JERSEY: Kingwood Twp., *Laport s.n.* (NCU); NORTH DAKOTA: Cass Co., Fargo, *Bergman s.n.* (A, PH, UC), Richland Co., Kindred, *Seiler 1500* (MO, NCU); OHIO: Butler Co., Oxford, *Kohlidakis s.n.* (WS), Hamilton Co., Cincinnati, *Lloyd s.n.* (MIN); PENNSYLVANIA: Chester Co., Malvern, *Stone s.n.* (NY, PH), Cumberland Co., Bloserville, *Wherry s.n.* (PENN); SOUTH DAKOTA: Dakota Co., Sioux City, *E. J. Palmer 37664* (A, MO), Minnehaha Co., Palisades State Park, *Sinnott 1634* (MARY); TENNESSEE: Davidson Co., Nashville, *Bicknell s.n.* (TENN); VIRGINIA: Warren Co., without location, *Hunnewell s.n.* (GH); WEST VIRGINIA: Adams Co., Easton, *Fassett 19895* (WIS), Dane Co., Festge Park, *Sinnott 1568* (MARY), Walworth Co., Whitewater *E. J. Palmer 27582* (A, MO).

8. **Ribes niveum** Lindl. (Figure 24)

Ribes niveum Lindl., Bot. Reg. 20: 1692. 1835. *Grossularia nivea* (Lindl.) Spach, Hist. Nat. Veg. 6: 179. 1838. TYPE: based on cultivated material, no date (see discussion) (HOLOTYPE: CGE!; ISOTYPE: K as a photograph!).

Ribes niveum Lindl. forma *pilosum* St. John, Fl. SE Washington 188. 1937. TYPE: UNITED STATES, Idaho, Nez Perce Co., N side of Snake River Canyon, Lewiston Grade, 12 Oct 1924, *St. John 6794* (HOLOTYPE: WS!).

Plant a medium to large shrub 1–2 m tall; *stems* erect to sprawling and rooting at the tips with the underground stems producing offshoot plants, the bark reddish-brown when young, becoming grey with exfoliation, the twigs usually glabrous, occasionally with internodal bristles; *nodal spines* greyish-brown to purplish-brown, (1–2) 3, 7–20 mm long, straight to slightly curved; *leaves* isodiametric, the blade 13–30 mm long and wide, trilobed above the midpoint, the lobes with rounded teeth, the upper surface glabrous or pilose with eglandular hairs, the lower surface similar, the apex rounded to broadly obtuse (90°), the base broadly cuneate to rounded (120–170°), the petiole 10–25 (30) mm long, glabrous or pilose with eglandular hairs and with scattered plumose glandular hairs near the base; *inflorescence* of 1–4 (5) flowers on glabrous or thinly pubescent, 8–20 mm long peduncles; *flowers* on 4–12 mm

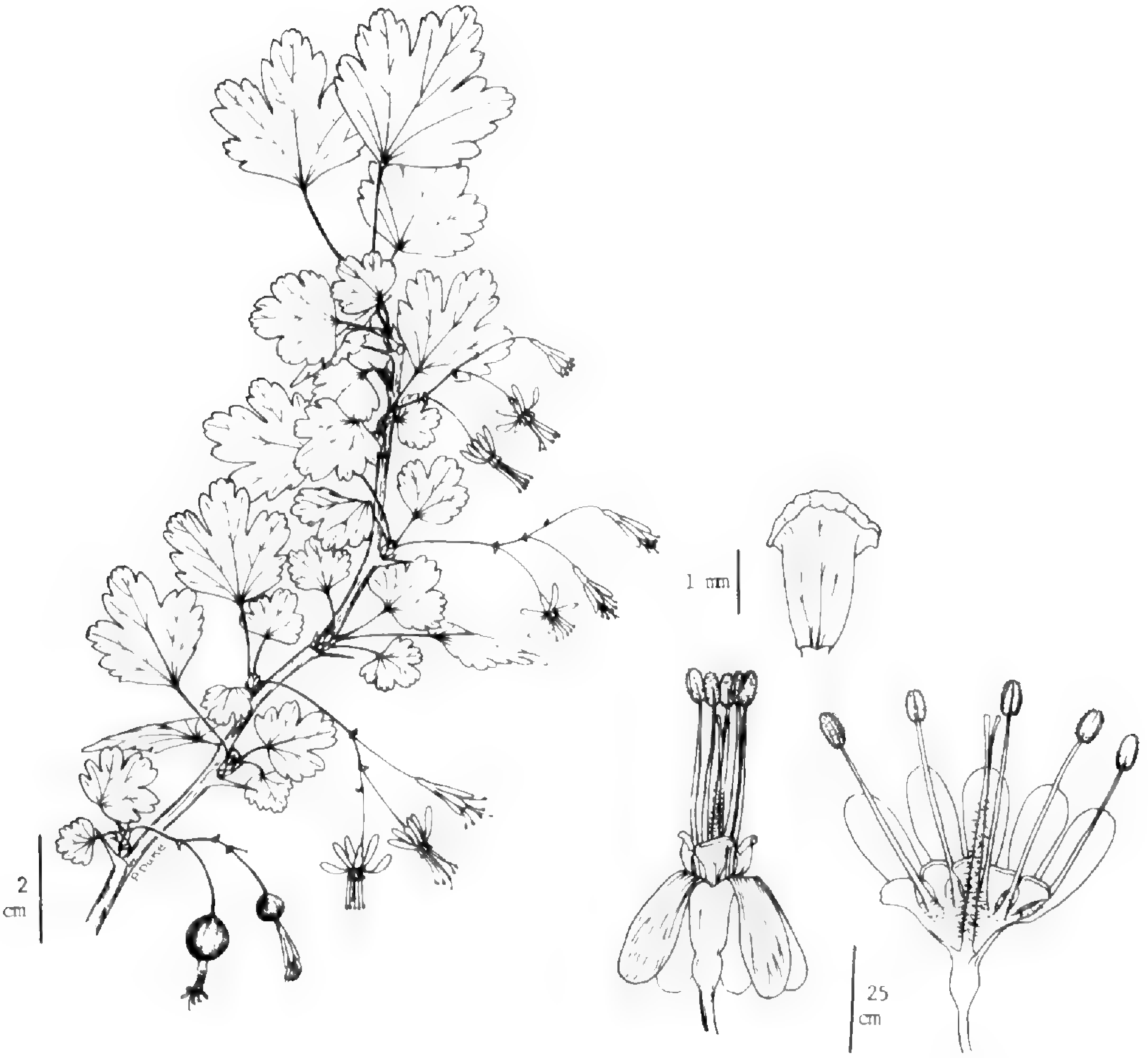


Figure 24. Illustration of *Ribes niveum*: habit, flower, open flower and petal.

long, glabrous pedicels, subtended by bracts 2–3 mm long, these glabrous or finely ciliate and glandular; *hypanthium* campanulate, white, the tube 2–2.5 mm long, 2–2.7 mm wide, glabrous or sparsely hairy, the calyx lobes 6–7.5 mm long, recurved at anthesis, glabrous or sparsely pubescent, the petals narrowly obovate, 2–3 mm long, white, the filaments 7–9 mm long, pilose or subglabrous, exserting the cream-colored, subglabrous to tufted hairy anthers well beyond the petals; *pistil* with a style 11–14 mm long, the ovary glabrous; *fruit* smooth and glabrous, 8–12 mm in diameter, purplish-green at maturity; $n = 8$ (Zielinski, 1952). Flowering from Apr–May, fruiting from May–Jul.

DISTRIBUTION. *Ribes niveum* consists of a series of populations which inhabit riparian communities of two independent watersheds

(Figure 25). The localities mapped in Washington, Oregon, Idaho and northeastern Nevada are all connected via the Columbia River watershed consisting of the Columbia and Snake rivers and their major tributaries, the John Day, Deschutes, Owyhee, Jarbridge and Brunneau rivers. The localities mapped in west-central Nevada are situated on the Humboldt River watershed, separated from the Columbia River watershed by the Jarbridge Range. Although independent, the two watersheds are separated by five miles or less in parts of Humboldt and Elko counties, Nevada, thus gene flow is likely.

The disjunct collections from New Mexico and Colorado could not be independently confirmed from field studies or other herbarium records. Neither specimen is recorded in existing floras for these states (Harrington, 1954; Martin & Hutchins, 1980).

It appears that *Ribes niveum* is declining in the Columbia River watershed. This conclusion is based on fieldwork and the low frequency of recent collections found in herbaria. The Columbia and Snake rivers have both been modified for commercial shipping uses, and the stream banks of many of their tributaries have been heavily impacted by grazing. During field studies along the Columbia and Snake rivers in 1982, large populations of *R. niveum* were rarely encountered and most populations consisted of only a single or few individuals. This is in stark contrast to Douglas' (1914) comment in his journal that in 1825, *R. niveum* was found "on all rocky soils from the Great Falls (The Dalles) to the junction of the Spokane River." Along the Humboldt River, however, populations are apparently more intact, at least according to herbarium records.

PLANT ASSOCIATIONS. *Ribes niveum* is usually associated with mesic reparian communities composed of *Salix, Prunus, Crataegus* and *Amelanchier.* In drier habitats it is associated with *Artemisia* and *Pinus,* as observed along the Snake River.

DISCUSSION. The holotype in Lindley's herbarium at CGE is annotated as a Horticultural Society specimen, presumably raised at one of the Society's gardens. In the original description, Lindley indicated the species was initially brought to England by David Douglas who gathered the plant in Northwest America. Douglas made two collecions of *R. niveum,* one in flower (April, 1826) and one in fruit (June, 1825). Both of the Douglas collections are mounted on one sheet with the isotype at K (Hooker's Herbarium).

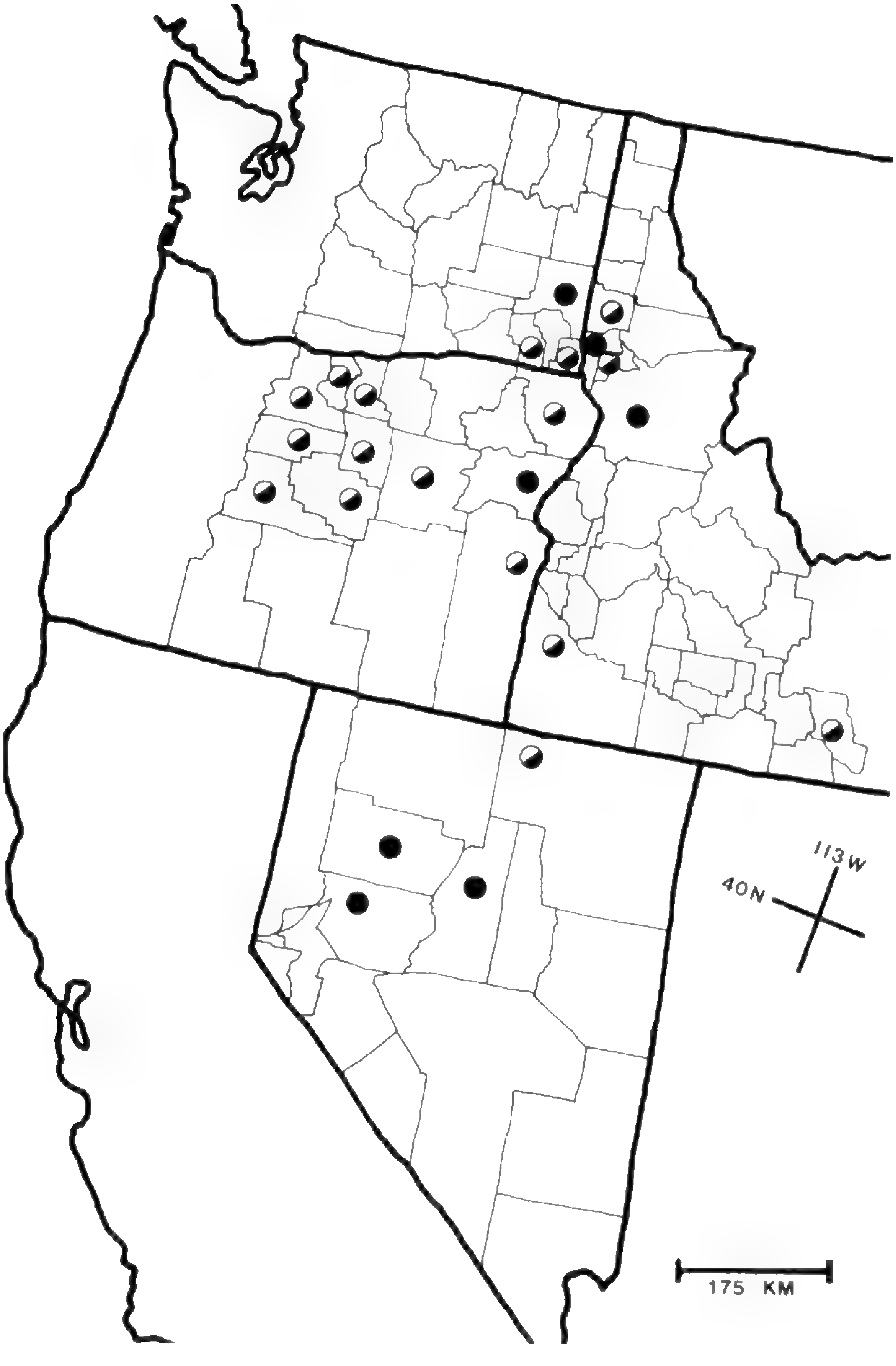


Figure 25. County dot distribution map of *Ribes niveum*. Solid circles represent post-1965 records. Unconfirmed reports from Colorado and New Mexico are not mapped.

If Lindley received his seed from the Douglas fruiting collection, the type material of *R. niveum* probably came from The Dalles along the Columbia River on the Oregon-Washington border. It is represented by *Douglas 317* (K).

Representative specimens. **United States.** COLORADO: Fremont Co., Wilson Cr., *Brandegee 697* (MO); IDAHO: Bannock Co., near Pocatello, *Ryan s.n.* (OSC), Idaho Co., Salmon R., *Cronquist 6200* (COLO, DAO, GA, MIN, ORE, OSC, RSA, SMU, TEX, UTC, WTU), Lawyer's Cr., *Sinnott 1765* (MARY); Latah Co., Kendrick, *Lawrence 386* (DAO), Lewis Co., Mission Cr., *St. John et al. 6331* (WS, WTU), Nez Perce Co., Lewiston, *Heller & Heller 2987* (A, AC, DAO, DS, KSC, MIN, MO, NY, PH, WS), Culdesac, *Sinnott 1824* (MARY), Owyhee Co., House Cr., *Nelson & Macbride 1759* (GH, MIN, NY, OSC, RM, SMU, US); NEVADA: Churchill Co., Pete Canyon, *Lott 112* (NY, RENO), Elko Co., Jarbridge R., *Train 774* (A, RENO), Lander Co., Big Creek Canyon, *Goodner & Henning 1270* (DAO, DS, F, MO, RENO), Pershing Co., Star Creek Canyon, *Ownbey & Ownbey 2827* (CAS, MIN, WS); NEW MEXICO: Bernalillo Co., Balsam Park, Sandia Mts., *Ellis 186* (MO); OREGON: Baker Co., Snake R., *Taylor s.n.* (BRY), Crook Co., Prineville, *Lawrence 3459* (OSC), Deschutes Co., Redmond, *M. E. Peck 24149* (CAS, WILLU), Gilliam Co., near Condon, *Cronquist 6345* (COLO, DAO, GA, MIN, NY, OSC, RSA, SMU, TEX, UTC, WS, WTU), Grant Co., Spray, *Thompson 11336* (A, DS, MO, NY, POM, WILLU, WTU), Jefferson Co., Cow Canyon, *M. E. Peck 15769* (DS, WILLU, WTU), Malheur Co., Owyhee R., *Dean 126* (OSC), Morrow Co., Buttermilk Canyon, *Leiberg 107* (ORE), Sherman Co., Grass Valley Canyon, *Evinger s.n.* (GH, OSC), Wallowa Co., Anatone, *Cronquist 5758* (CAN, COLO, DAO, DS, GH, MICH, MIN, RSA, SMU, TEX, US, UTC, WS, WTU), Wasco Co., Bakeoven Cr., *M. E. Peck 17322* (DS, NY, WILLU), Wheeler Co., Dayville, *Lawrence 4010* (DS, US); WASHINGTON: Asotin Co., Buffalo Rock, *G. N. Jones 1968* (PH, WTU), Columbia Co., Touchet R., *St. John et al. 7002* (GA), Whitman Co., Almota, *Piper s.n.* (DS, NY, POM, RM, US), Lower Granite Dam, *Sinnott 1823* (MARY).

9. **Ribes curvatum** J. K. Small (Figure 26)

Ribes curvatum J. K. Small, Bull. Torrey Bot. Club 23: 295. 1896. *Grossularia curvata* (J. K. Small) Coville & Britton, N. Amer. fl. 22: 221. 1908. Lectotype (here designated): United States, Georgia, DeKalb Co., base of Stone Mtn., 1–18 May 1895, *Small s.n.* (NY!; isolectotypes: A!, MIN!, NY!, TRT!).

Grossularia campestris J. K. Small, Fl. SE US 510. 1913. Type: United States, Louisiana, Red River, 1840, *Hall s.n.* (holotype: NY!).

Grossularia texensis Coville & Berger in A. Berger, New York Agric. Exp. Sta. Techn. Bull. 109: 95. 1924. *Ribes texense* (Coville & Berger in A. Berger) Standley, Field Mus. Nat. Hist., Bot. Ser. 8: 139. 1930. Type: United States, Texas, San Augustine Co., San augustine, *Crockett s.n.* (holotype: US!; isotype: NY!).

Plant a small to medium shrub 0.5–1.5 m tall; *stems* erect to recurving and rooting at the tips, the bark dark reddish-brown to chocolate in color, aging greyish when exfoliating, glabrous, occasionally with internodal bristles; *nodal spines* red-brown to dark

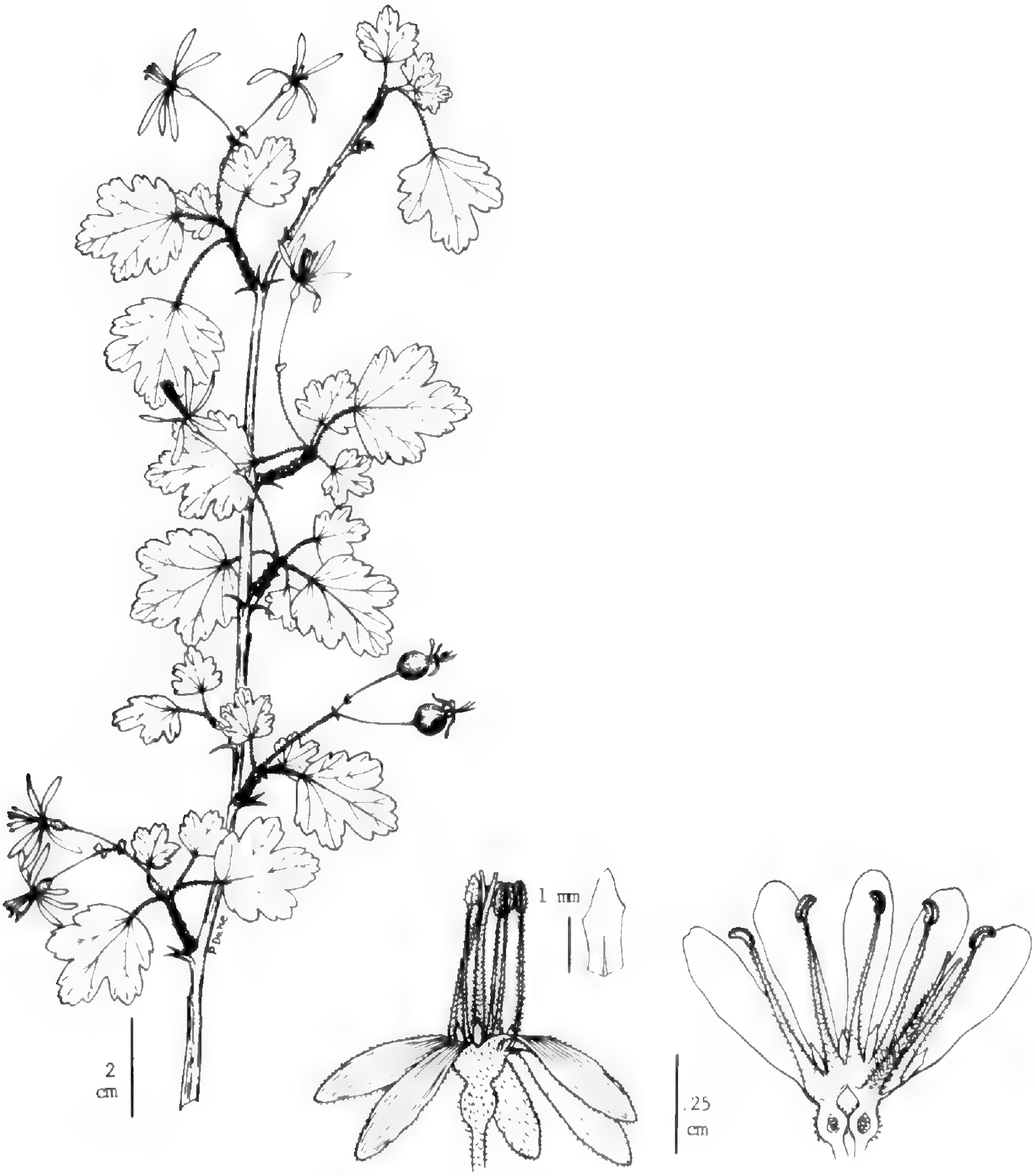


Figure 26. Illustration of *Ribes curvatum:* habit, flower, open flower and petal.

brown, (1–2) 3, 4–11 mm long, often curved; *leaves* isodiametric, the blade 10–30 mm long and wide, trilobed halfway to the midvein, the lobes toothed, occasionally appearing 5-lobed with an additional two lower lateral lobes, the upper surface pilose and usually glandular, becoming lustrous but still glandular with age, the lower surface with characteristic punctate glands intermixed with pilose hairs, the apex somewhat rounded to acute (about 90°), the base rounded to broadly cuneate (130–170°), the petiole 10–25 mm long, pilose and glandular with long-stalked glands, those nearest the base often plumose; *inflorescence* of 1–4 flowers on pilose, 10–27 mm long peduncles; *flowers* on 6–16 mm long, glabrous to pilose, glandular or eglandular pedicels, subtended by bracts 2–2.5 mm long, ciliate with pilose or occasionally glandular hairs on the margin; *hypanthium* broader than long, white, the tube 1–2 mm long, 2–2.8 mm wide, scattered hairy to subvillous, the calyx lobes 7.5–9 mm long, recurved in age, scattered hairy to subvillous, the petals white, 1.2–2 mm long, rhombic, entire or more commonly with a lateral appendage on each side near the apex, glabrous or occasionally hairy, the filaments 6–7.5 mm long, pilose, exserting the cream-colored, often pilose anthers beyond the petals; *pistil* with a style 8–11 mm long, the ovary usually glandular with sessile and short-stalked glands intermixed with pilose hairs; *fruit* smooth or occasionally retaining the glands and/or hairs, 7–12 mm in diameter, greenish to reddish-purple at maturity; $n = 8$ (Zielinski, 1952). Flowering from Mar–Apr, fruiting from Apr–Jul.

DISTRIBUTION. *Ribes curvatum* is bimodally distributed with one series of populations centered in eastern Texas and adjacent Oklahoma, Louisiana and Arkansas, and a second center concentrated in the mountains of southern Tennessee and adjacent parts of Alabama, Georgia and North Carolina (Figure 27). This distribution shows features of the relictual pattern found in species having disjunct populations in the southern Appalachians and the western United States (Wood, 1971). *Ribes echinellum* (Appendix) has a similar but more extreme disjunct relationship to the western species. Unlike any of its eastern neighbors, *R. echinellum* appears related to the western *R. lobbii* group.

PLANT ASSOCIATIONS. *Ribes curvatum* inhabits rich deciduous woods composed of *Quercus, Prunus, Cercis, Cornus, Aesculus* and *Staphylea.*

DISCUSSION. *Ribes curvatum* along with the western *R. niveum* and the midwestern *R. missouriense* form a relatively distinct subgroup within sect. *Grossularia.* All three species are characterized by long filaments that are often hairy (glabrous in *R. missouriense*), long styles, a short calyx tube and long recurved calyx lobes. With their profusion of conspicuous white flowers, these species represent some of the more horticulturally exploitable plants in sect. *Grossularia. Ribes curvatum* is somewhat variable in

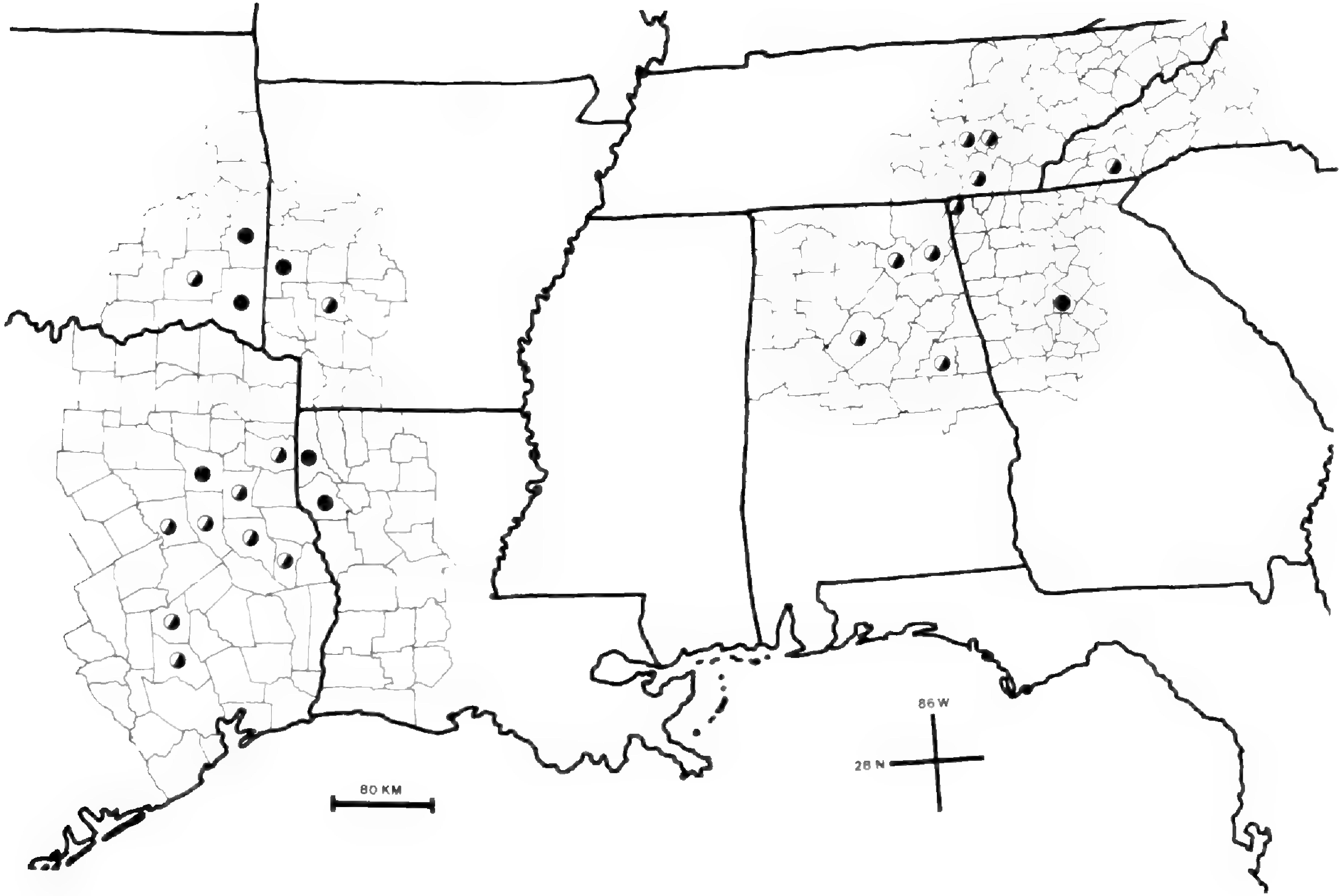


Figure 27. County dot distribution map of *Ribes curvatum*. Solid circles indicate post-1965 records.

its features, especially in floral vestiture, which has led to the segregation of additional species. Small (1913) described *R. campestris* based on its eglandular pubescence and entire petals. The degree to which the petals are lobed is variable throughout the range of *R. curvatum*, with specimens from the type area at Stone Mountain, Georgia, showing a complete range of variation from entire to apically-notched petals. This species was not recognized in a subsequent edition of the southeastern flora (Small, 1933).

In a letter to Britton dated 16 Nov 1918 and filed with the holotype of *Ribes campestris*, Coville stated, "My opinion is that *campestris* is a synonym of *curvata*," In the same letter he discussed the possibility of describing *Grossularia texensis* based on its hairy hypanthium, but concluded that "it is better to treat the unpublished *texensis* also as a variant form of *curvata*." Despite this conclusion, Berger (1924) published the species with Coville as senior author. Coville apparently was still opposed to the recognition of *G. texensis* because he annotated the holotype at US as *G. curvata* in 1926, two years after Berger published his paper.

Ribes curvatum has been confused by some with *R. gracile*, a synonym of *R. cynosbati* (see *R. missouriense* for a more detailed discussion).

REPRESENTATIVE SPECIMENS. **United States.** ALABAMA: Clay Co., Talladega Mts., *Small 5682e* (US), DeKalb Co., Desoto State Park, *Sherman 218* (SMU, TENN), Jefferson Co., Short Cr., *Mohr s.n.* (US), Marshall Co., Albertville, *Harper 8500* (A, GH, MO, NY, US, WIS); ARKANSAS: Pike Co., Newhope, *Demaree 9748* (A), Poke Co., Ouachita Region, Tall Peak, *Demaree 53351* (MASS, SMU); GEORGIA: Dade Co., Lookout Mtn., *Cronquist 5152* (GA, MICH, MO, NY, PH, US), DeKalb Co., Stone Mtn., *Bormann & Burbank 1422* (CAS, DAO, DS, GA, GH, LL, MO, NY, SMU, TENN), *Sinnott 1258* (MARY); LOUISIANA: Caddo Parish, Morringsport, *Hardin 509* (GH, MICH, TEX), Desoto Parish, Glouster, *Thieret 26040* (A, ASU, DAO, LL, MO); NORTH CAROLINA: Macon Co., Highlands, *Leeds 1958* (PH); OKLAHOMA: Leflore Co., Kiamachi Mts., *McKenzie 477* (GA), McCurtain Co., near Bethel, *Henry 5559* (PH), Pushmataha Co., Finley, *Henry 5592* (PH); TENNESSEE: Bledsoe Co., Morgan Spr., *Sharp 2414* (TENN, WIS), Hamilton Co., Walden's Ridge, *McGilliard 925* (GH), Rhea Co., Morgan Cr., *Shanks et al. 4377* (GA, TENN); TEXAS: Anderson Co., Palestine, *Palmer 13202* (A, MO, WIS), Cherokee Co., Larissa, *E. J. Palmer 9384* (A, CAS, DS, US), Harrison Co., Marshall, *E. J. Palmer 5302* (A, F, MIN), Montgomery Co., Willis, without collector data (MO), Nacogdoches Co., Nacogdoches, *Parks 28073* (A), Rusk Co., Henderson, *Reidel 44-20* (TEX), San Augustine Co., San Augustine, *E. J. Palmer 13233* (MIN, US, WIS), Smith Co., Van, *Butler & Butler s.n.* (SMU) Walker Co., Huntsville, *E. J. Palmer 13374* (A, MO, US).

APPENDIX

Ribes echinellum (Coville) Rehd. (Figure 28)

Grossularia echinella Coville, J. Agric. Res. 28: 71. 1924.

Ribes echinellum (Coville) Rehd., J. Arnold Arbor. 7: 148. 1926. TYPE: UNITED STATES, Florida, Jefferson Co., shores of Lake Miccosukee, 2 March 1924, *Coville 112* (HOLOTYPE: US!; ISOTYPES: GH!, US!).

Plant a medium to tall shrub 0.75–1.5 m tall; *stems* erect or recurving and rooting at the nodes, the bark grey to purple when young, glabrous to rarely pubescent, without internodal bristles; *nodal spines* brown, 2–3, 8–16 mm long, often slightly curved; *leaves* as broad as long to slightly longer than broad, the blade 15–22 mm long, 16–25 mm wide, trilobed, the lobes with 2–4 rounded teeth, the upper surface sparsely short pilose, becoming slightly lustrous at maturity, the lower surface scattered pilose to evenly pilose, the apex rounded to acute (90–100°), the base typically rounded-cuneate (130–160°), becoming truncate to subcordate on vegetative shoots, the petiole 10–24 mm long, evenly pilose with eglandular hairs with longer plumose glandular hairs near the base; inflorescence of 1–2 flowers on pilose and scattered glandular 8–18 mm long peduncles; *flowers* on 2–6 mm long pilose and glandular pedicels, subtended by bracts 1.5–2 mm long, these evenly pilose, rarely with intermixed glands; *hypanthium* cylindric or short tubular, greenish white, the tube 3–4.5 mm long, 2.7–3.5 mm wide, pilose, the calyx lobes 5–7 mm long, pilose, reflexed at anthesis, the petals 2–3 mm long, inrolled and appearing tubular, white, the filaments 9–12 mm long, scattered pilose, exserting the reddish-pink pilose anthers out from the petals; *pistil* with a shallowly divided style, cleft to about one fourth its length, 10–15 mm long, glabrous, the ovary densely covered with long glands, the tips of these glands expanded into a disk or cup-shaped apex; *fruits* purplish when mature, 2–3 cm in diameter, densely beset with spines developing from the ovary glands, the spines with flattened apices; $n = 8$ (Lewis et al., 1962). Flowering from Mar–May, fruiting from Apr–Jun.

DISTRIBUTION. *Ribes echinellum* is known only from two locations in eastern North America, Stevens Creek in McCormick Co., South Carolina and the type locality at Lake Miccosukee, Jefferson Co., Florida (Figure 29).

PLANT ASSOCIATIONS. This extremely rare gooseberry inhabits very rich deciduous woods at the two known localities. Tree associates are *Carya, Quercus, Acer, Celtis, Ulmus* and *Ostrya.*

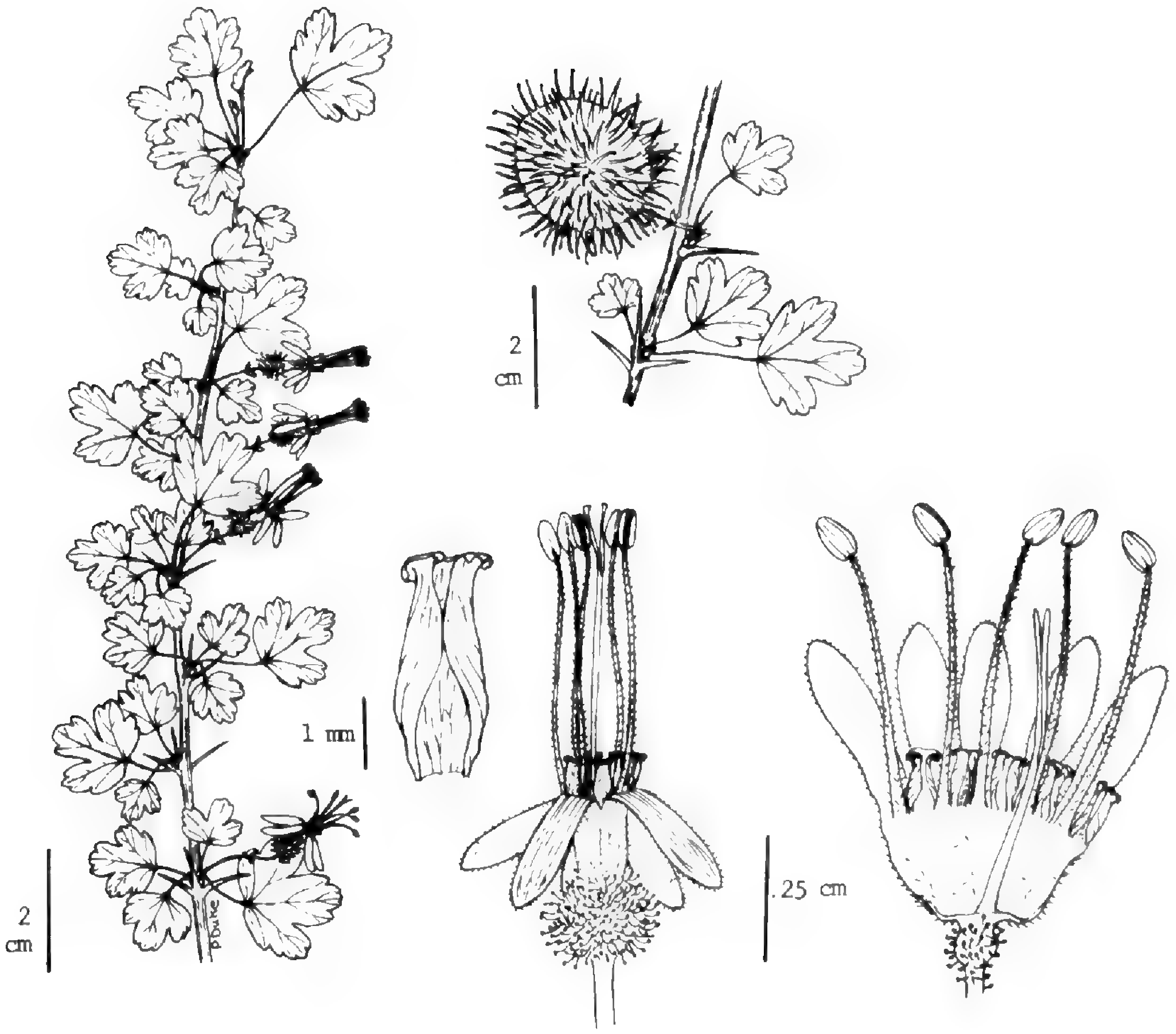


Figure 28. Illustration of *Ribes echinellum:* habit, flower, open flower and petal. Note the densely spiny fruits on the habit sketch.

DISCUSSION. Despite inhabiting a relatively well-collected region of North America, *Ribes echinellum* remained undetected to science until 1924 when two botanists, one from the Florida State Geological Survey, the other from a nearby college, encountered the species at Lake Miccosukee, about 30 miles from Tallahassee, Florida. After contacting F. V. Coville at the United States Department of Agriculture in Washington, DC, a field trip was organized to the region, and the species was first described (Coville, 1924). For 34 years, this population was believed to be the sole one of this southeastern gooseberry which appears unlike any of the other eastern species. Then, in the late 1950's, A. E. Radford located a second population of this unusual species over 200 miles to the north, at Stevens Creek in South Carolina (Radford, 1959;

Figure 29. County dot distribution map of *Ribes echinellum*. Both sites have been visited in the past five years and are still extant.

Radford & Ahles, 1959). To date, these sites remain the only two where the species is found.

Included by Berger (1924) with the hairy-styled species in sect. *Grossularia,* the lack of style pubescence, tubular petals and greenish calyx clearly isolate this species from the section. These features are found in species of the western group related to *Ribes lobbii,* and it appears likely that the affinities of *R. echinellum* belong with those species, not the eastern ones. Wood (1971) noted that many species exhibit a southeastern United States and western U.S. disjunct pattern. This pattern is also found in sect. *Grossularia* to a lesser extent with *R. curvatum,* whose nearest relative is the western *R. niveum.*

Ribes echinellum has been proposed as an endangered species at the state level in both Florida (Godfrey, 1979) and South Carolina (Rodgers and Clark, 1977, unpublished list) based on its infrequent occurrence. In addition, this species is included on the federal list of candidate plants (U. S. Fish & Wildlife Service, 1980), and efforts have been made to have the species officially listed as an endangered species. Currently, the species remains under review in the federal Endangered Species Program, U. S. Department of the Interior.

REPRESENTATIVE SPECIMENS. **United States.** FLORIDA: Jefferson Co., Lake Miccosukee, *Coville 113, 114, 115, 215* (US), *Godfrey 56238* (CAS, COLO, DS, GA, NY, TENN, TEX, UC, WIS) *Palmer 38463* (NY, US), *Small et al. 11206* (NY, TENN, US); SOUTH CAROLINA: McCormick Co., *Leonard & Radford 2328* (ARIZ, MONTU, UTC), *Radford 31713* (ASU, SMU, UC), *44800* (NY, TEX, WIS), *Sinnott 1253* (MARY).

ACKNOWLEDGMENTS

Acknowledgments are given the following five members of my examining and advising committee: James L. Reveal for supervising the entire research project and providing research facilities and funds, Bruce MacBryde for carefully examining the thesis and providing comments, Todd Cooke for thesis evaluation and suggestions, Glen Patterson for thesis evaluation and providing departmental funding and Conrad Link for thesis evaluation.

In addition, I acknowledge the assistance of the curators of the following herbaria for the loan of herbarium material needed for this project: A, ALTA, ASU, B, BH, BKL, BM, BRY, C, CAN, CAS, CGE, COLO, DAO, F, GA, GH, K, KRAM, KSC, LL,

MARY, MASS, MICH, MIN, MO, MONT, MONTU, MSC, MTMG, NCU, NDG, NEBC, NESH, NHA, NY, ORE, OSC, OXF, PENN, PH, RM, RSA, SMU, TENN, TEX, TRT, UBC, UC, UNM, US, UT, UTC, VT, WILLU, WIN, WIS, WTU, WS.

Finally, I thank Peggy Duke for providing the plant illustrations and Hollis Bedell for checking type material at P. I. acknowledge the Computer Science Center, University of Maryland, for providing computing funds.

LITERATURE CITED

ABRAMS, L. 1944. Illustrated Flora of the Pacific states. Vol. II. Stanford: Stanford University Press.

ADANSON, M. 1763. Familles des Plantes. Paris: Vincent.

AIRY-SHAW, H. K. 1973. A Dictionary of the Flowering Plants and Ferns. 8th ed. Cambridge: University Press.

BAYER, R. J., AND G. L. STEBBINS. 1981. Chromosome numbers of North American species of *Antennaria* Gaertner (Asteraceae: Inuleae). Amer. J. Bot. 68: 1342–1349.

BENNETT, F., W. H. PARKER AND J. MAZE. 1982. Needle flavonoids and population differentiation in *Abies procera* Rehd. (noble fir) and *A. magnifica* A. Murray (red fir.). 33rd annual AIBS meeting, Penn State Univ., abstract pp. 40.

BERGER, A. 1924. A taxonomic review of currants and gooseberries. New York Agric. Exp. Sta. Techn. Bull. 103: 3–118.

BERLANDIER, J. L. 1826. Mémoire sur la famille de Grossulariées. Mém. Soc. Phys. Genève 3: 43–60.

BRIZICKY, G. K. 1969. Subgeneric and sectional names: their starting points and early sources. Taxon 18: 643–669.

COVILLE, F. V. 1924. *Grossularia echinella*, a spiny-fruited gooseberry from Florida. J. Agric. Res. 28: 71–74.

———. 1935. Origin of the genus name *Ribes*. Science 82: 491–492.

———, AND N. L. BRITTON. 1908. Grossulariaceae. N. Amer. fl. 22: 193–225.

CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. New York: Columbia University Press.

DARLINGTON, C. D. 1929. A comparative study of the chromosome complement in *Ribes*. Genetica 11: 267–272.

DECANDOLLE, A. P. 1828. Prodromus Systematis Naturalis Regni Vegetabilis. Vol. 3. Paris: Treuttel & Wurtz.

DENTON, M. F. 1979. Factors contributing to evolutionary divergence and endemism in *Sedum* section *Gormania* (Crassulaceae). Taxon 28: 149–155.

———, B. GOLDMAN, C. L. HITCHCOCK, A. R. KRUCKEBERG AND M. MUELLER. 1977. A Working List of Rare, Endangered, Threatened and Endemic Vascular Plant Taxa for Washington. Seattle: University of Washington.

DILLENIUS, J. J. 1732. Hortus Elthamensis. London.

DIPPEL, L. 1893. Handbuch der Laubholzkunde. Berlin: Paul Parey.

Dodoens, R. 1578. A Nieuve Herball. London: Gerard Dewes.

Don, G. 1834. A General History of the Dichlamydeous Plants. Vol. 3. London: J. G. & F. Rivington.

Douglas, D. 1914. Journal, 1823–1827. Reprint. 1959. New York: Antiquarian Press.

Endlicher, S. 1839. Genera Plantarum. Wien: Fr. Beck.

Engler, A., and K. Prantl. 1891. Ribesioideae. Naturl. Pflanzenfam. 3 (2a): 97–142.

Farris, J. S. 1970. Methods for computing Wagner trees. Syst. Zool. 19: 83–92.

Fernald, M. L. 1905. Some lithological variations of *Ribes*. Rhodora 7: 153–156.

———. 1911. The varieties of *Ribes hirtellum*. Rhodora 13: 73–76.

———. 1935. Critical plants of the upper Great Lakes region of Ontario and Michigan. Rhodora 37: 238–262.

———. 1950. Gray's Manual of Botany, 8th ed. Boston: American.

Gaertner, J. 1789. De Fructibus et Seminibus Plantarum. Tubingen: G. H. Schramm.

Godfrey, R. K. 1979. *Ribes echinellum*, *In:* D. B. Ward (ed.). Rare and Endangered Biota of Florida, Vol. 5, Plants. Gainesville: University Presses of Florida.

Goldschmidt, E. 1964. Cytologische Untersuchungen an tetraploiden Pflanzen der Gattung *Ribes* L. Hereditas 52: 139–150.

Grant, V. 1971. Plant Speciation. New York: Columbia University Press.

———. 1981. Plant Speciation, 2nd. ed. New York: Columbia University Press.

Gray, A. 1876. Our wild gooseberries. Amer. Naturalist 10: 270–275.

Hamel, J. L. 1955. Matériaux pour l'étude caryo-taxonomique des Saxifragacées. Bull. Mus. Hist. Nat. (Paris) 27: 226–231.

Harlan, J. R., and J. M. J. DeWet. 1975. On O Winge and a prayer: The origins of polyploidy. Bot. Rev. (Lancaster) 41: 361–390.

Harrington, H. D. 1954. Manual of the Plants of Colorado. Chicago: Swallow Press.

Hooker, W. J. 1832. Flora Boreali-americana. Vol. I. London: Treuttel & Wurz.

Janczewski, E. 1903. Essai d'une disposition naturelle de espèces dans le genre *Ribes* L. Bull. Int. Acad. Sci. Cracovie Cl. Sci. Math. 1903: 232–241.

———. 1906a. Species generis *Ribes* L. II. Bull. Int. Acad. Sci. Cracovie Cl. Math. 1906: 1–13.

———. 1906b. Species generis *Ribes* L. III. Bull. Int. Acad. Sci. Cracovie Cl. Math. 1906: 280–293.

———. 1907. Monographie des groseillers, *Ribes* L. Mém. Soc. Phys. Genève 35: 199–517.

Jepson, W. L. 1936. A Flora of California, Vol. 2, pg. 151. California School Book Depository: San Francisco.

———. 1957. A Manual of the Flowering Plants of California. Berkeley: University Press.

Jones, S. B. and A. E. Luchsinger. 1979. Plant Systematics. New York: McGraw Hill.

Jussieu, A. L. 1789 Genera Plantarum. Paris: Herissant.

Keep, E. 1962. Interspecific hybridization in *Ribes*. Genetica 33: 1–23.

LAMARCK, J. B., AND A. P. DECANDOLLE. 1805. Flore Francaise. Paris: Desray.

LINDLEY, J. 1830a. A report upon new and rare plants. Trans. Hort. Soc. London 7: 243 244.

———. 1830b. *Ribes setosum*. Bot. Reg. 15: 1237.

LINNAEUS, C. 1737. Genera Plantarum. Leiden: C. Wishoff.

———. 1738. Hortus Cliffortianus. Amsterdam.

———. 1753. Species Plantarum. Stockholm: L. Salvii.

LÖVE, A., AND D. LÖVE. 1967. Polyploidy and altitude: Mt. Washington. Biol. Zentralblatt. Suppl. Vol: 307 312.

MACBRYDE, B. 1981. Information needed to use the Endangered Species Act for plant conservation, *In:* L. E. Morse and M. S. Hennefin (eds.). Rare Plant Conservation: Geographical data organization for rare plant conservation. New York: New York Botanical Garden.

MARTIN, W. C., AND C. R. HUTCHINS. 1980. A Flora of New Mexico. Vaduz: J. Cramer.

MAYR, E. 1963. Animal Species and Evolution. Cambridge: Harvard University Press.

———. 1976. Evolution and the Diversity of Life. Cambridge: Harvard University Press.

MCMINN, H. E. 1939. An Illustrated Manual of California Shrubs. San Francisco: J. W. Stacey.

MEDIKUS, F. K. 1789. Philosophische Botanik. Manneheim: Neuen.

MEURMAN, O. 1928. Cytological studies in the genus *Ribes* L. Hereditas 11: 289 356.

MICHAUX, A. 1803. Flora boreali-americana. Paris: Levrault.

MILLER, P. 1731. The Gardeners Dictionary. Folio ed. 1. London: C. Rivington.

———. 1754. The Gardeners Dictionary. Abridged ed. 4. London: J. & J. Rivington.

MUNZ, P. A. 1974. A Flora of Southern California. Berkeley: University of California Press.

———, AND D. D. KECK. 1959. A California Flora. Berkeley: University of California Press.

NILSSON, F. 1944. Tetraploida typer inom slaktet *Ribes*. Sveriges Pomol. Foren. Arsskr. 1944: 130-134.

———. 1955. Amphidiploid species in the genus *Ribes*. Report 14th Int. Hort. Cong. 1: 697-711.

NUTTALL, T. 1818. The Genera of North American Plants. Philadelphia: D. Heart.

PARKINSON, J. 1640. Theatrum Botanicum. London: T. Cotes.

PERSOON, C. H. 1805. Synopsis Plantarum. London.

PLUKENET, L. 1705. Amaltheum Botanicum. London.

PORSILD, A. E., AND W. J. CODY. 1980. Vascular Plants of Continental Northwest Territories, Canada. Ottawa: National Museums of Canada.

PURSH, F. 1814. Flora Americana Septentrionalis. London: White Cochrane and Co.

RADFORD, A. E. 1959. A relict plant community in South Carolina. J. Elisha Mitchell Sci. Soc. 75: 33 34.

______, AND H. E. AHLES. 1959. Species new to the flora of South Carolina. J. Elisha Mitchell Sci. Soc. 75: 35 43.

REHDER, A. 1910. Einige neve und kritische geholze. Mitt. Deutsch. Dendrol. Ges. 19: 248 254.

REICHENBACH, H. G. L. 1828. Conspectus Regni Vegetabilis. Leipzig: C. Cnobloch.

______. 1837. Handbuch des Naturlichen Pflanzensystems. Dresden: Arnoldischen.

RICHARD, A. 1823. Botanique medicale. Paris: Bechet Jeune.

ROBERTSON, C. 1929. Flowers and Insects. Lancaster: Science Press.

SAX, K. 1931. Chromosome numbers in the ligneous Saxifragaceae. J. Arnold Arb. 12: 198 206.

SCHOENAGEL, E. 1931. Chromosomenzahl und Phylogenie der Saxifragaceen. Bot. Jahrb. Syst. 64: 266 308.

SCOGGAN, H. J. 1978. Flora of Canada. Ottawa: National Museums of Canada.

SCOPOLI, A. 1772. Flora Carniolica. Wien: Vindobonensis.

SEYMOUR, F. C. 1969. The Flora of New England. Tokyo: C. E. Tuttle.

SIDDAL, J. L., K. L. CHAMBERS AND D. H. WAGNER. 1979. Rare, Threatened and Endangered Vascular Plants in Oregon. Salem: Division of State Lands.

SINNOTT, Q. P. 1981. A simple similarity coefficient for taxonomic comparisons. Taxon 30; 18 26.

______, K. A. SINNOTT AND M. W. STANTON. 1980. An annotated list of the vascular plants of Sky Ranch, Alameda Co., California. Wasmann J. Biol. 37: 1-17.

______, AND J. B. PHIPPS. 1983. Variation patterns in series *Pruinosae* (*Crataegus, Rosaceae*) in southern Ontario. Syst. Bot. 8: 59 70.

SMALL, J. K. 1913. Flora of the Southeastern United States. New York.

______. 1933. Manual of the Southeastern flora. Reprint. 1972. New York: Hafner.

SMILEY, F. J. 1921. A report upon the boreal flora of the Sierra Nevada of California. Univ. Calif. Publ. Bot. 9: 1-417.

SMITH, E. L. 1980. Laws and information needs for listing plants. Rhodora 82: 193-198.

SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical Taxonomy. San Francisco: Freeman.

SPACH, E. 1835. Revisio Grossularierum. Ann. Sci. Nat. Bot. II, 4: 16-31.

______. 1838. Histoire Naturelle des Végétaux. Phanerogames. Vol. 6. Paris: Revet.

SPONGBERG, S. A. 1972. The genera of Saxifragaceae in the southeastern United States. J. Arnold Arbor. 53: 409 498.

STAFLEU, F. A., et al. 1978. International Code of Botanical Nomenclature. Regnum Veg. 97: 1 457.

STEBBINS, G. L. 1938. Cytological characteristics associated with the different growth habits in the dicotyledons. Amer. J. Bot. 25: 189-198.

______. 1947. Types of polyploids: Their classification and significance. Advances Genet. 1: 403 429.

———. 1950. Variation and Evolution in Plants. New York: Columbia University Press.

———, AND J. MAJOR. 1965. Endemism and speciation in the California flora. Ecol. Monogr. 35: 1–35.

STERN, W. L., E. M. SWEITZER AND R. E. PHIPPS. 1970. Comparative anatomy and systematics of woody Saxifragaceae. *Ribes*.J. Linn. Soc., Bot. 63: 215–237.

TAYLOR, R. L., AND R. P. BROCKMAN. 1966. Chromosome numbers of some western Canadian plants. Canad. J. Bot. 44: 1093–1103.

THIERET, J. W. 1963. Botanical survey along the Yellowknife highway, Northwest Territories, Canada I. Catalogue of the flora. Sida 1: 117–170.

TISCHLER, G. 1927. Chromosomenstudien bei *Ribes gordonianum* und seinen Eltern. Planta 4: 617 650.

TORREY, J., AND A. GRAY. 1840. A Flora of North America. Reprint. New York: Hafner.

TOURNEFORT, J. P. 1700. Institutiones rei Herbariae, edito altera. Paris: J. Anison.

U. S. FISH AND WILDLIFE SERVICE. 1980. Endangered and threatened wildlife and plants: Review of plant taxa for listing as endangered or threatened species. Federal Reg. 45: 82479 82569.

VAARAMA, A. 1947. Morphological and cytological studies on colchicine induced tetraploid *Ribes nigrum*. Acta. Agric. Fenn. 67: 55–93.

———. 1948. A triple species hybrid in the genus *Ribes*. Hereditas 34: 369–370.

———. 1949. Spindle abnormalities and variation in chromosome numbers in *Ribes nigrum*. Hereditas 35: 136 162.

VENTENANT, E. P. 1799. Tableau du Règne Végétal. Paris: J. Drisonnier.

WASHINGTON Natural Heritage Program. 1981. An Illustrated Guide to the Endangered, Threatened and Sensitive Vascular Plants of Washington. Olympia: Dept. of Natural Resources.

———. 1982. Endangered, Threatened and Sensitive Vascular plants of Washington. Olympia: Dept. of Natural Resources.

WETZL, C. L. R. 1972. The significance of Niles Canyon in the phytogeography of the Coast Ranges of central California. Madroño 21: 177–264.

WHITTAKER, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30: 279 338.

———. 1961. Vegetation history of the Pacific Coast states and the "central" significance of the Klamath region. Madroño 16: 5–23.

WOOD, C. R. 1971. Some floristic relationships between the southern Appalachians and western North America. *In:* P. C. Holt, (ed.), The Distributional History of the Biota of the Southern Appalachians. Virginia Polytechnic Inst. and State Univ. Res. Div. Monograph 2: 331–404.

ZIELINSKI, Q. B. 1952. Chromosome numbers and meiotic studies in *Ribes*. Bot. Gaz. (Crawfordville) 114: 265 274.

DEPARTMENT OF BOTANY
UNIVERSITY OF MARYLAND
COLLEGE PARK, MD 20742

BOOK REVIEW

E. G. Lergh, Jr., A. S. Rand and D. M. Windsor (Eds). 1983. *The Ecology of a Tropical Rainforest—Seasonal Rhythms and Long-Term Changes.* 468 pp. Smithsonian Institution Press, Washington, D.C. 20560 $25.00.

There are only two words to describe this volume: *outstanding* and *innovative.* The contents (contributions by forty-nine authors) cover several fields—the physical setting, the biotic setting, seasonal rhythm in plants, frugivores, insects of tree crowns and their predators, litter arthropods and their predators, long-term changes.

The only unfortunate aspect of this most valuable book, which should be on the shelf of every biologist interested in the tropics, is its too-strict confinement to Barro Colorado Island in Panama, where many of the authors worked. There is, nonetheless, so much of a generally applicable nature to the humid tropics, especially of the New World, that this volume will long be read by serious students of the biology of the warm hemisphere.

RICHARD EVANS SCHULTES
BOTANICAL MUSEUM
HARVARD UNIVERSTIY
OXFORD ST.
CAMBRIDGE, MA 02138

BOOK REVIEW

MOLLIE BEATTIE, C. THOMPSON, L. LEVINE. *Working with Your Woodland – A Landowner's Guide.* Pp. xxii + 310, tt. 78. University Press of New England, Hanover, N.H. (1984) paper, $12.95; cloth, $27.50.

More than half a millon private landowners control about half of New England's productive forests – some 16,000,000 acres. It is probably safe to assume that a comparable figure could be cited for many other similarly populated areas. This fact, it seems, is not widely recognized, its extraordinary significance to conservation and development notwithstanding.

Undoubtedly few "small owners" are fully aware of the many facets of use to which their land may be constructively put: recreational, conservational and wise commercial exploitation for fire wood and timber. As the authors state: "When the woods are perceived as static, it is difficult to see how they can be guided and regulated... Human use is now so widespread, intense and frequent ...that the only realistic way to think of ourselves is as part of the forest environment. For landowners who intend to use their woods, understanding that relationship and its responsibilities engenders a concept of forest management for the benefit of both present and succeeding generations."

This neatly-published volume is a mine of diverse information, presented in eight chapters, each with its own wealth of coverage: 1) New England Forest History; 2) Assessing Woodland Potential; 3) Foresters; 4) Management Plans; 5) Management Techniques; 6) Harvesting Forest Products; 7) Financial Aspects of Forest Management; 8) Choosing a Future for the Forest. There are four appendixes and a comprehensive index.

The authors, representing a broad spectrum of experience, have obviously closely cooperated in expertly putting together their several contributions into an integrated whole. Beattie is a forester with the Windham Foundation in Vermont; Thompson's connections are with the Forestry Department of the University of Massachusetts and as president of Atlantic Forestry; Levine is a consulting forester to Forest Care, Vermont.

The outstanding importance of this book resides in its focus on the small owner. Much of our publication in forestry and allied fields concerns enormous extents of land owned and managed by huge and powerful industrial, commercial or governmental organizations. Furthermore, there is a wealth of material and coverage in this volume that can be directly applied to many other parts of the United States. Thus its appeal, though primarily oriented toward New England, should be of interest throughout the cooler forested regions of the country.

It is hoped that books of this scope will be harbingers of future publications that will impress upon the private citizen his/her personal role and importance in preservation and wise utilization of the natural wealth of the country.

RICHARD EVANS SCHULTES
BOTANICAL MUSEUM
HARVARD UNIVERSITY
OXFORD ST.
CAMBRIDGE, MA 02138

LITERATURE FOR NEW ENGLAND BOTANISTS

Bertness, Mark D. 1984. Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh. Ecology 65 (6): 1794–1807.

The author shows how this positive association leads to increased marsh net primary production and stability.

Foster, Jeffrey R. and William A. Reiners. 1983. Vegetation patterns in a virgin subalpine forest at Crawford Notch, White Mountains, New Hampshire. Bull. Torrey Bot. Club. 110 (2): 141–153.

Interesting examination of forest vegetation by direct gradient analysis, and a study of disturbance vegetation patches and old-age vegetation patches.

Hemond, H. E., W. A. Neiring, and R. H. Goodwin. 1983. Two decades of vegetation change in the Connecticut Arboretum Natural Area. Bull. Torrey Bot. Club 110 (2): 184–194.

Use of factor analysis in documenting vegetation change in a long-term study area.

Paillet, F. L. 1984. Growth-form and ecology of American Chestnut sprout clones in northeastern Massachusetts. Bull. Torrey Bot. Club 111(3): 316–328.

A study which shows that chestnut sprout trees are still an important percentage of the vegetation in northeastern forests.

Sprugel, Douglas, G. 1984. Density, biomass, productivity, and nutrient-cycling changes during stand development in wave-regenerated balsam-fir forests. Ecol. Monog. 54(2): 165–186.

Extensive quantitative analysis done in the Adirondacks—but a continuation of the work first done in the White Mountains by William Reiners, and therefore of interest to New Englanders.

Tippo, Oswald. 1982. Harry E. Ahles, 1924–1981. Bull. Torrey Bot. Club. 109(1): 84–86.

Biographical sketch, with portrait.

WHITNEY, GORDON G. 1984. The reproductive biology of raspberries and plant pollinator community structure. Amer. J. Bot. 71(7): 887–894.

One of the interesting Hubbard Brook studies which compares *Rubus idaeus* and *Rubus pubescens* with each other, and with associated taxa in their communities.

ZIKA, P. F., R. J. STERN, AND H. E. AHLES. 1983. Contributions to the flora of the Lake Champlain Valley, New York and Vermont. Bull. Torrey Bot. Club 110(3): 366–369.

These reports of range extensions, first-find collection records, and rare species, show that new finds are still to be made in local flora studies.

MARY M. WALKER
LIBRARIAN
NEW ENGLAND WILDFLOWER SOCIETY
FRAMINGHAM, MA 01701

NOTICE OF PUBLICATION

Biology 83: Current Titles in the Biological Sciences. Edwards, Stephen, managing editor. Association of Systematics Collections and Allen Press, Lawrence, KS, 1983–84. Vols. 1–4, 839 pp. (Write for current price: P.O. Box 368, Lawrence, KS 66044.)

A new quarterly periodical designed to help biologists keep abreast of current literature. Only titles published in 1983 are included. *Biology 84* will include only papers published in 1984, etc. Articles are listed first in a subject index, then a taxonomic index, finally in an author/title index.

Vol 87, No. 849, including pages 1–119, was issued January 31, 1985

INSTRUCTIONS TO CONTRIBUTORS TO RHODORA

Submission of a manuscript implies it is not being considered for publication simultaneously elsewhere, either in whole or in part.

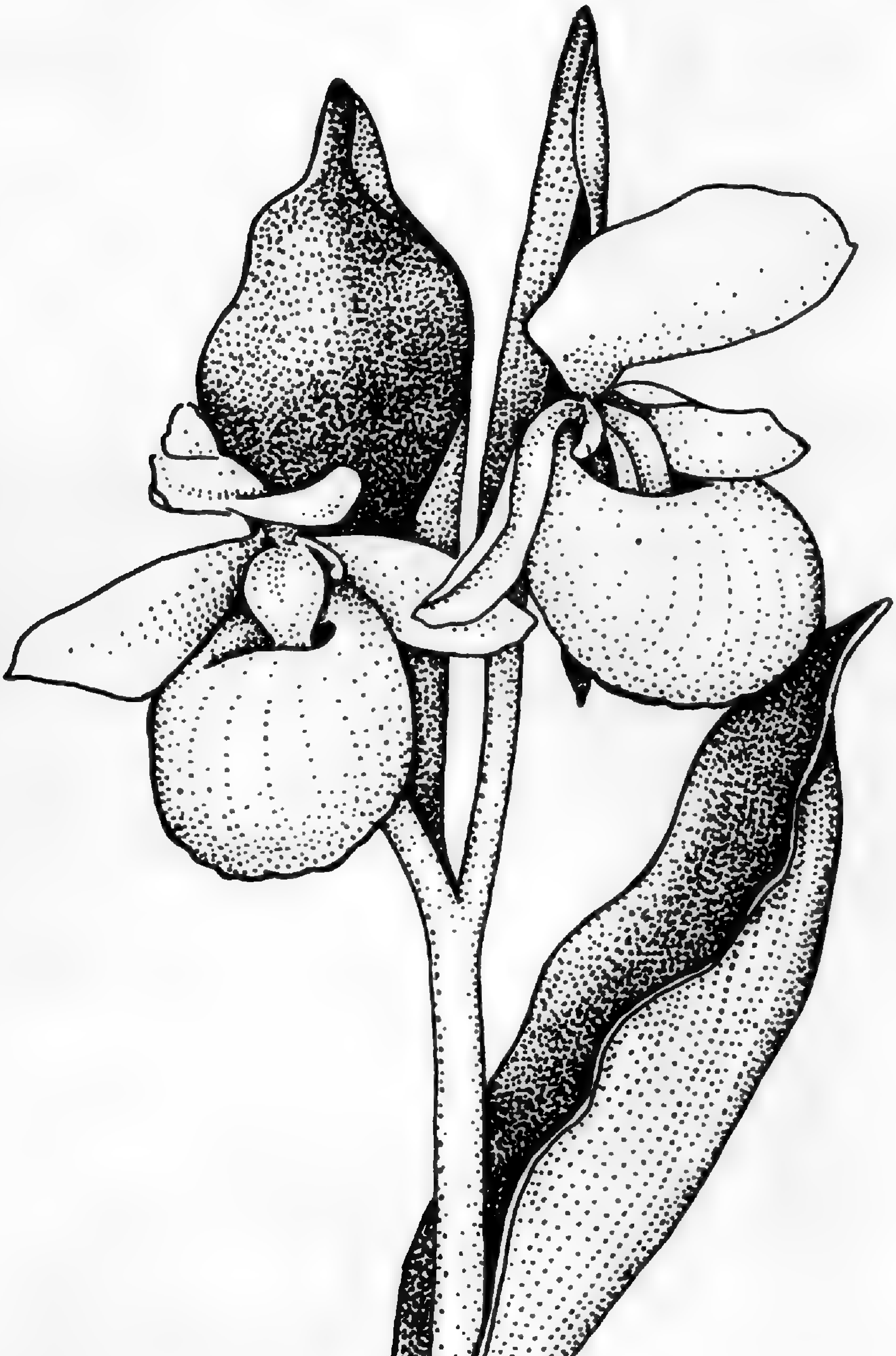
Manuscripts should be submitted in **triplicate** (an original and two xerographic copies) and *must be double-spaced* (at least 3/8 inch) **throughout** including footnotes, figure legends, and references. Please do not use corrasable bond. The list of legends for figures and maps should be provided on a separate page. Footnotes should be used sparingly. Do not indicate the style of type through the use of capitals or underscoring, particularly in the citation of specimens. Names of genera and species may be underlined to indicate italics in discussions. Specimen citations should be selected critically, especially for common species of broad distribution. Systematic revisions and similar papers should be prepared in the format of "A Monograph of the Genus Malvastrum", S. R. Hill, Rhodora 84: 1–83, 159–264, 317–409, 1982, particularly with reference to indentation of keys and synonyms. Designation of a new taxon should carry a **Latin diagnosis** (rather than a full Latin description), which sets forth succinctly just how the new taxon is distinguished from its congeners. Papers of a floristic nature should follow, as far as possible, the format of "Annotated list of the ferns and fern allies of Arkansas", W. Carl Taylor and Delzie Demaree, Rhodora 81: 503–548, 1979. For bibliographic citations, refer to the Botanico-Periodicum-Huntianum (B-P-H, 1968), which provides standardized abbreviations for journals originating before 1966. All abbreviations in the text should be followed by a period, except those for standard units of measure and direction (compass points). For standard abbreviations and for guidance in other matters of biological writing style, consult the *CBE Style Manual,* 5th ed. (original title: *Style Manual for Biological Journals*). In preparing figures (maps, charts, drawings, photos, etc.) please remember that the printed plate will be 4 × 6 inches; be sure that your illustrations are proportioned to reduce correctly, and indicate by blue pencil the intended limits of the figures. (Some "turn-page" figures with brief legends will be 3 1/2 × 6 in.) Magnification/reduction values given in text or figure legends should be calculated to reflect the actual printed size. An Abstract and a list of Key Words should be supplied at the beginning of each paper submitted, except for a very short article or note.

RHODORA **April, 1985** **Vol. 87, No. 850**

CONTENTS

Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB



Vol. 87 July 1985 No. 851

The New England Botanical Club, Inc.

Botanical Museum, Oxford Street, Cambridge, Massachusetts 02138

Conducted and published for the Club, by
NORTON H. NICKERSON, Editor-in-Chief

RHODORA.—Published four times a year, in January, April, July, and October. A quarterly journal of botany, devoted primarily to the flora of North America. Price $20.00 per year, net, postpaid, in funds payable at par in the United States currency at Boston. Some back volumes and single copies are available. Information and prices will be furnished upon request. Subscriptions and orders for back issues (making all remittances payable to RHODORA) should be sent to RHODORA, Botanical Museum, Oxford Street, Cambridge, Mass. 02138. In order to receive the next number of RHODORA, changes of address must be received prior to the first day of January, April, July or October.

Scientific papers and notes relating to the plants of North America and floristically related aras will be considered by the editorial committee for publication. Articles concerned with systematic botany and cytotaxonomy in their broader implications are equally acceptable. Brevity is urged whenever possible in all papers. Short items will be published on otherwise blank end pages as soon as possible, even if they appear ahead of longer articles already accepted. All manuscripts should be submitted in TRIPLICATE AND MUST BE DOUBLE (AT LEAST 3/8 OF AN INCH) OR TRIPLE-SPACED THROUGHOUT. **Please conform to the style of recent issues of the journal. See "Instructions to Contributors to RHODORA" at the end of each issue. Extracted reprints, if ordered in advance, will be furnished at cost. RHODORA assesses modest page charges.**

Address manuscripts and proofs to:
Joan Y. Nickerson
Managing Editor, RHODORA
Phippen-LaCroix Herbarium, Dept. of Biology
Tufts University
Medford, Mass. 02155

Second Class Postage Paid at Boston, Mass.

PRINTED BY
THE LEXINGTON PRESS, INC.
LEXINGTON, MASSACHUSETTS

Cover illustration

Cypripedium reginae Walt., the Showy Lady's-slipper, was presumed until recently to be extirpated from New Hampshire; five sites for this exquisite orchid are now known.

Original artwork by Tess Feltes, Illustrator.

Rhodora
(ISSN 0035 4902)
JOURNAL OF THE
NEW ENGLAND BOTANICAL CLUB

Vol. 87 July 1985 No. 851

RARE PLANTS ON ULTRAMAFIC SOILS IN VERMONT

PETER F. ZIKA AND KEVIN T. DANN

ABSTRACT

Nineteen dunite and serpentine (ultramafic) areas in Vermont were explored for rare vascular plants. Twenty-one new stations or re-locations for *Adiantum pedatum* var. *aleuticum*, *Arenaria macrophylla*, *Kalmia latifolia*, *Lycopodium selago*, and *Thelypteris simulata* are reported and the distribution of ultramafic areas in Vermont is mapped. Characteristic vegetation on dunite outcrops below 2000 feet elevation is described. Threatened or endangered classification of the rare species is discussed. *Lycopodium selago* is proposed as a threatened species in Vermont.

Key Words: Dunite, rare or endangered species, serpentine, ultramafic areas, Vermont.

INTRODUCTION

Soils derived from weathering of ultramafic rocks are usually referred to as "serpentine soils" by biologists, and like their parent rocks, these soils are extremely rich in magnesium and very poor in calcium, potassium, sodium, and aluminum. Serpentine soils are often rich in iron and contain unusually high amounts of the heavy metals nickel and chromium. Wherever they occur, serpentine soils are known for their extreme infertility and the peculiar nature of the vegetation they support. The two major characteristics of serpentine vegetation are: 1) physiognomic differences from vegetation of surrounding non-serpentine soils, and 2) high numbers of rare and endemic species as well as species of disjunct distribution. See Proctor and Woodell (1975), Whittaker (1954) and Kruckeberg (1954, 1969) for reviews investigating these effects.

In eastern North America, serpentine and related ultramafic rocks are confined to a distinct belt along the flank of the Appalachian Mountains. This belt, which averages 10 miles in width, extends for 1600 miles from Alabama to Newfoundland. The ultramafic rocks occur as imbricated bodies within highly metamorphosed sedimentary rocks of Paleozoic age. In Vermont, ultramafic rocks are confined to a narrow belt that extends northward through the central part of the state (Figure 1). Schists, phyllites, quartzites, slates, and marbles of Cambrian and Ordovician age make up this belt (Jahns, 1967). Most frequently the ultramafics intrude schists of the Hazen's Notch and Ottauquechee formations, although they also appear in the Giles Mountain formation further east (Billings and White, 1950).

The major concentration of ultramafic rock in Vermont is the Upper Missisquoi Valley in western Orleans County. This area is considered to be the southern end of the Quebec Serpentine Belt (Williams, 1978), and includes the region around Belvidere Mountain in Eden where chrysotile asbestos has been mined from the ultramafic rock for nearly a century. The ultramafic rocks of the region include dunite, peridotite, and serpentinite; dunite and peridotite are most abundant in the central parts of the plutons. The serpentinite occurs near the borders or makes up the whole of some of the smaller plutons. In most of the area, dunite and peridotite, which are more resistant to weathering and erosion than serpentinite, form hills, whereas serpentinite outcrops occur along lower slopes or underlay surficial material that fills valley bottoms (Cady et al., 1963).

There are two other large ultramafic deposits in Vermont. Near Proctorsville, a dunite deposit about two miles long and about a mile wide is bisected by the Black River. Further south is the East Dover ultramafic area, which is 4.5 miles long and slightly less than a mile wide. This body is also mostly dunite and is well exposed, being cut diagonally by the Rock River and three of its tributaries (Skehan, 1961). The rest of the ultramafic deposits in the state are considerably smaller and consist principally of serpentinite, which is white- or green-weathering, as opposed to the reddish-brown-weathering dunite. Exposed dunite seems to provide the best botanizing.

The distribution of plants on serpentine has largely been ignored by Vermont botanists, with the exception of several rare species. *Arenaria macrophylla* Hook. was added to the flora of New Eng-

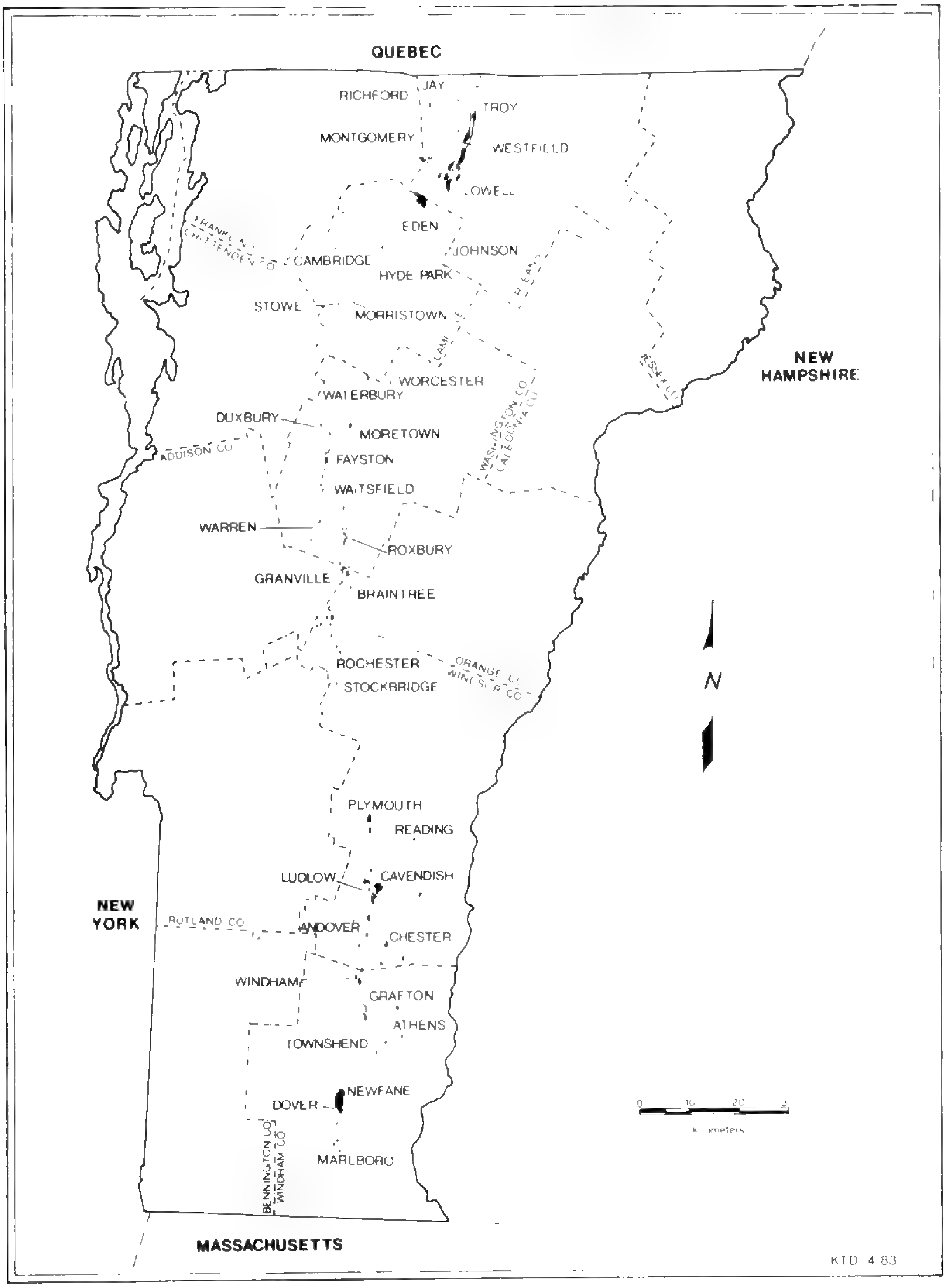


Figure 1. Ultramafic rock deposits in Vermont.

land when W. W. Eggleston discovered it in Proctorsville (Cavendish) in 1899 (Brainerd et al., 1900; Bartlett, 1905). But Eggleston and other botanists at the turn of the century failed to recognize the ultramafic substrate to which the plant was restricted, and their collection labels state the specimens came from "limestone ledges." Only when Douglass Ladd systematically began to search serpentine quarries in Washington Co. in the 1970's was the species relocated in Vermont. *Adiantum pedatum* L. var. *aleuticum* Rupr. was first discovered in New England on Mt. Belvidere's asbestos cliffs in Eden (Jolley, 1922; Flynn, 1922; Rugg, 1922). *Arenaria marcescens* Fern. was relatively recently established as a member of the United States flora. It was found on serpentine at high altitude, growing with a number of alpine species on Haystack Mountain in Lowell (Cook, 1959).

The prospect of locating new stations for disjunct or rare serpentine species prompted us to visit most of the larger ultramafic sites. At each site a careful search was made for rare taxa known to occur in other ultramafic areas of the northeast. These plants are listed in Table 1. Nomenclature follows Fernald (1970) and Tryon (1978).

Large ultramafic outcrops in Cavendish, Dover, Eden, and Lowell, and smaller deposits in Cambridge, Duxbury, Fayston, Moretown, Newfane, Plymouth, Reading, Roxbury, Troy, Waitsfield, Warren, Waterbury, and Westfield were explored.

The Vermont bedrock geological map (Doll et al., 1961) supplied sufficient detail, when combined with USGS topographical maps, to locate the larger sites. Small outcrops are numerous in Vermont, and these are more difficult to find. To pinpoint the deposits in the upper Missisquoi Valley, we used a geologic map at a scale of 1 : 62,500 (Cady et al., 1963). Much of the area mapped as ultramafic rock is covered by surficial material, which minimizes any effects on overlying vegetation, so natural and artificial edges were sought. Searches were primarily along roadcuts, streamcuts, ledges, quarries, and talus slopes. Maps at a scale of 1 : 62,500 or larger exist for most of the deposits in Vermont, and the authors can supply a list of those references to interested botanists. More than half of the mapped ultramafic rock in Vermont has not been botanized.

ULTRAMAFIC PLANT COMMUNITIES IN VERMONT

At sites where surficial deposits appeared to cover all the ultramafic bedrock, no rare species were found; the plant communities

Table 1. Rare Vermont plants known to occur on or near ultramafic deposits in the northeast.

Taxon	State or Province				
	CT	MA	ME	PQ	VT
Adiantum pedatum aleuticum (1)			+	+	+
Agrostis borealis					+
Arenaria macrophylla	+	+	+	+	+
Arenaria marcescens				+	+
Asplenium viride (2)			+		
Betula borealis (3)				+	
Carex scirpoidea (4)				+	
Dryopteris fragrans (4)				+	
Empetrum nigrum					+
Kalmia latifolia					+
Lycopodium selago (5)					+
Najas gracillima					?
Scirpus caespitosus					+
Thelypteris simulata					?
Vaccinium uliginosum					+
Vaccinium vitis-idaea (1)			+		

(1) A station reported by Carter (1979, unpubl. M. S. thesis, U. New Hampshire, Durham). Visited by the writers in September 1983: FRANKLIN CO., MAINE, **Seven Ponds:** Whitecap Mtn., ENE exposure, elev. 3100 3250 feet, 150 *Adiantum* seen with 100 *Vaccinium vitis-idaea.*

(2) A station reported by Carter (*op. cit.*).

(3) *See* Fernald (1970). There is no known extant New England station for *Betula borealis.*

(4) Reported from Quebec (Hamel, 1970, unpubl. Ph. D. thesis, U. Sherbrooke, Quebec).

(5) Reported from serpentine deposits on Mt. Belvidere in Eden, Vt. (D. S. Barrington, pers. comm.).

were indistinguishable from those on the surrounding bedrock types.

At many of the disturbed sites it was obvious there was no edaphic ultramafic plant community. This finding was especially true at quarries, tailings, and roadcuts. Plants of these sites were edge species and typical colonizers of disturbed xeric soil, responding to the available sunlight and lack of competition. Many of the dominants were European weeds. Sometimes *Adiantum pedatum* var. *aleuticum* or *Arenaria macrophylla* was found in association with weeds.

The ultramafic outcrop on the northwest face of the summit of Haystack Mountain at 3200 feet supports one species restricted to serpentine, *Arenaria marcescens,* and a number of alpine ledge species (Cook, 1959). *Agrostis borealis* Hartm., *Arenaria marcescens, Empetrum nigrum* L., *Lycopodium selago* L., *Scirpus cespitosus* L., and *Vaccinium uliginosum* L. are found together in Vermont only on Haystack Mt. The assemblange of plants there seems to be controlled strongly by climatic-geographic as well as edaphic factors, and it is unclear whether this group of species is strictly an edaphic ultramafic community. *Empetrum nigrum* and *Vaccinium uliginosum* are not found on ultramafics elsewhere in New England (Table 1), but they are recorded from serpentine in Newfoundland (Bouchard et al., 1978).

A well-developed edaphic ultramafic plant community exists at a number of sites with dunite outcrops below 2000 feet elevation in the Upper Missisquoi Valley and in Windsor County. This community is characterized by sparse tree cover and scattered herbaceous cover over dunite cliffs, talus, and gentle rocky slopes. These communities consistently had one or both of *Arenaria macrophylla* and *Adiantum pedatum* var. *aleuticum* as well as distinct native associates.

Trees were infrequent at these sites; included were *Acer rubrum* L., *Betula papyrifera* Marsh., *Picea rubens* Sarg., and *Pinus strobus* L. The most commonly seen shrubs were *Juniperus communis* L., *Spiraea latifolia* (Ait.) Borkh., *Vaccinium myrtilloides* Mich., and *Viburnum cassinoides* L.

The herbaceous associates were more numerous, though still sparse, and included most commonly (in decreasing abundance): *Pteridium aquilinum* (L.) Kuhn, *Polypodium virginianum* L., *Saxifraga virginiensis* Mich., *Deschampsia caespitosa* (L.) Beauv., *Deschampsia flexuosa* (L.) Trin., *Cerastium arvense* L., *Asplenium trichomanes* L., *Campanula rotundifolia* L., *Arenaria stricta* Mich., and *Achillea millefolium* L. At the top of a few of the dunite escarpments, *Epigaea repens* L., *Gaultheria procumbens* L., *Kalmia angustifolia* L., *Ledum groenlandicum* Oeder, and *Trientalis borealis* Raf. were conspicuous. *Pteridium aquilinum, Vaccinium myrtilloides,* and *Viburnum cassinoides* were more numerous than on the ledges below. Often there were talus slopes of large (2–6 feet wide) dunite boulders at the base of the ledges, and there only *Betula papyrifera, Juniperus communis, Pinus strobus,* and *Pteridium aquilinum* found a footing. *Adiantum pedatum* var. *aleuticum* also occurs on the talus slopes in the Upper Missisquoi Valley, but not in Windsor Co.

Although most of the community members are ubiquitous on rocky New England terrain, a number of them are characteristic plants on ultramafic rock throughout their ranges. This observation is particularly true of *Asplenium trichomanes, Campanula rotundifolia, Cerastium arvense, Deschampsia caespitosa,* and *D. flexuosa,* which are all conspicuous on serpentine and dunite from Quebec to Pennsylvania.

CONTEMPORARY STATIONS FOR RARE SPECIES

We found that 16 species of special interest in Vermont could occur in ultramafic areas (Table 1). Each of these species is rare in Vermont, in the sense that it is known from fewer than ten contemporary stations, or was included in the list of rare and endangered Vermont plants (Countryman, 1978). Contemporary stations (documented in the last five years) are marked with an *asterisk* after the collector's number in the following discussion. Population data are approximate.

Agrostis borealis, Arenaria marcescens, Empetrum nigrum, Scirpus caespitosus, and *Vaccinium uliginosum* are each known from only one ultramafic locality in Vermont (Cook, 1959); healthy populations were seen in 1982.

Kalmia latifolia L is reported here for the first time from ultramafic soils in Vermont.
WINDHAM CO., **Dover:** East Dover, elev. 1350 feet, 1000 stems, *Zika 6042** (VT).

Thelypteris simulata (Davenp.) Nieuwl. is probably found near ultramafics only coincidentally. We observed a single station.
WINDSOR CO., **Cavendish:** balsam fir swamp at the base of ultramafic bluff, elev. 1400 feet, 1 clump, *Jenkins & Zika 5994** (VT).

Najas gracillima (A. Br.) Magnus association with ultramafics is problematical Ladd (1979, unpubl. M. S. thesis, S. Ill. U., Carbondale) reported it from a series of beaver ponds at the base of serpentine outcrops in Roxbury. We have seen no specimens and were unable to re-locate the species in 1982 or 1983.

Adiantum pedatum L. var. *aleuticum* Rupr. The taxonomy of this striking form of maidenhair fern is still unsettled (Gawler, 1983). Cody (1983) has renamed all the eastern serpentine plants *A. pedatum* ssp. *calderi* Cody. Plants we saw on serpentine match Cody's new taxon, and are distinguished from the typical variety by their upright leaf posture, uncurved petiole branches and by growing in direct sunlight on dry serpentine. However, those distinctions blur on certain individual plants growing in partial shade, and one plant can display fronds of both var. *aleuticum* and var. *pedatum*. Tryon (1939) saw intermediate plants like these in Wisconsin.

FRANKLIN CO., **Berkshire:** cultivated, Mrs. Jolley's garden, *Ross s.n.* (VT). LAMOILLE CO., **Eden:** asbestos quarry, Mt. Belvidere, *Jolley s.n.* (NEBC); Mt. Belvidere, *Chisolm s.n.* (VT); Mt. Belvidere, *Rugg s.n.* (NEBC, NY); Mt. Belvidere quarry, elev. 2500 feet, 1100 plants, *Jenkins & Zika 6083* & 6087** (VT). ORLEANS CO., **Lowell:** dunite roadcut, Route 58, elev. 900 feet, 25 plants, *Dann & Zika 6156** (VT); dunite ledges N of Route 58, elev. 950 feet, 50 plants, *Dann & Zika 6159** (VT); Brown's Ledges, E- and W-facing dunite outcrops, elev. 1450 feet, 250 plants, *Dann & Zika 6168* & 6169** (VT); dunite roadcut, Route 100, elev. 840 feet, 200 plants, *Dann 8344** (VT). **Westfield:** dunite knob near Mineral Spring Brook, elev. 800 feet, 100 plants, *Dann 8323** (VT).

Jolley (1922) reported an abundance of the serpentine maidenhair fern at the original station near the then active quarry on the south slopes of Mt. Belvidere. The quarry has long since been abandoned; among the rubble and cliffs of the mangled mountainside, *Adiantum* is still common. Mining of asbestos now takes place lower and further east on Mt. Belvidere, and will undoubtedly create more habitat for this peculiar fern.

Arenaria macrophylla Hook. Historical stations documented in herbaria or reported in the literature from five counties including six different townships were visited; in all but one case the populations were easily re-located by merely driving to the ultramafic outcrops.

The singular exception is on Bird's Eye Mountain in Castleton, Rutland Co., as reported by Eggleston (1916). No ultramafic outcrops are mapped in this area and we were unable to re-locate the *Arenaria*.

We re-located previously unvouchered stations for *Arenaria macrophylla* in East Dover (Eggleston, 1916) and Newfane (Ballard, 1905) by using bedrock maps and literature descriptions of the sites. L. A. Wheeler found a station for *A. macrophylla* along the West River (Eggleston, 1916); presumably his colony was on a bank of the river or one of its tributaries. The only ultramafic exposure in the West River drainage is on the Rock River in East Dover. We have not visited the dunite outcrops there to try to find his population.

All the situations where we observed *Arenaria macrophylla* were lightly shaded or exposed to full sun on serpentine or dunite ledges, cliffs, or talus. Only rarely were plants seen under the full shade of a forest canopy, and these specimens were much less vigorous than open-grown plants. It was not surprising to see such a shade-intolerant species reproducing mainly by runners in deep shade and flowering more frequently in the open.

LAMOILLE CO., **Eden:** Mt. Belvidere, *Pease 31598* (NEBC); quarry road, Mt. Belvidere, elev. 2000 feet, 30 plants, *Jenkins & Zika 6078** (VT); asbestos quarry, Mt. Belvidere, elev. 2500 feet, 500 plants, *Jenkins & Zika 6086** (VT). ORLEANS CO., **Lowell:** dunite streamcut, elev. 870 feet, 75 plants, *Zika 6157** (VT); Brown's Ledges, W-facing dunite, elev. 1450 feet, 300 plants, *Dann & Zika 6170** (VT); dunite ledges and talus, E of Route 100, elev. 800 feet, 4500 plants, *Dann 8341** (VT). **Troy:** E -facing dunite bluffs, one mile S of village, elev. 800 to 900 feet, 50 plants, *Dann 8301** (VT). **Westfield:** dunite knob near Mineral Spring Brook, elev. 800 feet, 400 plants, *Dann 8320** (VT). RUTLAND CO., **Castleton:** Bird's Eye Mountain, *Carpenter s.n.* (VT). WASHINGTON CO., **Roxbury:** E of verde antique quarry, *Ladd 2320* (MOR); verde antique quarry, elev. 1100 feet, 25 plants, *Zika 7203** (VT). WINDHAM CO., **Dover:** wooded dunite knoll, between Bemis Brook and East Dover, elev. 1350 feet, 250 stems, *Zika 6043** (VT). **Newfane:** Roadcut between Brookside and East Dover, elev. 1200 feet, 750 stems, *Zika 6039** (VT). **Cavendish:** *Eggleston s.n., 1072, 1937, 2542* (NEBC, NY, VT); Proctorsville, *Rugg s.n.* (VT); Proctorsville, *Carpenter s.n.* (NEBC); Proctorsville, *Kittredge s.n.* (NY); dunite roadcut, Route 103, elev. 950 feet, 50 plants, *Jenkins & Zika 5991** (VT); dunite cliff, N of Proctorsville, elev. 1350 feet, 2500 plants, *Jenkins & Zika 5993** (VT); S-facing dunite knob NW of Proctorsville, elev. 1000 to 1400 feet, 10,000 to 15,000 plants, *Dann 8331** (VT).

RARE, THREATENED OR ENDANGERED CLASSIFICATION

Past efforts have classified the conservation needs of a number of the rare ultramafic species in Vermont in a general way. Countryman (1978) listed all of the ultramafic species in Table 1 (except *Betula borealis, Carex scirpoidea,* and *Scirpus caespitosus*) as *rare, threatened,* or *endangered* in Vermont, but did not attempt to assign the plants to one or another of those categories because of a lack of recent population data. *Adiantum pedatum* var. *aleuticum, Arenaria macrophylla, A. marcescens,* and *Thelypteris simulata* are rare in Quebec (Bouchard et al., 1983). Crow et al. (1981) gave four species as rare across the New England region: *Agrostis borealis, Carex scirpoidea, Dryopteris fragrans,* and *Lycopodium selago.* They further indicated four ultramafic species as threatened or endangered in the six-state area: *Adiantum pedatum* var. *aleuticum, Arenaria macrophylla, A. marcescens,* and *Asplenium viride.* More recently Crow (1982) noted *Asplenium viride* was nationally significant, and *Arenaria marcescens* was under consideration by the Fish & Wildlife Service for federal listing as a threatened or endangered species.

Recent field work and population data in Vermont suggest several changes in the classification of ultramafic species as rare, threatened or endangered. None of the plants in Table 1 qualify as endangered species on a federal or state level, based on existing definitions (Federal Endangered Species Act of 1973; 10 V.S.A., Chapter 123). None of the species discussed here should be considered threatened on a national level. Only one ultramafic species is visibly threatened in Vermont, *Lycopodium selago.* It qualifies as a state threatened species under current legislation because most of the population is concentrated in two small alpine (non-ultramafic) zones, where heavy hiker traffic has the potential to damage the colonies. We recommend *L. selago* be considered a threatened species in Vermont. *Adiantum pedatum* var. *aleuticum, Agrostis borealis, Arenaria marcescens, Asplenium viride, Carex scirpoidea, Dryopteris fragrans, Empetrum nigrum, Scirpus caespitosus, Thelypteris simulata, Vaccinium uliginosum,* and *V. vitis-idaea* should all be classified as rare but not threatened in Vermont; each is known from fewer than ten extant stations in the state. *Arenaria macrophylla* and *Kalmia latifolia* are now known from more than ten extant sites in Vermont and should no longer be considered rare. *Betula borealis* and *Najas gracillima* are not known to be extant in Vermont at this time and are not classified as rare, threatened, or endangered.

LITERATURE CITED

BALLARD, S. J. 1905. A second Vermont station for *Arenaria macrophylla.* Rhodora 7: 156.

BARTLETT, G. H. 1905. *Arenaria macrophylla* in Connecticut. Rhodora 7: 20.

BILLINGS, M. P., & W. S. WHITE. 1950. Metamorphosed mafic dikes of the Woodsville quadrangle, Vt. and NH. Am. Mineralogist 35(9 10): 629 643.

BOUCHARD, A., S. HAY, & E. ROULEAU. 1978. The vascular flora of St. Barbe South District, Newfoundland: an interpretation based on biophysiographic areas. Rhodora 80: 228 308.

———, D. Barabé, M. Dumais, & S. Hay. 1983. The Rare Vascular Plants of Quebec. Syllogeus No. 48. National Museum of Canada, Ottawa.

Brainerd, E., L. R. Jones, & W. W. Eggleston. 1900. Flora of Vermont. Free Press Association, Burlington, Vt.

Cady, W. M., A. L. Albee, & A. H. Chidester. 1963. Bedrock geology and asbestos deposits of the upper Missisquoi Valley and vicinity, Vermont. U.S.G.S. Bull. 1122-B: B1-B78.

Cody, W. J. 1983. *Adiantum pedatum* ssp. *calderi*, a new subspecies in northeastern North America. Rhodora 85: 93 96.

Cook, P. W. 1959. Discovery of *Arenaria marcescens* in the United States. Rhodora 61: 123 124.

Countryman, W. D. 1978. Rare and Endangered Vascular Plant Species in Vermont. New England Botanical Club in cooperation with the U.S. Fish and Wildlife Service, Newton Corner, Mass.

Crow, G. E. 1982. New England's Rare, Threatened, and Endangered Plants. U.S. Fish and Wildlife Service in cooperation with New Hampshire Agricultural Experiment Station, Univ. of New Hampshire, Durham.

———, W. D. Countryman, G. L. Church, L. M. Eastman, C. B. Hellquist, L. J. Mehrhoff, & I. M. Storks. 1981. Rare and endangered vascular plants in New England. Rhodora 83: 259 299.

Doll, C. G., W. M. Cody, J. B. Thompson, Jr., & M. P. Billings. 1961. Centennial geologic map of Vermont. Vermont Geologic Survey, Montpelier.

Eggleston, W. W. 1916. Additions and corrections to the new Vermont flora. Joint Bulletin of the Vermont Botanical and Bird Clubs 11: 19 28.

Fernald, M. L., with corrections supplied by R. C. Rollins. 1970. Gray's Manual of Botany. 8th edition. D. Van Nostrand Co., New York.

Flynn, N. F. 1922. Summer meeting of 1922. Joint Bulletin of the Vermont Botanical and Bird Clubs 8: 11 12.

Gawler, S. C. 1983. Note on *Adiantum pedatum* L. ssp. *calderi* Cody. Rhodora 85: 389 390.

Jahns, R. 1967. Serpentinites of the Roxbury district. *In:* P. J. Wyllie, Ed., Ultramafic and Related Rocks. Interscience Publishing, New York. pp. 137 160.

Jolley, L. F. 1922. A variety of maidenhair fern new to Vermont. Joint Bulletin of the Vermont Botanical and Bird Clubs 8: 40 41.

Kruckeberg, S. R. 1954. Plant species in relation to serpentine soils. Ecology 35: 267 274.

———. 1969. Plant life on serpentine and other ferromagnesian rocks in western North America. Syesis 2: 15-114.

Proctor, J., & S. R. J. Woodell. 1975. The ecology of serpentine soils. *In:* S. MacFadyen, Ed., Advances in Ecological Research. Vol. 9. Academic Press, San Francisco.

Rugg, H. G. 1922. *Adiantum pedatum* var. *aleuticum* in New England. American Fern Journal 12: 128 130.

Skehan, J. W. 1961. The Green Mountain Anticlinorium in the Vicinity of Wilmington and Woodford Vermont. Vt. Geol. Surv. Bull. 17. Vermont Development Dept., Montpelier.

Tryon, A. F. 1978. The New England ferns (Filicales). Rhodora 80: 558 569.

Tryon, R. M. 1939. Notes on the ferns of Wisconsin. American Fern Journal 29: 1–9.

Whittaker, R. H. 1954. The ecology of serpentine soils. Ecology 35: 258–259.

Williams, H. 1978. Tectonic lithofacies map of the Appalachian orogen. Map #1. Memorial Univ. of Newfoundland, St. Johns.

P. F. Z.
PRINGLE HERBARIUM
BOTANY DEPT.
UNIV. OF VERMONT
BURLINGTON, VT 05405

K. T. D.
GEOGRAPHY DEPT.
UNIV. OF VERMONT
BURLINGTON, VT 05405

SEX RATIO AND SEXUAL CONSTANCY IN SPICEBUSH (*LINDERA BENZOIN*)

RICHARD B. PRIMACK

ABSTRACT

Spicebush in two Massachusetts populations is a species in which a basic dimorphism exists with equal numbers of male plants and female plants that are sexually constant and vegetatively similar. A low percentage of individuals have both male and female flowers.

Key Words: Spicebush, *Lindera*, breeding systems, dioecy, shrub, Massachusetts

Several recent studies on plants of the western United States (Freeman et al., 1976; 1981) and common plants of eastern North America such as *Arisaema triphyllum* (Lovett-Doust & Cavers, 1982) and *Acer pensylvanicum* (Hibbs & Fischer, 1979) have shown that plants may be highly variable in their sex expression. In these studies, individual tagged plants have been found to change from having entirely male (staminate) flowers in one season to entirely female (pistillate) flowers in subsequent years (Freeman et al., 1981). Plants have been documented to change sex or vary their proportions of male and female flowers as they age or grow larger (Policansky, 1982). Sexual expression in plants might therefore become modified in order to achieve some advantage in terms of immediate or long-term fitness. However, many field biologists believe that plants of most dioecious species do not readily change sex (Lloyd & Bawa, 1984). The actual number of dioecious species that change sex is unknown because investigators have not followed tagged plants over several field seasons.

A long-term study was begun in 1980 of two populations of the spicebush, *Lindera benzoin* (L.) Blume, a common dioecious shrub of eastern North America. The purpose of the study was to determine if tagged plants change sex in successive years. This member of the Lauraceae is found along streams and in damp woods. The typical growth form is a clump of shoots coming from a central rootstock. While it is possible that stems may fall over and root to form new rootstocks, there was no evidence of this activity occurring at these two field sites.

The two populations of this study occurred in the Newton-Webster Conservation Area in Newton, Massachusetts. Population

I occurred along a small, rocky stream that runs through a narrow valley. Population II occurred on a flat, damp woodland along an old irrigation channel. The dominant trees at both sites were red maple, black birch and white ash. The dominant herbs at these sites were touch-me-not (*Impatiens capensis*) and skunk cabbage (*Symplocarpus foetidus*), with poison ivy (*Toxicodendron radicans*) also common.

Spicebush produced fascicles of small yellow flowers around April 20 at both locations. Male flowers bore bright, yellow, exerted stamens and are more conspicuous than the smaller female flowers in which the stigma and style are more off-white. The flowers are visited by small bees, flies and beetles. Pollinators apparently did not limit fruit set in Population I and fruit set was approximately 10% (McCall and Primack, unpublished). The fruit, a red drupe, matured in September.

In April 1980, 66 plants in each population were permanently tagged. These plants represented all of the individuals within an area of approximately 100 m^2. Each individual was examined for the sex of the flowers and measured for height, number of stems and diameter of the largest stem. In April of 1982, 1983 and 1984, the sex of each plant was checked again. More than 75% of the original plants in each population could still be found in the 1984 census. The remaining 25% of the plants had either died or the tags had fallen off.

In 1980 there was no evidence of an unequal sex ratio. In Population I, 33 plants were male and 33 plants were female. In Population II, 32 plants were male and 34 plants were female. There was no obvious pattern of aggregation of either male or female plants.

At Population I, no plant changed sex in 1982, 1983 or 1984. At Population II, 64 of the 66 plants did not change sex. Two plants (#38 and #48) were recorded as having only male flowers in 1980 and 1982. However, in 1983, Plant #38 produced 50% female flowers. In 1984, the plant produced 30% female flowers. The three stems of the plant had mixtures of male and female flowers. In 1983 and 1984, Plant #48 produced about 10% female flowers.

Two-way analysis of variance was used to compare differences between male and female plants in vegetative characters for the two populations. There were no significant differences between male and female plants in plant height, diameter of the largest stem or the number of stems (Table 1).

Table 1. Vegetative characteristics (mean and standard deviation) of male and female plants of spicebush at two populations.

	Number of Plants	Height (m)	Number of Stems	Diameter of Largest Stem (mm)
Population I				
Males	33	2.9 ± 1.1	2.8 ± 1.9	35 ± 16
Females	33	2.5 ± 1.1	2.8 ± 2.1	32 ± 17
Population II				
Males	32	2.7 ± 1.3	3.6 ± 2.5	30 ± 16
Females	34	2.7 ± 1.0	2.9 ± 1.9	33 ± 14

In these two populations, male plants and female plants occur with equal frequency in the populations and do not differ in their vegetative characteristics. Sex changing affects less than 2% of the population over the three time intervals and was only apparent in two male plants. The probability that an individual will have an altered sex expression in any yearly interval is less than 1%. The two plants that altered their sex expression were recorded as male in 1980 and 1982, and as having 50% or more male flowers in 1983 and 1984. Since male flowers were far more conspicuous than female flowers, it is possible that both of these plants actually produced some female flowers in 1980 and 1982, but they were not noticed. On the other hand, it can be said conclusively that no male flowers were produced on female plants at either site. In 1983 and 1984, all male plants were checked for scattered female flowers; none was present except on Plants #38 and #48. In conclusion except for a low percentage of individuals that have both male and female flowers, spicebush in these two populations is a species in which a basic dimorphism exists with equal numbers of male plants and female plants that are sexually constant and vegetatively similar.

ACKNOWLEDGMENTS

Helpful comments on this note were provided by Claire McCall, Pamela Hall, Kamal Bawa, Greg Anderson and John Silander.

LITERATURE CITED

Freeman, D. C., L. G. Klikoff, & K. T. Harper. 1976. Differential resource utilization by the sexes of dioecious plants. Science 193: 597-599.

———, E. D. McArthur, K. T. Harper, & A. C. Blauer. 1981. Influence of environment on the floral sex ratio of monoecious plants. Evolution 35: 194–197.

Hibbs, D. E., & B. C. Fischer. 1979. Sexual and vegetative reproduction of striped maple (*Acer pensylvanicum* L.). Bull. Torrey Bot. Club 106: 222–226.

Lloyd, D. G., & K. S. Bawa. 1984. Modification of the gender of seed plants in varying conditions. Evolutionary Biology 17: 255–338.

Lovett-Doust, J., & P. B. Cavers. 1982. Sex and gender dynamics in Jack-in-the-pulpit, *Arisaema triphyllum* (Araceae). Ecology 63: 797–807.

Policansky, D. 1982. Sex change in plants and animals. Ann. Rev. Ecol. Syst. 13: 471–495.

BIOLOGY DEPARTMENT
BOSTON UNIVERSITY
BOSTON, MA 02215

LAKESHORES IN THE TUSKET RIVER VALLEY, NOVA SCOTIA: DISTRIBUTION AND STATUS OF SOME RARE SPECIES, INCLUDING *COREOPSIS ROSEA* NUTT. AND *SABATIA KENNEDYANA* FERN.

PAUL A. KEDDY

ABSTRACT

The Tusket River valley in southwestern Nova Scotia has many rare Atlantic coastal plain plant species. Sixteen lakes were examined for some specific rare shoreline plants: seven lakes through which the Tusket River flows and nine similar-sized lakes adjacent to or discharging into the Tusket River. The seven Tusket River lakes had significantly more rare species ($P = 0.01$): the richest shoreline floras occurred lowest in the watershed ($P < 0.02$). Two environmental factors which could produce these distributions are water level fluctuations associated with the Tusket River and presence of different glacial tills. Shoreline species such as *Coreopsis rosea* and *Sabatia kennedyana* are threatened by the disruptive effects of cottage development and all-terrain vehicle use.

Key Words: Conservation, rare plants, *Coreopsis rosea, Sabatia kennedyana,* shorelines, wetlands, Tusket River, Nova Scotia

INTRODUCTION

The southwestern portions of Nova Scotia have long been known to support a rich flora disjunct from the Atlantic coastal plain of the eastern United States (Fernald 1921, 1922; Roland and Smith, 1969). Many of these species are considered rare and/or threatened in Nova Scotia and Canada (Maher et al., 1978). Some, such as *Coreopsis rosea* Nutt. (Compositae) and *Sabatia kennedyana* Fern. (Gentianaceae) are restricted to only a few lakeshores in Yarmouth County, apparently those specifically associated with the Tusket River.

The within-lake distributions of shoreline species in this river valley are the subject of ongoing ecological studies (Keddy, 1984 a, b). The distribution among lakes, however, was known only from scattered herbarium collections. It was important to locate concentrations of these species for future ecological studies and for conservation planning; the objective of this study was, therefore, to describe the distributions of these rare shoreline species in more detail.

METHODS

Field work was conducted during August 10–20, 1982, while canoeing from South Wallace Lake to Gavels Lake (*see* map, Figure 1). Since it was not possible in the time available to inventory fully the flora of each lake, two observers searched for two groups of target species: (i) some coastal plain species considered by Maher et al. (1978) to be rare or threatened in Nova Scotia, and (ii) typical shoreline species with wide distributions in eastern Canada (Table 1).

Where possible, the entire perimeter of each lake was examined using a canoe. When a lake was explored on foot instead, at least a kilometer of shoreline was carefully explored, paying particular care to visit both sheltered and exposed shorelines. Although species may have been missed, in those lakes which were fully inventoried, the first kilometer of shoreline usually revealed the presence or absence of all target species in that lake.

On lakes where *Coreopsis rosea* or *Sabatia kennedyana* were found, the entire shoreline was examined. Population size was estimated by counting the number of flowering stalks. Since both species had vigorous vegetative reproduction, and since many shoots in each population were not flowering, these data were only a crude measure of population size. It does, however, quantify the geographical distribution more accurately than simply presence or absence on a particular lake.

Species nomenclature follows Roland and Smith (1969). Statistical tests were carried out according to Siegel (1956).

RESULTS

Table 1 compares the shoreline floras of the lakes examined. There were significantly more rare Atlantic coastal plain species (Table 1, $P = 0.01$) on the Tusket River lakes. The other shoreline species occurred on all lakes. Within the Tusket River lakes, the number of rare species decreased with distance upstream (Spearman rank correlation coefficient corrected for ties, $n = 7$, $r_s = 0.93$, $p < 0.02$). Wilson's Lake had the richest shoreline flora and was the only lake with *Hydrocotyle umbellata* (*see also* Roland, 1980).

Figures 1 and 2 show the known Canadian distributions of *Sabatia kennedyana* and *Coreopsis rosea.* Both are largely restricted to the lower portions of the Tusket River basin. In addition, these maps show two populations (Fanning Lake, Salmon Lake) which are outside the Tusket River system; they were located later but are included here for completeness.

Figures 3 and 4 show the previously known distributions of these species based on herbarium specimens. Both once occurred on the shores of the lower lakes of the Tusket River, but apparently were eliminated when these lakes were turned into reservoirs for the Tusket Falls hydroelectric generating station. The specimen of *S. kennedyana* from Canoe Lake (Figure 3) was surprising since there appeared to be little suitable habitat there. The area which seemed most similar to other shorelines with *S. kennedyana* has several cottages adjacent to it; no *S. kennedyana* was found there.

DISCUSSION

It is difficult to explain the distribution of shoreline species in this region of Yarmouth County. The origin of Atlantic coastal plain species in southwestern Nova Scotia has been discussed by Roland and Smith (1969) and Holland (1981), but environmental factors influencing their present distributions have received less attention. Fluctuating water levels and glacial till may both be important.

Lakes in the Tusket River system have wide fluctuations in water level both within and among years, as shown by fluctuations in the water levels of the Tusket River (Figure 5). Occasional high water periods may eliminate shrubs which would otherwise dominate the shoreline. Shrubs have a major effect on the distribution of shoreline plants (Keddy, 1983), and more than a century ago Thoreau (1854) described how high water periods kill woody plants and produce open habitat on lakeshores in New England. Lakes without water level fluctuations often have little open habitat between shrubs and water line. The lakes associated with the Tusket River all had broad littoral zones. Keddy and Reznicek (1982) have found that water level fluctuations were associated with the presence of coastal plain species on Ontario lakes.

Southwestern Nova Scotia has a complex glacial history (Grant, 1977, 1980), and at least two till types can be found on lakeshores. One till has many large angular boulders of the surrounding greywacke of the Goldenville formation. The other till has rounded stones and gravels from the Caledonian igneous complex of New Brunswick. This latter till produces gently-sloping sand and gravel shorelines. *Coreopsis rosea, Hydrocotyle umbellata* and *Sabatia*

Table 1a. Shoreline species found on lakes associated with the Tusket River in Yarmouth County, Nova Scotia.

	Lakes Visited[1]						
	Tusket River						
Species	Bennetts	Wilsons	Gillfillan	Third	Pearl	Travis	South Wallace
(i)[2] *Hydrocotyle*[3] *umbellata*		√					
Coreopsis rosea[3]	√	√					
Habenaria flava	√	√	√				
Eupatorium dubium	√	√	√				
Sabatia kennedyana[4]	√	√	√	√	√	√	
Panicum longifolium	√	√	√	√	√	√	
(ii)[5] *Nymphoides cordata*	√	√	√	√	√	√	√
Eriocaulon septangulare	√	√	√	√	√	√	√
Lobelia dortmanna	√	√	√	√	√	√	√
Lysimachia terrestris	√	√	√	√	√	√	√

[1] Lowermost to uppermost within watershed (left to right) within each group (see maps); lakes below Bennett's are hydroelectric reservoirs with very little shoreline vegetation and are therefore not included.

[2] Atlantic coastal plain species rare in Nova Scotia (Maher et al., 1978); Mann-Whitney U Test (Siegel, 1956), one-tailed, $n_1 = 7$, $n_2 = 9$, $U = 9$, $P = 0.01$.

[3] Endangered in Canada

[4] Threatened in Canada

[5] Some widespread shoreline species

Table 1b. Shoreline species found on lakes associated with the Tusket River in Yarmouth County, Nova Scotia.

	Lakes Visited[1]								
	Other								
Species	Clear-water	Mill	Kege-shook	Canoe	Rushy	Kempt Snare	Beaver-house	Sun-day	Chur-chills
(i)[2] *Hydrocotyle*[3] *umbellata*									
Coreopsis rosea[3]									
Habenaria flava			√						
Eupatorium dubium			√						
Sabatia kennedyana[4]			√						
Panicum longifolium			√				√		
(ii)[5] *Nymphoides cordata*	√	√	√	√	√	√	√	√	√
Eriocaulon septangulare	√	√	√	√	√	√	√	√	√
Lobelia dortmanna	√	√	√	√	√	√	√	√	√
Lysimachia terrestris	√	√	√	√	√	√	√	√	√

kennedyana are all most abundant on, and largely restricted to, sand and gravel shorelines.

The anomalous rich flora in Kegeshook Lake is consistent with both of the above proposals since this lake had (1) broad littoral zones, suggesting past water level fluctuations, and (2) extensive sand and gravel shorelines.

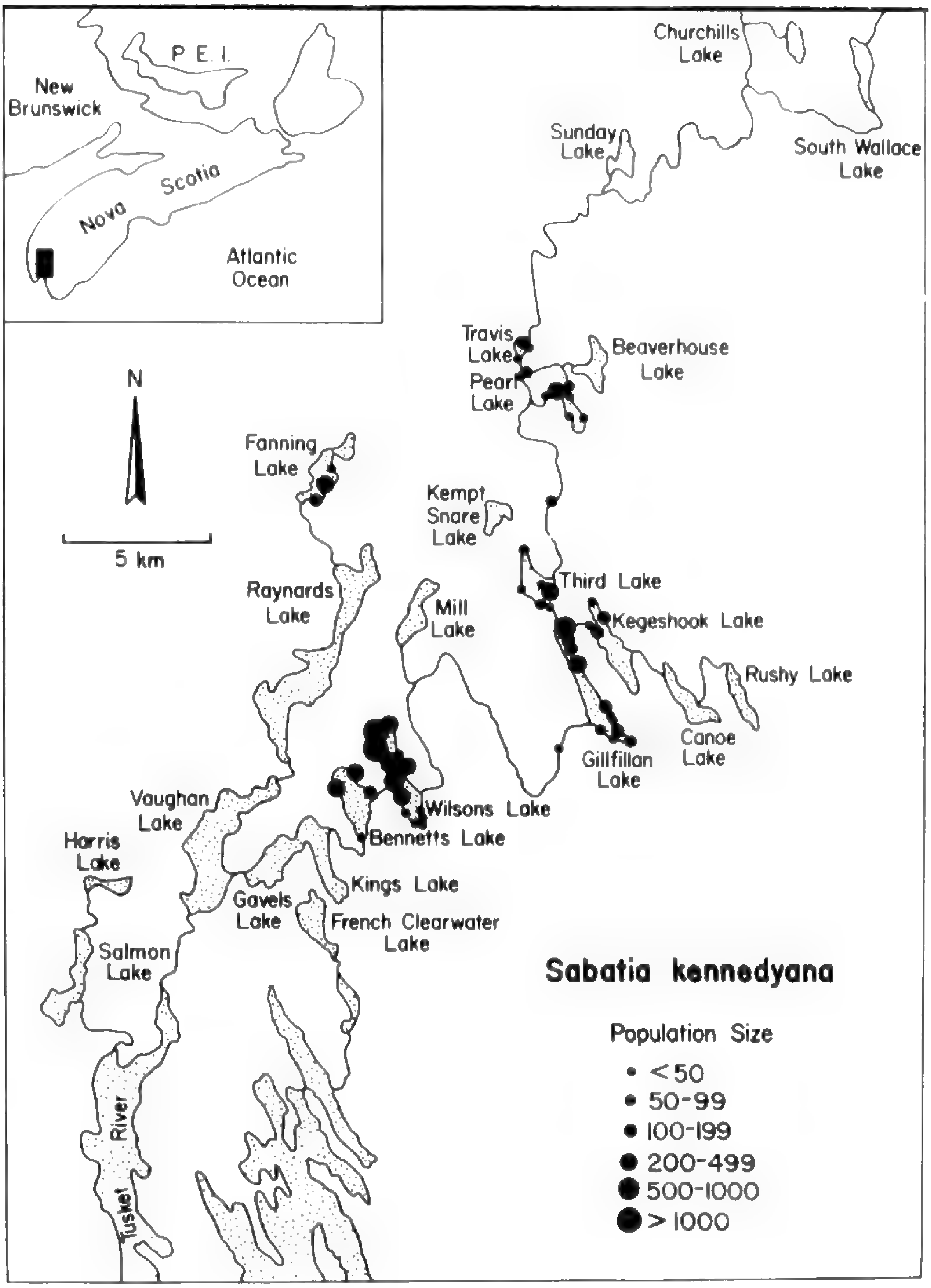


Figure 1. *Sabatia kennedyana* populations in Canada. Lake names follow Tusket 1:50,000 topographic map, Canada Department of Energy, Mines and Resources, 1976. The lowest two water bodies shown are brackish or salt water.

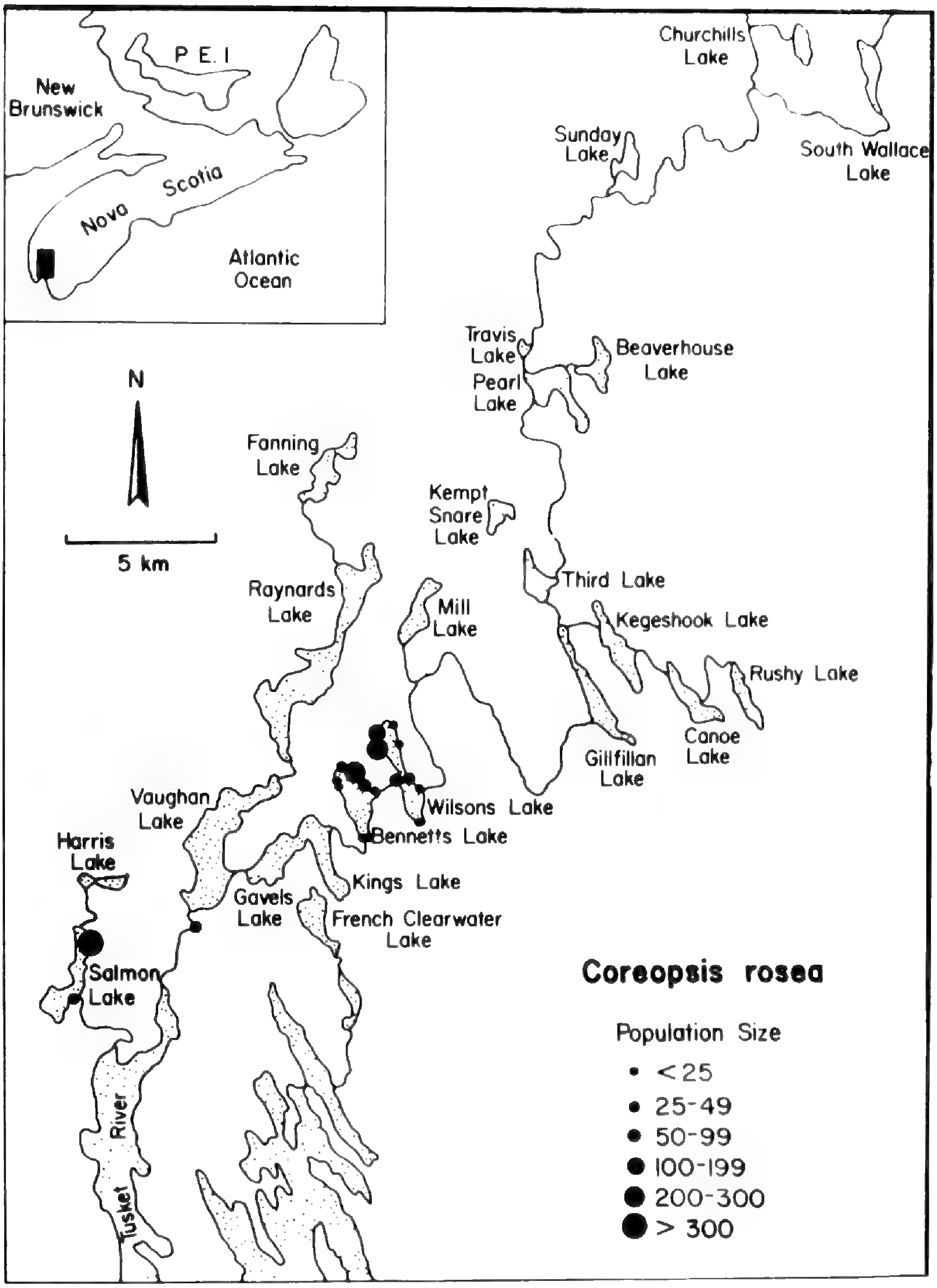


Figure 2. *Coreopsis rosea* populations in Canada.

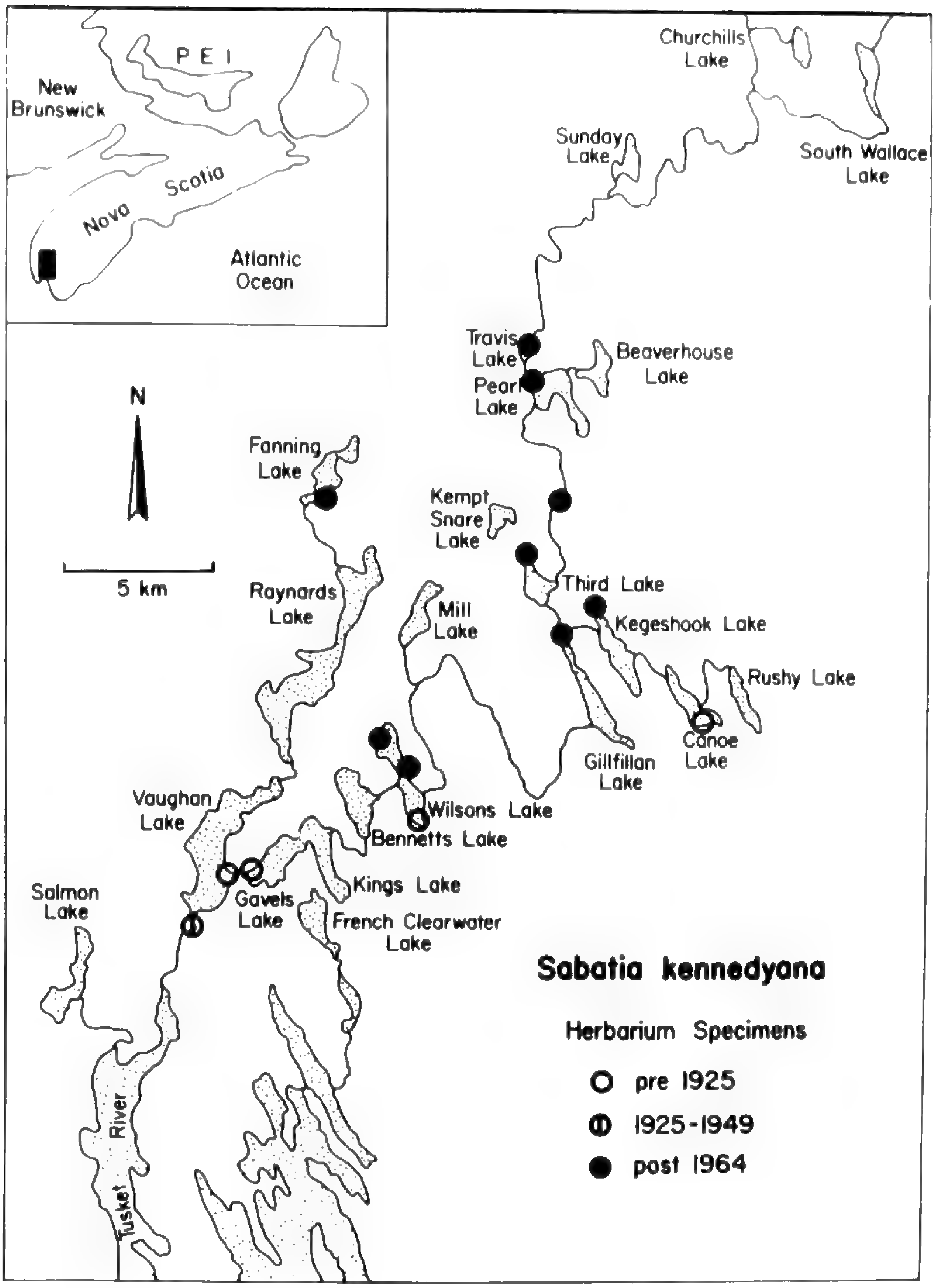


Figure 3. Past and present distribution of *Sabatia kennedyana* based on herbarium specimens (Courtesy of C. J. Keddy; herbaria consulted were ACAD, CAN, DAL, DAO, GH, NSAC, NSPM, TRT, US).

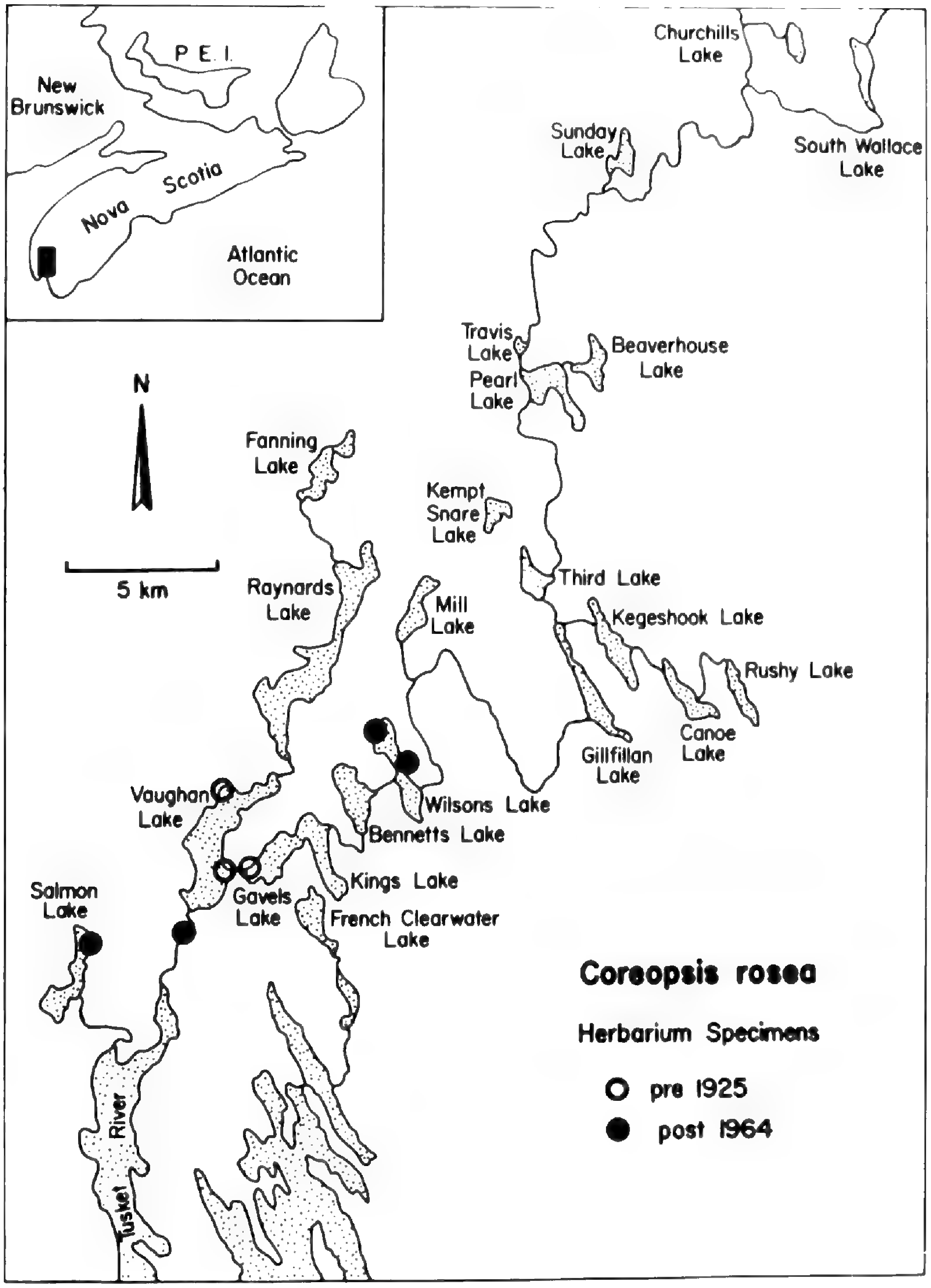


Figure 4. Past and present distribution of *Coreopsis rosea* based on herbarium specimens (Courtesy of C. J. Keddy; herbaria as in Figure 3).

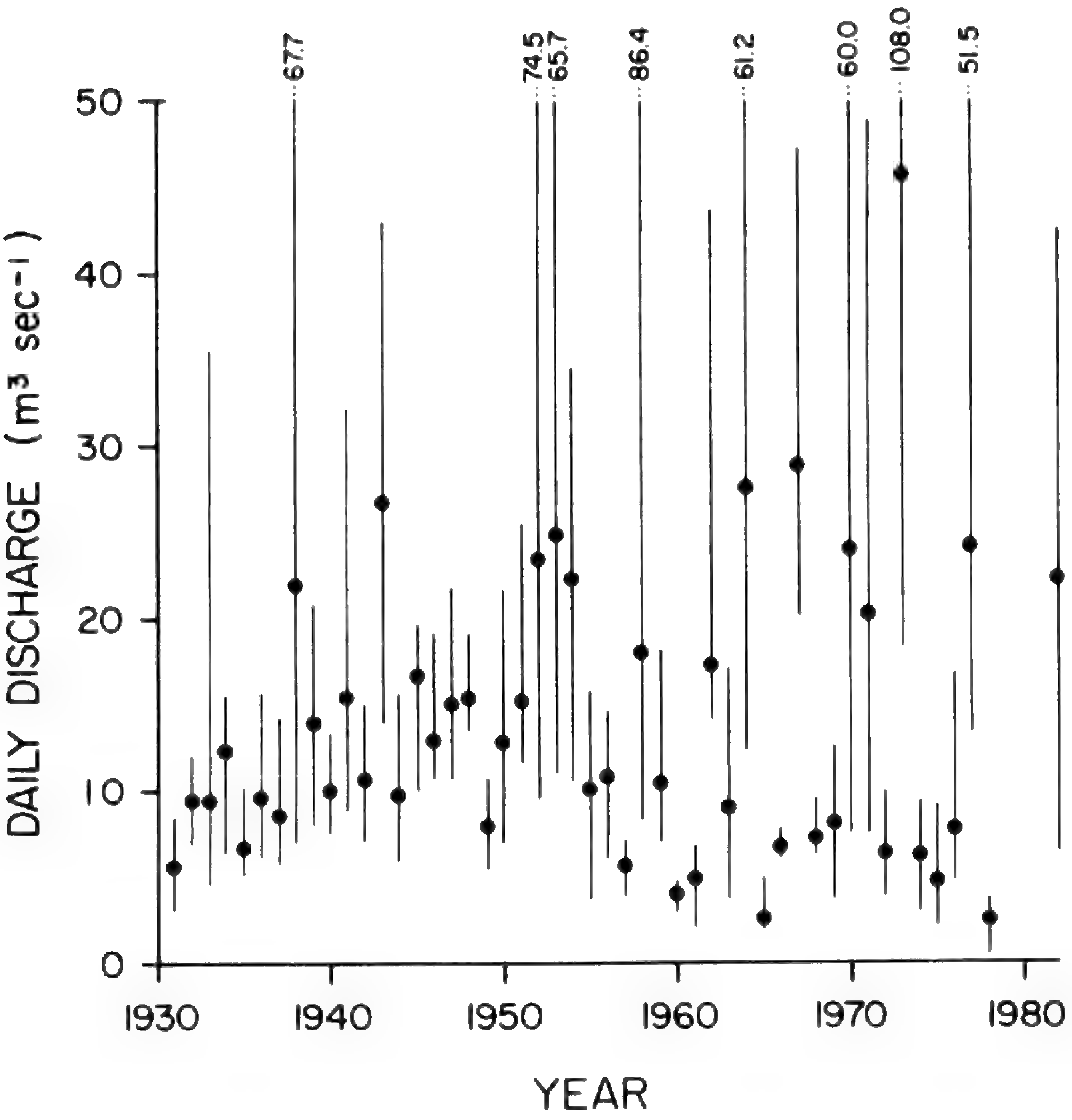


Figure 5. Water levels in the Tusket River measured just upstream from Wilson's Lake (means and range for August by year). Note fluctuations within and among years. (Data from station no. 01EA003 courtesy of the Inland Waters Directorate, Environment Canada).

STATUS OF FLORA

Older records (Fernald, 1921, 1922; Roland and Smith, 1969) indicate that these species were always rare in Nova Scotia, but habitat loss from human activity is now a growing threat. Raynards, Vaughan, Gavels and Kings Lake are now hydroelectric reservoirs, and species such as *Sabatia kennedyana* and *Coreopsis rosea* have apparently disappeared from them. Bennetts, Wilsons, Gillfillan, Kegeshook and Pearl Lakes are all being developed for cottages. Cottages not only lead to trampling, but vegetation is sometimes deliberately eliminated to provide swimming areas. All-terrain vehicles are causing increasing damage, and several *S. kennedyana* populations seen in 1982 were heavily damaged by 1984. Table 1 shows that Wilsons Lake should receive the highest priority in protecting a representative example of coastal plain vegetation in Nova Scotia. The Gillfillan-Kegeshook area also deserves consideration; although *C. rosea* and *Hydrocotyle umbellata* do not occur here, a wide range of vegetation types with other coastal plain species is represented.

ACKNOWLEDGMENTS

I thank C. J. Keddy for assistance with field work in the rain and P. Tufts for transportation in Nova Scotia. Thanks also to D. R. Grant for helpful discussions on geology. P. Catling, R. Day, A. E. Roland, I. Wisheu, and A. Payne provided many helpful comments on drafts of the manuscript. Maps were prepared by C. J. Keddy with financial assistance from the World Wildlife Fund (Canada). This study was funded by Natural Sciences and Engineering Research Council of Canada operating grant A6963.

LITERATURE CITED

FERNALD, M. L. 1921. The Gray Herbarium expedition to Nova Scotia 1920. Rhodora 23: 89–111, 130–152, 153–171, 184–195, 223–245, 257–278, 284–300.

______. 1922. Notes on the flora of western Nova Scotia 1921. Rhodora 24: 157–181, 201–208.

GRANT, D. R. 1977. Glacial style and ice limits, the Quaternary stratigraphic record, and changes of land and ocean level in the Atlantic provinces, Canada. Géogr. Phys. Quat. 31: 247–260.

______. 1980. Quaternary stratigraphy of southwestern Nova Scotia: glacial events and sea level changes. Geol. Assoc. Canada, Guidebook 9.

HOLLAND, P. G. 1981. Pleistocene refuge areas, and the revegetation of Nova Scotia, Canada. Progr. Phys. Geogr. 5: 535–562.

KEDDY, P. A. 1983. Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. Ecology 64: 331–344.

______. 1984a. Quantifying a within-lake gradient of wave energy in Gillfillan Lake, Nova Scotia. Can. J. Bot. 62: 301–309.

______. 1984b. Plant zonation on lakeshores in Nova Scotia, Canada: a test of the resource specialization hypothesis. J. Ecol. 72: 797–808.

______, AND A. A. REZNICEK. 1982. The role of seed banks in the persistence of Ontario's coastal plain flora. Am. J. Bot. 69: 13–22.

MAHER, R. V., D. J. WHITE, G. W. ARGUS, AND P. A. KEDDY. 1978. The Rare Vascular Plants of Nova Scotia. Syllogeus No. 18, National Museums of Canada, Ottawa.

ROLAND, A. E. 1980. *Hydrocotyle umbellata* in Nova Scotia. Rhodora 82: 517–518.

———, AND E. C. SMITH. 1969. The flora of Nova Scotia. Proc. Nova Scotia Inst. Sci. 26: 5–238, 277–743.

SIEGEL, S. 1956. Nonparametric Statistics for the Behavioral Sciences McGraw-Hill, N.Y.

THOREAU, H. D. 1854. Walden. Republished 1965. *In:* Walden and Civil Disobedience (pp. 132–133). Airmont Pub. Co., N.Y.

DEPARTMENT OF BIOLOGY
UNIVERSITY OF OTTAWA
OTTAWA, ONTARIO, CANADA
K1N 6N5

INVESTIGATIONS INTO THE EVOLUTIONARY HISTORY OF THE POLYPLOID COMPLEXES IN *ANTENNARIA* (ASTERACEAE: INULEAE).

II. THE *A. PARLINII* COMPLEX

RANDALL J. BAYER[1]

ABSTRACT

The *Antennaria Parlinii* polyploid complex is a widespread species occurring throughout deciduous forests of eastern United States and southern portions of adjacent Canada. This group consists of two variable subspecies, ssp. *Parlinii* and ssp. *fallax*. The complex is composed of both sexual and agamospermous populations with distinct geographic distributions. Crosses were made in all combinations among several sexual diploid species of *Antennaria* that morphologically resemble members of the *A. Parlinii* complex to aid in identifying its diploid ancestors. The hybrids were then compared by principal components, cluster, and discriminant analyses, to the naturally-occurring polyploids. Results indicated that *A. Parlinii* s.l. was of multiple hybrid origin involving three sexual diploid species, *Antennaria plantaginifolia*, *A. racemosa*, and *A. solitaria*.

Key Words: *Antennaria*, polyploidy, compilospecies, agamospermy, agamic complex, numerical taxonomy, interspecific hybrids

INTRODUCTION

The *Antennaria Parlinii* polyploid agamic complex occurs throughout deciduous forests from Georgia, west to Texas, north to the Thunder Bay District of Ontario, and east to Nova Scotia (Figure 7, Bayer and Stebbins, 1982). Populations of *A. Parlinii* are either sexually reproducing (with sex ratios near 1:1) or are asexual, and composed entirely of pistillate clones (Bayer and Stebbins, 1983). These sexual and asexual populations have distinct geographic distributions (Bayer and Stebbins, 1983), with the former occurring mainly in the southwestern portions of the range. Recently, Bayer and Stebbins (1982) defined *A. Parlinii* as consisting of two subspecies, *A. Parlinii* Fern. ssp. *Parlinii* and *A. Parlinii* Fern. ssp. *fallax* (Greene) Bayer and Stebbins. They differ in that the former has glabrous adaxial leaf surfaces and glands on the upper portion of the cauline stem while the latter has pubescent

---

[1] Present address: Department of Biology, University of Windsor, Windsor, Ontario, Canada N9B 3P4.

adaxial leaf surfaces and is glandless. Both subspecies are found over the entire range of the species, but ssp. *Parlinii* is rare in the southwestern portion of the range and more common in the northeast. Agamospermy in the *A. Parlinii* complex occurs via diplospory followed by diploid parthenogenesis, as was first demonstrated by Stebbins (1932b). Sexual members reproduce via the Polygonum-type embryo-sac (Stebbins, 1932a), as do sexual diploid members of the genus.

Antennaria Parlinii has basal leaves with 3–5 primary veins and capitulescences composed of 2–15 (median of 6) relatively large capitula. Chromosome numbers in the complex include tetraploids ($2n = 56$; $x = 14$), pentaploids ($2n = 70$), hexaploids ($2n = 84$), and octoploids ($2n = 112$) (Bayer and Stebbins, 1981; Bayer, 1984). Hexaploids are by far the predominant cytotype (Bayer, 1984), with pentaploids and octoploids so far only encountered rarely. Sexual tetraploids are occasional (Bayer, 1984), having been found at one site in Oklahoma, once in Missouri, and at five sites in the Driftless Area of Wisconsin. The frequent occurrence of tetraploid cytotypes in western portions of the range supports the hypothesis that the species originated in this area and spread eastward where it occurs both as sexual and agamospermous hexaploids (Bayer, 1984).

Workers on agamic complexes have often postulated that apomicts arise through hybridization between and among sexual diploid species (Gustafsson, 1947). Harlan and DeWet (1963) have termed polyploid complexes of multiple hybrid origin a *compilospecies*. The question can be asked: What were the most probable origins of the *Antennaria Parlinii* agamic complex? With this question in mind, crosses were made among five diploid species of *Antennaria: A. neglecta* Greene, *A. plantaginifolia* (L.) Richardson, *A. racemosa* Hook., *A. solitaria* Rydb., and *A. virginica* Stebb. to see whether any of the interspecific hybrids resembled members of the *A. Parlinii* complex (Bayer, 1985). These five diploid species were chosen for comparison with *A. Parlinii* because they are morphologically most similar to and largely sympatric with *A. Parlinii*. The five diploid species can be divided into two groups, the small-leaved section *Dioicae* with basal leaves having a single primary vein, and the large-leaved section *Plantaginifoliae* with basal leaves having 3–5 veins. Like the *A. Parlinii* complex, the diploids *A. plantaginifolia, A. racemosa,* and *A. solitaria* are of the large-leaved group and their hybrids most closely resemble members of *A. Parlinii*. Hybrids from crosses between diploids of the small- and large-leaved groups usually produce single-nerved basal leaves (Bayer, 1985). Consequently, the three diploid species of *Antennaria* chosen for analysis along with *A. Parlinii* were *A. plantaginifolia*, *A. racemosa*, and *A. solitaria* (*Antennaria neglecta* and *A. virginica* were eliminated from further analysis). Several crosses were also attempted between sexual clones of *A. Parlinii* and two of the putative diploid parents to test whether introgression could still be occurring under natural conditions. The purposes of this paper are (1) to discuss the relationship of the *A. Parlinii* polyploid complex to several sexual diploids, (2) to test the hypothesis that the *A. Parlinii* complex is of multiple hybrid origin, (3) to discuss the relationship of *A. Parlinii* to the morphologically similar *A. neodioica* polyploid agamic complex, and (4) to comment on the mode of inheritance of some important morphological features.

MATERIALS AND METHODS

Field observations of *Antennaria* were made each spring from 1978–83 and over 400 collections were cultivated in the greenhouse. Interspecific hybrids and other crosses were made as outlined previously (Bayer and Stebbins, 1982; 1983). Pollen viability of certain hybrids was ascertained through the use of Alexander's differential staining method (Alexander, 1980). Three hundred grains individual were scored for viability.

Morphological studies were aided by the use of specimens borrowed from the following herbaria: CAN, CM, GH, MO, MONTU, NDG, NY, OS, PAC, RM, SDU, US, VPI, WIS, and WVA. Herbarium vouchers of field collections and artificial hybrids produced during this study are on deposit at OS. Numerical methods are explained in detail in Bayer (1985), and are discussed here briefly. Thirty-eight characters (16 vegetative and 22 reproductive; *see* Bayer, 1985, Table 1) were used to construct the initial basic data matrix. The basic data matrix may be found in Bayer (Appendix, unpub. Ph.D. dissertation, 1984. Ohio State Univ., Columbus). The NT-SYS program of Rohlf, Kishpaugh, and Kirk (1974) was used to compute the principal components analysis (PCA), cluster analysis (UPGMA), and a table of correlation coefficients. A stepwise discriminant analysis and univariate statistics were generated by the BMDP program of Dixon (1981). Computations were carried out at The Instruction Research Computing Center at The Ohio State University. Several data matrices were used for this study: (1) a 149 OTU (operational taxonomic unit) matrix consisting of members of the *Antennaria Parlinii* (39 OTUs) complex, three related sexual diploids (34 OTUs of *A. plantaginifolia*, 34 of *A. racemosa*, and 35 of *A. solitaria*), and their interspecific hybrids (7 OTUs), (2) a 117 OTU data matrix composed of members of the *A. neodioica* (72 OTUs) and *A. Parlinii* (45 OTUs) polyploid complexes, (3) a 153 OTU data matrix, basically the same as matrix number 1 (41 OTUs of *A. Parlinii* s.l., 35 of *A. plantaginifolia*, 35 of *A. solitaria*, 35 of *A. racemosa*, and 7 interspecific hybrids), and (4) an 11 OTU matrix utilizing character averages for the three diploids and the *A. Parlinii* polyploid complex, plus the individual interspecific hybrids (7 OTUs) among the three diploids. *Antennaria Parlinii* is used in the sense of Bayer and Stebbins (1982) and includes all the agamospecies included in synonymy under *A. Parlinii* ssp. *Parlinii* and ssp. *fallax*. Specimens referable to several of the agamospecies (i.e. *A. Brainerdii* (= ssp. *Parlinii*), *A. calophylla* (= ssp. *fallax*), and *A. munda* (= ssp. *fallax*)) are occasionally discussed because some floras still recognize these taxa as distinct species. A three-dimensional plot of PCA computed from matrix number 1 is presented as Figure 1. Matrix number 2 was used to compute a PCA; the results are presented as two 2-dimensional plots (Figure 3) of the first three factors. A cluster analysis was performed using matrix number 3; the results are displayed as a phenogram (Figure 2). Matrix number one was used to execute a discriminant analysis. Pearson product-moment correlation coefficients (Sneath and Sokal, 1973) were used to compare OTUs of matrix number 4.

RESULTS

Phenetics of the diploids, interspecific hybrids, and polyploids

The first three factors of the PCA composed of the three diploids, their interspecific hybrids, and the *Antennaria Parlinii* complex (Figure 1) accounted for 54.6% of the variation. The first 11 factors have eigenvalues greater than 1.0, indicating that the characters are not highly correlated. High loadings for factor 1 are reproductive characters such as number of heads per capitulescence, flowering

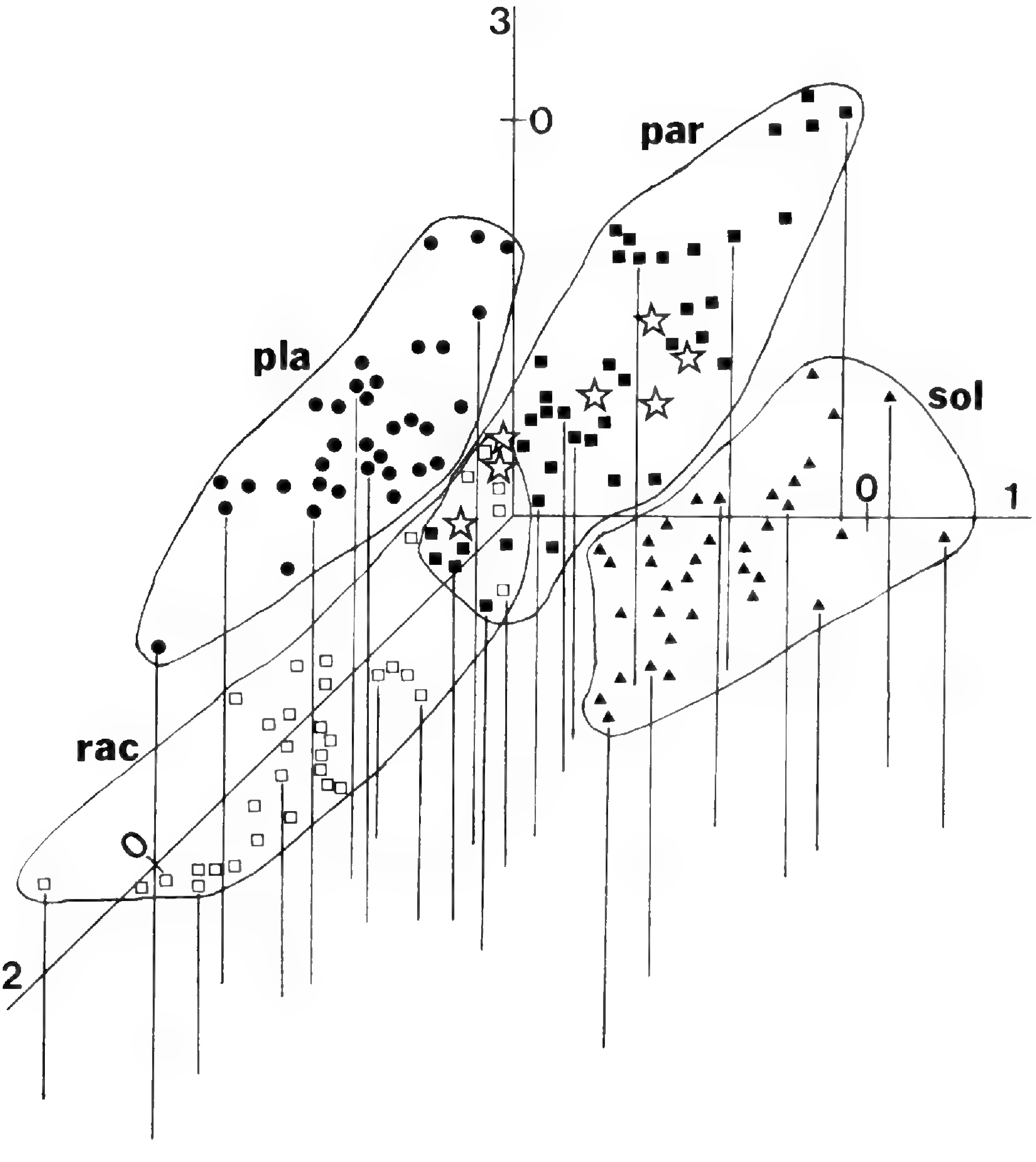


Figure 1. PCA composed of 149 OTUs including three diploid *Antennaria* species, interspecific hybrids, and the polyploid A. Parlinii s.l. Group outlines are indicated by a line. ● *A. plantaginifolia*, □ *A. racemosa*, ▲ *A. solitaria*, ■ *A. Parlinii*, and ☆ interspecific hybrids. Taxa are labeled with the first three letters of their specific epithets. Interspecific hybrid identifications are given as follows from uppermost to lowermost: HY41, HY01, HY42, HY02, HY03, HY04, HY40. Parentage of the hybrids is given in Table 1.

stem height, and width and length of the cauline leaves. A mixture of reproductive and vegetative characters such as degree of pubescence on the upper surface of the basal leaves, stolon length, and presence or absence of the scarious flag-like structure on the upper cauline leaves, have high loadings for factor 2. Factor 3 has high loadings for vegetative characters; the degree of pubescence of the upper leaf surfaces, width of the basal leaves, and number of stolons per basal rosette are examples. Inspection of Figure 1 shows that *A. Parlinii* is surrounded by the three diploids, *A. plantaginifolia, A. racemosa,* and *A. solitaria.* The diploid species are separated mainly by reproductive characters along component number 1. All of the interspecific hybrid combinations fall within the *A. Parlinii* group.

Although the two subspecies of *Antennaria Parlinii* are not shown as distinct in Figure 1, they do form somewhat distinct subgroups within *A. Parlinii* s.l. As expected, *A. Parlinii* ssp. *Parlinii* with its glabrous basal leaves and gland-bearing upper cauline stems, groups more closely to *A. racemosa,* with which it shares these characters. Subspecies *fallax* forms a subgroup in the upper portions of the *A. Parlinii* s.l. group and is most similar to *A. plantaginifolia* and *A. solitaria.* Several specimens referable to *A. calophylla* Greene (= *A. Parlinii* ssp. *fallax*) and *A. munda* Fern. (= *A. Parlinii* ssp. *fallax*) occupy positions at the upper end of the complex closest to *A. solitaria.*

The cluster analysis (Figure 2) has a cophenetic correlation coefficient of 0.857, and shows that the three diploids plus the *Antennaria Parlinii* polyploid complex each form a distinct group. The interspecific hybrids are either grouped within the *A. Parlinii* complex or with one of their parents. The two subspecies within *A. Parlinii,* although not represented separately in Figure 2, are scattered in small groups throughout the *A. Parlinii* complex. *Antennaria munda* Fern. (= *A. Parlinii* ssp. *fallax*) is a seldomly recognized agamospecies, which we have included within *A. Parlinii* s.l. (Bayer and Stebbins, 1982). In many respects it closely resembles *A. solitaria,* which is the reason it is grouped more closely to *A. solitaria* than to the remainder of *A. Parlinii.* Another seldomly recognized agamospecies, *A. Brainerdii* Fern., which has been included within *A. Parlinii* (Bayer and Stebbins, 1982), represents another extreme in the morphological variation of *A. Parlinii.* With its relatively small, glabrous, bright green leaves, *A. Brainerdii* closely resembles hybrids between *A. racemosa* and the other two diploids (Figure 2).

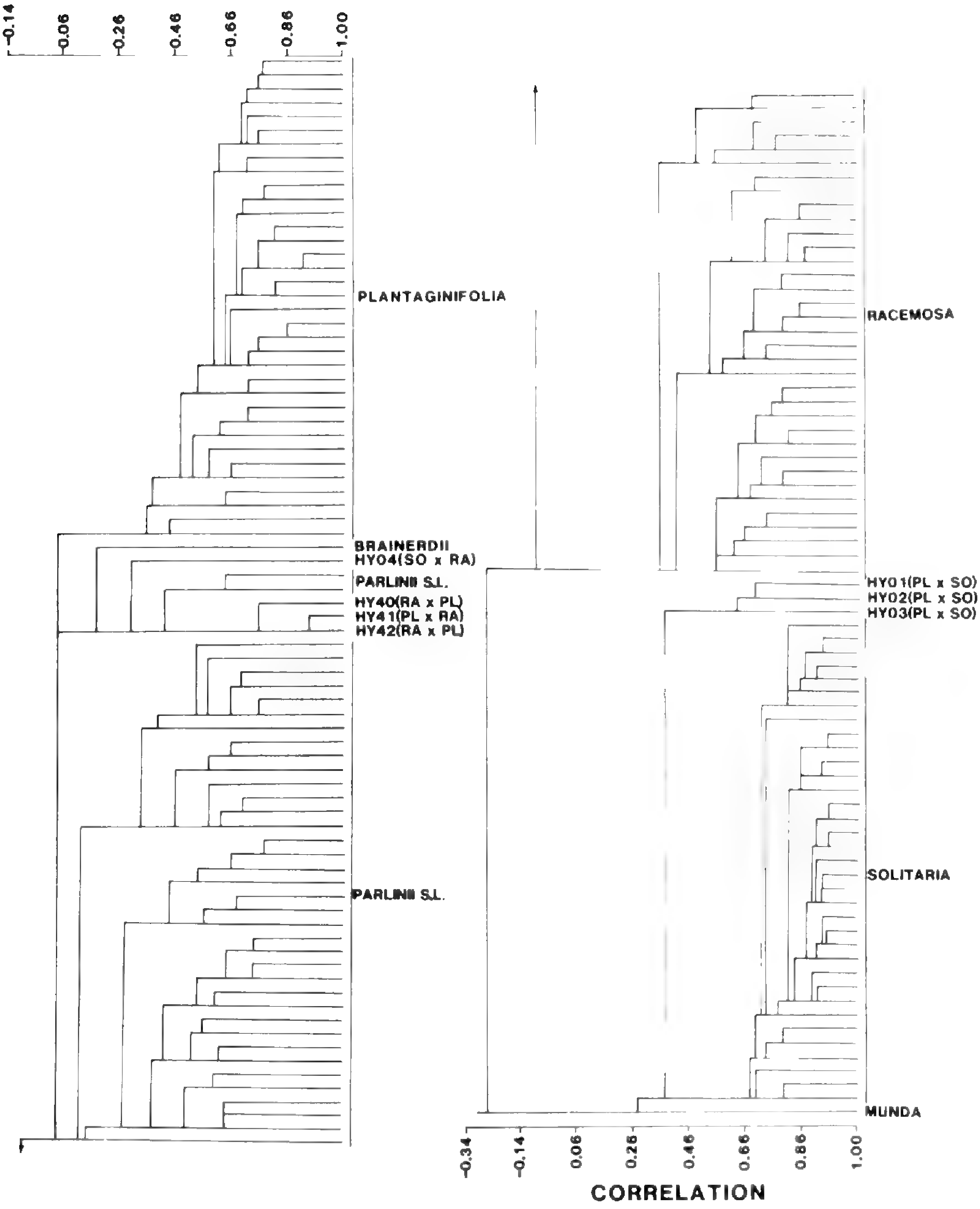


Figure 2. Correlation phenogram (UPGMA) composed of 153 OTUs including three diploid species of *Antennaria*, interspecific hybrids, and *A. Parlinii* s.l. Taxa are labelled with specific epithets. Two agamospecies, *A. munda* and *A. Brainerdii*, are represented separately from the remainder of *A. Parlinii* s.l. Parentage of hybrids is given in parentheses and are denoted by the first two letters of the parental specific epithets. Cophenetic correlation coefficient is 0.857.

Jensen and Eshbaugh (1976a, b) have demonstrated the utility of mean similarity matrices (correlation coefficients) for identifying hybrid taxa. A matrix of mean similarities (Table 1) shows that *Antennaria plantaginifolia* is most similar to *A. racemosa* and vice-versa. *Antennaria solitaria* is most similar to *A. Parlinii*, while *A. Parlinii* is about equally similar to *A. plantaginifolia* and *A. racemosa*. This analysis points to the overall similarity between the *A. Parlinii* polyploid complex and the three diploids. The interspecific hybrids are in all cases either most similar to one of their parents (e.g. HY02, HY03, and HY04) or to the *A. Parlinii* complex (e.g. HY01, HY40, HY41 and HY42). The method always associates the hybrid with one of its parents thereby showing the sensitivity of the technique. A discriminant analysis (Table 2), based on characters which best discriminate among the taxa, also demonstrates that these interspecific hybrids are always associated most closely with the polyploid complex or one of the diploid parents. A table of posterior probabilities derived from the discriminant analysis (Table 2) demonstrates that hybrids are identified as most probably belonging to either one of their parents (e.g. HY03 and HY42) or members of *A. Parlinii* (e.g. HY01, HY02, HY04, and HY41).

Relationship of the Antennaria neodioica complex to the A. Parlinii complex

The PCA (Figure 3) of members of *A. neodioica* (72 OTUs) and *A. Parlinii* (45 OTUs) was computed to demonstrate the morphological distinctness of the two closely related complexes. The first three principal components account for 51.5% of the variation. High loadings for factors 1 and 3 are vegetative characters, while those for factor 2 are reproductive characters. The *A. Parlinii* and *A. neodioica* complexes are separated chiefly on the basis of basal leaf characters along factor 1. The first eight factors have eigenvalues greater than 1.0, indicating that the characters are not highly correlated. The PCA (Figure 3) demonstrates that the two complexes do not overlap. Specimens of *A. neodioica* Greene ssp. *Howellii* (Greene) Bayer are morphologically closest to members of the *A. Parlinii* complex. *Antennaria Farwellii* Greene (= *A. Parlinii* ssp. *fallax*) is an agamospecies which has relatively small leaves when compared with the rest of *A. Parlinii* s.l. and is similar to members of the *A. neodioica* complex.

Table 1. Mean similarity matrix of *Antennaria* species with each other and with six artificial hybrid combinations. Taxa are labeled with the first three letters of the specific or subspecific epithet. Six artificial hybrids (HY— —) and their parentage are presented along with their mean similarities to naturally occurring taxa. ** highest and * second highest similarity between each hybrid and the taxa are indicated.

	PAR	PLA	RAC	SOL
PAR	1.000	0.578	0.502	0.114
PLA	0.578	1.000	0.599	−0.100
RAC	0.502	0.599	1.000	−0.154
SOL	0.114	−0.100	−0.154	1.000
HY01 (PLA × SOL)	0.547**	0.352	−0.010	0.489*
HY02 (PLA × SOL)	0.485*	0.312	−0.122	0.678**
HY03 (PLA × SOL)	0.228	0.322*	0.005	0.482**
HY04 (SOL × RAC)	0.502*	0.416	0.581**	−0.116
HY40 (RAC × PLA)	0.691**	0.449	0.591*	−0.042
HY41 (PLA × RAC)	0.644**	0.563*	0.513	0.084
HY42 (RAC × PLA)	0.650**	0.514*	0.474	0.155

Table 2. Table of posterior probabilities derived from a discriminant analysis. Six artificial interspecific hybrids of *Antennaria* (HY— —) and their parentage are presented along with the posterior probability to which of four naturally occurring groups of *Antennaria* they should belong. Taxa are labeled with the first three letters of the specific or subspecific epithet. Highest probabilities are **bold-faced.**

	PAR	PLA	RAC	SOL
HY01 (PLA × SOL)	**1.000**	0.000	0.000	0.000
HY02 (PLA × SOL)	**0.998**	0.002	0.000	0.000
HY03 (PLA × SOL)	0.001	0.000	0.000	**0.999**
HY04 (SOL × RAC)	**0.962**	0.000	0.038	0.000
HY41 (PLA × RAC)	**0.997**	0.003	0.000	0.000
HY42 (RAC × PLA)	0.329	**0.671**	0.000	0.000

Inheritance of morphological characters

Most of the morphological characters that I have considered in *Antennaria* are inherited polygenically (Bayer, 1985) and are probably controlled by a few (4–5) genes. *Antennaria Parlinii* ssp. *Parlinii* has glabrous adaxial leaf surfaces while subspecies *fallax* has leaves that are pubescent adaxially. When representative clones of each subspecies are crossed, the F_1 hybrids (total of 37 observed) range from glabrous to slightly pubescent, indicating that leaf pubescence is controlled by several genes, with glabrity being dominant to pubescence.

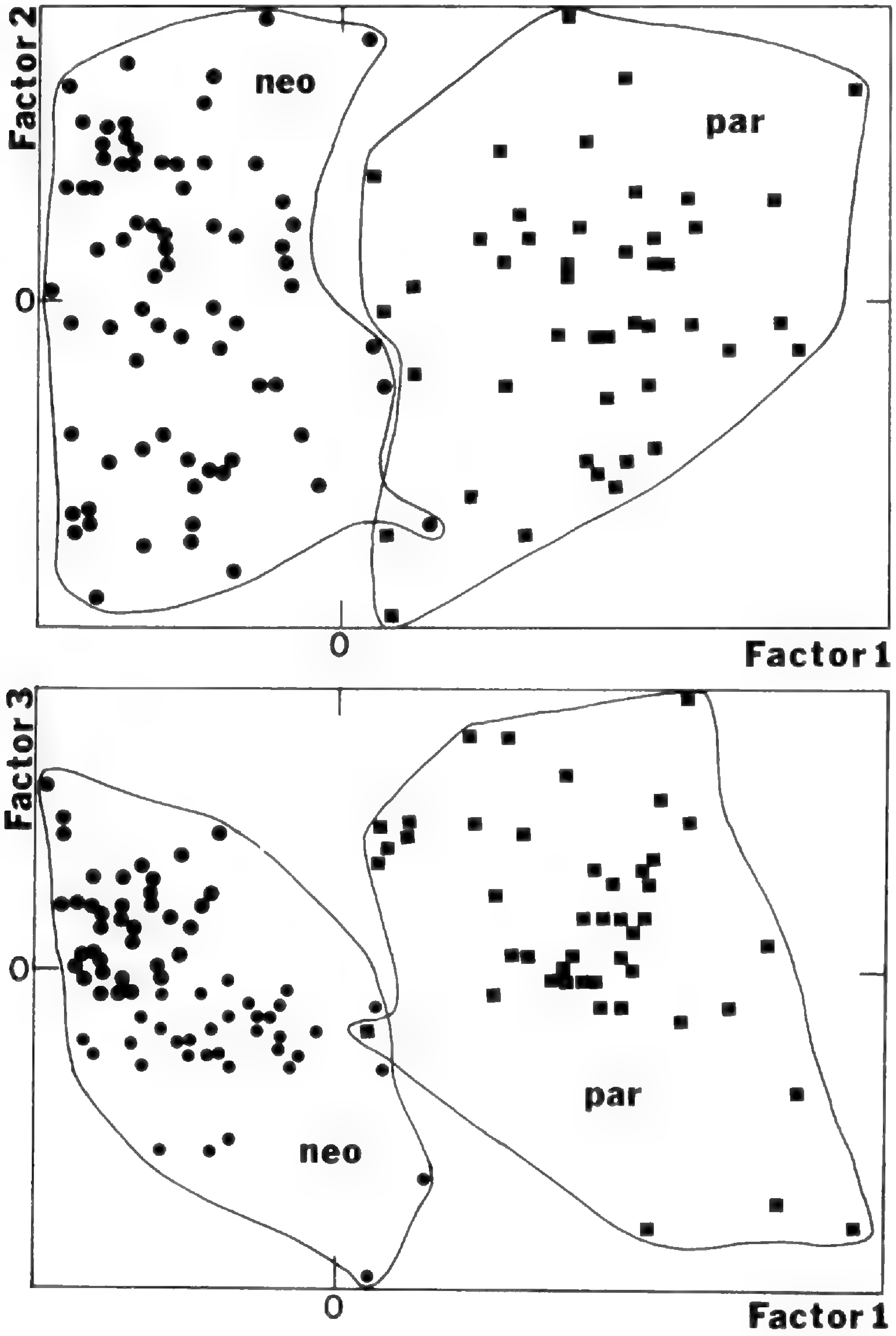


Figure 3. PCA composed of 117 OTUs of the *Antennaria Parlinii* (■) and *A. neodioica* (●) s.l. polyploid agamic complexes. Group outlines are indicated by a line. Taxa are labeled with the first three letters of their specific epithets.

DISCUSSION

Juel (1900) first concluded that the polyploid agamic species of *Antennaria* were probably the result of hybridization between sexual diploid species. It has been documented that most agamospermous groups arise in this way (Grant, 1981). With regard to the origins of *A. Parlinii*, Stebbins (1932b) suggested that while *A. fallax* Greene (= *A. Parlinii* ssp. *fallax*) was most closely related to *A. plantaginifolia*, other cytological features indicated *A. solitaria* or *A. neglecta* were also involved. *Antennaria Parlinii* Fern. (= *A. Parlinii* ssp. *Parlinii*), although similar to *A. plantaginifolia*, had several morphological features not present in *A. plantaginifolia* such as bright green adaxially glabrous leaves; it was undoubtedly of allopolyploid origin (Stebbins, 1932b). With respect to this character in ssp. *Parlinii*, Beals and Peters (1966) stated that "the very characteristic glabrous upper leaf surface and occasional purple glands on the stem suggest that introgression may have occurred in the past with some unknown, now extinct species." They were undoubtedly unaware of *A. racemosa*, the only sexual diploid *Antennaria* with adaxially glabrous leaves that are as large (3–5 veined) as those of *A. Parlinii* ssp. *Parlinii*. *Antennaria racemosa* also has the purple glands found in ssp. *Parlinii*.

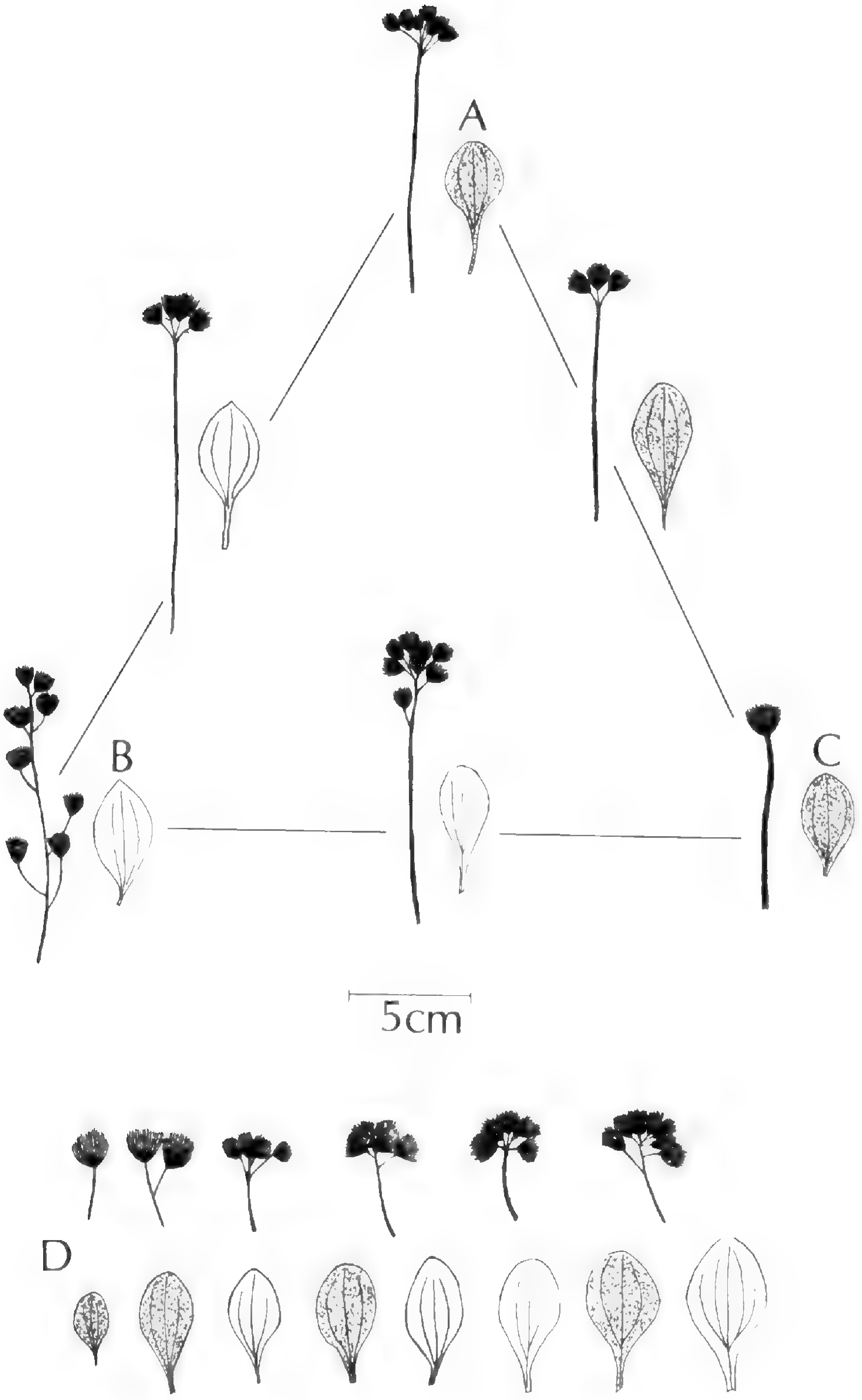
Previously, it was demonstrated by the use of PCA that the three diploids examined as progenitors of *Antennaria Parlinii* are morphologically distinct from one another (Bayer, 1985). It has also been shown (Bayer and Stebbins, 1982; Bayer, 1985) that the diploids are isolated by both spatial and reproductive factors. Further, it has been noted that these isolating mechanisms (Bayer, 1985) occasionally break down and allow hybridization among the diploid species. I have recently observed populations of *A. plantaginifolia*, *A. solitaria*, and polyploid *A. Parlinii* growing side by side in Kentucky; the same observation is reported from West Virginia (G. L. Stebbins, pers. comm.). Recently, field observations and crossing studies (Bayer and Stebbins, 1982) indicate ample opportunity for hybridization and introgression between the two eastern diploids, *A. plantaginifolia* and *A. solitaria*, and the polyploid *A. Parlinii* s.l. The existence of tetraploid, pentaploid, and octoploid cytotypes of *A. Parlinii*, in addition to the predominant hexaploid cytotype, could be cited as evidence of hybridization and introgression between polyploids and diploids. In the *A. neodioica* complex

($2n = 56, 84$), which is totally apomictic, there are only two cytotypes; this reduced number of cytotypes could be attributed to a reduction in crossing between the apomictic polyploids and diploids.

Both *Antennaria plantaginifolia* and *A. solitaria* are sympatric with the *A. Parlinii* complex throughout their entire ranges in the eastern United States (*see* Figures 2, 3, and 7, Bayer and Stebbins, 1982). *Antennaria solitaria* occurs in moist woodlands in the eastern United States mainly south of the Wisconsin glacial margin, while *A. plantaginifolia* is found throughout the Appalachian region, Atlantic Coastal Plain, and north into New York. *Antennaria plantaginifolia* also is known from disjunct populations in the Driftless Area of Wisconsin, as has been confirmed recently (Bayer, 1984; G. L. Stebbins, unpubl. obs.). A single specimen of *A. solitaria* from the Driftless Area of Jackson Co., Wisconsin, has been seen in the collection of WIS and thus it apparently occurs there. *Antennaria racemosa* is found in the coniferous forests of British Columbia and Alberta, south to Washington, Oregon, northern California, Montana, Idaho, and Wyoming. It has been reported as far east as the Black Hills of South Dakota (McIntosh, 1931; Dorn, 1977). Thus, although *A. racemosa* is not sympatric with *A. plantaginifolia* or *A. solitaria* at the present, they may have been sympatric during the last glacial period, 10,000 years ago, when forests probably extended across what is now prairie (Wells, 1970). It is likely that many Cordilleran species migrated eastward during the last glacial period (Wells, 1970; Whitehead, 1972; Marquis and Voss, 1981). For example, *A. rosea* Greene, a chiefly Cordilleran species which occurs sympatrically with *A. racemosa*, has disjunct populations on the north shore of Lake Superior (Hyypio, 1952). If *A. rosea* once migrated or dispersed eastwards, it is possible that *A. racemosa* could have similarly migrated.

The overlap of *Antennaria Parlinii* and *A. racemosa* in the PCA (Figure 1) indicates that *A. racemosa* was probably involved in the ancestry of the complex despite its present-day geographic isolation. The position of the diploid species also indicates that no single one of them is predominantly responsible for the genetic composition of the polyploids. In his original description, E. L. Greene (1898) made the perceptive observation that *A. calophylla* (= *A. Parlinii* ssp. *fallax*) was "related to the exclusively southern *A. solitaria*"; based on the PCA he was apparently correct. Likewise *Antennaria munda* (= *A. Parlinii* ssp. *fallax*) has basal leaves which are shaped like those of *A. solitaria.* Thus, these agamospecies (*A. calophylla* and *A. munda*) appear to have a predominance of genes from *A. solitaria;* this relationship is indicated by PCA in that the agamospecies occupy positions closest to *A. solitaria.* The positioning of certain OTUs of *A. Parlinii* s.l. beyond the morphological types found in *A. plantaginifolia* or *A. solitaria* (Figure 1) could be attributed either to the effects of polyploidy or to transgressive segregation. Transgressive segregation was earlier noted (Bayer, in press) in hybrids between *A. solitaria* and *A. neglecta.* Hiesey and Nobs (1982) have also reported this phenomenon in diploid and polyploid agamic complexes in *Poa.* The cluster analysis indicates that the two subspecies within *A. Parlinii* s.l. are scattered in small groups throughout the *A. Parlinii* complex. This lack of grouping of the two subspecies of *A. Parlinii* is probably the result of segregation of genes from the genomes of several diploids and also because ssp. *Parlinii* and ssp. *fallax* are separated mainly on the basis of only one character, namely pubescence of the adaxial surface of the basal leaves.

The PCA and the cluster analysis demonstrate that while many segregates of *Antennaria Parlinii* ssp. *fallax* morphologically resemble the diploid *A. plantaginifolia,* other segregates of the complex referable to ssp. *fallax* (including *A. calophylla* and *A. munda*) and ssp. *Parlinii* (including *A. Brainerdii*) have characteristics suggesting the presence of genes from both *A. solitaria* and *A. racemosa.* Both *A. Parlinii* s.l. and the *A. solitaria* × *A. plantaginifolia* hybrids are intermediate between *A. solitaria* and *A. plantaginifolia* with respect to number of heads and number of florets per head (Figure 4). Inspection of the basal leaves and capitulescences of the three diploid species, hybrids, and naturally-occurring polyploids demonstrates the close resemblance of all the artificial interspecific hybrids with *A. Parlinii* segregates. The resemblance is evident not only with respect to shape of the basal leaves, but also in the number and arrangement of heads, and on closer inspection the number of florets per head. The mean similarity matrix (Table 1) and the discriminant analysis (Table 2) also point to the similarity of most of the interspecific hybrids to members of the *A. Parlinii* complex. Many hybrids having *A. solitaria* as one of the their parents fre-


A
B
C
5cm
D

quently have high affinities with *A. solitaria* and this resemblance could be from the expression in these hybrids of several dominant traits present in *A. solitaria* (Bayer, 1985).

Antennaria Parlinii s.l. and *A. neodioica* s.l. both occur sympatrically in the deciduous forests of the eastern United States and adjacent Canada, but *A. neodioica* s.l. also occurs as far west as British Columbia and as far north as Hudson Bay and the Canadian Northwest Territories (Bayer and Stebbins, 1982; Bayer, 1985). The two polyploids are most easily separated taxonomically by the number of primary veins in the basal leaves, *A. Parlinii* having 3–5 and *A. neodioica* having only a single nerve. Beals and Peters (1966) and Beals (1968), in studying *Antennaria* in Wisconsin, came to the conclusion that members of these two complexes form a continuum and that species names are convenient labels when applied to them. They postulated that the complex was the product of hybridization and polyploidy. Although some segregates of the *A. Parlinii* complex do resemble members of the *A. neodioica* complex and vice-versa, they can always be positively identified on the basis of number of veins in the basal leaves. In addition, *A. neodioica* consists entirely of asexual populations (Bayer, 1985), while *A. Parlinii* s.l. is composed of both sexual and asexual populations (Bayer and Stebbins, 1983). The PCA (Figure 3) demonstrates that the two complexes are morphologically separable; their evolutionary history, reproductive mode differences, and chromosome number distinctions (Bayer, 1984) support this argument. The two complexes are morphologically similar at the extreme limits of their variation because they probably share the two sexual diploid progenitors *A. plantaginifolia* and *A. racemosa* (Figure 5). The *A. Parlinii* complex has one unique diploid progenitor, *A. solitaria*, while *A. neodioica* has two, *A. neglecta* and *A. virginica*. Figure 5 further portrays the proposed relationships of *A. Parlinii*, *A. neodioica*, and their extant

Figure 4. Line drawings of capitulescences and basal leaves of representative specimens among three diploid species of *Antennaria*, their interspecific hybrids, and *A. Parlinii* (both subspecies). Adaxial leaf pubescence is indicated by stippling. Variation among taxa is apparent with respect to leaf shape and pubescence, number of veins in basal leaves, and number, size, and arrangement of heads in the capitulescence. A. *A. plantaginifolia*, B. *A. racemosa*, C. *A. solitaria*, and D. *A. Parlinii* (both subspecies). Bar = 5.0 cm.

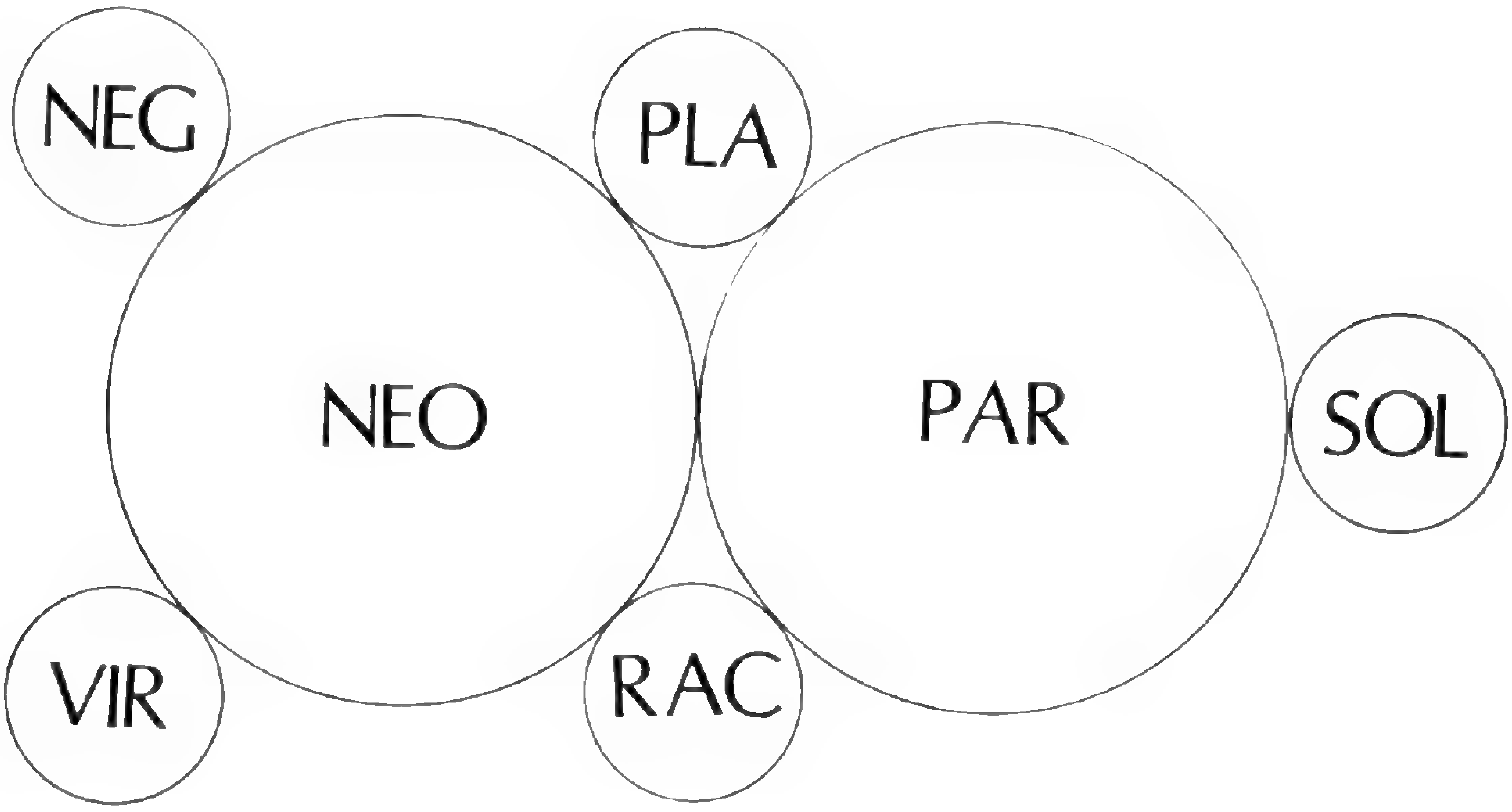


Figure 5. Proposed relationship of the *Antennaria neodioica* s.l. (NEO) and *A. Parlinii* s.l. (PAR) agamic complexes to the sexual diploids *A. neglecta* (NEG), *A. plantaginifolia* (PLA), *A. racemosa* (RAC), *A. solitaria* (SOL), and *A. virginica* (VIR). Degree or relatedness is indicated by proximity of the circles to each other. Relative morphological variability within each taxon is indicated by the size of the circles. See text for detailed explanation.

sexual diploid progenitors. *Antennaria plantaginifolia* and *A. racemosa* can be viewed as pivotal genomes because they are shared by both polyploids. The diploids unique to the ancestry of each complex are responsible for their morphological distinctness.

Antennaria Parlinii s.l. is often found growing with two of its probable diploid progenitors, *A. plantaginifolia* and *A. solitaria.* The question arises whether introgression is still possible between the polyploid and its diploid progenitors. Many populations exist in which asexual clones of *A. Parlinii* s.l. are found growing with sexual clones of *A. plantaginifolia* (Bayer and Stebbins, 1981); in such cases the species are obviously reproductively isolated. In populations where sexually reproducing clones of the polyploids and diploids are sympatric, introgression may still be occurring. In crosses conducted in the greenhouse between *A. Parlinii* s.l. and the diploids *A. plantaginifolia* and *A. solitaria,* the *A. Parlinii* s.l. × *A. plantaginifolia* crosses set 1.0% of their seeds (Bayer and Stebbins,

1982) while the *A. Parlinii* s.l. × *A. solitaria* hybrids set 0.5%. As a result of the crosses, a single hybrid from each was obtained; both were expected to be and were confirmed as tetraploids ($2n = 56$). The *A. Parlinii* × *A. plantaginifolia* hybrid was pistillate and was not analyzed further with respect to fertility, but the *A. Parlinii* × *A. solitaria* hybrid had a pollen stainability of 77.3%. The stainability is high, especially when compared with results obtained for interspecific crosses among diploid species (Bayer, 1985). Diploid species of *Antennaria* have pollen stainabilities greater than 85.0% (Bayer, 1985). The *A. Parlinii* × *A. solitaria* hybrid should be quite fertile; it is likely that introgression is still occurring among the polyploids and diploids.

The contention that polyploid agamic complexes should be retained as distinct from their diploid relatives at the specific level (Bayer and Stebbins, 1982) is viewed as the most desirable solution to the species problem in *Antennaria.* Because the polyploids are of multiple hybrid origin, it is inappropriate to include them simply as varieties of one of the diploid relatives as did Cronquist (1945) when he included members of *A. Parlinii* as varieties of *A. plantaginifolia. Antennaria Parlinii* is certainly of hybrid origin because it has characteristics not found in diploid *A. plantaginifolia.* Although one can not rule out the possibility that diploid progenitors have become extinct, the most simple and plausible explanation is that which has been presented.

ACKNOWLEDGMENTS

This study is part of a dissertation submitted to the graduate school of The Ohio State University in partial fulfillment of the degree of Doctor of Philosophy. The investigation was conducted under the guidance of Daniel J. Crawford and was supported by NSF Doctoral Dissertation Improvement Grant DEB-8200359. I thank D. J. Crawford, G. Ledyard Stebbins, and T. F. Stuessy for their comments on an earlier version of the manuscript.

LITERATURE CITED

ALEXANDER, M. P. 1980. A versatile stain for pollen, fungi, yeast, and bacteria. Stain Technol. 55: 13–18.

BAYER, R. J. 1984. Chromosome numbers and taxonomic notes for North American species of *Antennaria* (Asteraceae: Inuleae). Syst. Bot. 9: 74–83.

———. 1985. Investigations into the evolutionary history of the polyploid complexes in *Antennaria* (Asteraceae: Inuleae). I. The *A. neodioica* complex. Pl. Syst. Evol. (In press).

———, AND G. L. STEBBINS. 1981. Chromosome numbers of North American species of *Antennaria* Gaertner (Asteraceae: Inuleae). Amer. J. Bot. 68: 1342–1349.

———, AND ———. 1982. A revised classification of *Antennaria* (Asteraceae: Inuleae) of the eastern United States. Syst. Bot. 7: 300–313.

———, AND ———. 1983. Distribution of sexual and apomictic populations of *Antennaria parlinii*. Evolution 37: 555–561.

BEALS, E. W. 1968. A taxonomic continuum in the genus *Antennaria* in Wisconsin. Amer. Midl. Naturalist 79: 31–47.

———, AND R. F. PETERS. 1966. Preliminary reports on the flora of Wisconsin no. 56. Compositae V-Compositae family, tribe Inuleae (*Antennaria, Gnaphalium, Anaphalis, Inula*). Trans. Wisconsin Acad. Sci. 55: 223–242.

CRONQUIST, A. J. 1945. Notes on the Compositae of the northeastern United States. I. Inuleae. Rhodora 47: 182–184.

DIXON, N. J. 1981. BMDP statistical software. Berkeley, California: Univ. of California Press.

DORN, R. D. 1977. Flora of the Black Hills. Authors. 377 p.

GREENE, E. L. 1898. New or noteworthy species. Pittonia 3: 347–8.

GRANT, V. 1981. Plant Speciation (2nd ed.) New York: Columbia.

GUSTAFSSON, Å. 1947. Apomixis in higher plants. Acta Univ. Lund. Kungl. Fysiogr. Sallsk. Handl. N. R. Avd. 2. 42–44: 1–370.

HARLAN, J. R., AND J. M. J. DEWET. 1963. The compilospecies concept. Evolution 17: 497–501.

HIESEY, W. M., AND M. A. NOBS. 1982. Experimental studies on the nature of species. A VI. Interspecific hybrid derivatives between facultatively apomictic species of bluegrasses and their responses to contrasting environments. Publ. Carnegie Inst. Wash. 636: 1–119.

HYYPIO, P. A. 1952. *Antennaria rosea* Greene in the Lake Superior region. Rhodora 54: 291.

JENSEN, R. J., AND W. H. ESHBAUGH. 1976a. Numerical taxonomic studies of hybridization in *Quercus*. I. Populations of restricted areal distribution and low taxonomic diversity. Syst. Bot. 1: 1–9.

———, AND ———. 1976b. Numerical taxonomic studies of hybridization in *Quercus*. II. Populations with wide areal distributions and high taxonomic diversity. Syst. Bot. 1: 10–19.

JUEL, H. O. 1900. Vergleichende Untersuchungen über typische und parthenogenetische Fortpflanzung bei der Gattung *Antennaria*. Kongl. Svenska Vetenskaps-akad. Handl. 33(5): 1–59.

MCINTOSH, A. C. 1931. A botanical survey of the Black Hills of South Dakota. Black Hills Engineer. 19(3): 159–276.

MARQUIS, R. J., AND E. G. VOSS. 1981. Distributions of some western North American plants disjunct in the Great Lakes region. Michigan Bot. 20: 53–82.

Rohlf, F. J., J. Kishpaugh, and D. Kirk. 1974. Numerical taxonomy system of multivariate statistical programs. Stony Brook, New York: State Univ. of New York.

Sneath, P. H. A., and R. R. Sokal. 1973. Numerical Taxonomy. San Francisco: W. H. Freeman and Co.

Stebbins, G. L. 1932a. Cytology of *Antennaria*. I. Normal species. Bot. Gaz. (Crawfordsville) 94: 134–151.

———. 1932b. Cytology of *Antennaria*. II. Parthenogenetic species. Bot. Gaz. (Crawfordsville) 94: 322–345.

Wells, P. V. 1970. Postglacial vegetational history of the Great Plains. Science 167: 1574–1582.

Whitehead, D. R. 1972. Approaches to disjunct populations: the contribution of palynology. Ann. Missouri Bot. Gard. 59: 125–137.

THE OHIO STATE UNIVERSITY
DEPARTMENT OF BOTANY
COLUMBUS, OHIO, 43210.

DISTRIBUTION AND EXTENT OF *PINUS RESINOSA* AIT. IN NEWFOUNDLAND[1]

B. A. ROBERTS

ABSTRACT

Red pine, the rarest coniferous tree species in Newfoundland, was earlier known from only eight locations of unknown ecological and mensurational characteristics. This study identifies 20 stands in three distinct geographic areas. Stands range from a few trees of varying density to those exceeding 100 ha containing several thousand trees. Red pine is found principally on coarse-textured sands and gravels of glacial outwash or lake bottom material, but is not entirely thus restricted, as two stands (Charles Arm and near Birchy Lake) are growing on bedrock or shattered bedrock with some mor humus cover. Repeated large wildfires around the turn of the century and more recently in 1946, 1961, 1977 and 1979, gravel extraction, and severe competition from more shade-tolerant coniferous trees have contributed to its decline.

Key Words: Red pine, rare plant, distribution, Newfoundland

INTRODUCTION

Red pine, *Pinus resinosa* Ait., is presently the rarest indigenous coniferous tree species in Newfoundland. Prior to this study the ecological status of the present red pine stands and their locations were relatively unknown. The object of this study was to locate and verify the number and extent of rare red pine stands, and make recommendations for preservation and future utilization of the species.

Red pine once occupied a greater range in Newfoundland than it does today, especially after the Wisconsin glaciation when there was a greater abundance of coarse-textured sand and gravel sites, which is the preferred habitat (Roberts, 1981). The post-glacial pine period (Fernald, 1911, 1925, 1933; Dansereau, 1953; Field and Coddington, 1980) involved successful migration of drought-tolerant *Pinus resinosa* from coastal New England to Newfoundland via a land bridge at Sable Island.

The marine limit of the West Coast lowland related to the Wisconsin (Roberts, 1983) is approximately 130 m (Grant, 1969) and

---

[1] Aspects of this paper were presented at the Canadian Botanical Association Annual Meeting held at Guelph, June 7 11, 1981. Abstract published: No. 37, p. 44.

decreases southward. Concentrations of red pine around Sandy Lake, Newfoundland, for example, are presently less than 100 m in elevation, which suggests that red pine could not have survived at present locations until later when the coastline uplifted; thus present populations are definitely post-glacial.

Although the existence of nunataks and related features proposed by Fernald (1925) has been substantiated (Grant, 1969, 1977; Brookes, 1970, 1982), there is little chance that red pine could have survived in the Alpine nunataks of the Long Range Mountains. Elevations greater than 700 m with a cold, harsh climate would prevent establishment and growth. Robertson and Roberts (1982) did not even list white pine (*Pinus strobus* L.) in these nunatak areas, yet white pine is known to have a greater ecological amplitude than red pine.

In addition to alpine refugia, Ives (1978) mapped a coastal nunatak in the central northeastern part of the Island. This area is reasonably close to an existing red pine stand but this stand owes its existence to the more central localities. It would be difficult for red pine to migrate against the prevailing wind and it is certain that this red pine site, which is ≤5 m above sea level at present, was under water during the early Wisconsin.

The land bridge dispersal corridor appears to be the most plausible explanation for distribution of red pine in Newfoundland. The post-glacial pine period which is known (Holland, 1981) outweighs, I believe, the uncertain conditions that red pine could have survived at the alpine or other plant refugia sites. In using lower plants which are typical of alpine refugia, however, Belland and Brassard (1980) and Brassard (1983) suggested that the nunatak theory works well for the bryophyte group in the Long Range Mountains of western Newfoundland.

METHODS USED IN LOCATING STANDS

The first task of this study was to establish the location of red pine stands outlined in the general map (Damman, 1976). Natural colour airphotos at a scale of 1:12,500, and black and white airphotos at a scale 1:50,000 were assembled for the general areas outlined by Damman (1976). These general areas were visited in the fall of 1978. All but one of the eight locations were known to me through my past forestry experience and were in easily accessible areas. The seven red pine stands were plotted on 1:50,000 and 1:250,000 topographic maps and were given a stand name and map reference.

I thought at the time that there was no more than the one remaining stand; however, in conversations with various forestry-related people, a suggestion that there likely were more stands always seemed to surface. I began a series of interviews with people in communities nearby the known red pine stands. I asked former loggers and woods personnel if they knew of any stands of pine. Most of the respondents stated that they did, but could not answer whether they were red pine or white pine (*Pinus strobus*), or even planted Scots pine (*Pinus sylvestris* L.). On many occasions, journeys led to stands of white or planted Scots pine; however, the Mint Brook and Traytown stands, both representing new locations, were located using this method.

Key forestry personnel assisted greatly with their knowledge of certain stand locations and logistics for reaching those stands. In addition, the kind cooperation of all forest industry and government personnel was very evident. Helicopter trips to remote stands were on most occasions a courtesy of the Provincial Department of Forestry on their way to fires, insect sampling or other Provincial matters.

Field work commenced in the fall of 1978 and continued through summer and fall of 1979 to 1983 with the same techniques. Areas having stands were traversed to determine whether there were possible separate stands between known localities. Time expended in the field including travel time was as follows: 1977—six days; 1978—90 days; 1979—106 days; 1980—80 days; 1981—31 days; 1982—86 days and 1983—30 days. Field work was conducted while I worked on three field studies as part of soils and autecology projects of the Newfoundland Forest Research Centre.

RANGE IN NORTH AMERICA

The range of red pine extends from Newfoundland, the Maritime Provinces and Quebec, west to Ontario and southeastern Manitoba, south to northeastern Minnesota, Wisconsin, Michigan, Illinois, northern Pennsylvania, New York, Connecticut and Maine (Rudolf, 1957; Horton and Bedell, 1960; Fowells, 1965; Critchfield and Little, 1966; Mirov, 1967; Stiell, 1978). The area of its natural distribution is bounded by latitudes 44–50° N, (2400 km) and longitudes 60–95° W (800 km). Isolated patches occur in northeastern Illlinois and locally in northeastern West Virginia. The altitudinal range is sea level to 800 m with two locations in West Virginia which are at 1150 and 1300 m (Rudolf, 1957). In Newfoundland, red pine occurs at elevations of 5–300 m.

PAST AND PRESENT DISTRIBUTION IN NEWFOUNDLAND

The earliest recorded map showing the general range of red pine (Fernald, 1911) is shown as it appeared in Rhodora 13: Plate 89.8 (Figure 1). The map is fairly accurate considering that Fernald visited the interior by rail and the coastline by boat at that time. The range of red pine shown by Rudolf (1957) indicated a more diminished range, which did not include the northwestern central stands. Horton and Bedell (1960) showed two concentrations of red pine but the locations are obviously incorrect. Fowells (1965) provided a more accurate distribution of two concentrations of red pine, as did the general distribution of Mirov (1967). The most detailed map showing distribution of red pine prior to this study is that of Damman (1976), who gave eight locations in two lines of occurrence.

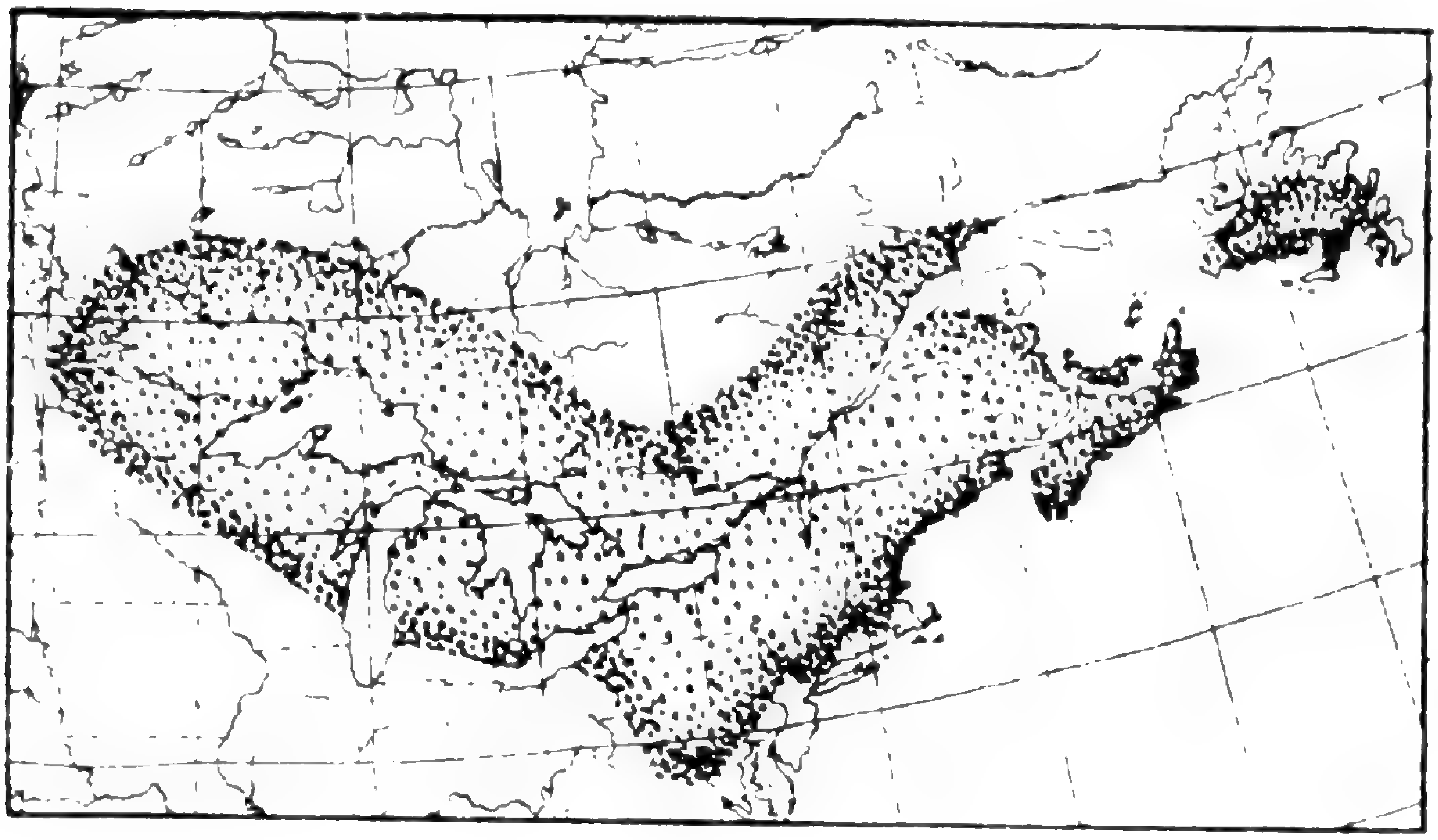


Figure 1. The distribution of *Pinus resinosa* Ait. (Fernald, 1911).

This study has identified some 20 stands (Table 1, Figure 2) along three distinct lines of occurrence: I) northwestern central Newfoundland (11 stands, Figure 3); II) central Newfoundland (two stands, Figure 4); and, III) northeastern central Newfoundland (seven stands, Figure 5). The stands vary from a few scattered trees or clumps of trees to stands exceeding 100 ha containing several thousand trees (Table 1, Figure 6). The number of individual stands added in the west-north-central line near Sandy Lake and in the east-central line from Terra Nova to the east coast of Bonavista Bay are not quite as significant as the two stands that occur along the Exploits River area in the coastal area of Charles Arm. These latter stands had not been previously recorded. The Charles Arm site (outside Fernald's 1911 map), and the Old Stands (all trees ≥ 225 years old) east of Birchy Narrows represent two red pine sites not restricted to dry sandy soils as reported by Damman (1976). The red pine at Charles Arm is growing on exposed coastal diritic rocks (Figure 7), and the old stand east of Birchy Narrows is growing on mor humus (10–15 cm) over shattered silicic and basic volcanic rocks (Figure 8).

Older residents (Mr. T. Curran, pers. comm.) from the region indicated that the seven stands in northeast central Newfoundland (line III) were previously contiguous. Prior to the large forest fires in the late 1890's, 1904 and 1946, red pine grew right to the coast in this part of its range. Red pine were cut for railway ties and structural timber throughout the Terra Nova and Gambo areas from the turn of the century. Extraction of gravel and fill for railway road beds and later the Trans-Canada Highway have also contributed to decline of the species.

Fernald (1911), journeying by train, identified stands of red pine just east of Howley at the Goose Ponds; however, he did not quantify the number (their extent). This site is obviously the Howley Stand (H) (Table 1, No. 1) near the railway line at Goose Ponds of Steadies, the western-most red pine site in Newfoundland. In Fernald's other trips to Newfoundland he did not record much on red pine distribution though he used the species to further support the land bridge theory.

It was pointed out above that alpine nunataks were not ecologically suitable for red pine. Red pine stand origin can best be related to a gradual migration into the northern and eastern limit of its range. In support of the ecological requirements of red pine, Damman (1983) indicated that *Pinus resinosa* and a number of angiosperms are restricted to central Newfoundland, his Ecoregion II. Ecoregion II has the highest mean annual maximum temperature for Newfoundland, ~ 30° C (Damman, 1976). This study shows that the two red pine stands at Charles Arm and Traytown fall within Damman's (1983) Ecoregion III, the North Shore. Perhaps some refinement of the Ecoregion lines based on the new red pine distributions is warranted.

PALYNOLOGICAL STUDIES

There have been only a few palynological investigations in Newfoundland, recently summarized by Macpherson (1981, 1982). Earlier studies from three bog sites on the Avalon Peninsula (Terasmae, 1963) suggested that red pine may have been more generally distributed and abundant in early post-glacial time in Newfoundland. These studies also indicated that the now rather erratic occurrence of red pine is mostly attributable to greater development of shade-tolerant coniferous forest, bogs, heaths or mesic conditions which have effectively eliminated pine from most sites. However, Macpherson (1981) did not find enough pine pollen in two sites in the northeastern Avalon region to suggest the local presence of the tree. Both these sites, however, are not in the mapped distribution of red pine (Fernald, 1911).

In the central part of the island near the coast (Macpherson, pers. comm.) there is sufficient pine pollen (not yet differentiated as to red or white) to indicate that pines were much more common in the central region than in the Avalon region of Newfoundland. The approximate dates of the pine pollen deposits ranged from 6–7000 years B.P.

RESERVE AREAS

Because of its relative rarity, there has been some movement to protect the remaining red pine in Newfoundland. In 1978 the Pine Acres or Grants Siding area was designated as a development area and under the Development (Areas) Land Act. The Provincial Department of Forestry and Agriculture subsequently took legislative action to protect and conserve this important stand of red pine.

Table 1. Natural red pine stand locations, map and air photo references, extent and estimates of the number of trees in each stand.

	Stand name	Map reference	1:50,000 Map sheet	Air photo 1:12,500	Approx. area* (ha)	Approx. No. of trees
1.	Howley (H)	932-468	12 H 3 Deer Lake	NF 78040-68	< 15 ha	< 650
2.	Sandy Lake (SL1)	950-475	12 H 3 Deer Lake	NF 78040-69	< 20 ha	< 1000
3.	Sandy Lake (SL2)	963-486	12 H 3 Deer Lake	NF 78040-128	< 5 ha	< 250
4.	Sandy Lake (SL3)	988-498	12 H 3 Deer Lake	NF 78040-125	< 5 ha	< 350
5.	Sandy Lake (SL4)	023-528	12 H 2 The Topsails	NF 78041-26	< 5 ha	< 200
6.	Sandy Lake (SL5)	033-535	12 H 2 The Topsails	NF 78041-150	< 5 ha	< 200
7.	Sandy Lake (SL6)	047-541	12 H 2 The Topsails	NF 78041-203	< 5 ha	< 200
8.	Sandy Lake (SL7)	055-548	12 H 2 The Topsails	NF 78041-202	< 10 ha	< 250
9.	Birchy Narrows (BN)	098-588	12 H 7 Sheffield Lake	NFA 31077-9	< 1 ha	< 25
10.	Old Stand (OS)	207-632	12 H 7 Sheffield Lake	NF 78058-58	< 1 ha	< 15
11.	Rowsells Brook (RB)	489-582	12 H 8 Springdale	NFA 31076-164	< 200 ha	< 3000
12.	Exploits River (ER)	147-319	2 E 3 Botwood	NFA 31034-5	< 1 ha	< 15
13.	Charles Arm (CA)	246-687	2 E 5 Point Leamington	NFA 31106-73	< 5 ha	< 300
14.	David Smallwood Pk (DSP)	042-090	2 D 16 Gambo	NF 78018-1	< 5 ha	< 150
15.	Mint Brook (MB)	007-017	2 D 9 Glovertown	NFA 31109-142	< 1 ha	< 15
16.	Pine Acres (Grants Pit) (PA)	080-015	2 D 9 Glovertown	NFA 311069-154 **	< 400 ha	< 5000
17.	Traytown (TT)	948-798	2 C 12 Eastport	NFA 31108-79	< 5 ha	< 50
18.	Georges Pd. (GP)	889-753	2 D 9 Glovertown	NF 78030-125	< 20 ha	< 500
19.	Terra Nova 1 (TN1)	060-756	2 D 9 Glovertown	NFA 31096-177	< 2 ha	< 50
20.	Terra Nova 2 (TN2)	034-750	2 D 8 Port Blandford	NFA 31096-180	< 50 ha	< 250
TOTALS					< 761 ha	< 12470

*Area of the land form

**< 100 ha is reserved by the provincial government with the remaining 300 ha privately owned.

Figure 2. The present distribution of *Pinus resinosa* Ait. showing the geographical area of 20 stands in three lines of occurrence.

The red pine stand at David Smallwood Park is also protected under the Provincial Parks legislation. The small red pine stand at Birchy Narrows is now a privately owned park which offers some protection as well. As a result of this present study a recommendation has been given to the new Wilderness and Ecological Reserve Advisory Council to include most of the red pine stands as ecological reserves, especially the stands at Charles Arm, Rowsells Brook, the Old Stand and some of the stands along Sandy Lake.

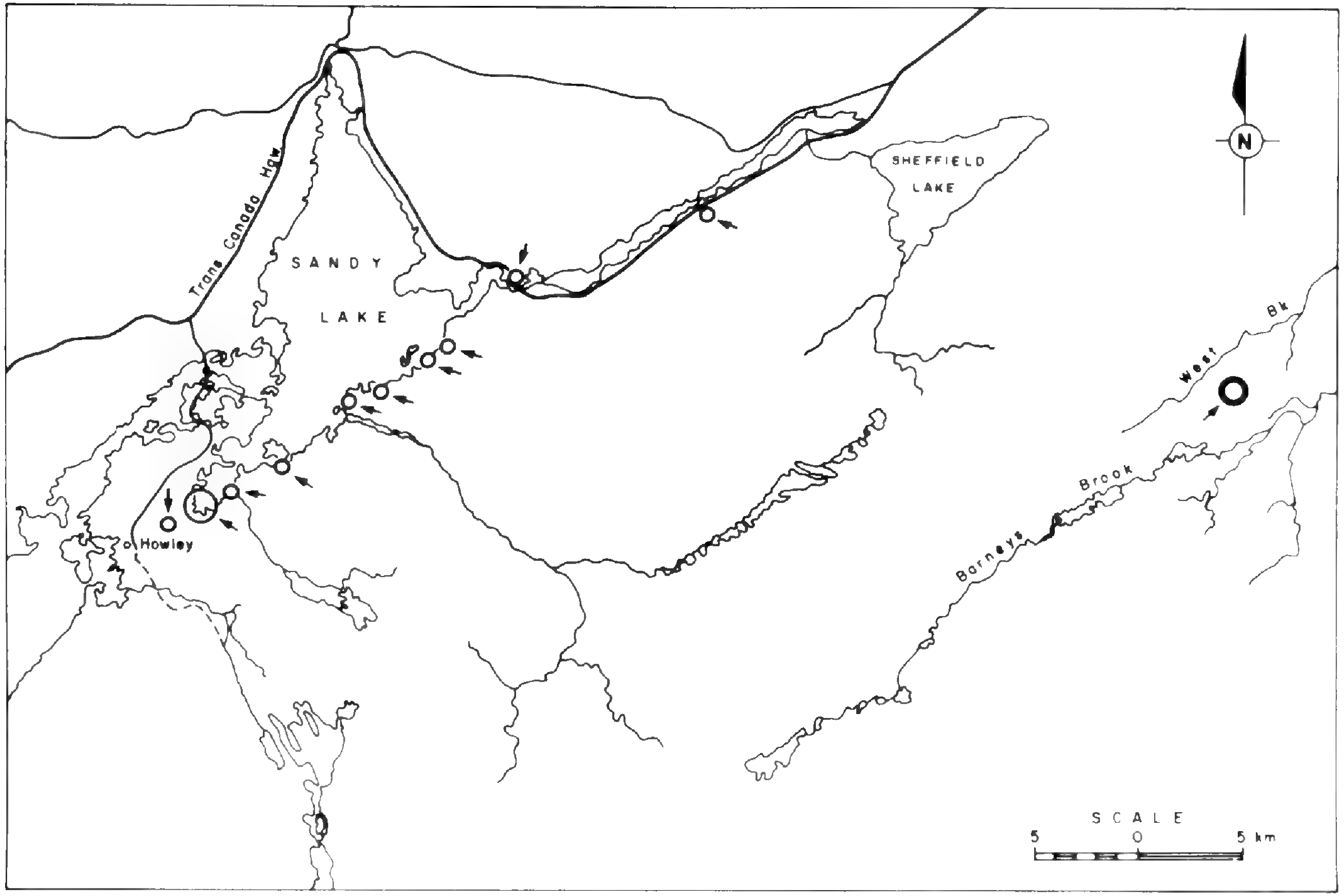


Figure 3. Detailed map showing the 11 stands of *Pinus resinosa* Ait. in northwestern central Newfoundland, geographical line I.

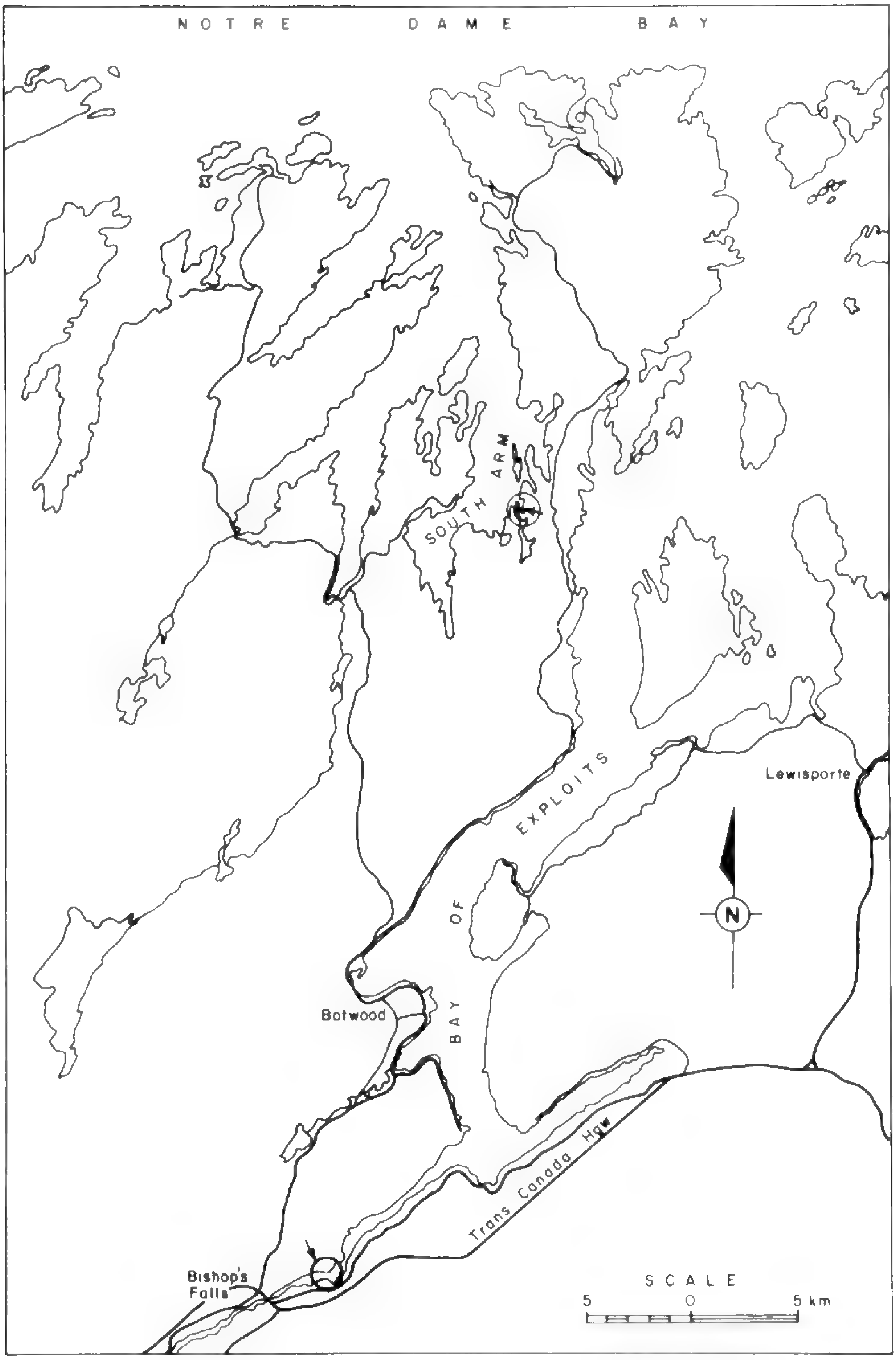


Figure 4. Detailed map showing the two stands of *Pinus resinosa* Ait. in central Newfoundland, geographical line II.

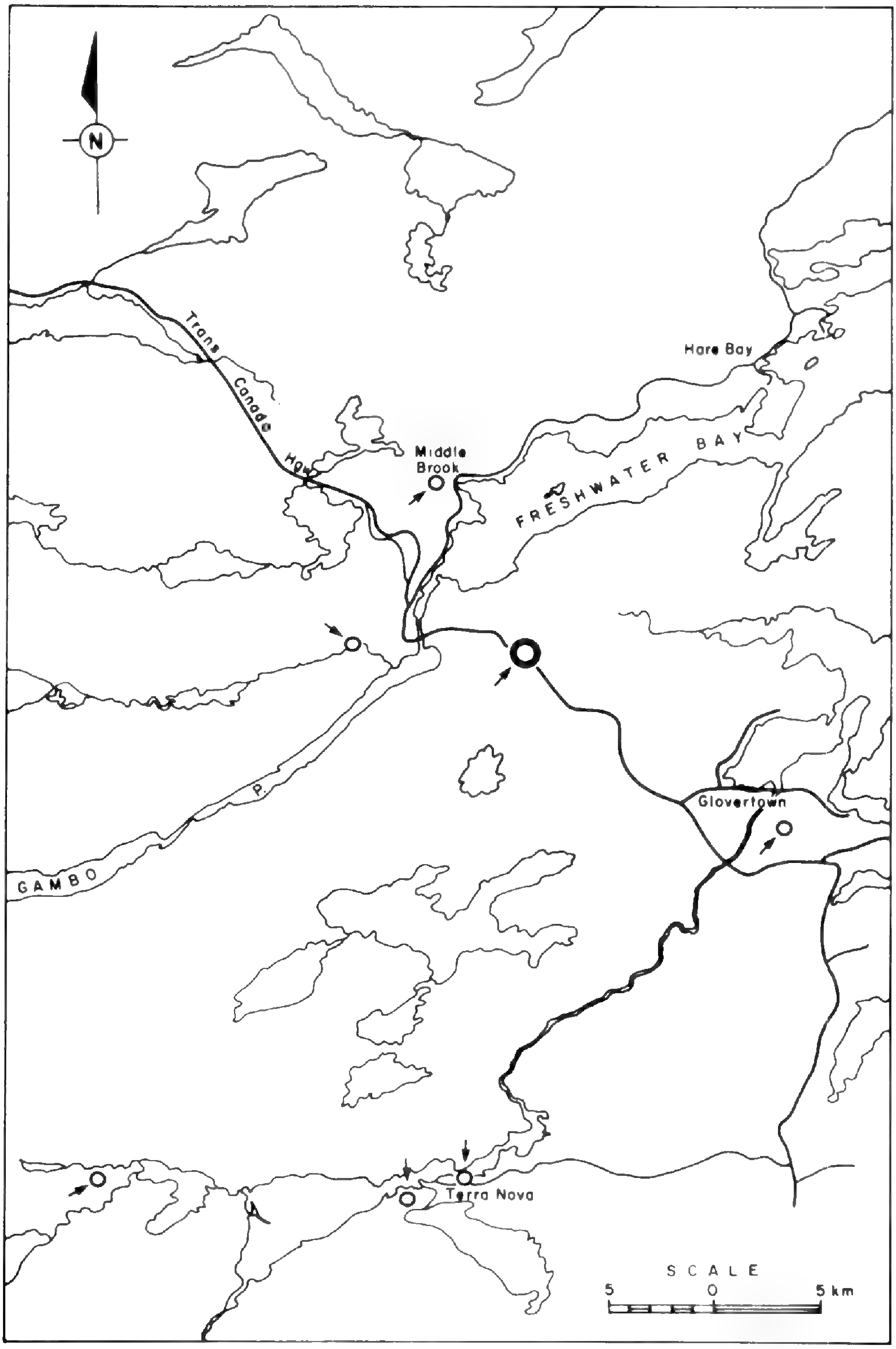


Figure 5. Detailed map showing the seven stands in northeastern central Newfoundland, geographical line III.

Figure 6. Typical open grown red pine stand at Sandy Lake on dry coarse-textured lake bottom material. The ground vegetation is dominated by the shrub *Kalmia angustifolia*. The lichens *Cladina stellaris* and *C. rangiferina* give the white mottled effect.

ACKNOWLEDGMENTS

I am grateful to many of the Provincial Forestry Unit Foresters, the pulp and paper forestry personnel, the Canadian Forestry Service and members of the general public who have contributed to this study. In particular I would like to acknowledge the following: Mr. M. Squires, former Chief Forester, Abitibi-Price, and Mr. W. A. Dickson, former Chief Forester of Bowater Newfoundland Limited. From the Provincial Forestry Department: Mr. L. Lavers, Mr. N. Turner, Mr. D. Joy, Mr. L. Boyd, Mr. D. Mifflin, Mr. E. Blackmore, Mr. D. Elliott, and Mr. A. Kelly who aided greatly with the knowledge of certain stands and logistics. I have benefited greatly in discussion about red pine with Dr. Guy R. Brassard, Dr. L. K. Thompson, Dr. D. Bajzak, Dr. R. Lee, Dr. A. W. H. Damman, Dr. J. B. Macpherson, Dr. M. A. K. Khalil, Mr. W. J. Meades, Mr. A. W. Roberston, Mr. A. B. Case, Mr. G. Milne, Mr. M. Chalil, Mr. J.

Figure 7. Coastal red pine stand at Charles Arm growing on bedrock. **A.** face view. **B.** profile view.

Figure 8. Old Stand of red pine growing on shattered bedrock near Birchy Lake. The trees in this stand are greater than 250 years old. **A.** face view. **B.** view at right angles to A.

P. Bouzane, Mr. R. S. van Nostrand, Mr. L. J. Clarke and Mr. T. Curran. I especially acknowledge Ms. B. A. Janes for her excellent technical assistance and Ms. M. F. Gillingham and Ms. B. M. Bartlett for expertly typing the manuscript.

LITERATURE CITED

Belland, R. J., and Guy R. Brassard. 1980. A major range for *Encalypta longicolla*. The Bryologist 83: 563.

Brassard, Guy R. 1983. Bryogeography with special references to mosses. *In:* Biogeography and Ecology of the Island of Newfoundland. G. R. South (Ed.) Monographiae Biologicae 48: 361–384. Dr. W. Junk Publishers, The Hague.

Brookes, I. A. 1970. New evidence for an independent Wisconsin-age ice cap over Newfoundland. Canad. J. Earth Sci., 7: 1374–1382.

———. 1982. Ice marks in Newfoundland: A history of ideas. Geographie physique et quaternaire XXXVI: 139–163.

Critchfield, W. B., and E. L. Little, Jr. 1966. Geographic distribution of the pines of the world. U.S. Dept. of Agriculture. Miscellaneous Pub. 991, Forest Service, p. 11, Map No. 26.

Damman, A. W. H. 1976. Plant distribution in Newfoundland especially in relation to summer temperatures measured with the sucrose inversion method. Canad. J. Bot. 54: 1561–1585.

———. 1983. An ecological subdivision of the Island of Newfoundland. *In:* Biogeography and Ecology of the Island of Newfoundland. G. R. South (Ed.) Monographiae Biologicae 48: 163–206. Dr. W. Junk Publishers, The Hague.

Dansereau, P. 1953. The post-glacial pine period. Transactions of the Royal Society of Canada XLVII, Series III, Section V: 23–38.

Fernald, M. L. 1911. A botanical expedition to Newfoundland and southern Labrador. Rhodora 13: 109–162.

———. 1925. Persistence of plants in unglaciated regions of Boreal America. Mem. Amer. Acad. Sci. N.S. 15: 237–242.

———. 1933. Recent discoveries in the Newfoundland flora. Rhodora 35: 80–107.

Field, K. G., and J. Coddington. 1980. Rare plant species in Massachusetts. Rhodora 82: 151–162.

Fowells, H. A. 1965. Red pine (*Pinus resinosa* Ait.). Silvics of Forest Trees of the United States. U.S. Dept. of Agriculture, Agriculture Handbook No. 271: 432–446.

Grant, D. R. 1969. Late pleistocene re-advance of piedmont glaciers in western Newfoundland. Maritime Sediments 5: 126–128.

———. 1977. Glacial style and ice limits, the quaternary stratigraphic record, and changes of land and ocean level in the Atlantic Provinces, Canada. Geographie physique et quaternaire XXXI: 247–260.

Holland, P. G. 1981. Pleistocene refuge areas, and the revegetation of Nova Scotia. Progress in Physical Geography 5: 535–562.

Horton, K. W., and G. H. D. Bedell. 1960. White and red pine. Ecology, Silviculture and Management. Canada Dept. of Northern Affairs and National Resources, Forestry Branch, Bulletin 124.

Ives, J. D. 1978. The maximum extent of the Laurentide ice sheet along the east coast of North America during the last glaciation. Arctic 31: 1–33.

Macpherson, J. B. 1981. The development of the vegetation of Newfoundland and climatic change during the Holocene. *In:* The Natural Environment of Newfoundland Past and Present. A. G. Macpherson and J. B. Macpherson (Eds). 189–217. Dept. of Geography, Memorial University of Newfoundland, St. John's, Nfld.

———. 1982. Post-glacial vegetational history of the eastern Avalon Peninsula, Newfoundland and Holocene climatic change along the eastern Canadian seaboard. Geographie physique et quaternaire XXXVI: 175–196.

Mirov, N. T. 1967. The Genus *Pinus*. The Ronald Press Co., New York.

Roberts, B. A. 1981. Ecology of red pine in Newfoundland. I. Location and extent. Paper presented at Canadian Botanical Association Meeting and Symposium. Abstract No. 37, p. 44.

———. 1983. Soils. *In:* Biogeography and Ecology of the Island of Newfoundland. G. R. South (Ed.) Monographiae Biologicae 48: 107–161. Dr. W. Junk Publishers, The Hague.

Robertson, A. W., and B. A. Roberts. 1982. Checklist of the Alpine flora of Western Brook Pond and Deer Pond areas, Gros Morne National Park. Rhodora 84: 101–115.

Rudolf, P. O. 1957. Silvical characteristics of red pine (*Pinus resinosa* Ait.). Lake States For. Exp. Station. Paper No. 44. USDA.

Steill, W. M. 1978. Characteristics of eastern white pine and red pine. *In:* White and Red Pine Symposium: 7–51. Great Lakes Forest Res. Centre, Sault Ste. Marie, Ontario, 0-P-6.

Terasmae, J. 1963. Three C-14 dated pollen diagrams from Newfoundland, Canada. Adv. Frontiers Plant Sci. 6: 149–162.

SOILS-AUTECOLOGY
NEWFOUNDLAND FOREST RESEARCH CENTRE
CANADIAN FORESTRY SERVICE
P.O. BOX 6028
ST. JOHN'S, NEWFOUNDLAND
CANADA A1C 5X8

CHANGES IN THE STANDING CROP OF EELGRASS, *ZOSTERA MARINA* L., AT CAPE ANN, MASSACHUSETTS, SINCE THE EPIDEMIC OF 1932

RALPH W. DEXTER

ABSTRACT

Over a period of 52 years (1933–84) 43 annual surveys were made to monitor changes in the abundance and distribution of eelgrass (*Zostera marina*) at Cape Ann, Massachusetts. Intensive observations were made throughout the length of the Annisquam Tidal River and adjacent coves in Annisquam Harbor. After the epidemic of eelgrass disease (1930–32), eelgrass persisted only as a small patch in Goose Cove. Gradually additional patches appeared in the Annisquam System and a peak was reached in 1971–72, then eelgrass declined during 1973–77, with a recovery during 1978–82. This recovery was followed by almost total disappearance again in 1984.

Fluctuations in annual precipitation, with consequent changes in salinity, were not always related to changes in eelgrass abundance. Wet years were favorable for the growth and spread of eelgrass, but with the exception of drought years related to a general epidemic along the north Atlantic coast (1930 and 1941), dry years did not retard eelgrass recovery at Cape Ann.

Key Words: *Zostera marina*, marine ecology, sea grass, Cape Ann, Mass.

INTRODUCTION

In 1930–32 a wasting disease caused by a slime mold (*Labyrinthula* sp.) wiped out nearly all beds of eelgrass (*Zostera marina*) along the entire Atlantic Coast from Maine to Florida. Recovery has been slow, but in recent years it has fully returned in some localities. At Cape Ann, Mass., recovery has been very slow, never complete, and has had periodic recessions. Only two coves (Upper Goose Cove and Upper Lobster Cove) had complete recovery after 50 years. In 1984 another epidemic occurred which again nearly eliminated all eelgrass from this area.

Periodic surveys (43 annual surveys, 1933–84) were conducted in order to obtain a long-term picture of *Zostera* population fluctuations in the Cape Ann area. Observations were made from the shoreline and from a shallow-draft skiff during low tide along the entire length of the Annisquam Tidal River. During certain years the coves of Annisquam Harbor were also included. Small patches were measured and the area of large patches was estimated. Bottom dredging in deeper water occasionally brought up single plants, but eelgrass was largely confined to the shoreline. Detailed results have been published through 1952 (Dexter, 1944, 1945, 1946, 1947, 1950, 1951, 1953). Since then, marked increases have been noted in some areas, with peak return in 1971–72, followed by a gradual decline between 1973–77, a gradual restoration during 1978–82, followed by the epidemic of 1984.

Periods of greatest decline on the North Atlantic Coast have been recorded for 1854, 1889, 1894, 1908, 1915, 1921, 1930–32, and 1941, usually following severe drought, perhaps because at these periods coastal water became more saline (Martin, 1954), and at times of extreme north declination of the moon (Stevens, 1936; 1939). Wheat (1962) pointed out that eelgrass declines seem to follow solar cycles fairly well, while Rasmussen (1976) and Phillips (1982) believed that warmer sea water was the cause of epidemics. Some of the periodic reports of the standing crop of eelgrass showing major changes along the northeastern coast of North America other than Cape Ann have been published by Cottam (1933, 1945), Renn (1936, 1937), Lynch and Cottam (1937), Cottam and Addy (1947), Stevens, Ellis and Stevens (1950), Orth (1976), and Orth and Moore (1983). The latter reported similar fluctuations of sea grasses for Chesapeake Bay as reported here for the Annisquam inlet at Cape Ann.

This paper summarizes changes in abundance and distribution observed in eelgrass beds at Cape Ann, Massachusetts, over a period of 52 years, and shows that differences in annual precipitation with consequent changes of salinity, long thought to be a major factor, may be only one parameter concerned, and not necessarily always relevant to population changes in this particular area.

SYNOPSIS OF ANNUAL SURVEYS AT CAPE ANN

Following the epidemic of 1930–32 eelgrass survived at Cape Ann only as a small patch in Goose Cove (*see* Figure 1 for localities mentioned). Gradually small scattered clumps appeared in adjacent areas, and increased in Goose Cove where maximum growth was attained by 1949 (total area 5.8 ha).

In 1952, this stand was completely destroyed by impoundment of freshwater behind a temporary dam. With removal of the dam, eelgrass reappeared in 1953 and increased each year, reaching a

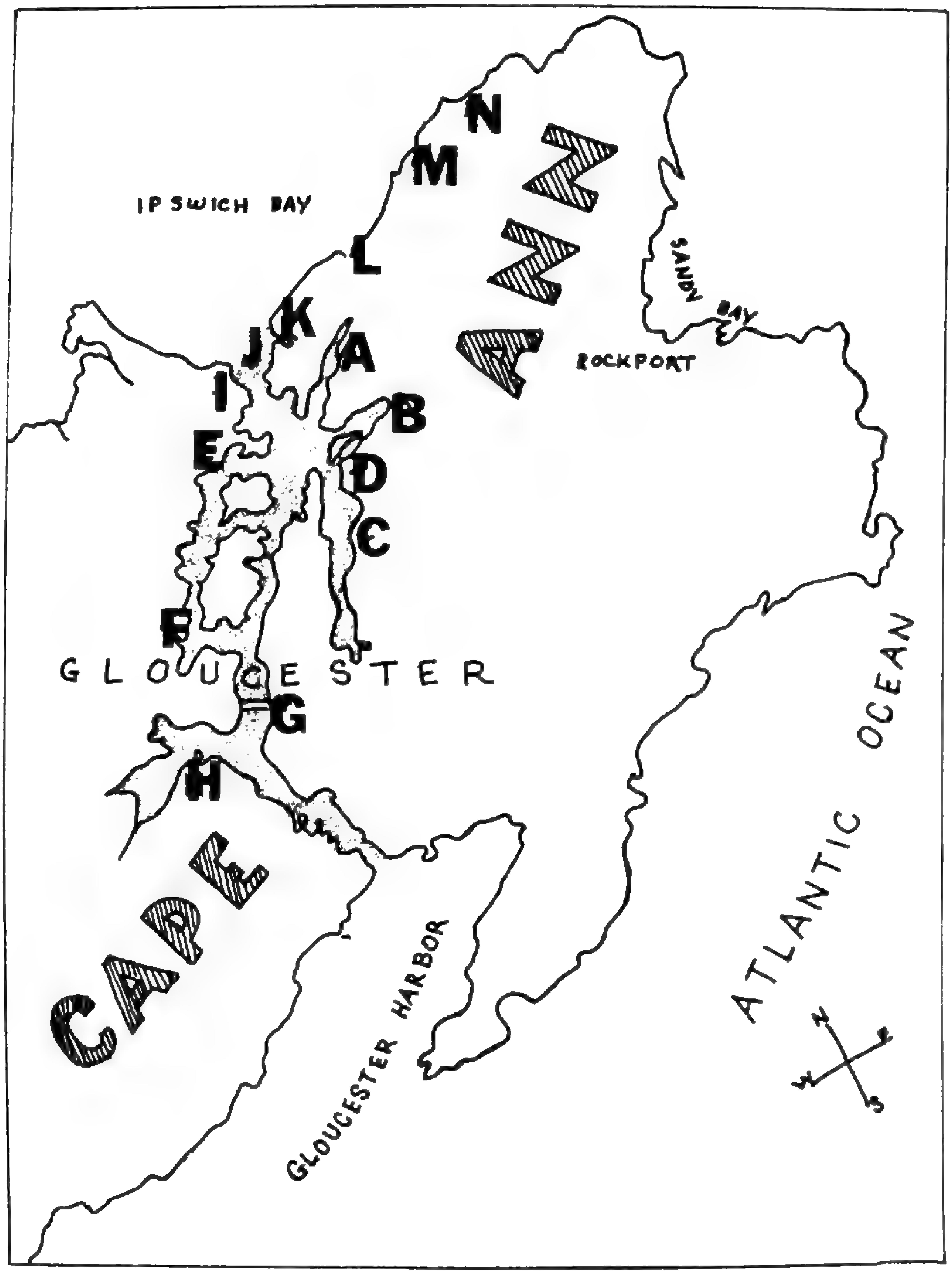


Figure 1. Map of Cape Ann, Mass., with tidal inlet (Annisquam River) running between Ipswich Bay and Gloucester Harbor. **A** = Lobster Cove; **B** = Goose Cove; **C** = Mill River; **D** = Back Creek; **E** = north Section of Jones Creek; **F** = south section of Jones Creek; **G** = A. Piatt Andrew Bridge; **H** = Little River; **I** = Wingaersheek Beach; **J** = Annisquam Harbor; **K** = Lighthouse Cove; **L** = Diamond Cove; **M** = Hodgkins Cove; **N** = Plum Cove.

maximum stand again in 1963, which remained until 1984 when only one patch of 36m² of eelgrass was found.

Since 1963 outer Goose Cove had about 50% of the subtidal bottom (total area 0.4 ha) covered with eelgrass until 1967 when it disappeared from the central basin. Small patches persisted around the margins, reaching best recovery in 1970, but they declined to scattered marginal patches on occasional years. Growth around the margins was restored to about 50% by 1980–81, but disappeared by 1984.

The growth in the upper end of Lobster Cove increased rapidly from 29 patches (16m²) in 1962 to cover about 25% of the subtidal bottom in 1964 (total area 1.3 ha), about 50% of the bottom in 1965, and about 75% cover in 1967. It then declined to 50% cover in 1969, but increased to about 75% cover during 1971–75. In 1976 it was reduced again to 50% cover and further reduced the next year to about 25% coverage, but returned to 50% coverage in 1978, increasing in 1979 to 75% cover. A solid stand became established in 1980–81, but it disappeared in 1984.

By 1966, a narrow fringe of eelgrass was found around the basin of outer Lobster Cove, but after 1974, it was reduced to a few small patches which remained until 1984.

In upper Mill River, one plant was found in 1947 and again in 1951. Several small patches were observed in 1953, which spread to form nearly continuous beds in the subtidal channel by 1965 (total area 2.0 ha). These beds declined about 50% during 1967–69, were back to nearly continuous beds in 1970, but were reduced to one patch by 1975. None has been found there since then.

In middle Mill River, scattered small patches in 1966 increased to a nearly continuous margin on both sides of the channel until 1970. After 1973, growth was restricted to the south border of Riggs Point in scattered patches, increasing annually and extending into the channel during 1979–81 (ca. 40m²), and disappeared by 1984.

In lower Mill River, scattered patches were found on the east side in 1967, with a large patch (ca. 12m²) on a sand bar at the mouth. These patches increased in 1975, were reduced in 1978 (largely replaced by green algae), then restored themselves in 1979–82, lasting until 1984.

In Back Creek (connecting Mill River with Goose Cove) patches of eelgrass were found at the southwest end in 1965 which increased to cover about 25% of the subtidal bottom by 1968 (total area 14m^2), about 50% by 1970, and were largely continuous in 1971. Scattered seedlings occurred in the remainder of the creek. From 1975 to 1978, eelgrass declined to a small number of scattered patches, but increased annually after that time to form a nearly continuous stand. At the northeast end of Back Creek where it joins Goose Cove, about 50% of the subtidal bottom was covered only during 1980 81 (total area 14m^2).

In Jones Creek, one seedling of eelgrass was found at the north end in 1954. Beginning in 1960, small clumps of scattered seedlings increased each year. One side channel (total area 50m^2) was about 25% covered in 1965, and was about 75% covered the following year.

In 1965, several small patches were located at the south end; they persisted through 1971, but all were gone by 1976. From 1979 to 1981, a narrow margin of eelgrass 15m long was found at the mouth of the north section of Jones Creek in the main channel of the Annisquam Tidal River.

Occasional fragments and a few plants were dredged from the main channel, north section, of the Annisquam River between 1934 and 1937. In 1958, 3 plants were dredged up; in 1963, 2 patches totaling 20m^2 were located; in 1966, 6 patches totalling 27m^2 were found. An increase was noticed each year until 1970; that year a narrow margin of eelgrass was found on the west side along the shore of Rust Island just north of the A. Piatt Andrew Bridge. From 1974 to 1976, small patches were observed in that same area on both sides of the channel, but these were gone the following year. However, they reappeared on the west side between 1979 and 1981, expanded by 1982, (ca. 80m^2), but were gone in 1984. A small patch was seen on the east side north of the bridge only in 1980 and 1981.

On the west side, south of the A. Piatt Andrew Bridge, a series of patches was found in 1970, which merged to form one large patch (ca. 80m^2) at the entrance to Little River in 1975; it remained through 1977, disappeared the following year, and was restored in 1980 and 1981. This patch declined again in 1982, was restored in 1983, but was gone in 1984. In 1981, a new patch of similar size on the opposite shore at the entrance to Little River was discovered; this patch lasted only three years.

In Little River, a side channel of the Annisquam Tidal River, the upper and lower sections never developed eelgrass. The upper section has no water during low tide. In middle Little River, a single patch of several plants was found in 1951. Ten years later a similar patch was located in the same place. Between 1962 and 1966, eelgrass expanded from a single small patch of $0.2m^2$ to about $210m^2$ in 50 patches. During 1968–70, 25% to 50% of the subtidal bottom (0.4 ha) was covered, but this stand subsequently declined. None was found after 1975 until it was largely restored in 1980 and 1981, when it was last observed.

In the south channel of the Annisquam River, no eelgrass has been observed from Little River to Gloucester Harbor since the epidemic of 1932.

Beginning in 1949, an annual survey was made of eelgrass at Wingaersheek Beach on the shores of Ipswich Bay. A two-meter-wide transect across the beach at or near spring low-water line was sampled each year. From 1949 to 1958, widely-spaced single plants or very small patches were observed. Leaves at this site never grow very long, probably because of the shifting sand, water currents, and surf. Also, from 1953 to 1965, single plants and small patches with short leaves were found in several shallow tidal pools at the upper level of the beach along the margin of the Annisquam River. With the exception of 1963, there was a general decline of eelgrass at the beach after 1958. Very little eelgrass remained in 1965, but there was a slight increase the following year. Severe winter storms in 1966–67, 1968–69, and 1977–78 wiped out most of the eelgrass at this beach. However, eelgrass did reappear in 1979, although little remained after that time. In 1984, Ellen Mellen (personal communication) found sparse growth still surviving when it was nearly all gone from the Annisquam inlet.

In Annisquam Harbor, occasional fragments and a few plants of eelgrass were dredged between 1956 and 1961. One seedling was found on the shoreline in 1956. During the decade of 1960–70, there was a gradual annual increase which was never very extensive.

In Lighthouse Cove (north of Annisquam Harbor), eelgrass increased from several patches and scattered small clumps in 1961 (total $8m^2$) to a broad band of continuous patches across the cove at spring low-water line by 1965 (ca. $1200m^2$). Over the next five years there was a general decline. In the summer of 1984, Ellen Mellen (personal communication) found eelgrass surviving in a broad band across the cove, the only thriving stand of eelgrass known from this area.

In Diamond Cove, extensive patches were found from 1955 to 1959. These patches remained rather stable through 1961, but declined approximately 50% in 1962, and then restored again the following year when nearly 50% of the subtidal bottom (ca. 400m^2) was covered along the spring low-water line. This recovery was then followed by a gradual decline through 1970.

Between 1955 and 1962, large patches developed in the center of Hodgkins Cove (ca. 80m^2); these patches remained until 1981, when they were last observed.

In Plum Cove, eelgrass increased from about 20m^2 to about 150m^2 between 1956 and 1963, remaining essentially the same through 1970.

RELATION OF PRECIPITATION TO CHANGES IN EELGRASS DENSITIES

Annual reports and occasional summaries of weather data are published by the U.S. Weather Bureau (National Climatic Data Center) on a calendar year basis (U.S. Dept. Agriculture 1931–32; U.S. Dept. Commerce, 1954–84, 1958). The mean annual precipitation for Cape Ann is 43.22 inches. Annual field surveys were made in the months of July–September. Precipitation records were analyzed for the preceding October through the following September. Unfortunately there are no continuous records of seawater salinity for Cape Ann, but at Boston, 30 miles south, salinity records reflect changing precipitation records at Cape Ann (i.e., higher precipitation resulted in lower salinity and vice versa). Mean annual salinity at Boston is 27.83$^0/_{00}$ (parts per thousand). It is clear from examination of weather records that during years of high precipitation [1933 (60.78 in.), 1938 (60.82 in.), 1946 (57.68 in), 1954 (63.02 in.), 1958 (57.45 in.), 1972 (60.41 in.)] eelgrass increased considerably in extent. Contrary to expectation, during some years of low precipitation [1947 (35.31 in.), 1950 (29.19 in.), 1957 (34.19 in.), 1965 (32.08 in.), 1980 (31,38 in.)] eelgrass often continued to increase slightly, but during the drought years of 1930 (32.04 in.) and 1941 (33.71 in.), eelgrass decline was drastic and widespread throughout the area. It seems generally true that very high precipitation, with consequent low salinity, was favorable for the growth and spread of eelgrass, but low precipitation (except for extreme records) was not detrimental to eelgrass recovery in the Cape Ann area during the period 1933–1984.

DISCUSSION AND CONCLUSIONS

Since 1932, only upper Goose Cove and upper Lobster Cove had reached a maximum stand of eelgrass following the epidemic. Gradual local increases through the years, with minor fluctuations, reached a peak in 1971 and 1972, with a general decline from 1973 to 1977, and a return to another peak from 1978 to 1983. By 1984, nearly all eelgrass was gone again.

Major declines over large geographic areas may be correlated with drought years, especially 1930 and 1941, but local variations in annual precipitation are not always reflected by eelgrass changes in a uniform manner. Periods of high precipitation were years of increasing eelgrass for the most part, and peak recovery was at a time of very high precipitation. However, periods of low precipitation were not generally characterized by decline of eelgrass. Except for drought years and wet years, local fluctuations were not clearly related to precipitation with consequent change of salinity. In addition to annual precipitation, other factors such as disease, turbidity, light reduction, and temperature changes probably influenced annual changes in the occurrence of eelgrass on Cape Ann.

ACKNOWLEDGMENTS

Many persons have aided with the field work, but special acknowledgment is made to Dr. William Beardslee, Dr. Thomas Hruby, Winthrop Davis, George Gleason and Ellen Mellen for their aid in this project, especially for information they provided when I was unable to be at Cape Ann. I am also indebted to George Robinson, Jr. and Richard Salo for precipitation data on Cape Ann, and to James R. Hubbard, Chief, Tidal Datums Section, Tides and Water Levels Branch, NOAA, for salinity records compiled at Boston, Mass.

LITERATURE CITED

Cottam, C. 1933. Disappearance of eelgrass along the Atlantic Coast. Plant Disease Reporter 17: 46–53.

———. 1945. Eelgrass conditions along the Atlantic seaboard of North America. Plant Disease Reporter 29: 302 310.

———, and C. E. Addy. 1947. Present eelgrass conditions and problems on the Atlantic Coast of North America. Trans. 12th North American Wildlife Confer. 12: 387 397.

Dexter, R. W. 1944. Ecological significance of the disappearance of eelgrass at Cape Ann, Mass. Jour. Wildlife Mgt. 8: 173 176.

———. 1945. A report on the eelgrass situation in the Annisquam (Mass.) and Mystic (Conn.) tidewater rivers in the summer of 1945. Plant Disease Reporter 29: 702 704.

———. 1946. The eelgrass situation in the Annisquam (Mass.) and Mystic (Conn.) tidewater rivers in the summer of 1946. Plant Disease Reporter 30: 424 425.

———. 1947. Status of eelgrass in the Annisquam Tidal River and Menemsha Saltwater Pond in Mass. during the summer of 1947. Plant Disease Reporter 31: 448 449.

———. 1950. Restoration of the *Zostera* faciation at Cape Ann, Mass. Ecology 31: 286 288.

———. 1951. The eelgrass situation at Cape Ann, Mass., in the summer of 1951. Plant Disease Reporter 35: 507 508.

———. 1953. Recession of eelgrass at Cape Ann, Mass. Ecology 34: 229 231.

Lynch, J. J. and C. Cottam. 1937. Status of Eelgrass (*Zostera marina*) on the North American Coast. U.S.D.A. Biol. Survey. Leaflet 94.

Martin, A. C. 1954. A clue to the eelgrass mystery. Trans. 19th North American Wildlife Confer. 19: 441 449.

Orth, R. J. 1976. The demise and recovery of eelgrass, *Zostera marina*, in the Chesapeake Bay, Virginia. Aquatic Bot. 2: 141 159.

———, and K. A. Moore. 1983. Chesapeake Bay: an unprecedented decline in submerged aquatic vegetation. Science 222: 51 53.

Phillips, R. C. 1982. Seagrass meadows. *In:* Lewis, R. R. III (ed.) Creation and Restoration of Coastal Plant Communities. C.R.C. Press, Boca Raton, Fla.

Rasmussen, E. 1976. The wasting disease of eelgrass (*Zostera marina*) and its effect on environmental factors and fauna. *In:* McRoy, C. P. and C. Helfferick (eds.) Seagrass Ecosystems: a Scientific Perspective. Marcel Deikker, Inc., New York, pp. 1 52.

Renn, C. E. 1936. Persistence of the eelgrass disease and parasite on the American Atlantic Coast. Nature 138: 507 508.

———. 1937. The eelgrass situation along the Middle Atlantic Coast. Ecology 18: 323 325.

Stevens, N. E. 1936. Environmental conditions and the wasting disease of eelgrass. Science 84: 87 89.

———. 1939. Environmental factors and the wasting disease of eelgrass. Rhodora 41: 260 262.

———, H. R. Ellis, and R. B. Stevens. 1950. Wasting and recovery of *Zostera marina* on the Atlantic Coast of the United States. Plant Disease Reporter 34: 357 362.

U.S. Dept. Agriculture. Weather Bureau. 1931 32. Report of the Chief of the Weather Bureau for 1929 and 1930. U.S. Gov. Printing Office, Wash. D.C.

U.S. DEPT. COMMERCE. 1954–84. Annual Summary Climatological Data for New England (1953–83). U.S. Gov. Printing Office, Wash. D.C.

———. 1958. Climatic Summary of The United States Supplement for 1931 through 1952. (New England). U.S. Gov. Printing Office, Wash. D.C.

WHEAT, M. C., JR. 1962. Eelgrass. A controversial link in the chain of life in our marine waters. The Conservationist 16: 28–30.

DEPARTMENT OF BIOLOGICAL SCIENCES
KENT STATE UNIVERSITY
KENT, OHIO 44242

THE CYTOGEOGRAPHY OF *ASTER PILOSUS* (COMPOSITAE-ASTEREAE)
II. SURVEY OF THE RANGE, WITH NOTES ON *A. DEPAUPERATUS, A. PARVICEPS* AND *A. PORTERI*

John C. Semple and Jerry G. Chmielewski

ABSTRACT

Chromosome numbers of one or more individuals from 269 collections of *Aster pilosus* were determined from throughout the range of the species. Two cytotypes were commonly encountered: $4x$ and $6x$ ($x = 8$). In var. *pilosus*, tetraploids and hexaploids were allopatric for the most part. Hexaploids occurred in the northwestern portion of the species' range. Intervarietal and infravarietal pentaploids encountered came from interface areas. All plants of *A. pilosus* var. *pringlei* (including var. *demotus*) were hexaploid and occurred in the northeastern portion of the range of the species. Only 3 plants were found to have supernumerary chromosomes. Two plants were putative heptaploids. In comparison, diploids have been found in the 3 related species *A. porteri*, *A. depauperatus*, and *A. parviceps*. First reports: *A. parviceps*, $2n = 16$; *A. pilosus* var. *pilosus*, $2n = 35$ and $2n = 42$; *A. pilosus* var. *pringlei*, $2n = 48 + 2$–8 supernumeraries and $2n = 56$; *A. pilosus* var. *priceae*, $2n = 32$.

Key Words: *Aster pilosus*, chromosome numbers, polyploidy, cytogeography

INTRODUCTION

Four species are recognized in *Aster* sect. *Porteriani* (Compositae: Astereae): *A. pilosus* Willd., *A. depauperatus* (Porter) Fernald, *A. parviceps* (Burgess) Mackenzie & Bush, and *A. porteri* A. Gray. All species of the section have phyllary morphology that distinguishes them from other $x = 8$ taxa, and are therefore a well delimited phylogenetic line (Semple, 1978; Jones, 1980; Semple and Brouillet, 1980a). *Aster pilosus* is the most widely distributed (Figure 1) and morphologically variable species of the section. Cronquist (1968, 1980) recognized four varieties in *A. pilosus:* var. *demotus* Blake, var. *pilosus*, var. *priceae* (Britton) Cronquist and var. *pringlei* (Gray) Blake. In this paper we recognize only three varieties in *A. pilosus*, placing var. *demotus* within var. *pringlei*. *Aster pilosus* is known to occur at two ploidal levels at scattered locations in the United States (Van Faasen, 1963; Van Faasen and Sterk, 1973; Semple, 1978; Jones, 1980; Semple and Brouillet, 1980b; Semple, Chmielewski and Chinnappa, 1983). The distribution of cytotypes was studied in Ontario where var. *pilosus* (tetraploid and hexaploid populations) and var. *pringlei* (hexaploid populations) are allopatric except along the north shore of Lake Ontario (Semple, 1978). Also, in Ontario the distributions of the cytotypes within var. *pilosus* are, for the most part, allopatric. To determine the overall pattern of cytotype distribution for the species, we sampled plants over the entire range of *A. pilosus.* The results of this field work are reported in this paper.

When we began our study of *A. pilosus,* nothing was known about the cytology of the other species of the *Aster* sect. *Porteriani.* We therefore included them in our investigation. Subsequently, at least one count for each of these related species has been reported. Morton (1981) reported a count of $2n = 16 + 2$ supernumeraries for *A. depauperatus,* which is endemic to serpentine soils in southeastern Pennsylvania, northeastern Maryland, possibly eastern West Virginia, and Delaware (Wherry et al., 1979; Cronquist, 1980). Semple et al. (1983) reported a tetraploid ($2n = 32$) count for the Ozark Plateau endemic *A. parviceps. Aster porteri* was reported to be diploid in two counties in Colorado (Jones, 1980; Semple et al., 1983); the species occurs at lower elevations in the Front Range of the Rocky Mountains in Colorado and New Mexico (Harrington, 1954). Additional, previously unreported counts for *A. depauperatus, A. porteri* and *A. parviceps* are reported in this paper along with comments on their significance to *A. pilosus.*

MATERIALS AND METHODS

Chromosome numbers were determined from mitotic configurations observed in root tip cells. Rootstocks, viable achenes, and voucher specimens were collected in the wild and handled as described in Chmielewski and Semple (1983). One to three plants were usually collected per site. Morphologically dissimilar plants at the same site were given separate collection numbers. Field work was conducted during the fall when plants were generally in full bloom or slightly past this stage. Counts reported in this paper were obtained from plants collected between 1977 and 1984.

The range of each species was determined from field observations and collections at CAN, DAO, GH, MO, MT, NY, US and WAT.

RESULTS AND DISCUSSION

Chromosome count determinations for 276 collections of *Aster* sect. *Porteriani* are listed in Table 1. The majority of the counts (208) was for individuals of *A. pilosus* var. *pilosus:* $2n = 32$, 157 collections; $2n = 35$ ($= 32 + 3$), one plant from New York; $2n = 40$, 3 plants from Missouri and Pennsylvania; $2n = 42$ ($= 40 + 2$), one plant from Pennsylvania; and $2n = 48$, 46 collections. The hexaploid chromosome number of a plant thought to be from Georgia was determined early in the study, before any distribution patterns were apparent. The origin of this plant is now questionable due to the general patterns discussed below, since no other hexaploids were found within several hundred miles of the location. Previous counts of $2n = 32$, 40 and 48 have been published for the variety (Van Faasen, 1963; Van Faasen and Sterk, 1973; Semple, 1978; Semple and Brouillet, 1980b; Semple et al., 1983); $2n = 35$ and 42 are reported for the first time.

The distributions of the tetraploid and hexaploid races of var. *pilosus* are almost completely allopatric (Figure 1). Tetraploids occur from northcentral Ontario to Florida, occupying a wide range of habitats. A few disjunct tetraploids populations were sampled from the northernmost portion of the distribution of var. *pilosus* in Quebec and Ontario. These disjuncts are either a result of chance long-distance dispersal from more southern Great Lakes populations, or are remnants of a once more extensive northern distribution of a tetraploid race during warmer post-glacial times. Both possibilities may be true.

Generally, hexaploids of var. *pilosus* occur in the northwestern portion of the range of the variety. This area corresponds well with the Central Lowlands Geologic Province (Shimer, 1972), is underlain by sedimentary bedrock, and is covered in some places with glacial deposits several hundred feet thick (Shimer, 1972). In Ontario hexaploids grow on glacial till and sand deposits, but not on exposed limestone or clay plains (Semple, 1978). However, the correlation between physiographic features and cytotypes found in Ontario is not a cause-effect relationship. In the United States hexaploids grow on limestone outcrops, glacial lake-sediment deposits, and soil-covered unglaciated bedrock plains as well as till deposits (Figure 1, large dots).

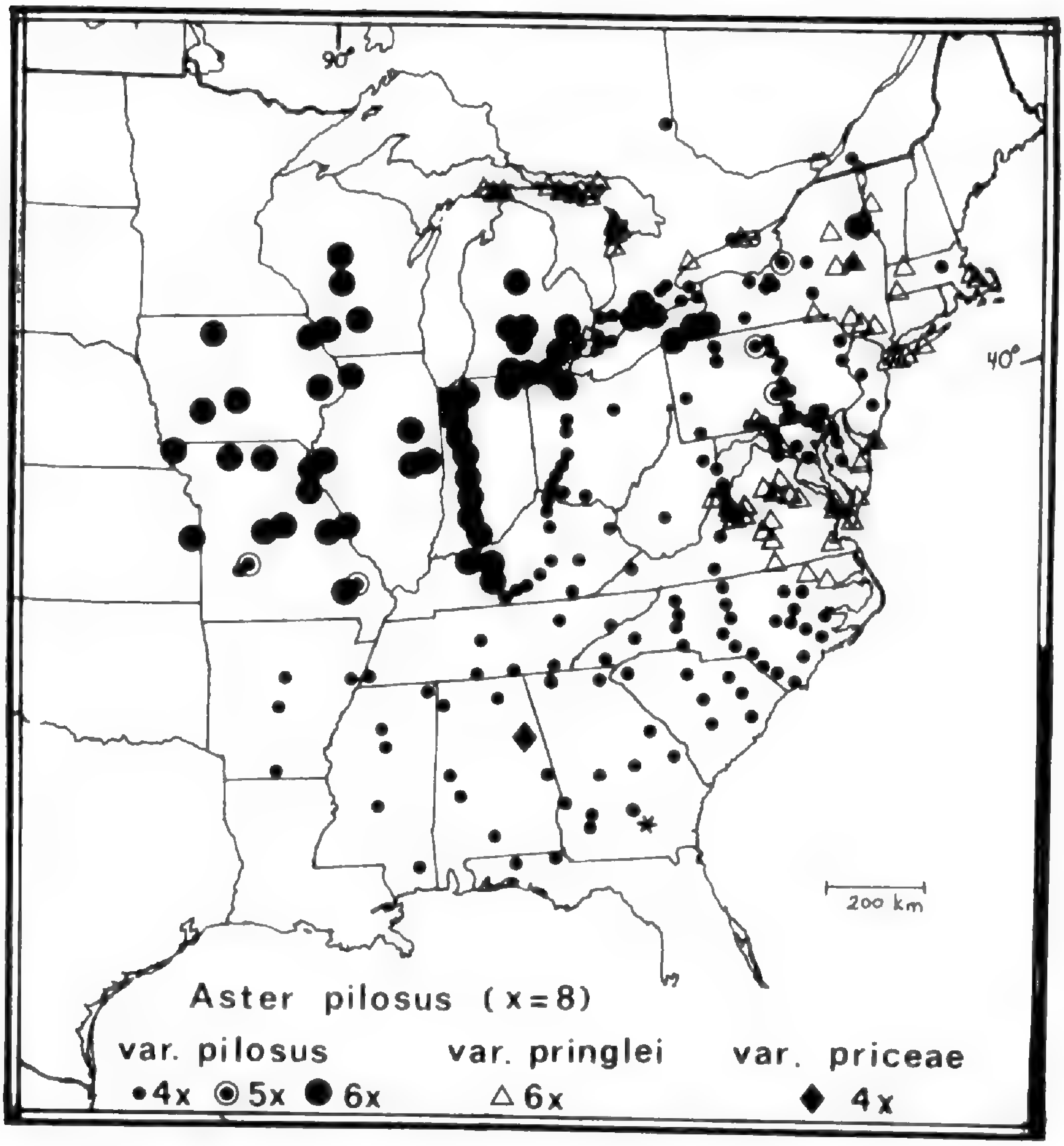


Figure 1. The cytogeography of *Aster pilosus*. The asterisk (*) in southern Georgia indicates the questionable location of the hexaploid individual discussed in the text.

The allopatry of the tetraploid and hexaploid races of var. *pilosus* appears to be as pronounced along the entire southern portion of the range of hexaploids as in southern Ontario (Semple, 1978). Every collection examined from Michigan, Wisconsin, Iowa, Illinois, and Indiana was hexaploid, as were those from western Kentucky and the northern half of Missouri. Hexaploids were also found in northwestern Ohio and near Lake Erie in Pennsylvania and New York. With the noted possible exception in Georgia, one hexaploid collection from northeastern New York and the pentaploids discussed below, all collections of var. *pilosus* from elsewhere in the range were tetraploid.

Only a few pentaploids $2n = 40$ of var. *pilosus* were collected, these came from areas where the tetraploid and hexaploid races are potentially sympatric. Occurrence of pentaploids in the wild indicates that tetraploid and hexaploid races do hybridize and must, therefore, occasionally occur in very close proximity. In Ontario we have found the two races occurring within 100 m of each other, but nonetheless in separate habitats. Pentaploids should be expected in low frequency in any area where the two races come in close contact.

A chromosome count of $2n = 32$ for an individual of var. *priceae* from Alabama (Figure 1, solid diamond) is listed in Table 1 and is the first report for the taxon. The plant had the bluish rays and glabrate stem characteristic of var. *priceae* (Cronquist, 1968, 1980); this variety was encountered only once during our field work. Bluish- or pink-rayed plants of var. *pilosus,* however, were encountered a number of times throughout the entire range and always had pubescent stems.

In this paper we have included var. *demotus* within var. *pringlei,* thereby grouping together into one variety all the plants of northern distribution that normally have white rays and glabrate-glabrous stems. Cronquist (1968, 1980) distinguished the two varieties on the basis of stem height and the number of heads per shoot, but we have found these traits to be very plastic. Short plants (1–3 dm) collected from limestone pavements on the Bruce Peninsula in Ontario produced shoots nearly 1 m tall when grown in deep, humus-rich soil in an experimental garden. Alternatively, tall plants (5–12 dm) from both Ontario and North Carolina produced short shoots when grown in confining pots in the greenhouse in Ontario. The usefulness of stem height as a taxonomic character to delimit the varieties is therefore questioned. Likewise, the number of heads and the number of florets per head varied greatly with growth conditions.

Aster pilosus var. *pringlei* as delimited here was found to be hexaploid (Table 1; 44 collections). Plants of three collections had 2–8 supernumerary chromosomes. The supernumeraries were somewhat smaller than the smallest A-set chromosomes. Two plants were $2n = 56$, which may be either heptaploid or $2n = 48 + 8$ supernumeraries. The distribution of these collections and those reported previously are shown in Figure 1.

Aster pilosus var. *pringlei* was found to occur on a wide variety of soil types in the northeastern portion of the range of the species. Habitats varied from sand dunes near the Great Lakes and along the Atlantic Coast to exposed limestone and shale rock faces in the northern Appalachians and near Lake Michigan and Lake Huron. The variety is also known to occur in scattered locations in Wisconsin, northcentral Ontario and Quebec, southern Nova Scotia, and along the coast of northeastern Maine. Our cytological sample did not include plants from these outlying locations. However, herbarium specimens (CAN, DAO, GH, NY) from these locations were not morphologically distinct from individuals native to cytologically sampled parts of the variety's range.

Aster sect. *Porteriani* includes three diploid species, each of which has a limited distribution compared to that of *A. pilosus*. We have seen collections (GH, MO, NY, US) of *Aster depauperatus* from serpentine soils in Pennsylvania and Maryland. The species was reported to be diploid at one site in Lancaster County, PA. (Morton, 1981). The vouchers for this count (WAT) were collected in 1972 and 1973 from a plant cultivated from transplanted wild rootstock; it had small involucres comparable in size to those of the diploid plants of *A. parviceps*. The 1973 shoots were very robust and highly branched compared to the gracile 1972 collection. Thus, the habit of a single individual is quite plastic. We visited one large population of *A. depauperatus* (Table 1) which contained diploids that ranged in size from less than 1 dm tall and sparsely branched, to 5 dm tall and profusely branched. The phyllaries were always tightly appressed forming cylindrical involucres in fresh plants. At nearby sites (e.g., *S & R 7616, S & Ch 7683*) hexaploid individuals of *A. pilosus* var. *pringlei* were found to be very similar in size and habit, but the tips of the phyllaries were somewhat spreading and the involucres were slightly turbinate. Upon drying, the phyllaries of both taxa usually spread apart resulting in very similar-looking involucres. Thus, it is easy to confuse dried collections of the two taxa; this ambiquity was found to be the case with herbarium specimen identifications as well. Cytologically, the two taxa are readily distinguished.

Populations of *Aster parviceps* may be either diploid or tetraploid. The only diploid count for the species is reported here for the first time (Table 1); the plants were from western Illinois. The only

Table 1. Chromosome number determinations in *Aster* sect. *Porteriani* from Canada and the United States. Collections by Semple & Chmielewski unless otherwise indicated: Bt = L. Brouillet; C = J. Canne; Ch = J. Chmielewski; H = Calvin Hart; Hart = Chris Hart; R = G. Ringius; S = J. Semple.

COUNT	LOCATION AND VOUCHER DATA (WAT)
A. depauperatus (Porter) Fern.	
$2n = 16$	U.S.A. **Pennsylvania:** Chester Co.: S of Nottingham, *7681*.
A. parviceps (Burg.) Mack. & Bush.	
$2n = 16$	U.S.A. **Illinois:** Adams Co.: W of Paloma, *S & Bt 7378*.
A. pilosus Willd. var. *pilosus*	
$2n = 32$	CANADA. **Ontario:** Nipissing Dist.: S of Temagami, *Ch 1305*. Wellington Co.: Arkell, *S 7395*. U.S.A. **Alabama:** Chambers Co.: S of Lafayette, *6316;* Conecuh Co.: E of Cohassett, *6352;* Franklin Co.: W of Atwood, *6375;* Greene Co.: S of Eutaw, *6364;* Madison Co.: Owens Crossing, *6294;* Wilcox Co.: S of Millers Ferry, *6359*. **Arkansas:** Cleburne Co.: S of Quitman, *6396*. Crittendon Co.: W of Memphis, *6389;* Saline Co.: NW of Haskell, *6399;* Union Co.: Eldorado, *6410*. **Florida:** Walton Co.: S of Florala, *6350*. **Georgia:** Dougherty Co.: N of Newton, *6329;* Houston Co.: S of Cinchfield, *S 7407;* Johnson Co.: E of Wrightsville, *S, Bt & C 4043;* Lee Co.: NW of Albany, *6328;* McDuffie Co.: S of Cobbham, *6141;* Rockdale Co.: Milstead, *6150;* Screven Co.: S of Hilltonia, *6140;* Steward Co.: N of Lumpkin, *6325;* Telfair Co.: *C 1875;* White Co.: N of Robertstown, *6212;* Whitfield Co.: Rocky Face, *S & S 7399*. **Kentucky:** Adair Co.: US-80, W of KT-127, *Ch & H 966;* Allen Co.: N of Scottsville, *Ch & H 958;* S of Scottsville, *Ch & H 957;* Barren Co.: US-31 by Barren River, *Ch & H 959;* Boyle Co.: Mercer Co. line, US-127, *Ch & H 974;* Casey Co.: S of Dunneville, *Ch & H 974; Ch & H 972;* Fayette Co.: *Baskin s.n.;* Grant Co.: N of Corinth, *Ch & H 979 & 980;* Kenton Co.: US-25 S of KT-330, *Ch & H 982;* Lawrence Co.: N of Paintsville, *6272;* Metfcalfe Co.: I-80, E of county line, *Ch & H 960;* I-80, W of county line, *Ch & H 961;* Rockcastle Co.: Mt. Vernon, *S 5329;* Scott Co.: US-25, S of KT-32, *Ch & H 976;* Warren Co.: US-231 at KT-626, *Ch & H 955*. **Maryland:** Anne Arundel Co.: S of Priest Bridge, *S. & R 7653;* Cecil Co NE of Rising Sun, *S & R 7618;* S of Warwick, *S & R 7624;* Frederick Co.: US-806 at US-15, *Ch & H 301 & 302;* Howard Co.: N of Damascus, *S, Brammall & Hart 3073;* Kent Co.: NE of Galena, *S & R 7629;* Washington Co.: N of Greenbrier State Park, *S & R 7660*. **Massachusetts:** Middlesex Co.: E of Concord, *S 6864*. **Mississippi:** Alcorn Co.: E of Strictland, *6386;* George Co.: W of Benndale, *S, Bt & C 3851;* Grenada Co.: S of Grenada, *S, Bt & C 3759;* Rankin Co.: NW of Star, *S, Bt & C 3812;* Yalobusha Co.: NW of Tillatoba, *S, Bt & C 3789*. **Missouri:** Hickory Co.: W of Hermitage, Hicomo Park, *5275*. **New Jersey:** Burlington Co.: N of Chatsworth, *6257;* Cape May Co.: N of Burleigh, *6248;* Linvale Co.: N of Linvale, *6260*. **New York:** Cayuga Co.: S of Victoria, *S*

Table I. *Continued*

COUNT	LOCATION AND VOUCHER DATA (WAT)
	6918; Chautauqua Co.: W of Jamestown, *Ch & H 441;* Cortland Co.: N of Homer, *S 6800;* Fulton Co.: N of Mayfield, *S 6913;* Monroe Co.: Scottsville, *Ch & H 244;* Oneida Co.: E of Camden, *S 6915;* Ontario Co.: E of Cliffton Springs, *S 3378;* Steuben Co.: S. Kanona, *Ch & H 257 & 260.* **North Carolina:** Brunswick Co.: S of Belville, *Ch & H 356;* Wilmington, *Ch & H 355;* Catawba Co.: S of Millersville, *S, Bt & C 4078,* S of Newton, *S, Bt & C 4075;* Columbia Co.: US-74 E of US-76, *Ch & H 359;* Craven Co.: NW of Vanceboro, *6053;* Edgecombe Co.: E of Rocky Mount, *6237;* Franklin Co.: W of New Hope, *6236;* Gaston Co.: Dallas, *S, Bt & C 4068;* Guilford Co.: S of Greensboro, *Ch & H 391;* Johnson Co.: S of Princeton, *Ch & H 347;* Jones Co.: US-258 N of NC-41, *Ch & H 351;* Lenoir Co.: S of Kinston, *Ch & H 350;* Macon Co.: N of Gneiss, *6216;* Montgomery Co.: S of Seagrove, 21 km S, *Ch & H 377 & 378;* 5.7 km S, *384 & 385;* Pender Co.: N of Hampstead, *Ch & H 354;* Richmond Co.: S of Norman, *Ch & H 370;* Robertson Co.: US-74 1 km E of US-41, *Ch & H 361;* US-74 18 km E of US-41, *Ch & H 362;* Rockingham Co.: US-220 at state line, *Ch & H 396;* Sampson Co.: NE of Clinton, *6030;* Scotland Co.: E of Hamlet, *Ch & H 364;* Wayne Co.: US-70 N of US-903, *Ch & H 348;* Wilkes Co.: McGrady, *S, Bt & C 4082;* Wilson Co.: S of Wilson, *6011.* **Ohio:** Adams Co.: E of West Union, *6271;* Ashland Co.: NW of Savanah, *S, Bt & C 4110;* Clark Co.: N of Hustead, *Ch & H 998;* Clermont Co.: I-275 S of US-50, *Ch & H 986;* Greene Co.: US-42 at West Krepps Rd., *Ch & H 997;* Hamilton Co.: US-22 E of I-275, *Ch & H 987;* Hancock Co.: US-68 Madison Twp. Rd-149, *Ch & H 1009;* Harron Co.: US-68 at Co. Rd.-135, *Ch & H 1006;* Logan Co.: N of Bellfountaine, *Ch & H 1002;* Warren Co.: NW of Maineville, *Ch & H 989, 990, 993.* **Pennsylvania:** Adams Co.: N of state line on US-15, *Ch & H 295 & 298;* Butler Co.: E of Slippery Rock, *Ch & H 435;* Chester Co.: S of Nottingham, *7682;* Dauphin Co.: Dauphin, *Ch & H 286;* Elk Co.: S of Wilcox, *S & R 7584;* Fayette Co.: US-119 N of state line, *Ch & H 428;* Franklin Co.: Tuscarora Mt. W of Ft. Loudon, *S & R 7667;* Fulton Co.: E of Amaranth, *5862;* Lancaster Co.: E of Little Britain, *S & R 7613;* Quarryville, *S 6506;* Lycoming Co.: near Bald Eagle Mt., *Ch & H 271;* S of Hepburnville, *Ch & H 269 & 270;* McKeene Co.: Custer City, *S & R 7577;* Northampton Co.: N of Easton, *6262;* Perry Co.: W of Montgomery Ferry, US-322, *7684;* Pike Co.: S of Hawley, *6265;* Snyder Co.: N of Montgomery, *Ch & H 278 & 279;* Tioga Co.: S of Mansfield, *Ch & H 264, 265, 267;* Union Co.: Lewisburg, *Ch & H 273, 274, 275;* York Co.: E of Sunnyburn, *S & R 7615;* Warren Co.: S of Warren, *Ch & H 437;* Washington Co.: S of Lorne Pines, *Ch & H 431;* York Co.: N of Clear Spring, *Ch & H 291;* N of Dillsburg, *Ch & H 288.* **South Carolina:** Chester Co.: E of Chester, *6094;* Darlington Co.: Darlington, *6105;* Florence Co.: N of Evergreen, *6106;* Georgetown Co.: S of Andrews, *6125;* Orangeburg Co.: S of Bowman, *6134;* Pickens Co.: N of Liberty,

Table I. *Continued*

COUNT	LOCATION AND VOUCHER DATA (WAT)
	6160; Richland Co.: N of Columbia, *S, Bt & C 4063.* **Tennessee:** Bradley Co.: Cleveland, *S 5330;* Giles Co.: S of Pulaski, *6291;* Grundy Co.: Mounteagle, *6287;* Shelby Co.: SE of Memphis, *6387.* **Virginia:** Botetourt Co.: S of Fincastle, *Ch & H 401;* Franklin Co.: S of Boones Mill, *Ch & H 399;* US-220 N of county line, *Ch & H 397;* Loudoun Co.: N of Leesburg, *Ch & H 306;* Wise Co.: NE of Appalachia, *6278.* **West Virginia:** Fayette Co.: N of Beckley, *S, Bt & C 4100;* Pendelton Co.: N of Franklin, *5895;* Taylor Co.: E of Grafton, *Ch & H 422;* US-119 S of US-48, *Ch & H 424;* US-219 N of county line, *Ch & H 419.*
$2n = 35$	U.S.A. **New York:** Wayne Co.: E of Clyde, *S 6919.*
$2n = 40$	U.S.A. **Missouri:** Hickory Co.: US-54 W of county line, *5279;* Madison Co.: US-64 N of Co. Rd-A, *S, Bt & C 3770.* **Pennsylvania:** Tioga Co.: S of Mansfield, *Ch & H 266.*
$2n = 42$	U.S.A. **Pennsylvania:** Perry Co.: NE of Newport, *S 6510.*
$2n = 48$	U.S.A. **Georgia:** Coffee Co.: N of Douglas, *S, Bt & C 4017.* (See text for discussion of this count.) **Illinois:** Adams Co.: Bluff Hall, *S & Bt 7368;* W of Paloma, *S & Bt 7377.* Carroll Co.: S of Palisades State Park, *5204;* Livingston Co.: E of Forrest, *S & Bt 7389.* **Indiana:** Dubois Co.: N of Jasper, *Ch & H 948;* Greene Co.: S of Bloomfield, *Ch & H 944;* Lagrave Co.: IN-775 N of IN-120, *Ch & H 923;* Montgomery Co.: SE of Whitesville, *Ch & H 938;* Owen Co.: N of Carp, *Ch & H 940;* S of Freedom, *Ch & H 942;* Porter Co.: N of Chesterton, *S & Bt 4521;* Putnam Co.: N of Cloverdale, *S, Bt & C 3735;* St. Joseph Co.: N of Mill Creek, *Ch & H 924;* Starke Co.: W of Grovertown, *Ch & H 931;* Tippecanoe Co.: S of LaFayette, *Ch & H 936;* White Co.: US-231 at Carrol Co. line, *Ch & H 934.* **Iowa:** Clayton Co.: W of Mcgregor, *5177;* Clinton Co.: E of Oxford Junction, *5206;* Kossuth Co.: W of Wesley, *5161.* **Kansas:** Douglas Co.: N of Baldwin City, *5246.* **Kentucky.** Butler Co.: US-231 at Carson Bridge Rd., *Ch & H 953;* Daviess Co.: US-231 at US-60, *Ch & H 949;* Ohio Co.: US-231 at Green River, *Ch & H 952.* **Michigan:** Branch Co.: US-12 by Wheeler Rd, *Ch & H 920;* Clare Co.: N of Clare, *4971;* Hillsdale Co.: S of Ann Arbor, *Ch & H 917;* E of Moscow, *Ch & H 915;* Lenawee Co.: US-12 W of MI-52, *Ch & H 912;* Oakland Co.: Lake Orion, *Ch & H 1016;* Washtenaw Co.: US-12 at US-23, *Ch & H 910.* **Missouri:** Atchison Co.: W of Rock Port, *S & Bt 7361;* Callaway Co.: S of Fulton, *5303;* Franklin Co.: St. Clair, *S & Bt 3760;* Harrison Co.: E of Bethany, *5227;* Moniteau Co.: S of California, *5298;* Pike Co.: E of Bowling Green, *5316;* Putnam Co.: E of Unionville, *5217;* St. Louis Co.: Times Beach, *S & Bt 3744.* Wayne Co.: US-67 at MO-19, *S, Bt & C 3780.* **Ohio:** Warren Co.: S end of Loon Lake, *S 6911;* Wood Co.: OH-199 at Jerry City Rd., *Ch & H 1014.* **Wisconsin:** Crawford Co.: S of Prairie du Chien, *5183;* Marathon Co.: S of Knowlton, *5048;* Sauk Co.: Wisonsin Dells, *S & Bt 6936;* Wood Co.: N of Babcock, *5060.*

Table 1. *Continued*

COUNT	LOCATION AND VOUCHER DATA (WAT)
A. pilosus var. *pilosus* × *pringlei*	
$2n = 40$	U.S.A. **Maryland:** Cecil Co.: N of Rising Sun, *S & R 7616a*. **New York:** Oswego Co.: E of Texas, *S 6917*. **Pennsylvania:** Perry Co.: W of Montgomery Ferry, US-322, *7685*.
A. pilosus var. *priceae* (Britt.) Cronq.	
$2n = 32$	U.S.A. **Alabama:** Cleburne-Calhoun count line; SE of Anniston, *6305*.
A. pilosus var. *pringlei* (Gray) Blake	
$2n = 48$	CANADA. **Ontario:** Bruce Co.: Georgian Bay, Bears Rump Island, *Morton & Venn NA 7769*. U.S.A. **Delaware:** Sussex Co.: E of Georgetown, *S & R 7645*. **Maryland:** Caroline Co.: SE of Denton, *S & R 7640;* Cecil Co.: N of Rising Sun, *S & R 7616, 7680*. **Massachusetts:** Franklin Co.: W of Riverside, *S 6875-1;* Plymouth Co.: SE of Manomet, *S & Bt 3550;* White Horse Beach, *S & Bt 3548*. **Michigan:** Mackinac Co.: Gros Cap, *4998, 4999;* E of Naubinway, *5012;* W of Naubinway, *5013;* Pt. Aux Chenes, *5002*. **New Jersey:** Cape May Co.: W of Burleigh, *6249*. **New York:** Broome Co.: W of Windsor, *S 6809 & 6810;* Delaware Co.: W of Horton, *S 6814;* Dutchess-Putnam Co. line, Taconic State Pkwy, *S 6831;* Fulton Co.: N of Mayfield, *S 6912;* Hamilton Co.: N of Long Lake, *S & B 3675;* Nassau Co.: E of Norwich, *S 6842;* Suffolk Co.: W of East Moriches, *S 6854;* NE of Central Islip, *S 6850;* Sullivan Co.: E of Wurtville, *S 6825;* Ulster Co.: E of Woodburne, *S 6822*. **North Carolina:** Bertie Co.: S of Lewiston, *6238*. **Pennsylvania:** Chester Co.: E of Unionville, *7683;* Franklin Co.: Tuscarora Mt. W of Ft. Loudon, *S & R 7668;* Fulton Co.: E of Amaranth, *5863;* Perry Co.: W of Montgomery Ferry, US-322, *7686*. **Virginia:** Accomack Co.: N of Temperenceville, *6246;* Albermarle Co.: N of Coveville, *5937;* Augusta Co.: W of West Augusta, *5912;* Botetourt Co.: N of Fincastle, *Ch & H 403;* Buckingham Co.: N of Curddsville, *Ch & H 336;* N of Dillwyn, *Ch & H 329;* Culpepper Co.: NW of Lignum, *5950;* Essex Co.: US-17, near Spotsylvania county line, *5962;* Fluvanna Co.: N of Fork Union, *Ch & H 328;* Greene Co.: N of Ruckersville, *5940;* Highland Co.: E of Monterey, *5906 & 5907;* Isle of Wight Co.: US-258 by James River, *5993*. Madison Co.: SW of Culpepper, *5943;* Mecklenburg Co.: S of Clarksville, *Ch & H 341;* Middlesex Co.: NE of Harmony Village, *5977;* Nelson Co.: W of Crabtree Falls, *5929;* Northampton Co.: S of Eastville, *6245;* Northumberland Co.: Reedville, *5956;* Prince William Co.: N of junction of US-15 and US-55, *Ch & H 314;* Spotsylvania Co.: S of Fredericksburg, *5956*. **West Virginia:** Berkeley Co.: Harpers Ferry, *5873*.
$2n = 48 + 2$ supernumeraries	
	U.S.A. **Virginia:** Augusta Co.: W of West Augusta, *5918*.

Table 1. *Continued*

COUNT	LOCATION AND VOUCHER DATA (WAT)
$2n = 48 + 6$ supernumeraries	U.S.A. **Virginia:** Albermarle Co.: N of Coveville, *5932*.
$2n = 48 + 6 - 8$ supernumeraries	U.S.A. **Vermont:** Addison Co.: N of Middlebury, *S 6907*.
$2n = 56$	U.S.A. **Virginia:** Fauquier Co.: Opal, *Ch & H 317*. Spotsylvania Co.: S of Fredericksburg, *5955*.
Aster porteri A. Gray	
$2n = 16$	U.S.A. **Colorado:** Boulder Co.: N of Nederland, *S & S 5810;* El Paso Co.: Manitou Springs, Garden of the Gods, *S & Bt 7277;* W of Manitou Springs, *S & Bt 7268;* Larimer Co.: S of Estes Park, *S & S 5834;* Teller Co.: E of Florissant, *S & Bt 7258*

other cytologically known population was tetraploid and from eastern Kansas (Semple et al., 1983). Diploid plants of *A. parviceps* at the Illinois site were sympatric with *A. pilosus;* the two taxa differed in that *A. parviceps* was sparsely pubescent, had small cylindrical heads compared to the larger, turbinate heads of *A. pilosus*, and had an earlier flowering period.

Aster porteri has been previously reported to be diploid (Jones, 1980; Semple et al., 1983). Five additional, previously unreported diploid chromosome counts are listed in Table 1. The list includes plants which had not been sampled earlier from the southern end of the species' distribution in Colorado. The species is diploid throughout the range in Colorado. Populations isolated in north-central New Mexico have not been sampled yet. Plants of *A. porteri* can be similar in appearance to smaller individuals of *A. pilosus* var. *pringlei* but the two are not likely to be mistaken for each other since the ranges are markedly different.

Only a few other species of *Aster* that are native to eastern North America have been extensively investigated cytologically, excluding the virguloid asters (Semple, 1984). Several $x = 8$ species with generally more northern distributions have been studied and were found to have non-random cytotype distributions. *Aster lanceolatus* Willd. has a complex pattern of sympatric and allopatric cytological races (Semple, Chmielewski, Rao and Allen, 1983). *Aster* *puniceus* L. was found to be predominantly diploid with a few tetraploids occurring in the southwestern portion of its range (Semple et al., 1983). *Aster praealtus* Poir. was found to have two allopatric cytotypes corresponding to varieties (Semple et al., 1983). None of these cytotype distribution patterns is similar to those occurring in *A. pilosus;* these species have rather different distributions and habitat preferences. The restricted distribution pattern of diploids in sect. *Porteriani* is also unique in the genus *Aster.* Within the section only the polyploid species *A. pilosus* is widely distributed, perhaps partly as a consequence of being polyploid.

ACKNOWLEDGMENTS

This research was supported by National Research Council of Canada and Natural Sciences and Engineering Research Council of Canada Operating Grants to JCS. The following people are thanked for their assistance in the field: Dr. J. Baskin, R. Brammall, Dr. L. Brouillet, Dr. J. Canne, Calvin Hart, Chris Hart, and Brenda Semple. The reviewers are thanked for their suggestions.

LITERATURE CITED

Chmielewski, J. G. & J. C. Semple. 1983. The cytogeography of *Aster lanceolatus.* III. Cyteocology in southern Ontario. Canad. J. Bot. 61: 1879-1886.

Cronquist, A. 1968. *Aster. In:* H. A. Gleason, Ed., The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada. Hafner Pub. Co., New York.

———. 1980. Vascular Flora of the Southeastern United States. I. Asteraceae. Univ. North Carolina Press, Chapel Hill.

Harrington, H. D. 1954. Manual of the Plants of Colorado. Swallow Press, Chicago.

Jones, A. G. 1980. Data on chromosome numbers in *Aster* (Asteraceae), with comments on the status and relationships of certain North American species. Brittonia 32: 240-261.

Morton, J. K. 1981. Chromosome numbers in Compositae from Canada and the U.S.A. J. Linn. Soc., Bot. 82: 357-368.

Semple, J. C. 1978. The cytogeograph of *Aster pilosus* (Compositae): Ontario and the adjacent United States. Canad. J. Bot. 56: 1274-1279.

———. 1984. Cytogeography of North American asters. I. Range surveys of *Virgulus adnatus, V. concolor, V. georgianus, V. grandiflorus, V. novae-angliae, V. oblongifolius, V. patens,* and *V. walteri.* Amer. J. Bot. 71: 522-531.

———, & L. Brouillet. 1980a. A synopsis of North American asters: the subgenera, sections and subsections of *Aster* and *Lasallea.* Amer. J. Bot. 67: 1010-1026.

______, & ______. 1980b. Chromosome numbers and satellite chromosome morphology in *Aster* and *Lasallea*. Amer. J. Bot. 67: 1027–1039.

______, J. G. Chmielewski, & C. C. Chinnappa. 1983. Chromosome number determinations in *Aster* L. (Compositae) with comments on cytogeography, phylogeny and chromosome morphology. Amer. J. Bot. 70: 1432–1443.

______, J. G. Chmielewski, K. S. Rao & G. A. Allen. 1983. The cytogeography of *Aster lanceolatus*. II. A preliminary survey of the range including *A. hesperius*. Can. J. Bot. 61: 434–441.

Shimer, J. 1972. Field Guide to Landforms in the United States. Macmillan Co., New York.

Van Faasen, P. 1963. Cytotaxonomic studies in Michigan asters. Mich. Bot. 2: 17–27.

______, & F. F. Sterk. 1973. Chromosome numbers in *Aster*. Rhodora 75: 26–33.

Wherry, E., J. Fogg, & H. Wahl. 1979. Atlas of the Flora of Pennsylvania. Morris Arboretum, Philadelphia.

DEPARTMENT OF BIOLOGY
UNIVERSITY OF WATERLOO
WATERLOO, ONTARIO
CANADA N2L 3G1

CHROMOSOMES OF MEXICAN *SEDUM* V. SECTION SEDUM AND SUBGENUS SULCUS

CHARLES H. UHL

ABSTRACT

Chromosome numbers in 39 species of *Sedum* Section Sedum and Subgenus Sulcus range from $n = 11$ to $n =$ ca. 100, with about 38 different numbers known and no basic or ancestral number apparent. Dysploidy and/or polyploidy, up to 12-ploidy, occur within most of the more widespread species, and B-chromosomes were found in seven species. Common chromosome numbers are $n = 12$ (four species), $n = 18$ 19 (ten species), and $n = 34$ (nine species), with each of these numbers including some species that are similar and obviously related. Many crosses have been attempted, with some success, and in several cases pairing of the chromosomes in hybrids provides useful evidence regarding degree of relationship between parents. Most species occur as relatively small, scattered populations in restricted pioneer habitats; evidently this distribution has promoted rapid evolution of morphological and cytological diversity.

Key Words: Mexican *Sedum*, chromosome numbers, dysploidy, polyploidy, hybrids, small populations

INTRODUCTION

This paper is the fifth in a series reporting the chromosomes of about 100 species of *Sedum* native to Mexico and adjacent parts of the United States and Central America. Preceding papers dealt with 10 annual and biennial species (Uhl, 1976b), with 20 mostly large and woody species of section (or subgenus) Pachysedum and three probable hybrids that have been given names as species (Uhl, 1978), with 24 other more or less woody species (Uhl, 1980), and with *S. moranense*, which is remarkable for the many different chromosome numbers found in different populations (Uhl, 1983). Materials and methods and acknowledgements were given in Uhl (1976b).

This paper reports the chromosomes of 39 species of relatively small "typical" perennial species (chamaephytes). Although they are classified together, they show considerable morphological and cytological diversity, and some of these species are probably more closely related to certain annual or biennial species or to certain woody species that were reported previously than they are to each other. The species are discussed alphabetically, with comments regarding their distinguishing characters, distribution, chromosomes, possible relationships and hybrids. In Table 1, the collections are listed alphabetically by species, then arranged roughly from north to south and from west to east.

In certain collections and hybrids that are irregular at meiosis, univalents usually are easily distinguished by their generally smaller size, by their strong tendency to lie around the fringes of the metaphase plate or often completely off the plate, and especially by their much shallower depth in focusing. These characteristics are not always shown in photographs. With the small chromosomes that characterize Mexican *Sedum* it is generally not possible to distinguish all multivalents from all bivalents with any confidence, and so in some cases the two are classed together as "paired elements".

Drawings of some of these species, many from fresh material, have been published (in some cases under other names) by Praeger (1921), Fröderström (1935), and Clausen (1959). Photographs of several living plants were published with their original descriptions by Rose (1911), and many photographs of herbarium specimens by Fröderström (1935). Keys that include many of the species have been published by Berger (1930), Fröderström (1935), and Clausen (1959, 1984). Jacobsen (1974) has published brief descriptions of most of these species, generally following Berger's (1930) treatment.

SPECIES

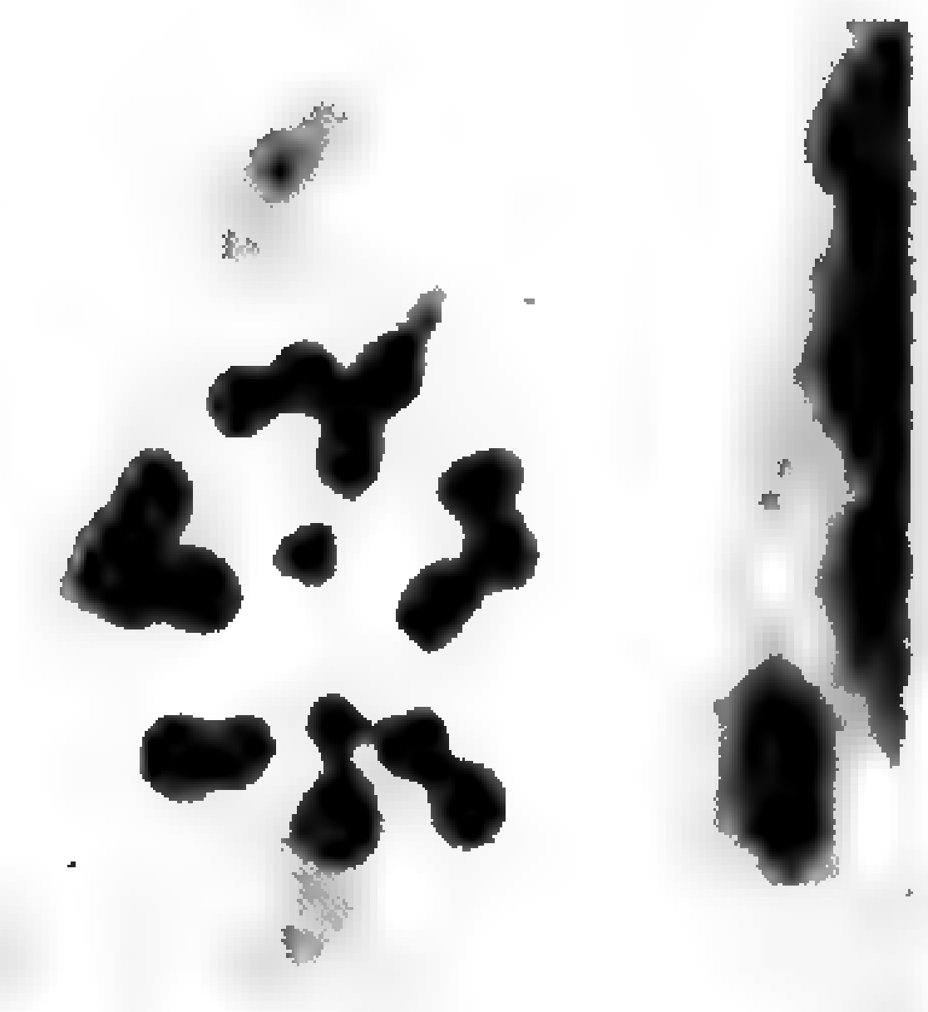
Sedum alamosanum

Sedum alamosanum S. Watson has tightly crowded leaves that are terete, erect, and densely covered with white papillae, thereby appearing glaucous. Its petals are white with tiny pink dots, often appearing flesh-colored. It occurs in Baja California Sur and across northwestern Mexico from southern Sonora and Chihuahua into western Coahuila. Two collections from Baja California Sur, two from Alamos Mountain, Sonora, the type locality, and two from Chihuahua were diploid ($n = 18$, Fig. 2), and one from western Coahuila consistently had 17 bivalents and one univalent of standard size (Fig. 1), apparently a monosomic ($2n - 1$) of a basic 18. Plants from the Barranca del Cobre in southwestern Chihuahua were tetraploids with $n = 36$ (Fig. 3), and others from the bottom of the same canyon were hexaploids with $n = 54$ (Fig. 4). Clausen (1981) studied plants that later were found to represent all three levels of ploidy and found that "clear evidence for subspecies is lacking" in *S. alamosanum*.

Diploid *Sedum alamosanum* has been hybridized with three other species of Section Sedum (*S. greggii, S. lumholtzii,* and *S. multiflorum*), with *S. latifilamentum* of Subgenus Sulcus, with *S. guatemalensis* of Section Fruticisedum, with *S. cremnophila* (= *Cremnophila nutans*), and with two diploid and one tetraploid species of *Villadia* (*V. albiflora, V. levis,* and *V. grandisepala*). Only *S. alamosanum* ($n = 18$) × *S. lumholtzii* ($n = 19$) (*U1647* × *UC68.144*) showed much chromosome pairing: 12–17 bivalents and multivalents and 1–13 univalents (average 15.6 + 4.3) in 12 cells analyzed (17 + 1 in Fig. 5, with two other univalents out of focus). In the other hybrids few chromosomes were paired at metaphase I, most of them occurring as univalents. For example, only 2–6 paired elements + 17–26 univalents were seen at metaphase I in 14 cells analyzed of *S. alamosanum* ($n = 18$) × *S. multiflorum* ($n = 12$) (*U1647* × *U2088*) (3 + 24 in Fig. 6, with the larger chromosomes of *S. multiflorum* conspicuous), and 4–12 paired elements + 26–42 univalents were seen in 16 cells of *S. alamosanum* ($n = 18$) × *Cremnophila nutans* ($n = 33$) (*U1647* × *M10174*) (5 + ca. 38 in Fig. 7). These other species probably are only distantly related to *S. alamosanum*.

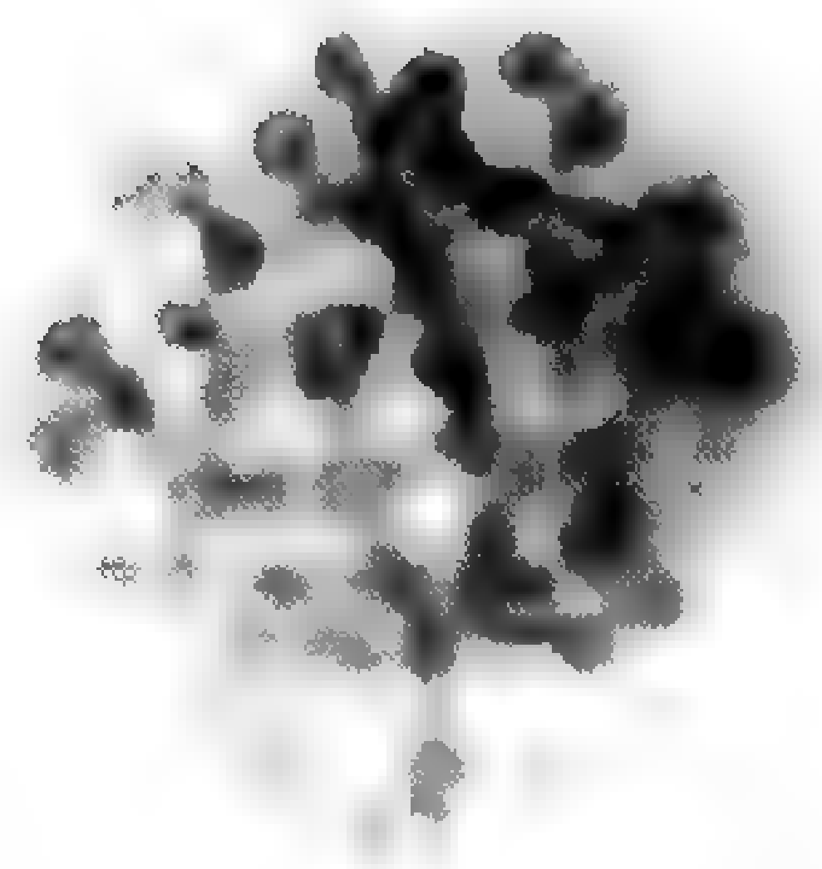
Efforts to cross diploid *Sedum alamosanum* with 11 other species of Section Sedum, with ten species of other sections of *Sedum*, four other species of *Villadia*, and with one species each of *Graptopetalum* and *Pachyphytum* were unsuccessful. These unsuccessful efforts include an attempt to cross diploid *S. alamosanum* with one of the species most similar to it, diploid *S. diffusum* ($n = 19$) (*U1647* × *U2086*), as well as attempted reciprocal crosses between tetraploid *S. alamosanum* and *S. bellum* (both $n = 36$).

A hybrid between hexaploid *Sedum alamosanum* (*U2045*, $n = 54$), which has faintly pinkish flowers, as pollen parent, and the yellow-flowered *S. greggii* (*U1535*, $n = 26$, considered diploid, *q.v.*) closely resembled the hexaploid pollen parent, as expected, and produced pale yellow flowers. At metaphase I, this hybrid formed 18–20 bivalents and multivalents and 23–40 univalents in ten cells that could be analyzed with moderate accuracy. Most or all of the bivalents here are believed to consist of paired homologues from two of the three sets of chromosomes that the hybrid received from *S. alamosanum*. The third homologues from *S. alamosanum* in many cases probably pair for part(s) of their length with one of the other two of each kind to produce a trivalent. The large number of

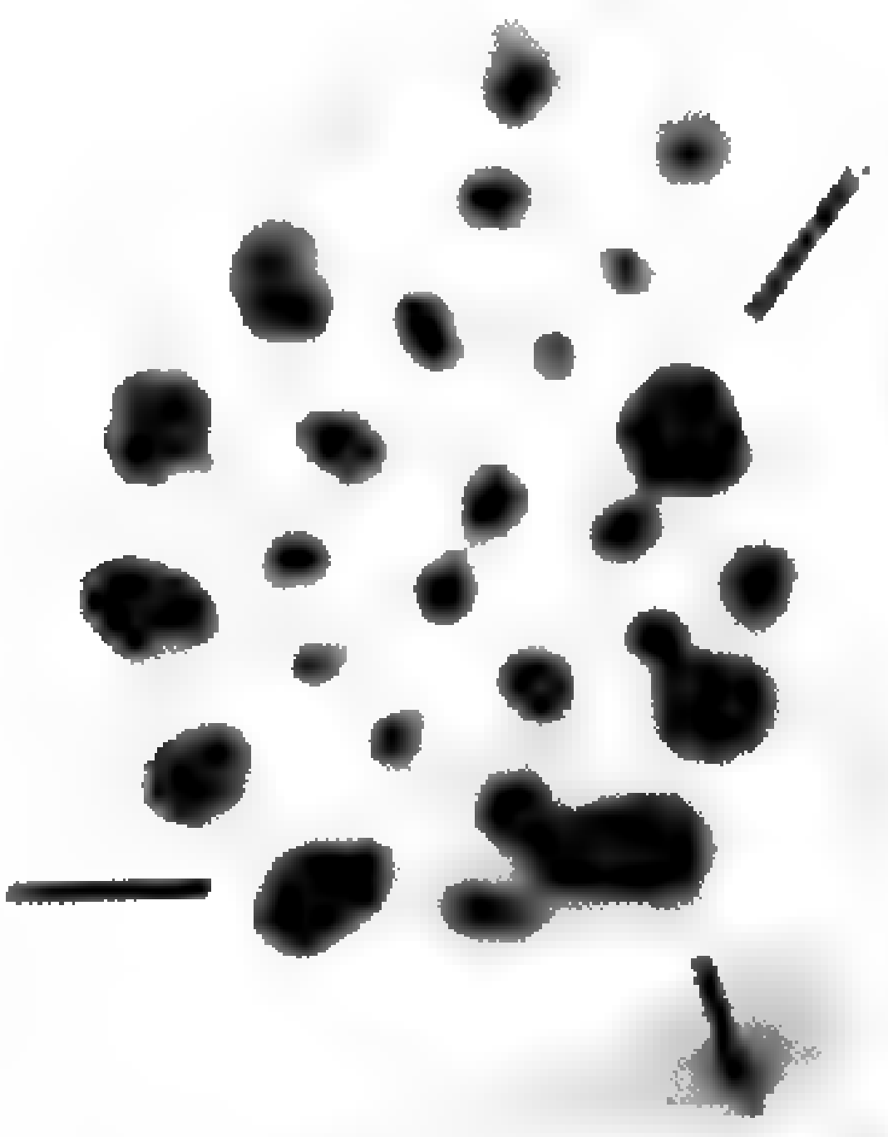

1

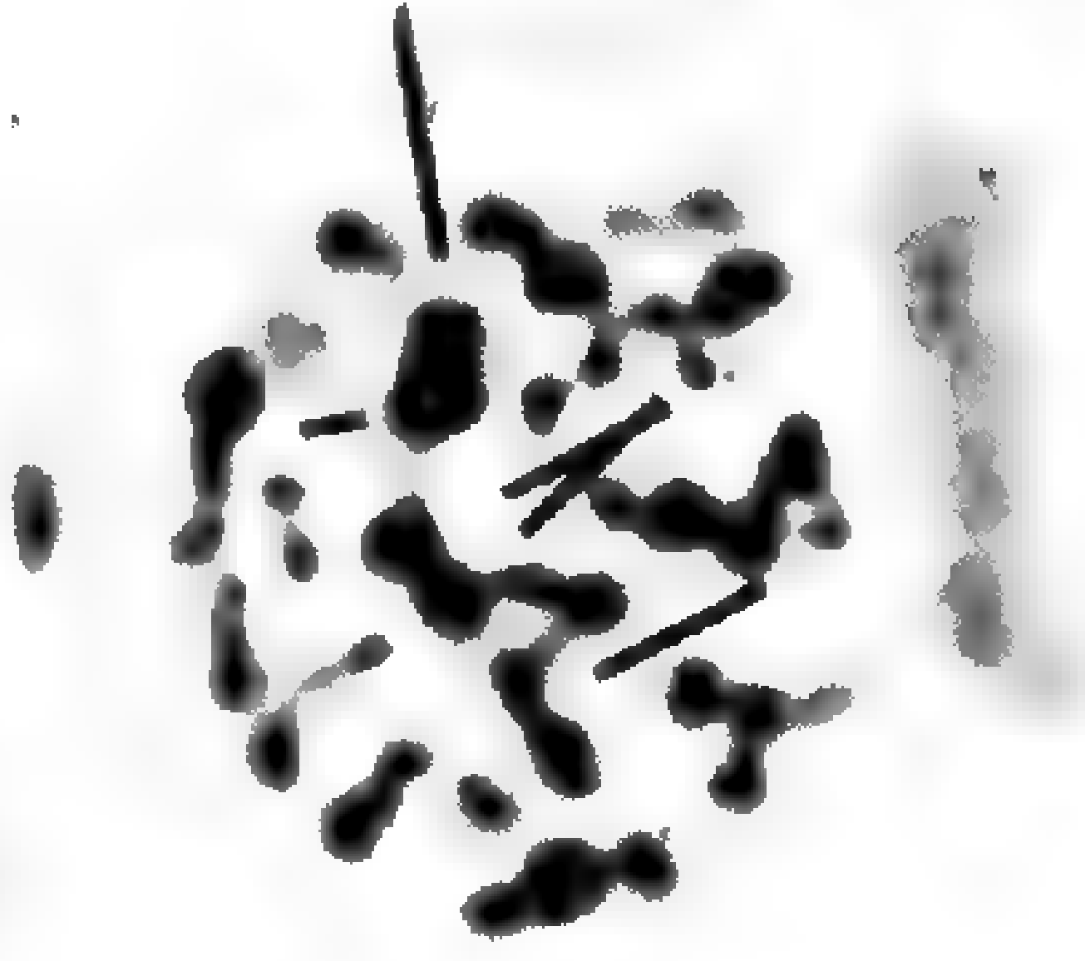

2


3

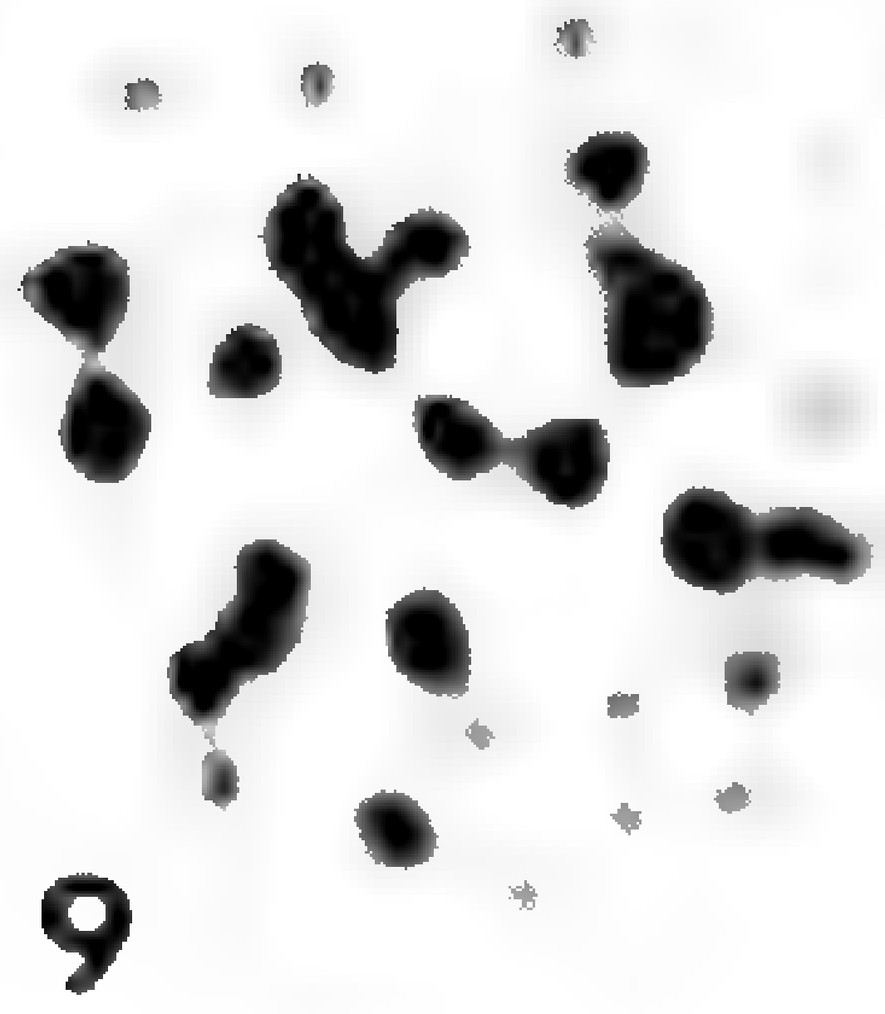

4

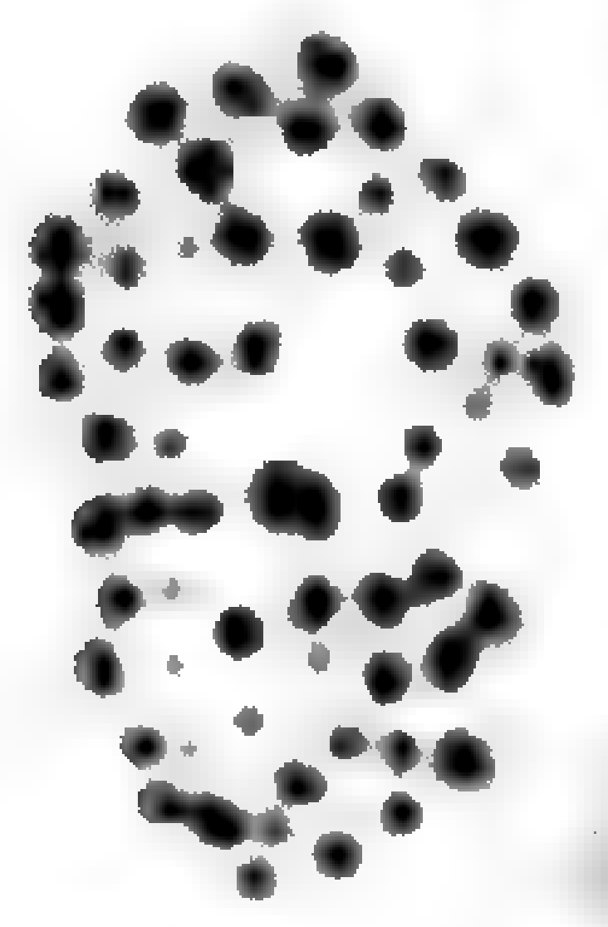

5

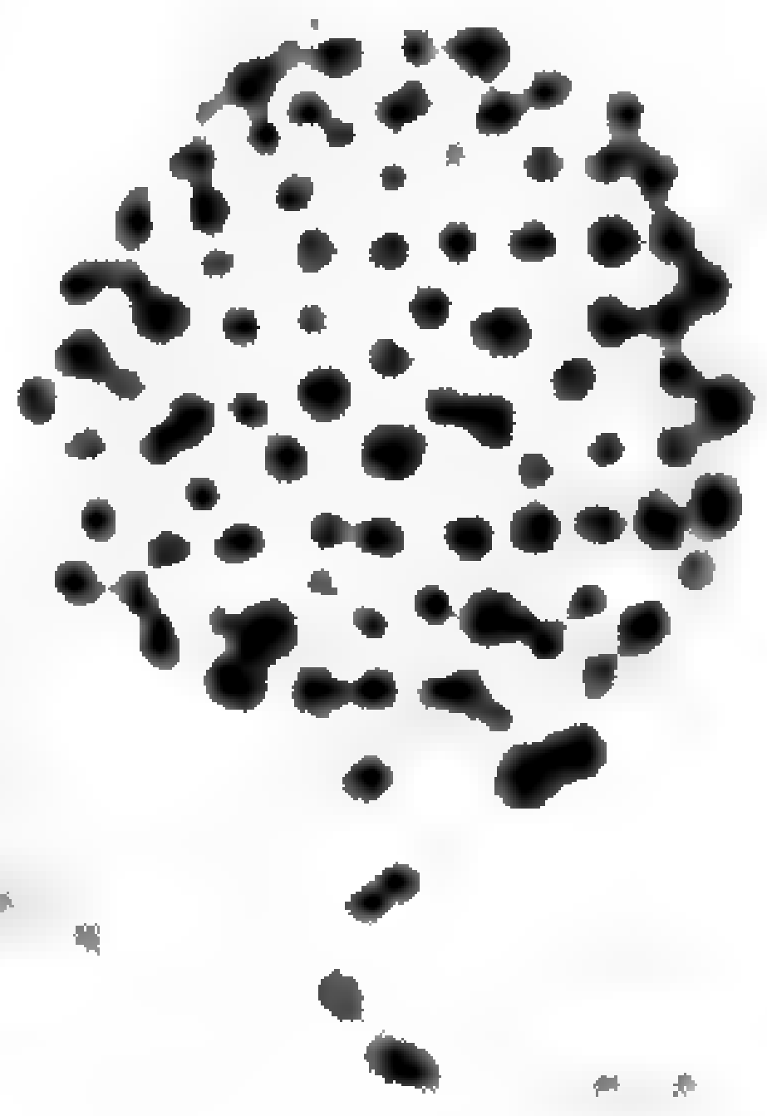

6

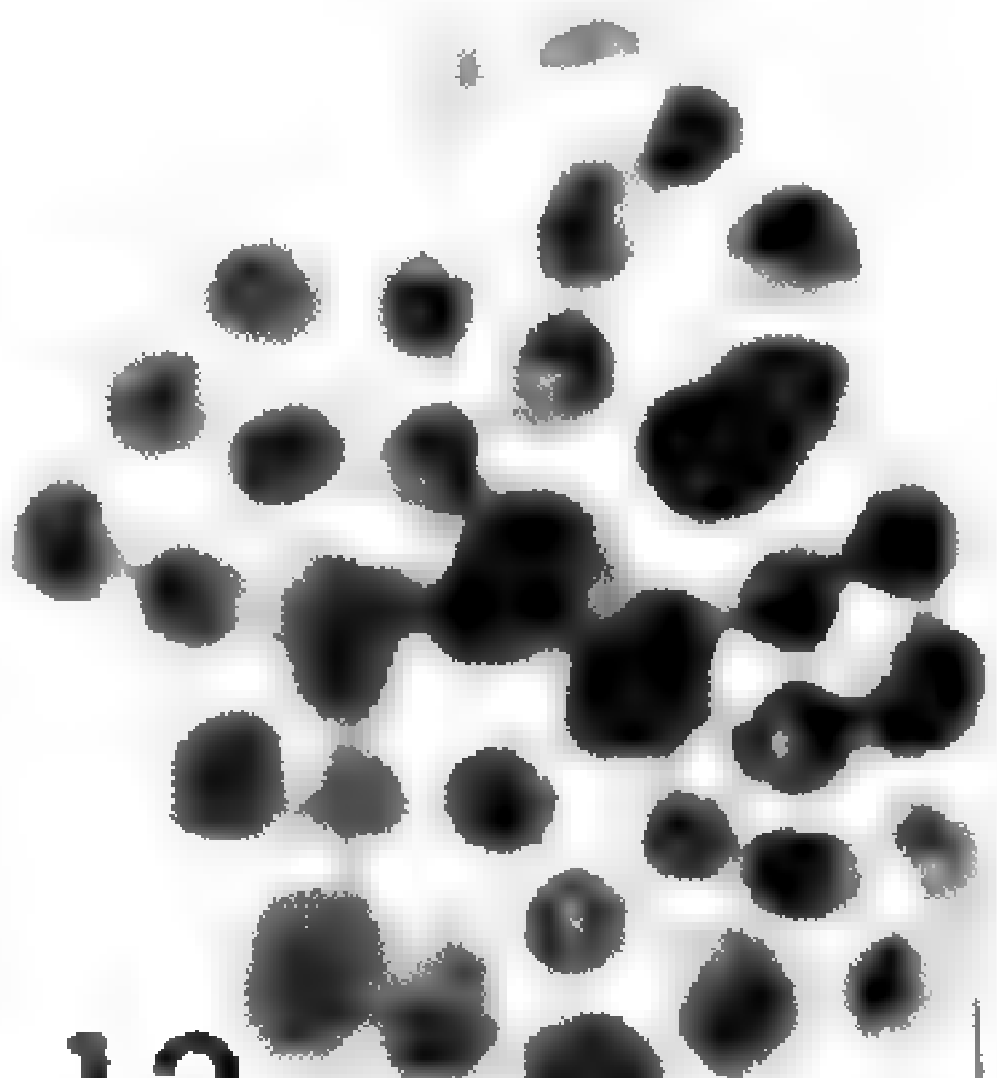

7

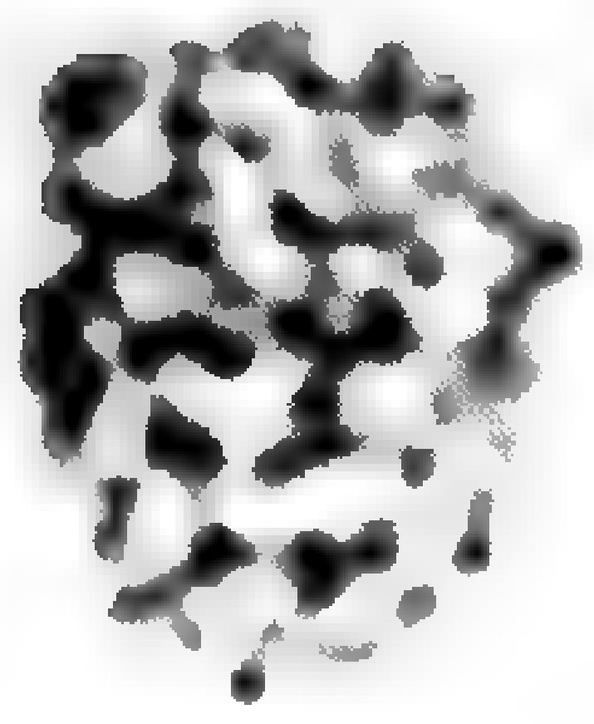

8


9

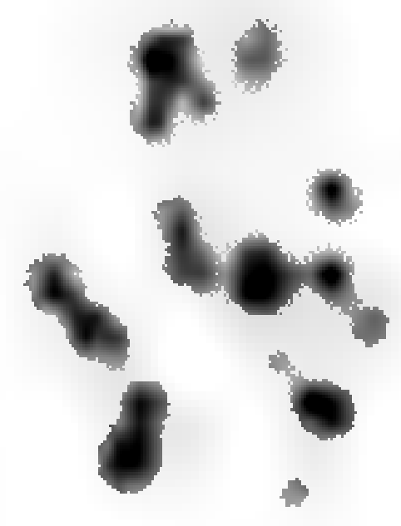

10

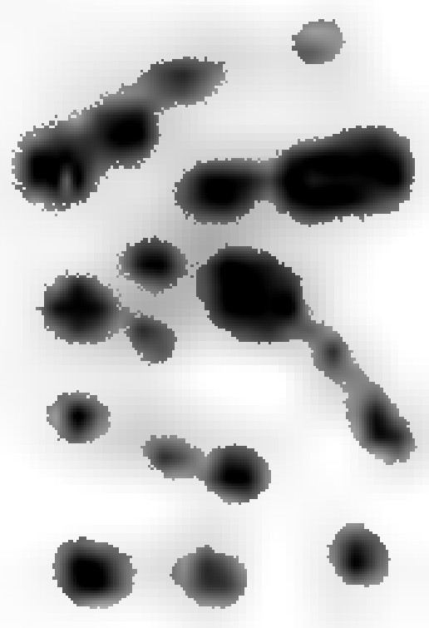

11

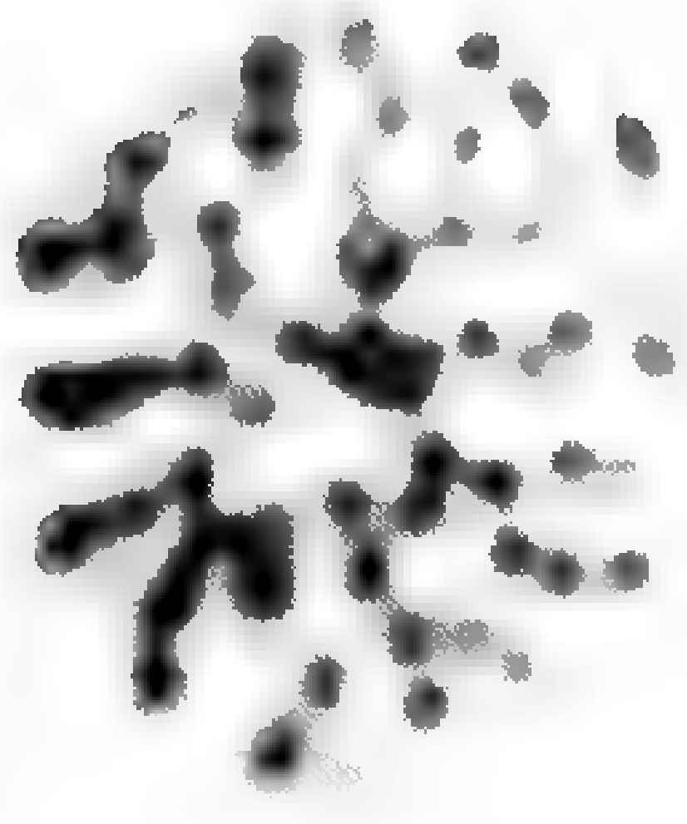

12

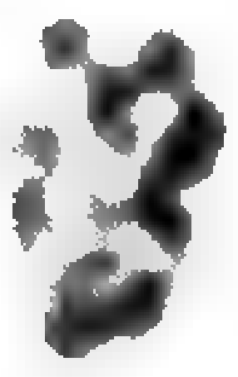

13

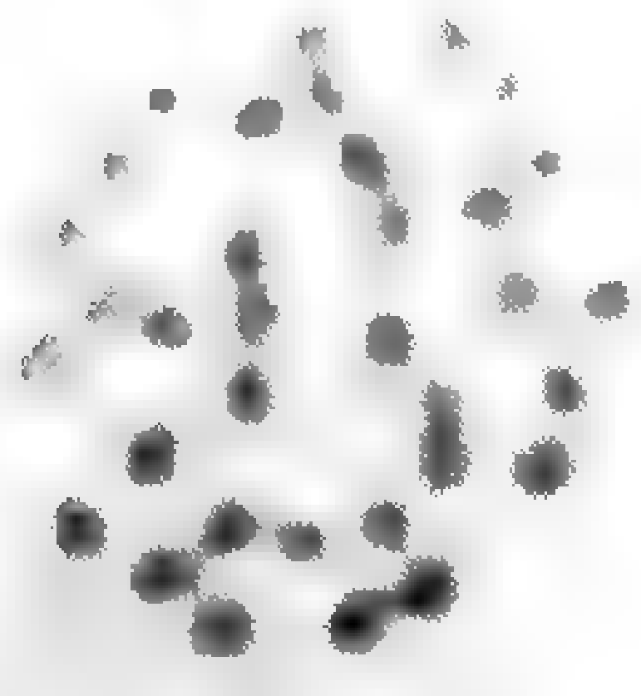

14

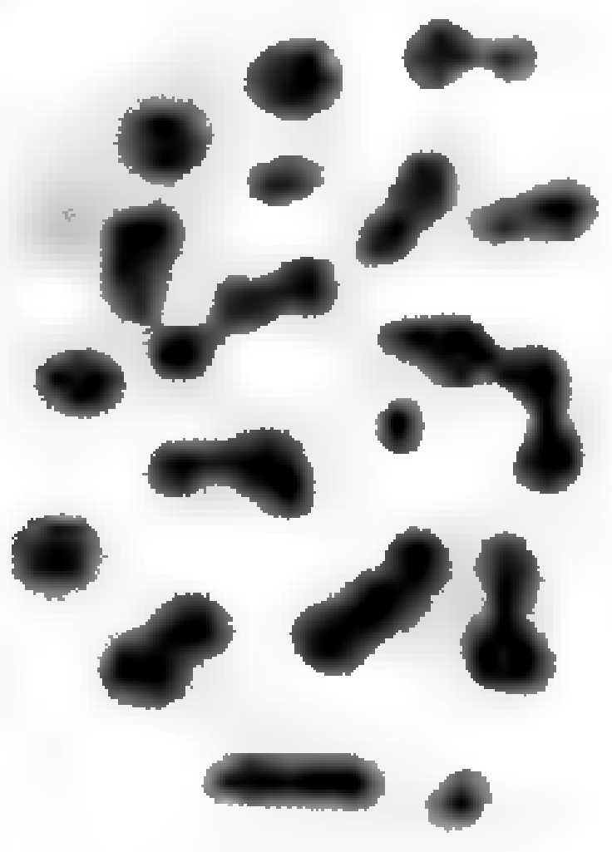

15


16


17


18


19


20

univalents probably consist of most or all of the 26 chromosomes from *S. greggii,* plus some of the third homologues of *S. alamosanum.* Evidently no more than a very little pairing occurs between chromosomes received from the different parents of this hybrid, or else a larger number of paired elements would have been seen. A hybrid between diploid *S. alamosanum* ($n = 18$) and the same *S. greggii* (*U1535* × *U1647*) showed considerable chromosome pairing, but it appears loose and unstable, and the genomes of these two parents, consisting of 18 and 26 chromosomes respectively, must differ very substantially in their organization.

Sedum australe

Sedum australe Rose is often confused with *S. oaxacanum* (*cf.* Clausen, 1946), but it differs from the latter in its linear, terete leaves and its reddish yellow flowers with mucronate petal tips. The type locality is in southwestern Guatemala, but one polyploid collection ($n =$ ca. 100) from adjacent Mexico may belong here, or it may represent a narrower-leaved form of *S. oaxacanum.*

Sedum bellum

Sedum bellum Rose ex Praeger was first named *S. farinosum* Rose (1911), but that name had been used earlier for a species from Madeira. It has elongated rosettes of flat, spatulate, farinose leaves, ca. 20 mm. long and 10 mm. broad, and white flowers. A living

---

Figures 1 20. Chromosomes of *Sedum* species and various hybrids in pollen mother cells at metaphase I unless otherwise indicated, all X2000. In some cells, univalents and or B-chromosomes are indicated with thin lines, certain paired elements (bivalents and or multivalents) with thick lines. **1–4.** *S. alamosanum:* **1,** *U2408,* $n = 17 + 1$; **2,** *C44-19,* $n = 18$; **3,** *U2021,* $n = 36$; **4,** *U2683,* $n = 54$; **5,** *S. alamosanum* ($n = 18$) × *S. lumholtzii* ($n = 19$), *U1647* × *UC68.144,* 17 bivalents + 1 univalent (+ 2 univalents out of focus); **6,** *S. alamosanum* ($n = 18$) × *S. multiflorum* ($n = 12$), *U1647* × *U2088,* 3 bivalents + 24 univalents—larger chromosomes from *S. multiflorum;* **7,** *S. alamosanum* ($n = 18$) × *Cremnophila nutans* ($n = 33$), *U1647* × *M10174,* 5 paired elements + ca. 38 univalents; **8,** *S. bellum, U2648,* $n = 36$; **9,** *S. bellum* hybrid, *U1944,* 18 paired elements + 18 univalents; **10–11,** *S. caducum:* **10,** *U2777,* $n = 64$; **11,** *U2779,* $n = 96$; **12,** *S. clavifolium, U1762,* 34 elements, including 2 univalents; **13,** *S. compactum, U1509,* $n = 60$ probably; **14,** *S. cupressoides, U2358,* $n = 30$; **15–17,** *S. diffusum:* **15,** *U1922,* $n = 19$; **16,** *C7363,* $n = 19 + 1$; **17,** *M7727a,* $n = 54$; **18,** *S. globuliflorum, U2643,* $n = 12$; **19,** *S. grandipetalum, U1755,* $n = 34$; **20,** *Pachyphytum hookeri* ($n = 32$) × *S. grandipetalum, M13349* × *U1755,* 32 paired elements + 1 univalent.

clonotype was obtained by R. T. Clausen in 1947 from the New York Botanical Garden, still bearing Rose's original collection number. The type locality is western Durango, and I know of no other collections of this species. This plant has $n = 36$, or the equivalent when several multivalents that are usually present are allowed for (Fig. 8), and apparently it is an autotetraploid. Reciprocal attempts to cross *S. bellum* with tetraploid *S. alamosanum* (also $n = 36$) were unsuccessful, as was also an attempted cross with tetraploid *S. palmeri* ($n = 68$).

A rather similar plant that is widely cultivated as *Sedum bellum* appears to be a triploid garden hybrid between *S. bellum* and an unknown diploid species. This hybrid differs from true *S. bellum* in its larger size and flowers, and Clausen (1981) suggested that the other parent might have been an *Echeveria*. However, flowers of the hybrid show none of the compromises in petal orientation that are seen in other hybrids between *Sedum* and *Echeveria*, and this suggestion does not seem reasonable to me. Meiosis in this hybrid is highly irregular, with 17 or 18 bivalents and multivalents observed at metaphase I, plus 18–22 univalents (18 + 18 in Fig. 9), and with many laggards at anaphase I. The close morphological resemblance of the hybrid to *S. bellum* and the behavior of its chromosomes at meiosis suggest that it received a double dose of hereditary information in the form of two sets of 18 chromsomes each from *S. bellum*. At meiosis the homologous chromosomes of these two sets tend strongly to form pairs, while the chromosomes from the other parent generally remain unpaired. The other parent must have been a diploid *Sedum* that contributed a single set of probably at least 22 chromosomes to the hybrid. At meiosis these chromosomes have no homology at all with each other and relatively weaker homology with those of *S. bellum*, and most of them remain unpaired.

Sedum caducum

Sedum caducum Clausen (1950) has leaves that are thick, heavily spotted with red and easily detached, resembling *Lenophyllum* for which it was at first mistaken. However, its petals spread from the base and do not recurve, and this character classes it with *Sedum*. The species occurs at relatively low elevations on the east slopes of the Sierra Madre Oriental in southern Tamaulipas. A plant of the type collection had $n = 96$ (Fig. 11), but another collected earlier apparently nearby had $n = 64$ (Fig. 10), as did a third plant from a higher elevation about 70 km. northwest. The counts suggest a basic chromosome number of 32, but no plants with that number have been found.

Originally Clausen (1950) classified *Sedum caducum* near *S. cockerellii* (n = 14–16, 29–32) of southwestern United States and northwestern Mexico and *S. wrightii* (n = 12 and multiples), which ranges from nearby to southeastern New Mexico. Later (1981) he suggested that it might have originated by hybridization between *Lenophyllum acutifolium* (n = 22), which occurs with it, and *S. calcicola* (n = 32, 48, 64) or *S. wrightii*. Such an origin seems highly unlikely to me.

Sedum clavifolium

Sedum clavifolium Rose is small, with branched rhizomes, greenish white petals, and conspicuous red nectaries. It is known only from high on the west slope of the Iztaccihuatl volcano, southeast of Mexico City (Clausen, 1959). Three plants were studied cytologically, but none yielded an exact count, although the gametic chromosome number is probably in the range of 34 to 38 (Fig. 12). Univalents and/or multivalents were noted at metaphase I in many cells, and after meiosis some "quartets" included one or more extra and/or undersized microspores. Attempted crosses with *S. retusum* and *S. stelliforme* were unsuccessful.

Sedum cockerellii

Sedum cockerellii Britton has a tufted habit, with somewhat fleshy roots and small vegetative rosettes that elongate their second year to produce stems up to 20 cm. long, bearing cymes of white to faintly pinkish flowers (Clausen, 1975). The species is variable morphologically, but the variation seems more or less continuous; hence a broad concept of the species is followed here, to include also *S. anomiosepalum* Fröderström, *S. griffithsii* Britton, *S. puberulum* S. Wats., and *S. wootoni* Britton (Uhl, 1972; Clausen, 1975). It ranges from north central New Mexico and Arizona to northern Sonora and far south into Chihuahua. Several different chromosome races have been found, but plants from the same mountain range have all had the same chromosome number (ignoring occasional B-chromosomes): n = 14, 15, 16, 29, 30, 32. Clausen (1975, p. 196) reported counts of n = 17 and n = 14 for plants from Tuerto Mountain and from Cuba respectively, both in New Mexico. These numbers differ from the pattern reported here, but I have recently made new slides from the same plants that he studied (*U2729* and *U2768*), and I find that both have $n = 16$, although the former also has 2–4 B-chromsomes. These new counts conform to the distribution of chromosome races that I have reported previously (Uhl, 1972).

Additional plants reported here also support the earlier report in all respects and add the new information that the plants from Chihuahua, like those from the Davis Mountains of western Texas, all have $n = 15$. A near topotype of *Sedum wootoni*, the first report from the Organ Mountains of southern New Mexico, had $n = 32$, which is a new number for the species. An attempt to cross *S. cockerellii* ($n = 15$) with *S. stelliforme* ($n = 13 + 3$) (*U2529* × *U2245*) was unsuccessful, perhaps because of the cytological irregularity of the prospective seed parent.

Sedum compactum

Sedum compactum Rose of Oaxaca is small and moss-like, with papillose leaves and floral parts and globular flowers. Petals are white, flecked at the base with red, upcurving and with tips that spread very little, as in *S. globuliflorum*. The only specimen studied had $n = 60$, probably (Fig. 13). A hybrid with autotetraploid *S. allantoides* of section Centripetalia ($n = 58$, Uhl, 1980) (*M6358* × *U1509*) was morphologically intermediate between the parents and had nearly normal meiosis, with 59 bivalents or the equivalent in most cells at metaphase I. This hybrid produced 10.2% stainable pollen at anthesis, and it is fertile, since ten seedlings similar to it were grown from seed that it produced spontaneously. This behavior is expected if the hybrid received from autotetraploid *S. allantoides* two similar sets of 29 chromosomes each and from *S. compactum* two other sets of 30 each that are similar to each other. At meiosis the most similar chromosomes usually pair preferentially, forming 59 pairs (29 + 30) in most cells. This behavior means that *S. compactum*, or at least the plant studied here, is an autotetraploid. A similar situation has been documented in detail for autotetraploid *Echeveria secunda* (Uhl, 1982b). Attempted crosses of *S. compactum* with *S. versadense*, with polyploid *S. reptans* (*M13381*) and with polyploid *S.* cf. *semiteres* (*U2251*) resulted in no viable seeds.

Sedum cupressoides

Sedum cupressoides Hemsley is one of several small species of southern Mexico and Guatemala that are poorly known and often confused. As conceived here (*U2358*), it has white to faintly pinkish flowers and spreading, closely crowded, awl-shaped leaves about 3 mm. long that taper from a base about 1.5 mm. in diameter and persist on the stem after drying, as in *S. liebmannianum*. A collection from Oaxaca, perhaps from the region of the type locality, and another from about 300 km. to the north-northwest in Puebla both had $n = 30$, the latter also with a small, unpaired B-chromsome (Fig. 14). This species has sometimes been confused with *S. muscoideum* (Clausen, 1959; Praeger, 1921), but that species has yellow flowers, tightly appressed, almost scale-like leaves and $n = 34$. Attempts to cross *S. cupressoides* (*U2358*) with *S. alamosanum* ($n = 18$), *S. greggii* ($n = 33$), and *S. semiteres* ($n = 19$) were unsuccessful.

Sedum diffusum

Sedum diffusum S. Watson resembles *S. alamosanum* and appears to replace it to the southeast, but it forms mats and its leaves are smooth and blue glaucous, not papillose, and its petals are white, not pinkish. *Sedum potosinum* Rose seems not distinguishable (Clausen, 1981). *Sedum diffusum* occurs mainly on limestone on the eastern slopes of the northern Sierra Madre Oriental within 50 km. of Monterrey, with outlying populations to the northwest in Coahuila and apparently Chihuahua and, when *S. potosinum* is included, to the south in San Luis Potosi. Six collections had $n = 19$ (Fig. 15), one trisomic, with an extra standard chromosome (Fig. 16), but one collection from cultivation was tetraploid with $n = 38$, and five others, four of them from cultivation (most of them received as *S. potosinum*), were hexaploid with $n = 57$ (Fig. 17). The occurrence of diploids, tetraploids, and hexaploids here parallels the situation in *S. alamosanum* ($n = 18, 36, 54$). Seven attempts to cross *S. diffusum* with five other species of section *Sedum*, including *S. alamosanum*, and with *Graptopetalum fruticosum* were all unsuccessful.

Sedum globuliflorum

Sedum globuliflorum Clausen (1979) has strongly ciliate leaves and white petals that are erect, incurved and slightly connate at the base, giving the flowers a nearly spherical shape at anthesis, rather like those of *S. compactum*. The carpels are grooved ventrally and incompletely sealed, and Clausen (1979) thought the species so distinctive that he created a new subgenus, Sulcus, for it. It is known only from its type locality in northwestern Hidalgo. A plant of the same clone as the type had $n = 12$ (Fig. 18), with the spindles very slender and the chromosomes always tightly clumped at metaphase I and II. Clausen believed that the species is self-pollinated, and no crosses have been attempted.

Sedum grandipetalum

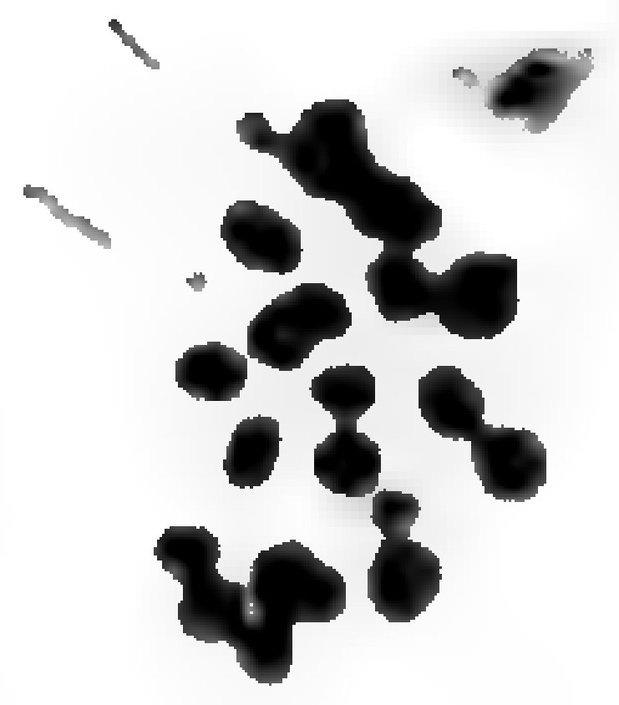
Sedum grandipetalum Fröderström of southwestern Jalisco somewhat resembles *S. greggii* but is substantially larger in all respects and has pendent branches and floral stems (Clausen, 1959). Two plants from a population on the north side of the Nevado de Colima had $n = 34$ (Fig. 19), as did also a third plant from the Sierra de Minatlan, about 65 km. west. This chromosome number also occurs in *S. greggii*. A hybrid with *Pachyphytum hookeri* ($n = 32$) (*M13349* × *U1755*), considered a very wide cross, resembled the pollen parent (*Sedum grandipetalum*) rather more closely and showed a surprising amount of chromosome pairing: 29–32 paired elements plus 0–5 univalents in 12 cells analyzed at metaphase I (32 + 1 in Fig. 20). A hybrid with *S. greggii* ($n = 26$) (*U1535* × *U1755*) died without flowering, and attempted crosses with *S. alamosanum*, *S. palmeri*, and *S. tortuosum* were unsuccessful.

Sedum greggii

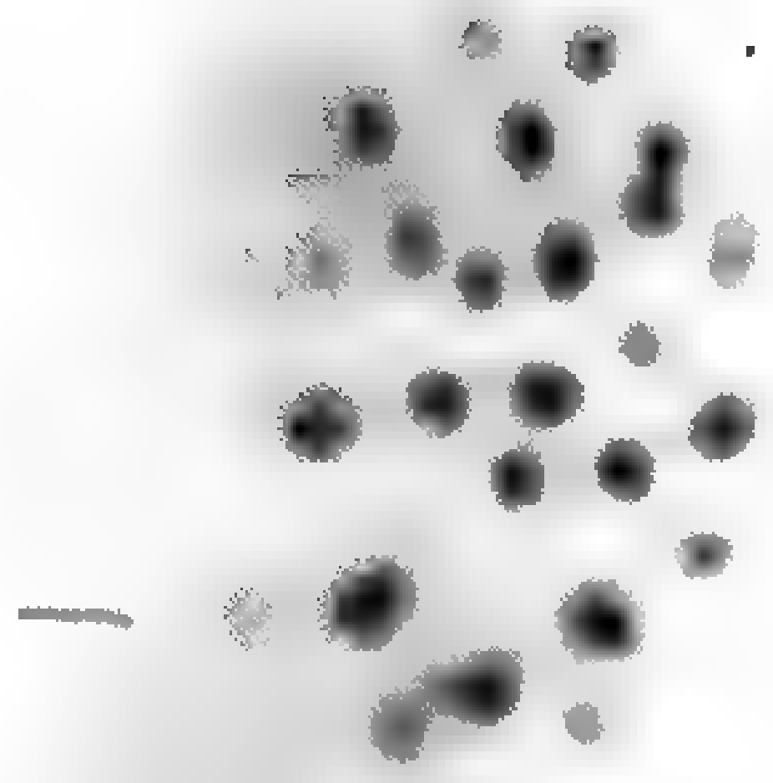
Sedum greggii Hemsley forms small, dense vegetative rosettes which extend to form often relatively long and lank floriferous stems with larger and more loosely arranged leaves, and eventually produce small cymes of yellow flowers. Both types of leaves are papillose. *Sedum humifusum* is similar but generally smaller and has ciliate leaves and solitary flowers. *Sedum greggii* occurs from northwestern Puebla west across central Mexico to southern Jalisco and north to southern San Luis Potosi. The species is very diverse cytologically, with polyploids and considerable dysploidy. A chromosome race with $n = 33$ (Fig. 25), one plant with 6 additional B-chromosomes (Fig. 26), appears to be relatively common from northern Hidalgo and adjacent Queretaro to the northwestern part of the state of Mexico (9 collections, plus 3 others of uncertain origin). This region includes the type localities of both *S. greggii* and

S. diversifolium Rose, which, following Clausen (1959), is reduced here. A second chromosome race with $n = 26$ (Fig. 23) occurs in southwestern San Luis Potosi and adjacent Guanajuato (5 collections, one with a B-chromosome). These two dysploid chromosome races must represent at least incipient species. Closer study, including chemotaxonomic methods, e.g., might reveal other consistent differences between them and especially whether the 26-chromosome race has any particular affinity to *S. nanifolium* from farther north, also $n = 26$. Other dysploid plants had $n = 24 + 1$ (Fig. 22) from central Guanajuato, apparently a deviant from the 26-chromosome race, and $n = 18 + 6B$ (Fig. 21) from northwestern Puebla. The westernmost collection, from southern Jalisco, had $n = 30$ (Fig. 24), and plants from Hidalgo and Michoacan had $n = 34$ (Fig. 27), probably variants from the 33-chromosome race. An apparent triploid was from northwestern Puebla. Three plants from two collections of subspecies *angustifolium* Clausen from the Volcano of Tequila, in Jalisco, including the type clone, were polyploids of some sort and cytologically very irregular. About 80–90 elements, including univalents, bivalents, and multivalents, were present at metaphase I and many laggards at anaphase I, with extra and/or abnormal microspores in nearly every quartet after meiosis. Clausen (1978) noted that vegetative propagation is very common here, with leaves easily detached and sprouting readily to produce new plants, and this ability may compensate for the apparent sexual sterility.

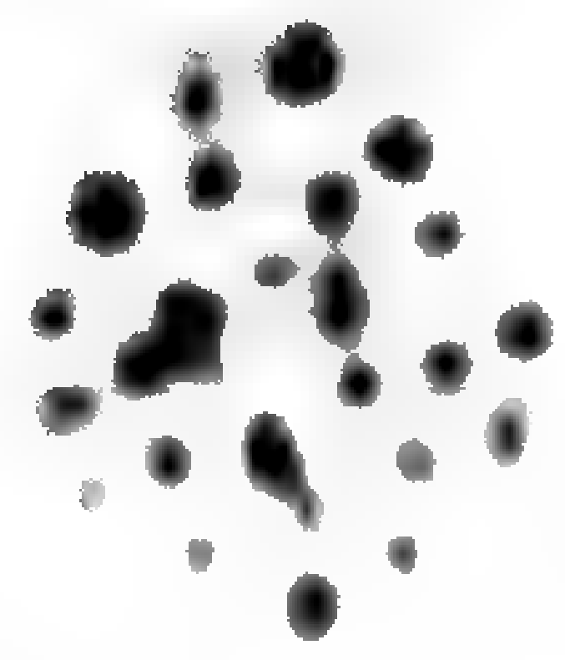
A hybrid between the 33- and 26-chromosome races of *Sedum greggii* (*M7807* × *U1535*) was irregular at meiosis, as expected, and produced very few stainable pollen grains. The number of paired chromosomal elements at metaphase I in 24 cells ranged from 24 to 26 with from 0 to 4 univalents (average 25.6 + 1.8) (26 paired elements in Fig. 28). As many as three laggards (univalents) and occasionally a bridge were noted at anaphase I, and 28 to 31 elements on each of 11 metaphase II plates. In fact, one cell at metaphase II had 28 elements on one plate, 31 on the other, thus accounting for all 59 of its somatic chromosomes. Evidence from chromosome pairing in other hybrids of *S. greggii* supports a conclusion that neither parent here contributes any chromosomes to its gametes that can pair with each other and therefore that both the 26- and 33-chromosome parents are now effectively diploid (*cf.* Uhl, 1976a, 1982a). Thus all pairing at meiosis in this hybrid occurs between



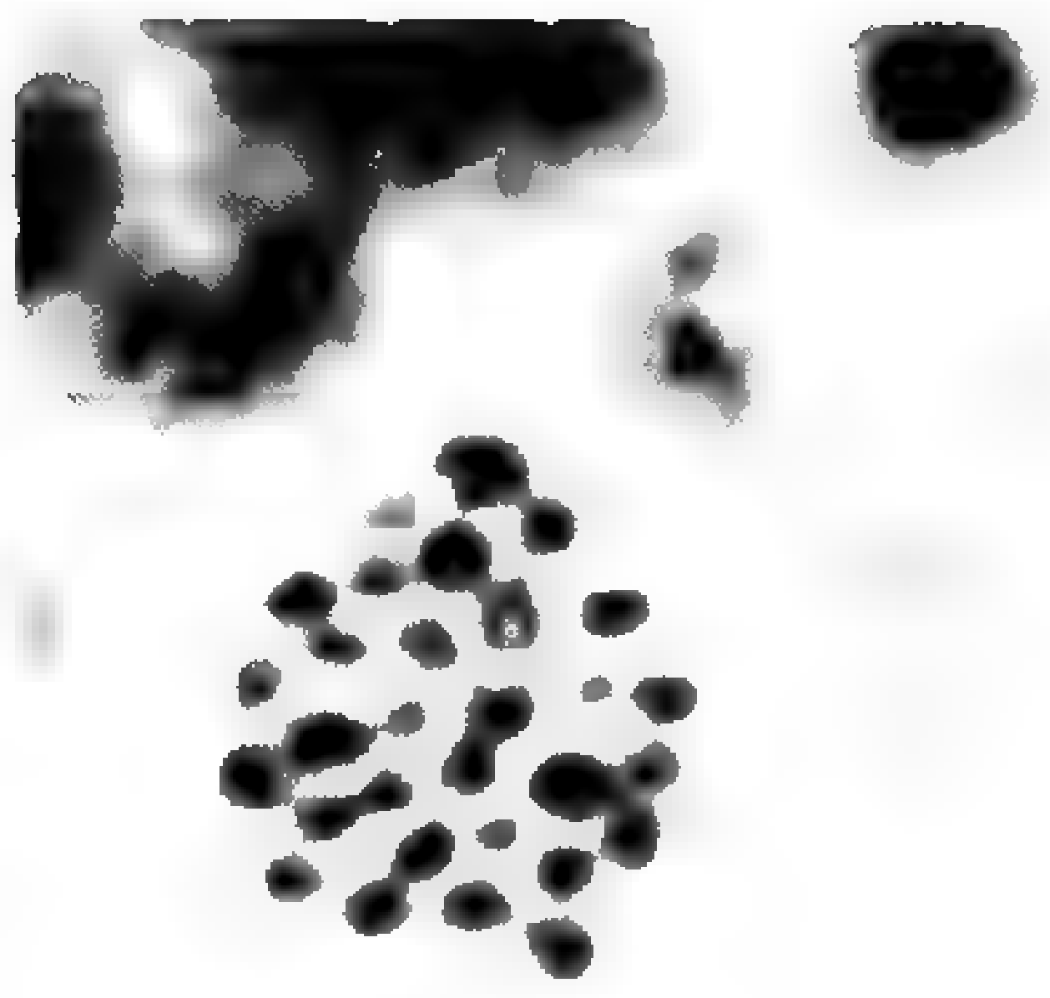
21



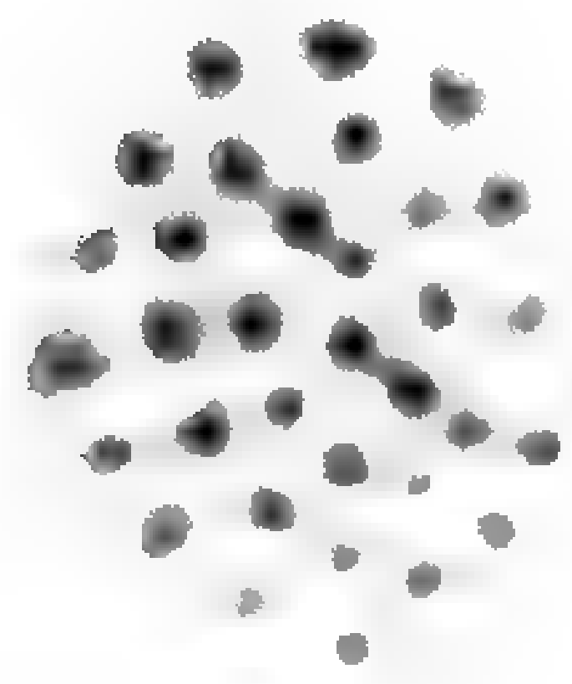
22



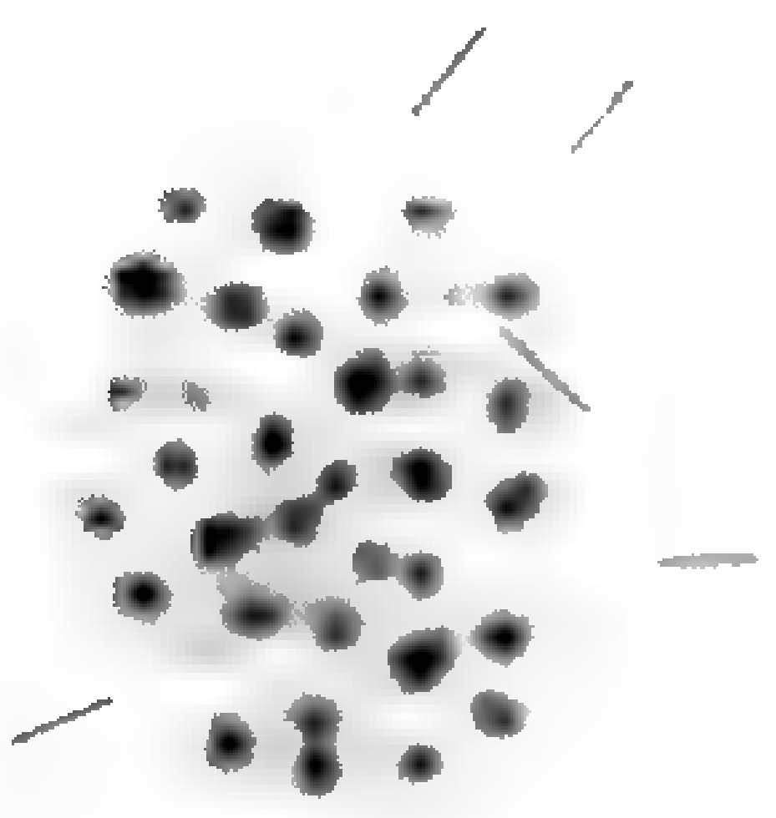
23



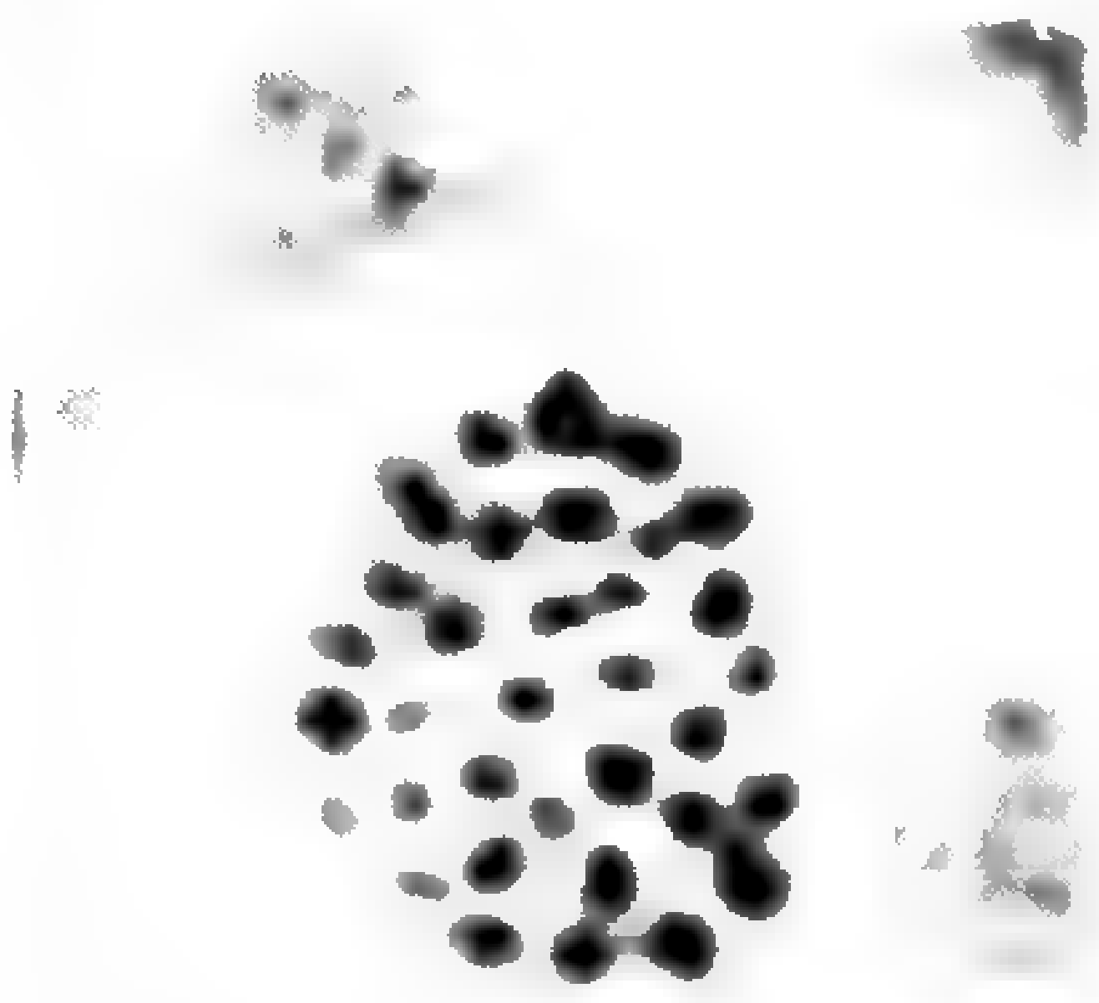
24



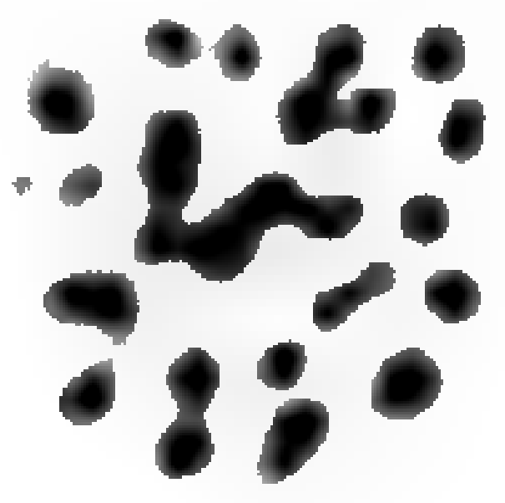
25



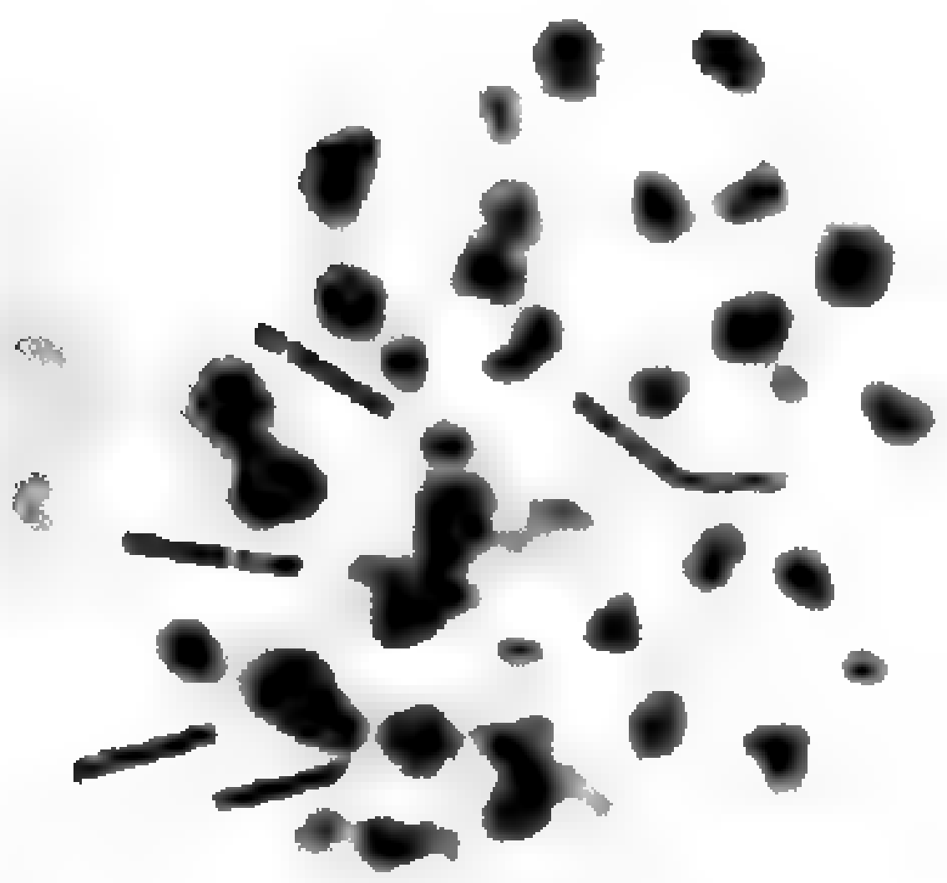
26



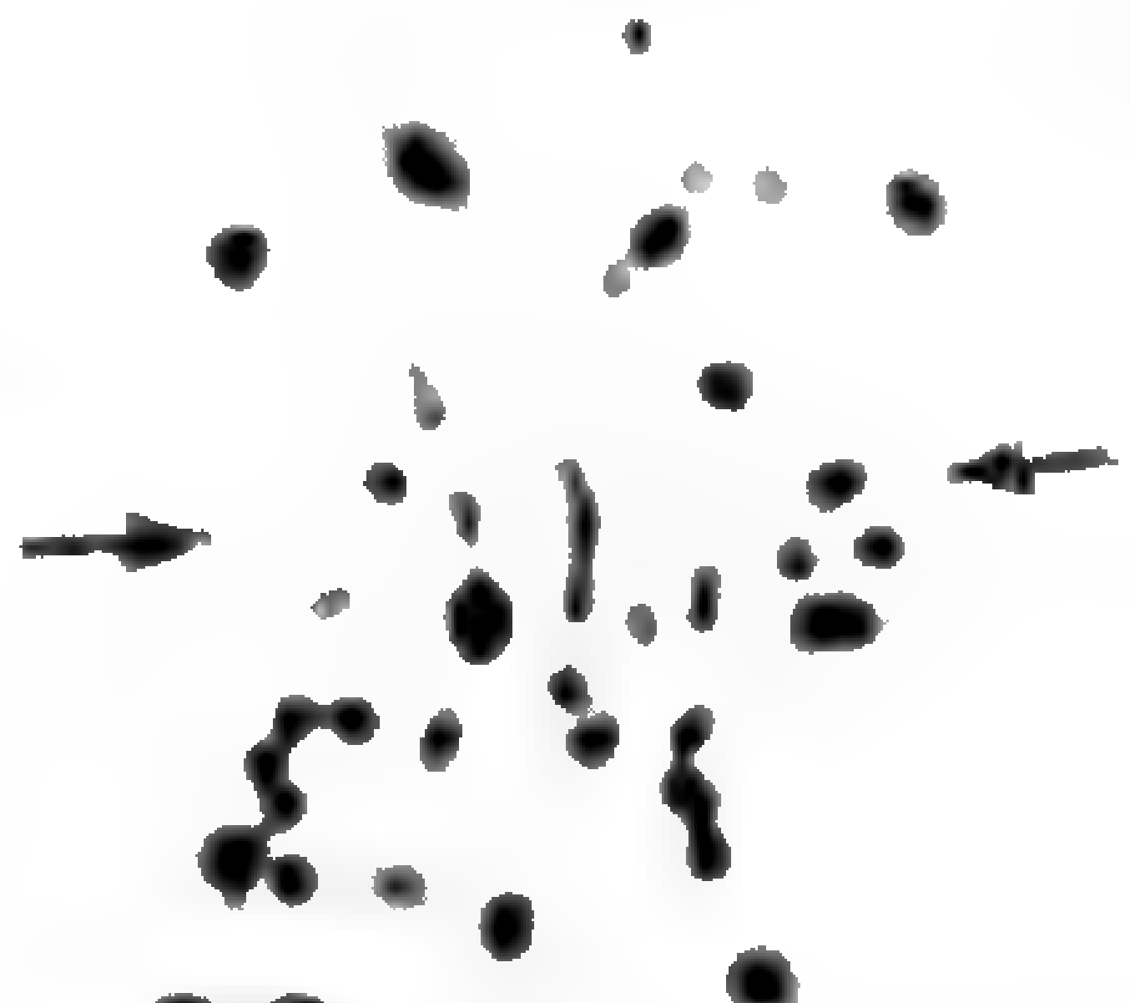
27



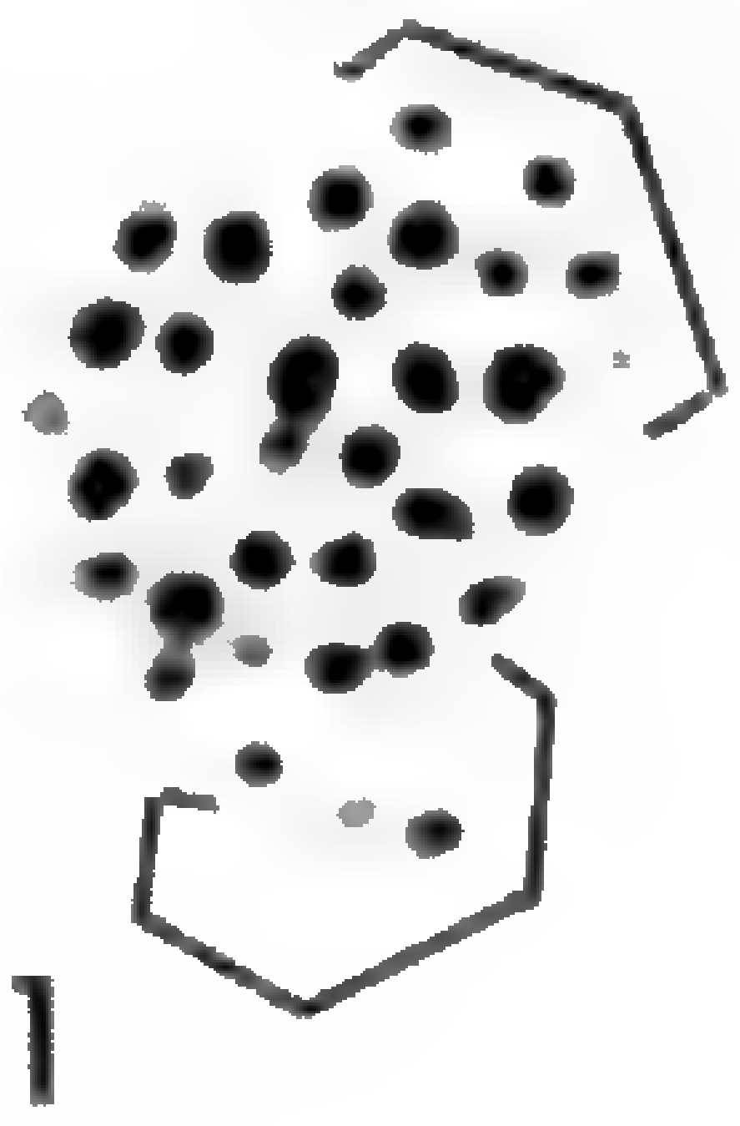
28



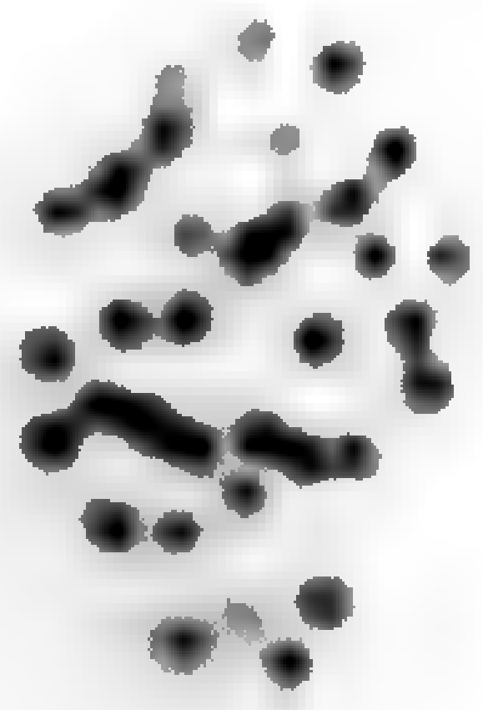
29



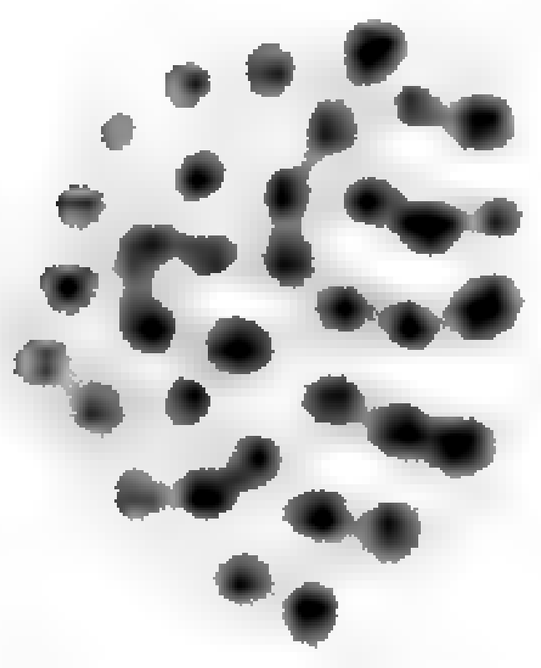
30



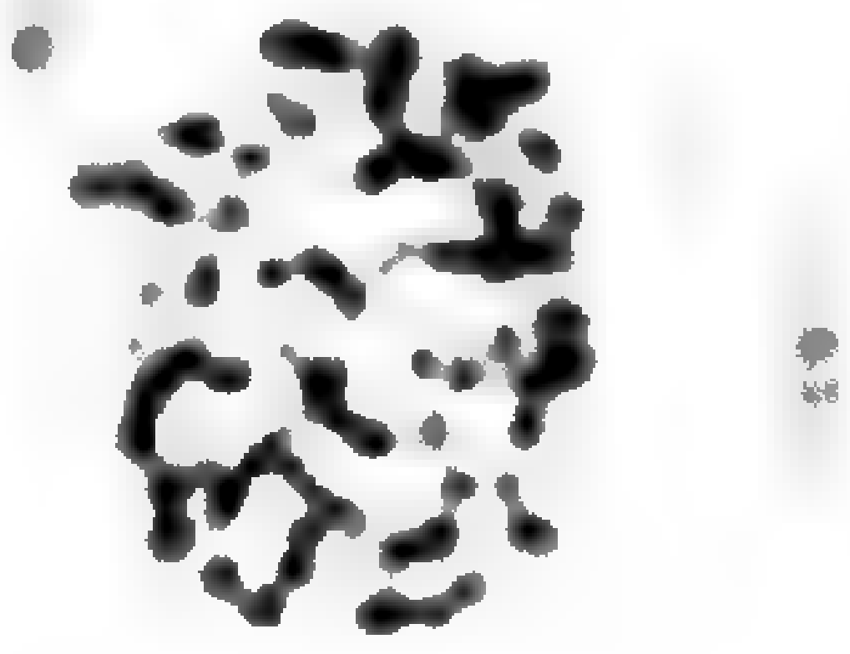
31



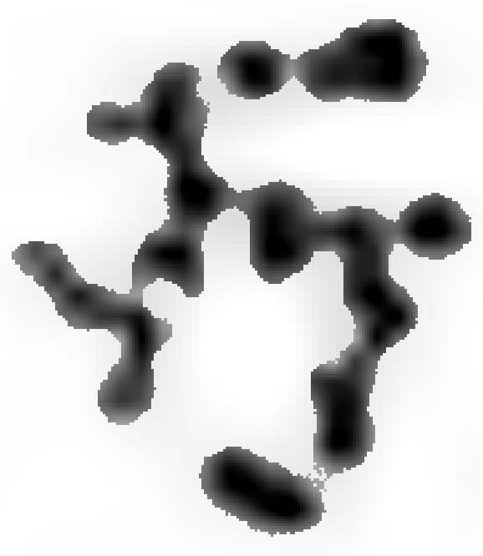
32



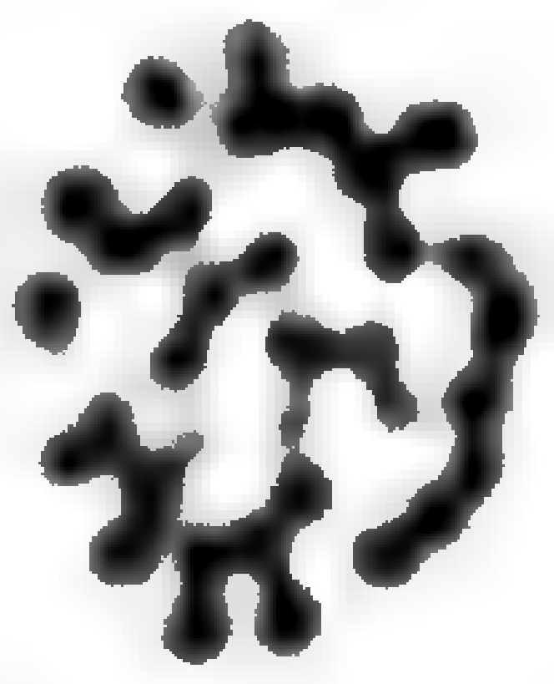
33



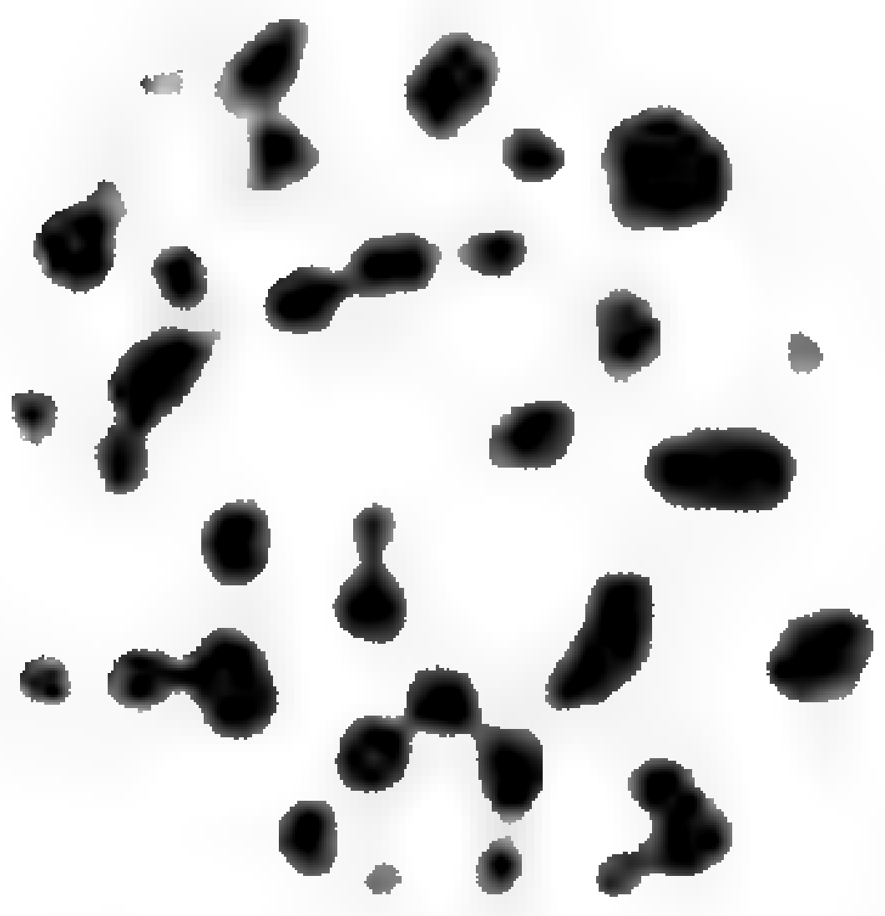
34



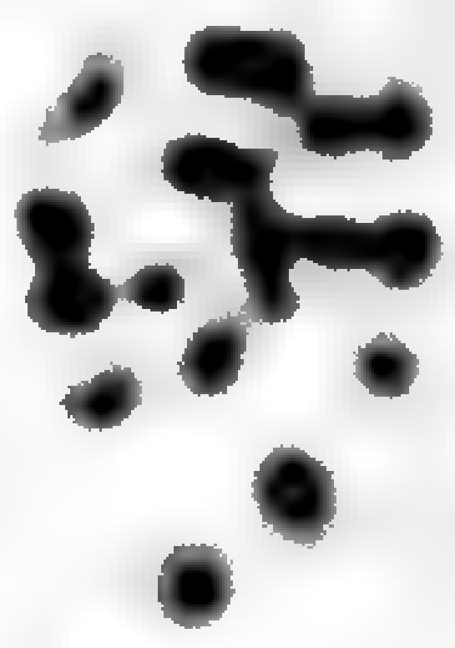
35



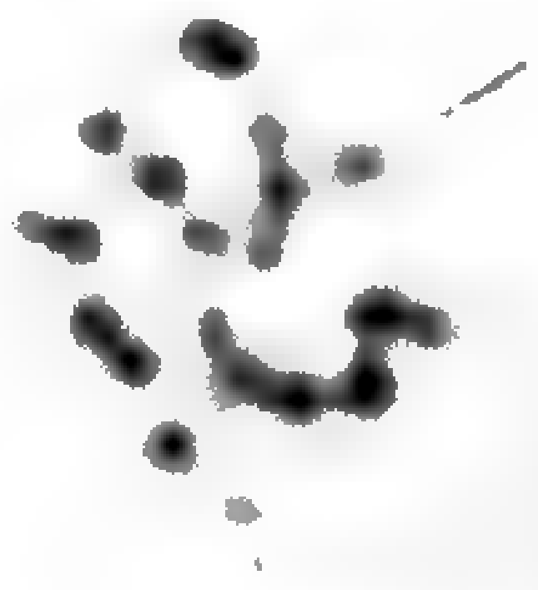
36



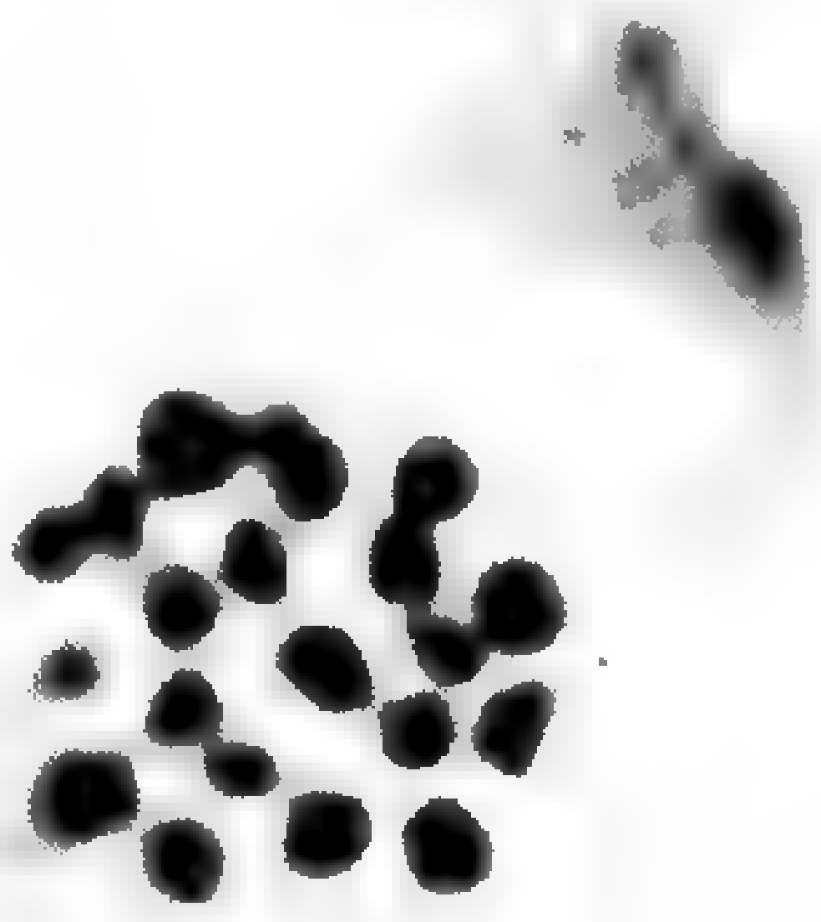
37



38



39



40

chromosomes of the different parents. Evidently the chromosomes of their putative common ancestor have undergone considerable rearrangement of corresponding parts by translocations and inversions while still retaining enough homology among the rearranged parts that most or all of the chromosomes still have regions that can pair with each other. Extensive rearrangements of this sort can lead to differences in chromosome number (dysploidy), and this sort of thing is common in the Mexican species of *Sedum*.

Sedum luteoviride Clausen is meiotically irregular and is considered to be a natural hybrid, probably *S. greggii* × *S. praealtum* ssp. *parvifolium* (Uhl, 1978). Two attempts to cross these two species artificially were unsuccessful.

Sedum greggii with $n = 33$ (*U1491, M7807*) has also been crossed successfully with nine other species, some of them very different and only distantly related: *S. cremnophila* (= *Cremnophila nutans*, $n = 33$), *S. cuspidatum* ($n = 34$), *S. furfuraceum* ($n = 34$), *S. obcordatum* ($n = 34$), *S. platyphyllum* ($n = 29$), *Echeveria* (*Cremnophila*) *linguifolia* ($n = 33$), *Graptopetalum fruticosum* ($n = 31$), *Villadia* cf. *pringlei* ($n = 15$), and an unidentified *Villadia* (*M10107*, $n = 14$). *Sedum greggii* with $n = 26$ has been hybridized with 12 species, including both cremnophilas (*S. cremnophila* and *E. linguifolia*) and *S. platyphyllum*—all three of these also hybridized with 33-chromosome *S. greggii*—and in addition: *S. alamosanum* (both diploid and hexaploid), *S. bourgaei* ($n = 29$), *S. grandipetalum* ($n = 34$), *S. griseum*

Figures 21–40. Chromosomes of *Sedum* species and various hybrids in pollen mother cells at metaphase I unless otherwise indicated, all X2000. In some cells, univalents and/or B-chromosomes are indicated with thin lines, certain paired elements (bivalents and/or multivalents) with thick lines. **21–27**, *S. greggii*: **21**, *U2354*, $n = 18 + 2B$; **22**, *M14738*, $n = 24 + 1$; **23**, *U1535*, $n = 26$; **24**, *U2675*, $n = 30$; **25**, *UC52.1765*, $n = 33$; **26**, *U2034*, $n = 33 + 5B$; **27**, *U2676*, $n = 34$; **28**, *S. greggii* ($n = 33$) × *S. greggii* ($n = 26$), *M7807* × *U1535*, 26 paired elements; **29**, *S. greggii* ($n = 26$), × *S. hultenii* ($n = 26$), *U1535* × *U1868*, 6 paired elements + ca. 40 univalents; **30**, *S. greggii* ($n = 33$) × *Cremnophila nutans* ($n = 33$), *U1491* × *M10174*, spindle view of poorly organized plate at metaphase I (arrows) with 2 paired elements plus many univalents off the plate; **31**, *S. greggii* ($n = 33$) × *Cremnophila linguifolia* ($n = 33$), *M7807* × *M14778*, 28 paired elements + 9 univalents (brackets); **32–34**, *S. humifusum*: **32**, *M14751*, $n = 34$; **33**, *M14754*, $n = 35$; **34**, *U1847*, $n = 68$; **35**, *S. latifilamentum*, *U2688*, $n = 20$; **36–37**, *S. liebmannianum*: **36**, *U2023*, $n = 34$; **37**, *M6379*, ca. 28 paired elements + 12 univalents; **38–40**, *S. longipes*: **38**, *U1412*, $n = 19$; **39**, *M10175*, $n = 19 + 1$; **40**, *Tep. 7*, $n = 20$.

($n = 30$), *S. hintonii* ($n = 25$), *S. hultenii* ($n = 26$), *S. multiflorum* ($n = 12$), *S. semiteres* ($n = 19$), and *Villadia levis* ($n = 20$). Twenty of these hybrids have flowered, and most of them show some pairing between chromosomes of the different parents, although nearly all of them also have large numbers of unpaired chromosomes (univalents) at metaphase I. For example, *S. greggii* ($n = 26$) × *S. hultenii* ($n = 26$) (*U1535* × *U1868*) had 5–16 paired elements + 18–40 univalents in 10 cells analyzed at metaphase I (6 + ca. 40 in Fig. 29), and *S. greggii* ($n = 33$) × *Cremnophila nutans* ($n = 33$) (*U1491* × *M10174*) had 6–18 paired elements + 26–48 univalents in 12 cells (side view of metaphase I showing mostly univalents in Fig. 30). Surprisingly, the greatest pairing was seen in a hybrid of 33-chromosome *S. greggii* with *Cremnophila linguifolia* (also $n = 33$) (*M7807* × *M14778*), where 24–31 paired elements and 3–15 univalents (average 27.5 + 9.5) were seen in 13 cells analyzed (28 + 9 in Fig. 31) (Uhl, 1976a). Fifty-eight attempted crosses involving other combinations with some of those that were crossed successfully, as well as attempts with 21 additional species, were unsuccessful.

Some interesting studies have been made of the physiology of these plants. *Sedum greggii* is a C–3 plant, fixing its CO_2 for photosynthesis in daylight, and *Cremnophila* (*Echeveria*) *linguifolia* is a CAM plant, which fixes its CO_2 in the dark. Different enzymes are employed in the two cases for the initial steps of photosynthesis, and it is surprising that plants so different can be hybridized. Teeri (1982) has found convincing evidence that both processes occur in the hybrid (*U1535* × *UC61.583*).

Sedum havardii

Sedum havardii Rose has creeping stems with small spreading linear leaves and white to pale pinkish flowers. It is known only from the Big Bend region of western Texas and adjacent Mexico (Clausen, 1984). I have previously reported counts of $n = 54$ and $n = 81$ for this species (Uhl, 1972) and now report two new counts of $n = 54$. The chromosome number of $n = 54$ in most collections of this species might suggest that it is some sort of hexaploid based on $x = 18$, as in the rather similar *S. alamosanum*. However, the occurrence of $n = 81$ here (Uhl, 1972) indicates that the basic chromosome number in this species is probably 27, although no such number has yet been found. Another theoretical possibility is that the ancestral number is 9, but that number has not been found in any perennial

Sedum in North America; it is known in Mexico only in two plants of one collection of the biennial *S. jaliscanum* ssp. *angustifolium* Clausen (1981) (reported as *S.* cf. *chihuahuaense* in Uhl, 1976b) and in one collection of a perennial *Villadia* (Uhl, unpub.).

Sedum humifusum

Sedum humifusum Rose is tiny, almost moss-like, with ciliate leaf margins and solitary yellow flowers. It occurs from eastern Guanajuato across Queretaro into western Hidalgo. Clausen (1981) considered it a "reduced type adapted to drier, warmer conditions than *S. greggii*," which is probably its closest relative. Three collections from western Hidalgo had $n = 34$ (Fig. 32), a number that is known also in *S. greggii*, but one from ca. 50 km. north in Queretaro had $n = 35$ (Fig. 33), and another plant from 30 km. farther north, in Guanajuato, was tetraploid with $n = 68$, probably (Fig. 34). The easternmost collection was evidently triploid, with about 34 bivalents and multivalents plus up to 6 or 7 univalents at metaphase I and a few laggards at anaphase I, then about 100 elements altogether on the two metaphase II plates. Attempts to cross diploid *S. humifusum* with *S. alamosanum*, *S. greggii*, *S. griseum*, and *S. obcordatum* and with *Cremnophila nutans* were all unsuccessful.

Sedum latifilamentum

Sedum latifilamentum Clausen (1979) somewhat resembles *S. globuliflorum* ($n = 12$) in its carpels, which are briefly sulcate and lack styles, and Clausen (1979) classified the two species together in his new subgenus Sulcus. However, in its other characters *S. latifilamentum* is very different from *S. globuliflorum*, and it closely resembles *Villadia* in overall aspect, in its tuberous roots, and in its petals that are connate basally and erect for most of their length. Its type locality is in northwestern Hidalgo, with a second collection, apparently the same species, from 50 km. west in northeastern Queretaro and a third from 70 km. farther west in eastern Guanajuato (Clausen, in herb.). A plant of the same clone as the type and another plant from the Queretaro population both had $n = 20$ (Fig. 35), which is a chromosome number that is known in several species of *Villadia* (Uhl, unpub.). In short, I think that the species would be more appropriately assigned to *Villadia* than to *Sedum* subgenus *Sulcus*. A hybrid with diploid *S. alamosanum* ($n = 18$) (*U1647* × *U1855*) showed very little chromosome pairing at metaphase I.

Sedum liebmannianum

Sedum liebmannianum Hemsley resembles *S. moranense*, but its dried leaf bases persist along the stem and give it a distinctive appearance. Moreover, it appears to be a calciphile, found generally on limestone in Oaxaca and southern Puebla, whereas *S. moranense* is a plant of old lava flows mostly farther north. One collection from southern Puebla had $n = 34$ (Fig. 36), as did another from 125 km. to the south in northwestern Oaxaca. However, seven other collections from throughout the range were irregular at meiosis, forming multivalents and univalents at metaphase I (ca. 28 paired elements + 12 univalents in Fig. 37), showing lagging chromosomes at anaphase I, and producing many abnormal and undersized microspores. The meiotically irregular collections appear to represent at least three different levels of ploidy. Since very similar plants are meiotically normal, it seems unlikely that the plants with irregular meiosis are hybrids, and perhaps they represent odd levels of ploidy ($3x$, $5x$, etc.). *Sedum moranense* has many different chromosome numbers, most of them multiples of 18 to 21, and $n = 34$ is not known there (Uhl, 1983). No crosses of *S. liebmannianum* have been attempted.

Sedum longipes

Sedum longipes Rose has creeping stems, like *S. pentastamineum*, but it is substantially larger and has ten stamens and large, conspicuous nectaries. It occurs from Morelos west to Michoacan (Clausen, 1959). One plant from the type locality, near Tepoztlan, Morelos, had $n = 20$ (Fig. 40), whereas another plant from nearby was apparently monosomic with $n = 19 + 1$ unpaired chromosome of standard size (Fig. 39). Plants from localities 35 and 150 kilometers to the west in the state of Mexico and in eastern Michoacan both had $n = 19$ (Fig. 38), as does *S. pentastamineum*. Subspecies *rosulare* Clausen, known only from cultivation, also had $n = 19$ in a clone of the type. Twelve attempts to cross *S. longipes* with eight other species of *Sedum* were all unsuccessful.

Sedum lumholtzii

Sedum lumholtzii Robinson and Fernald of the northern Sierra Madre Occidental has minutely hairy stems and leaves. It seems closest to *S. semiteres*, but leaves of that species are merely papillose. The only collection available had $n = 19$ (Fig. 41), as does *S. semiteres*. A hybrid with *S. alamosanum* ($n = 18$, q. v.) showed considerable chromosome pairing at meiosis (Fig. 5). Seven other attempted crosses, with *S. greggii, S. longipes, Cremnophila nutans,* and a reciprocal with *S. alamosanum* were unsuccessful.

Sedum madrense

Sedum madrense S. Wats. of northwestern Mexico is distinguished by its pink flowers. Clausen (1979) observed that in dried condition it closely resembles *S. stelliforme,* which flowers nearby at the same time. However, the two do not intergrade, and he concluded that they are best regarded as sibling species. A plant from the Barranca del Cobre is clearly some sort of polyploid. It showed some multivalents and univalents at metaphase I but had the equivalent of about 64 bivalents when these irregularities are allowed for.

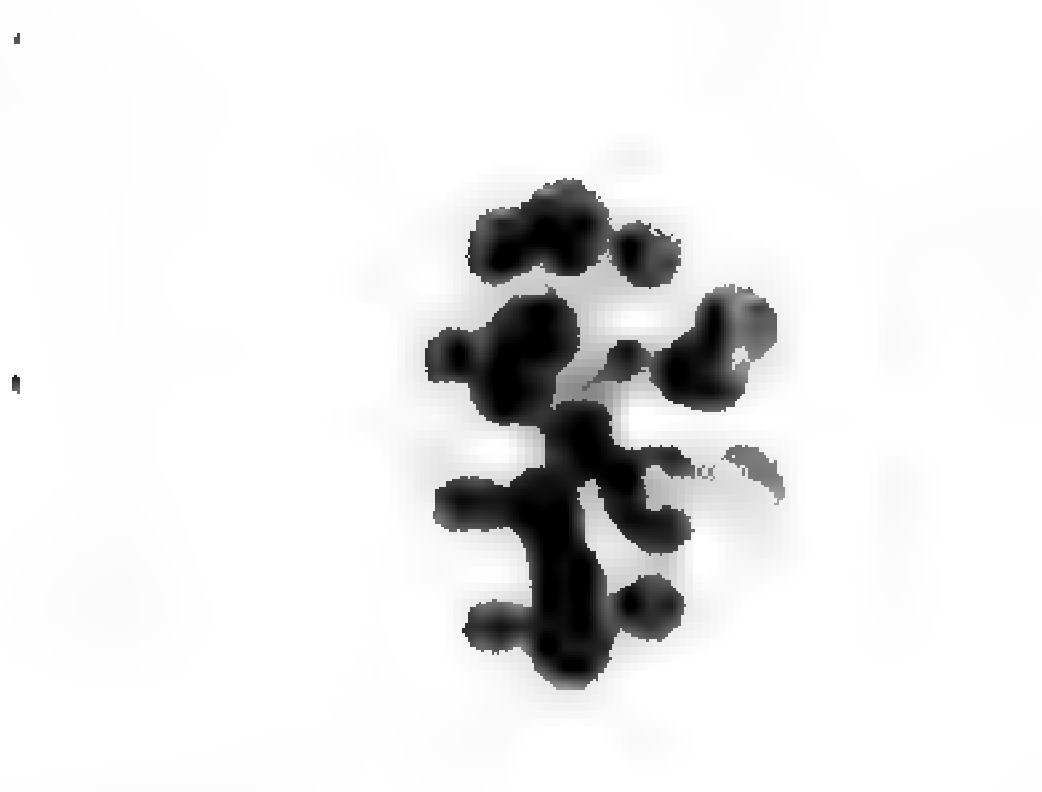
Sedum mellitulum

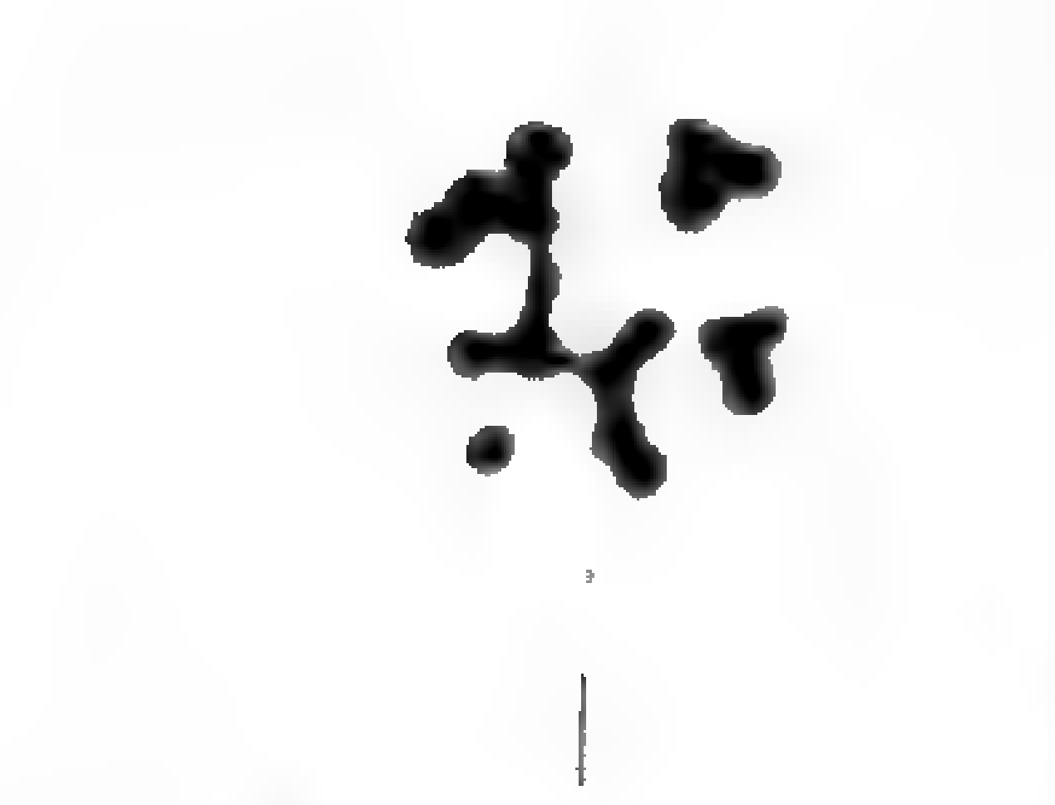
Sedum mellitulum Rose differs from *S. stelliforme,* with which it sometimes occurs, in its smaller size, its papillose (not smooth) leaves, and the erect (not spreading) beaks of its follicles, and it differs from *S. alamosanum* in the latter character and also in its white (vs. pinkish) petals (Clausen, 1979). I have seen collections only from the northern Sierra Madre Occidental in southwestern Chihuahua and southeastern Sonora, but Clausen (1981) reported that similar plants from far to the south in Michoacan and Guerrero might be *S. mellitulum.* The species is very diverse cytologically and includes some high polyploids. Plants from the vicinity of the Barranca del Cobre in southwestern Chihuahua had $n = 18$ (Fig. 42) (as does also *S. alamosanum*), one of them with a B-chromosome (Fig. 43), but other plants nearby had $n = 19$ (Fig. 44) and $n =$ ca. 50 (48 paired elements + 3 univalents in Fig. 45). High polyploids with $n =$ ca. 66, $n = 80$–84 (Fig. 46), and $n = 95$ (Fig. 47) came from 150–200 km. to the northwest. An attempted cross between *S. mellitulum* ($n = 18$) and *S. multiflorum* ($n = 12$) was unsuccessful.

Sedum mexicanum

Sedum mexicanum Britton has bright green linear leaves borne in whorls of three to five, at least below. Although described from plants grown from seed collected near Mexico City in 1896, it has never been found (again?) in the wild. Three collections studied here, all from cultivation, had $n = 18$ (Fig. 48), as did a plant reported long ago by Skovsted (1934). Morphologically the species

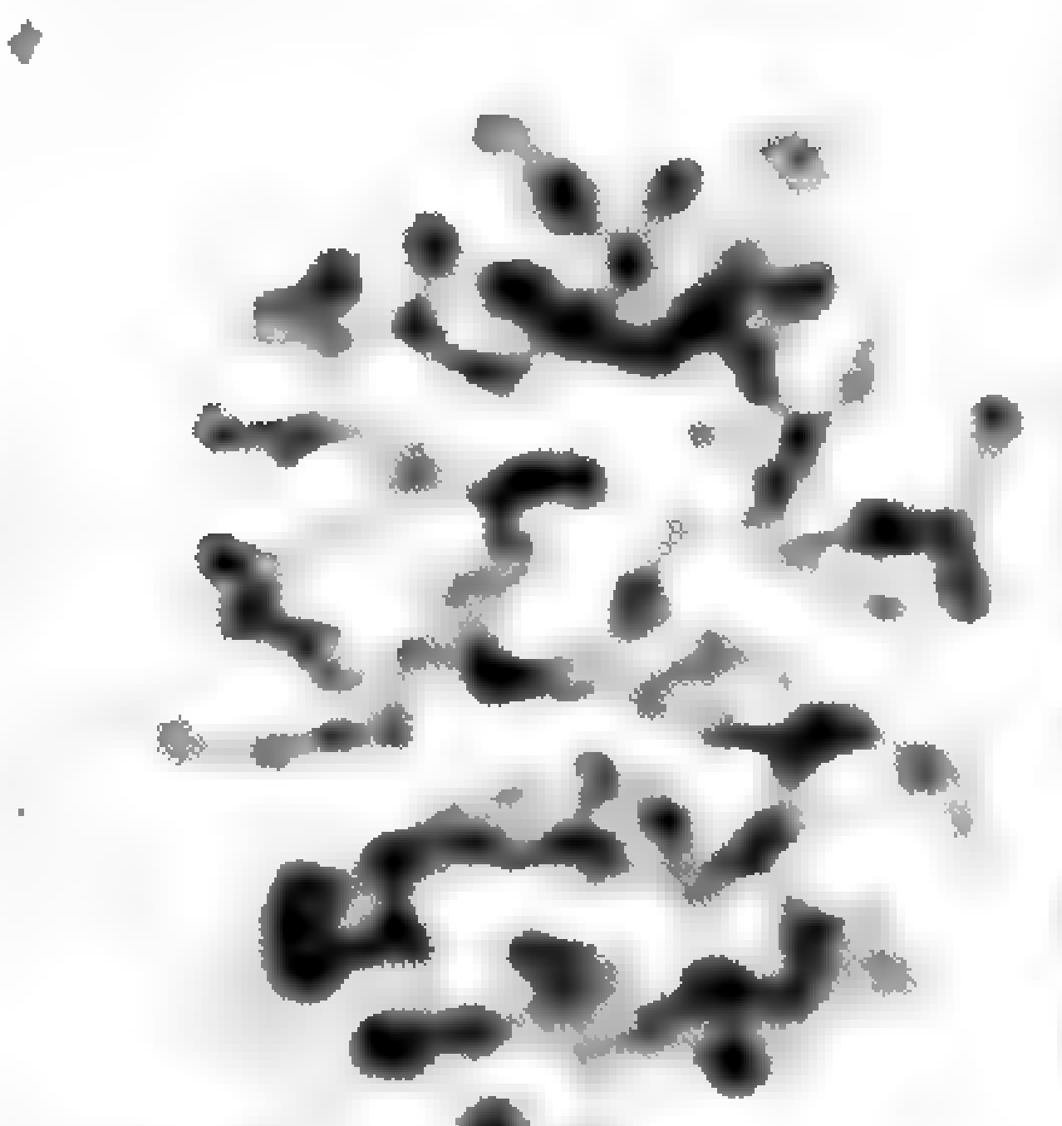

41

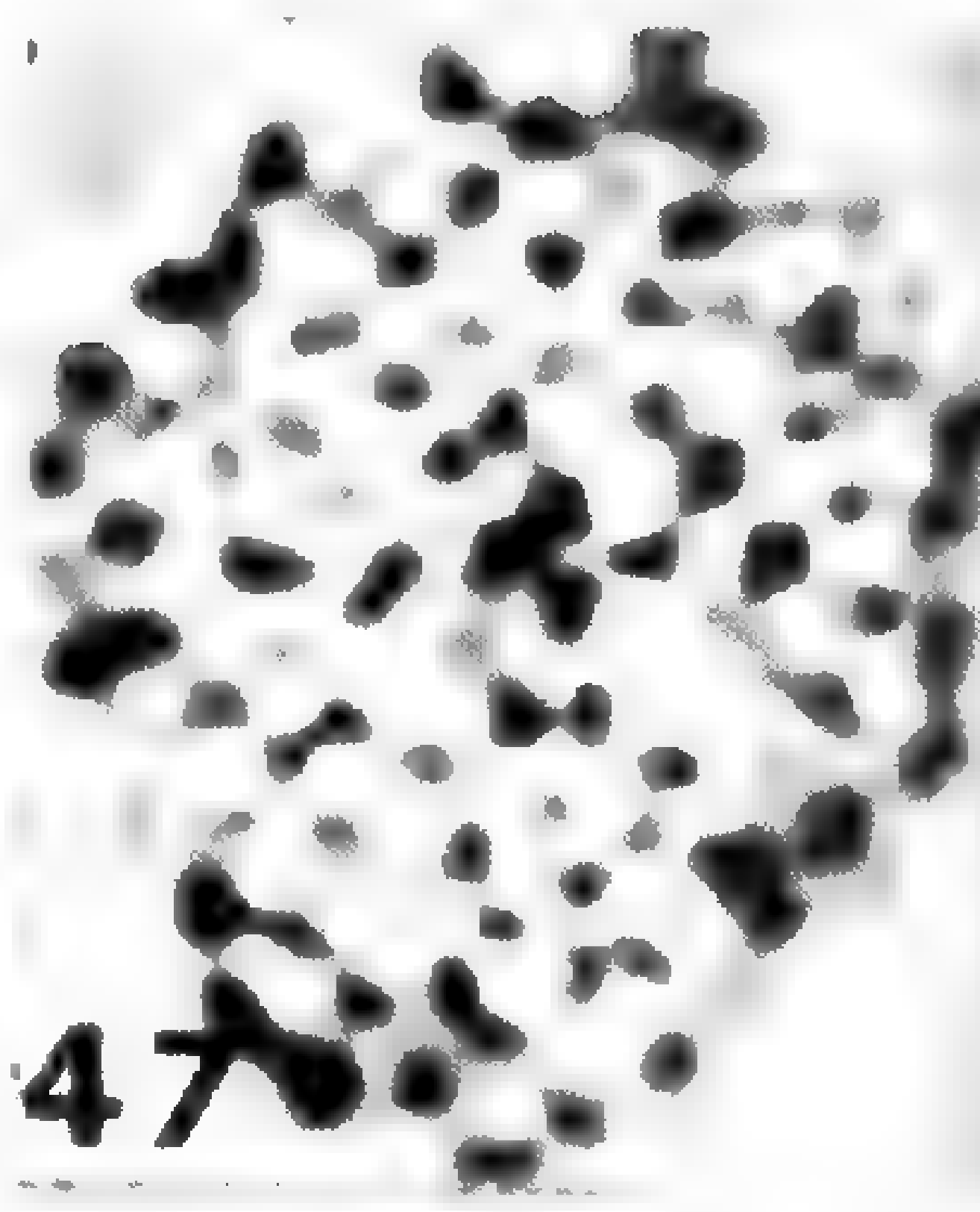

42

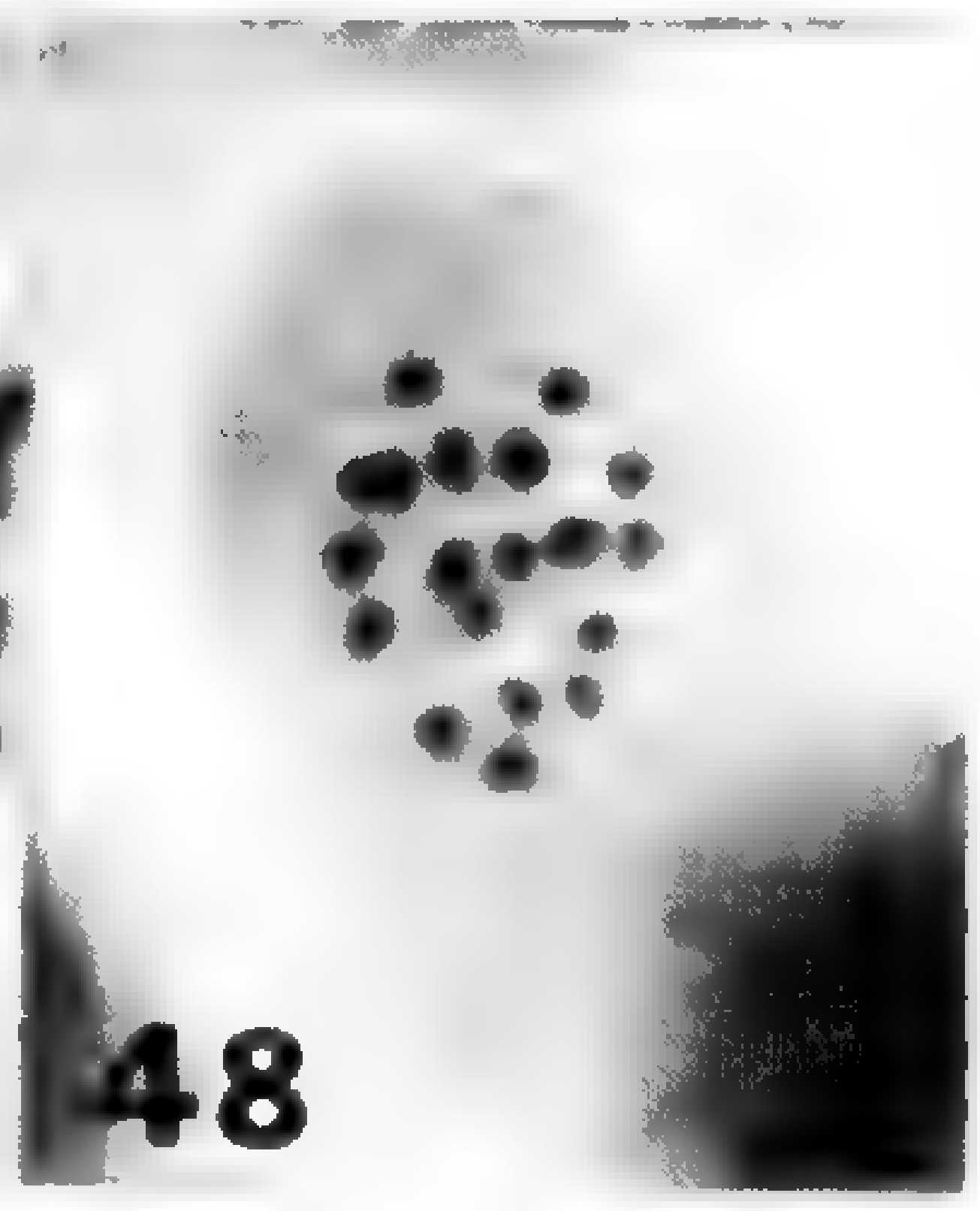

43

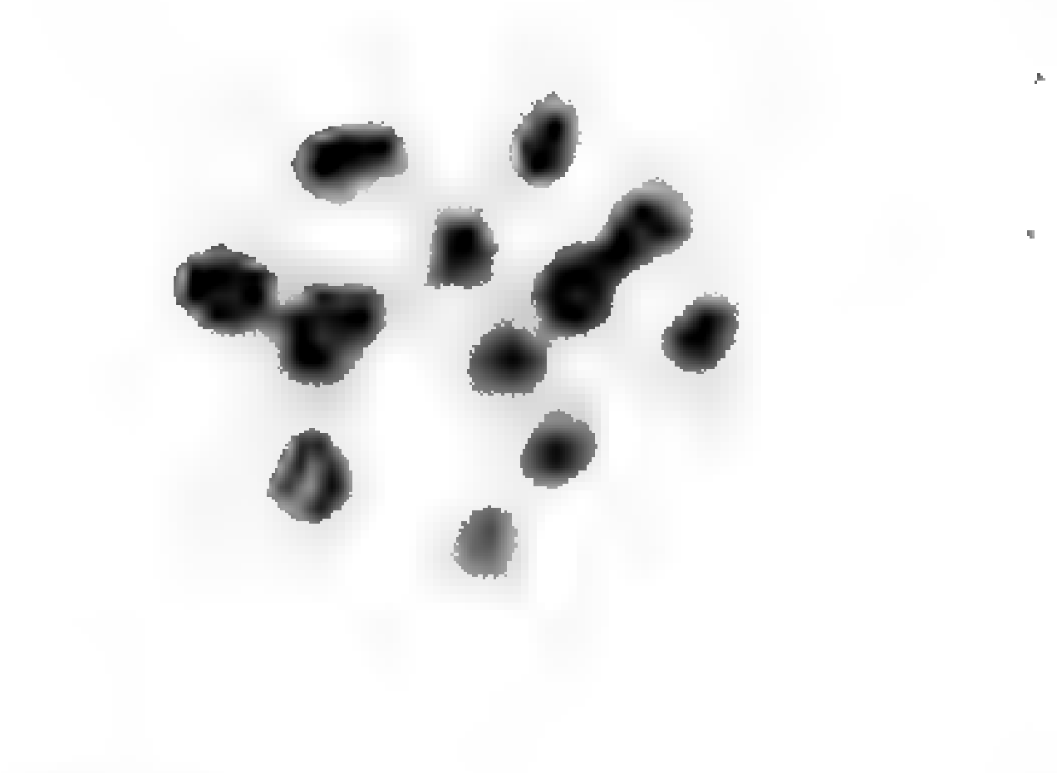

44


45

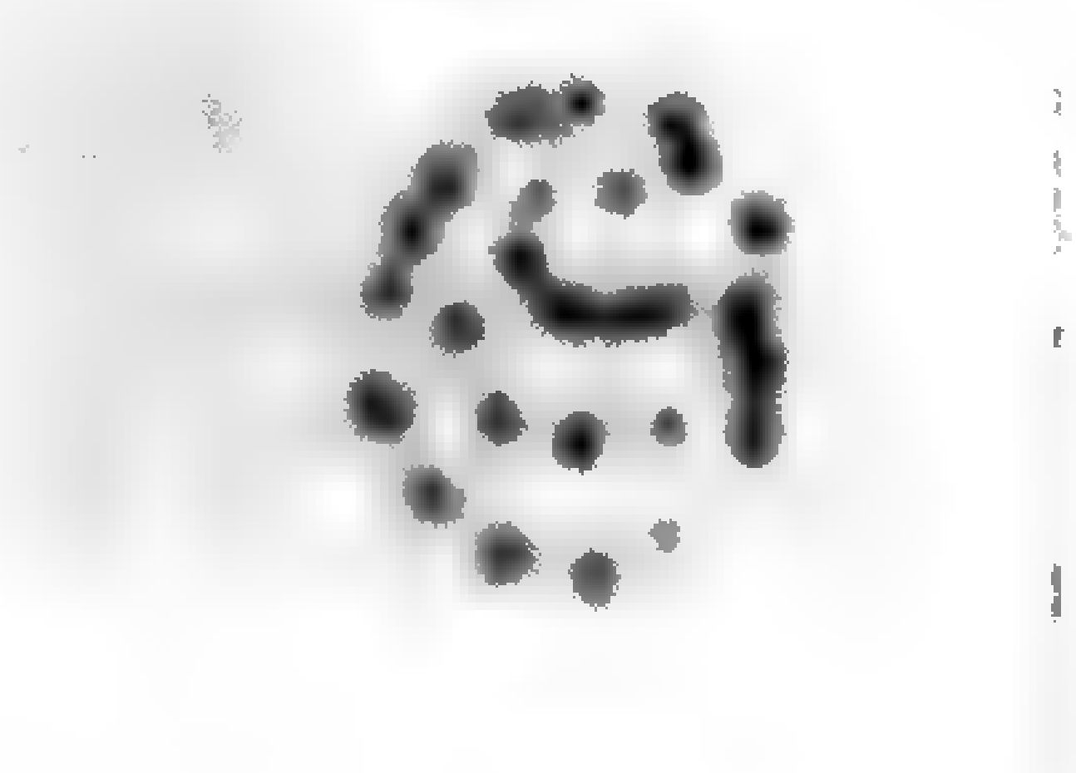

46

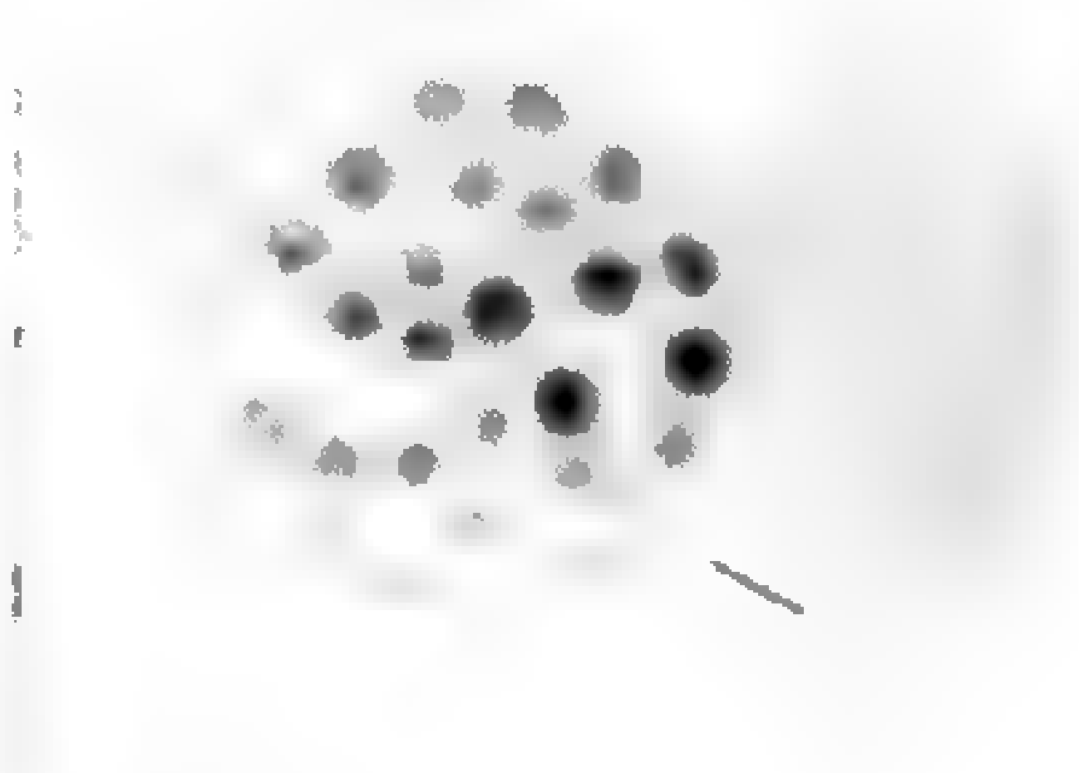

47

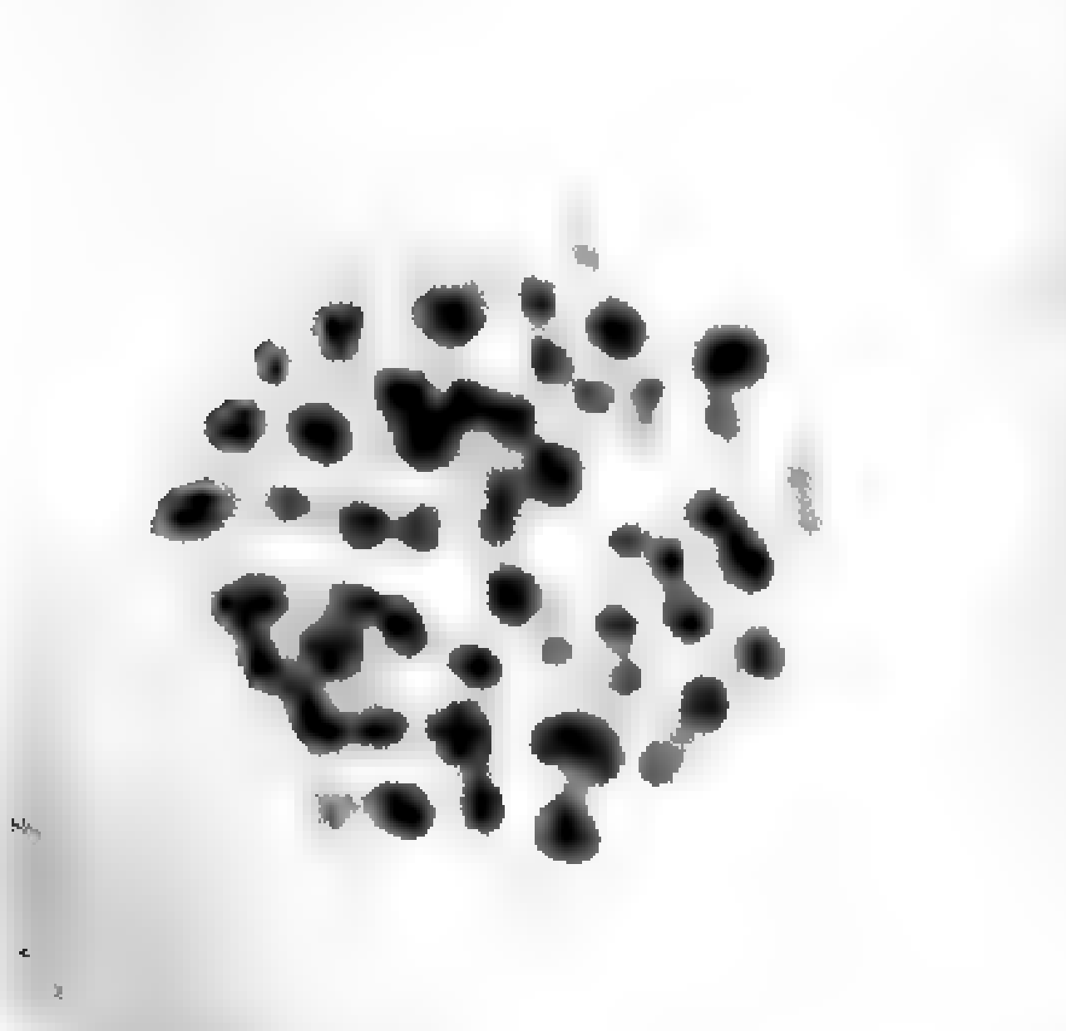

48

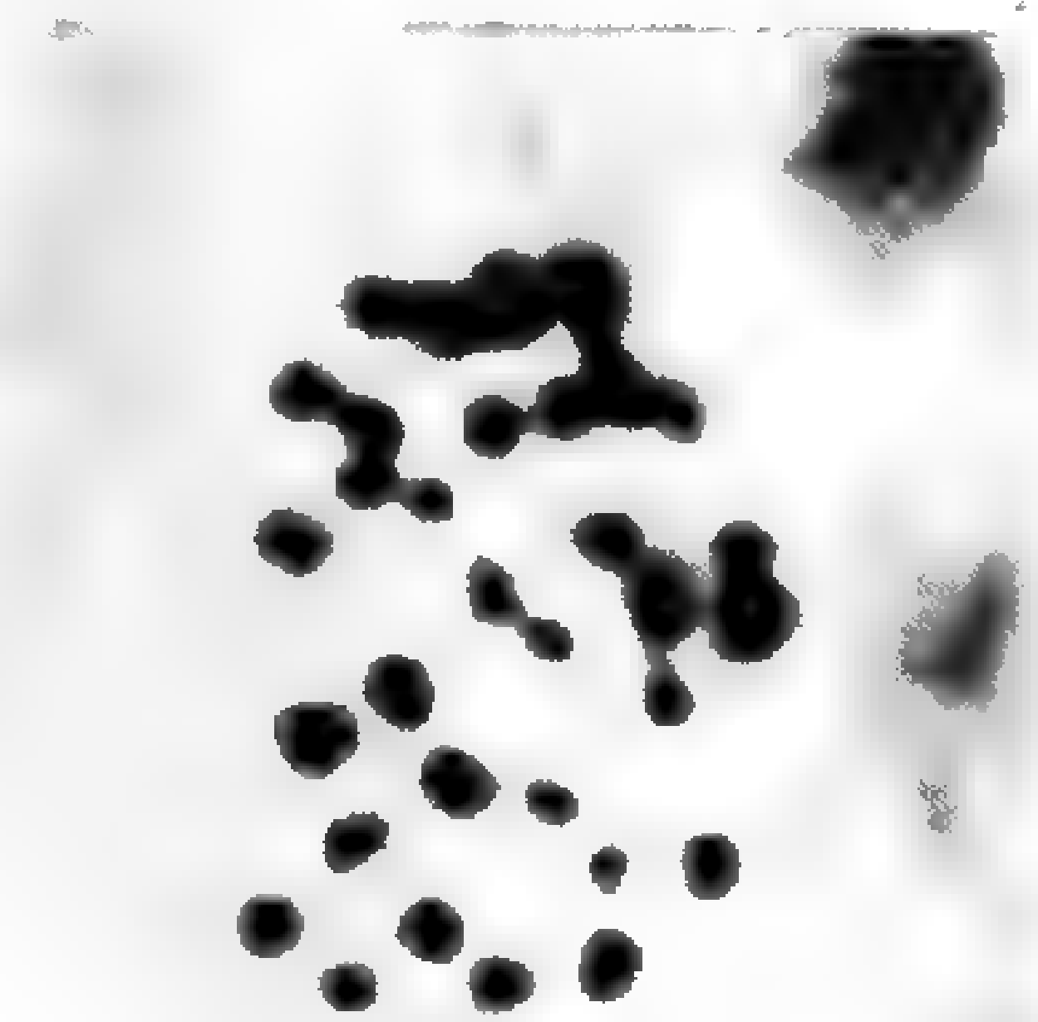

49

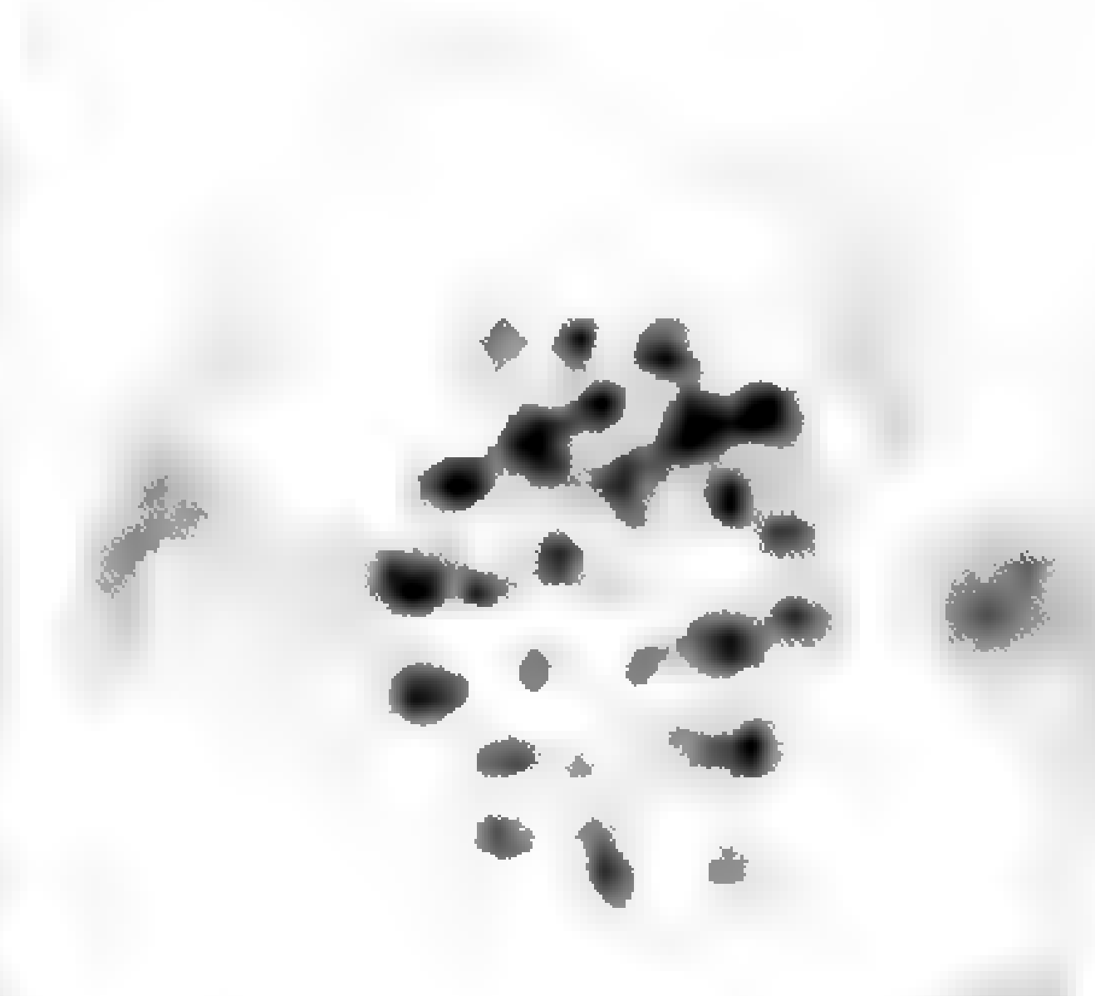

50


51

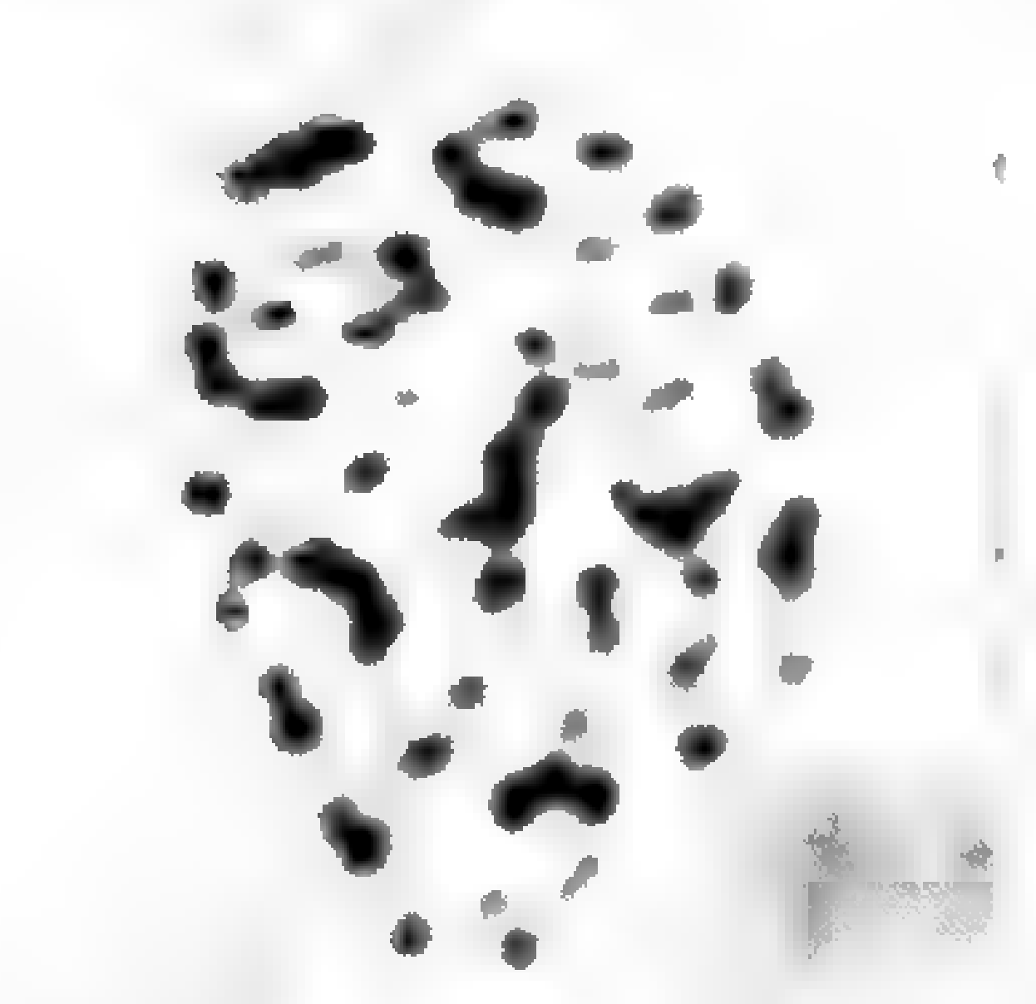

52

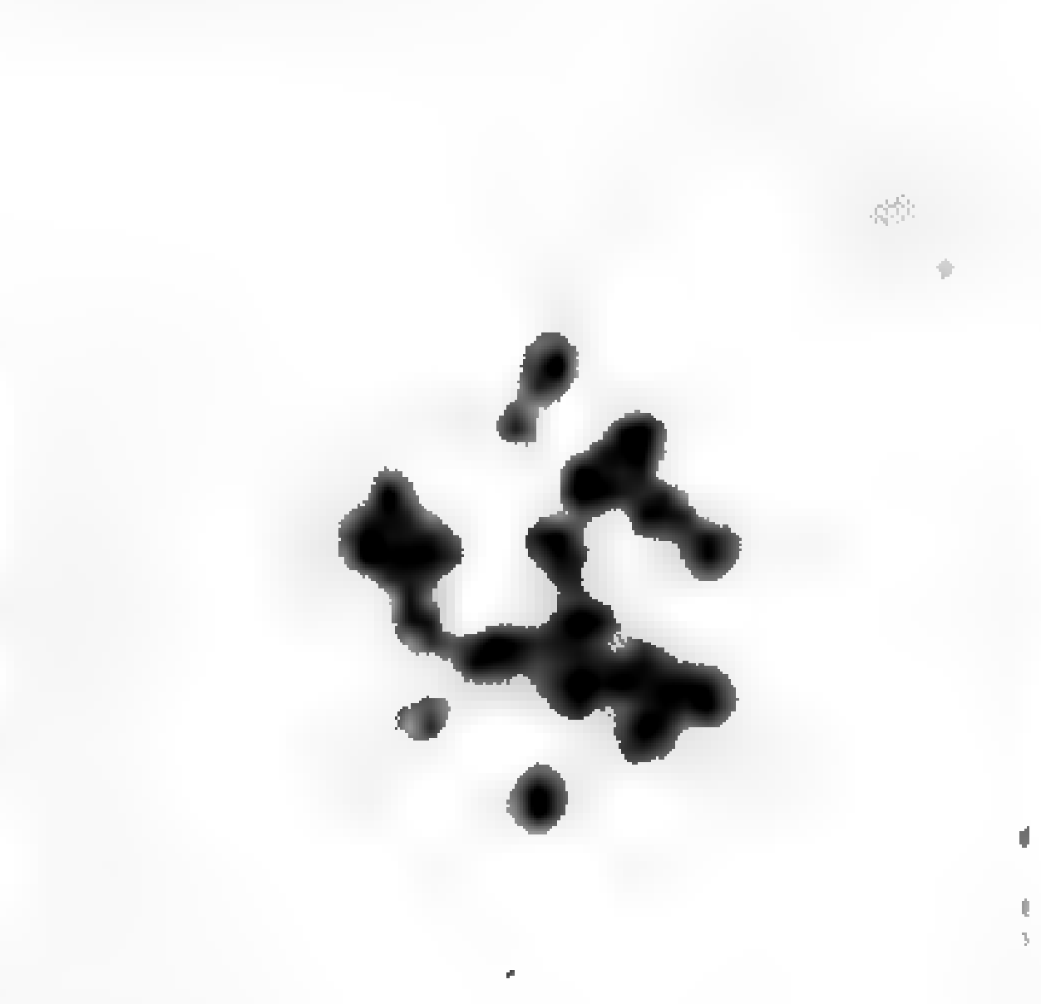

53

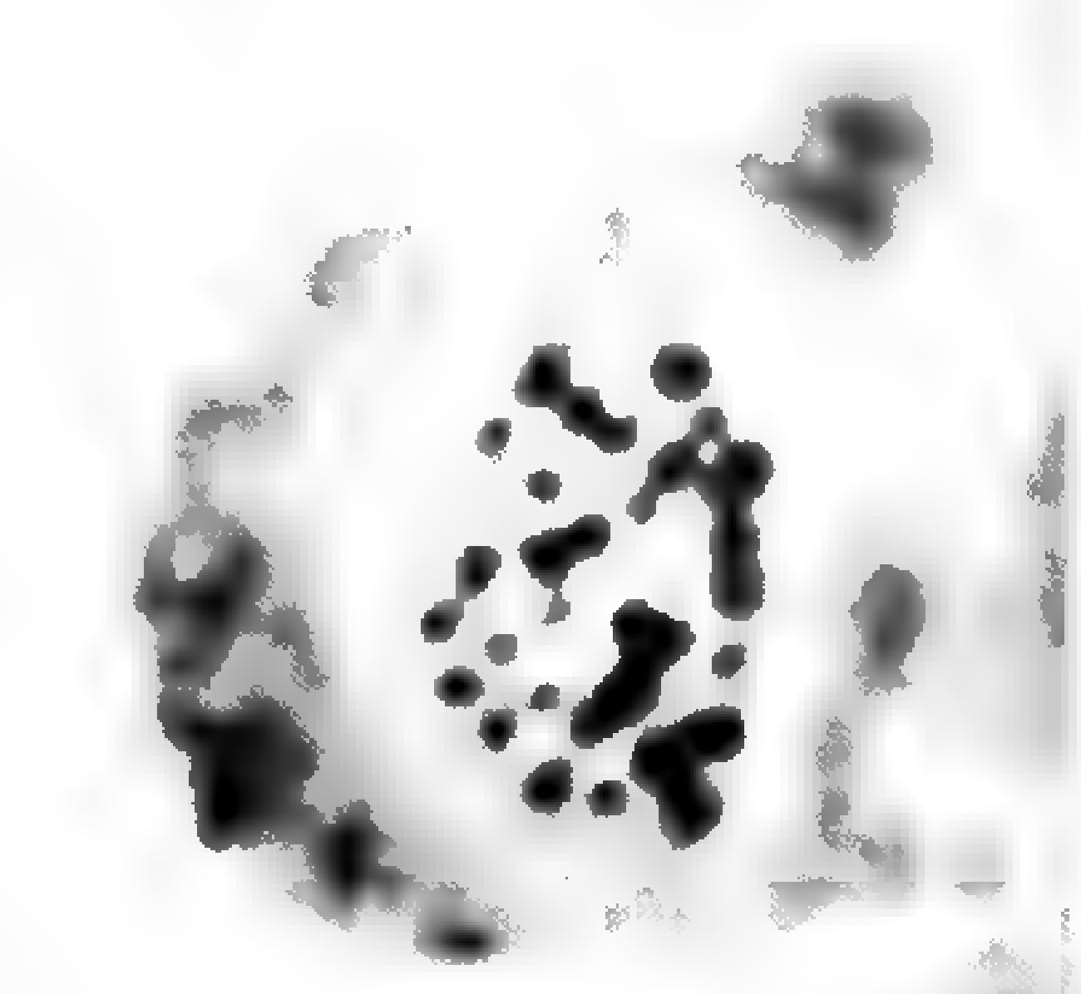

54

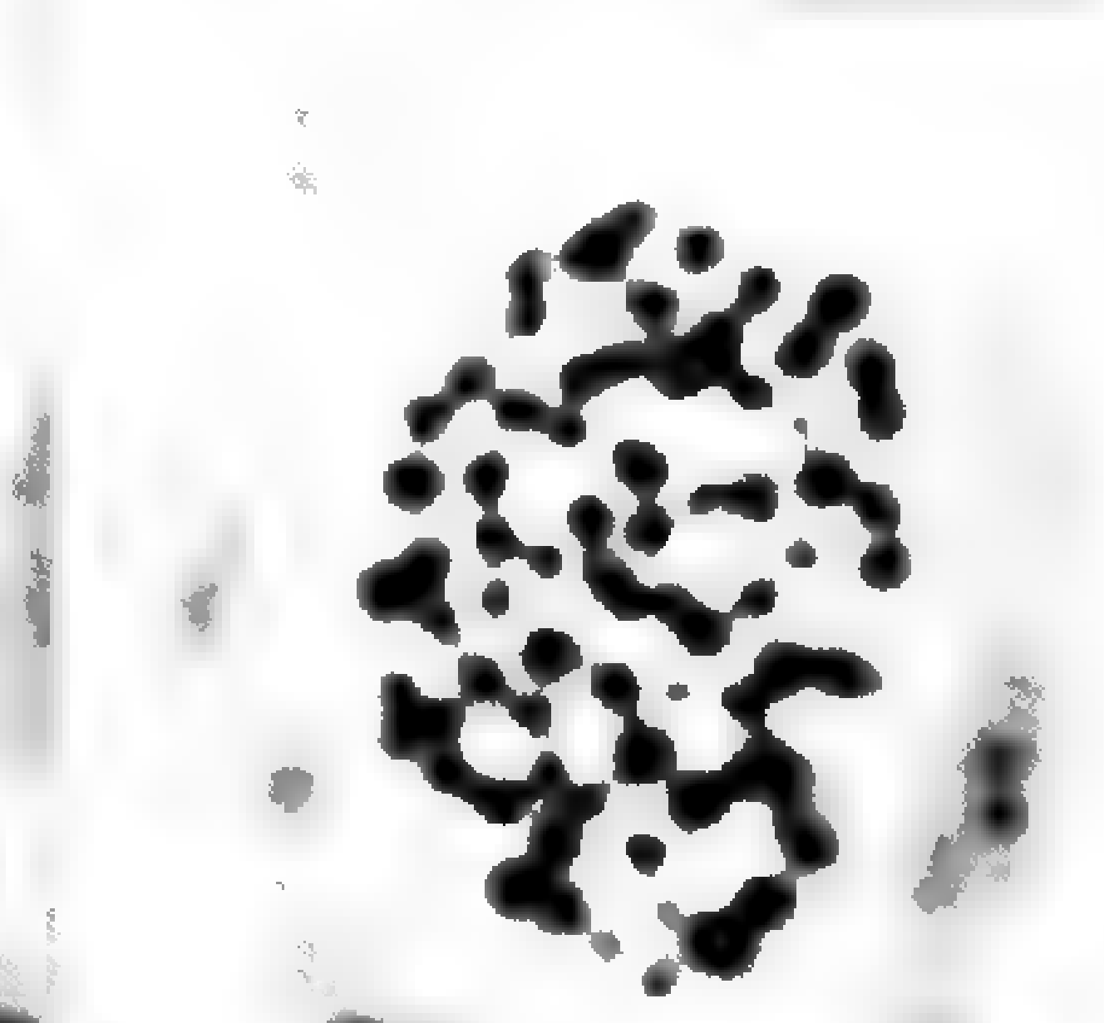

55


56


57


58


59


60

seems closest to certain Oriental species, notably *S. lineare* ($n = 36$, Uhl and Moran, 1972). Clausen (1959) found both *S. mexicanum* and *S. lineare* under cultivation in Mexico, and Standley and Steyermark (1946) reported *S. mexicanum* as common in gardens in Guatemala and Salvador, but of uncertain origin. Praeger (1921) reported that the species was cultivated in Europe before its type was collected in Mexico. If this species is really native to Mexico, it is the only one that appears to have relatives anywhere in the Eastern Hemisphere.

Sedum millspaughii

Sedum millspaughii Hamet of Guatemala was apparently described from a few fragments and has been poorly known. It has tuberous roots and rather thick floral stems up to 10 cm. long, bearing flowers with white petals and pink styles and carpel sutures. Two collections from the same locality south of Guatemala City had $n = 24$. (I am indebted to the late Professor R. T. Clausen for identifying this puzzling plant.)

Sedum multiflorum

Sedum multiflorum Clausen (1978) has thickened roots and forms compact vegetative rosettes with stems that elongate to as much as 40 cm. or more when flowering, at least in cultivation. Leaves of the floral stems are easily detached and root readily, and the flowers are white and pungently scented. Most of these characters also apply to *S. wrightii* (q. v.), but the petals of *S. multiflorum* are widely spreading. The species is known only from the vicinity of its type locality,

---

Figures 41–60. Chromosomes of *Sedum* species and various hybrids in pollen mother cells at metaphase I unless otherwise indicated, all X2000. In some cells, univalents and/or B-chromosomes are indicated with thin lines, certain paired elements (bivalents and/or multivalents) with thick lines. **41,** *S. lumholtzii, UC68.144,* $n = 19$; 42–47, *S. mellitulum;* **42,** *U2733,* $n = 18$; **43,** *U2042,* $n = 18 + 1B$; **44,** *U2734B,* $n = 19$; **45,** *M17272,* $n = 48$ paired elements + 3 univalents; **46,** *M23248,* $n =$ ca. 80; **47,** *U2772,* $n = 95$; **48,** *S. mexicanum, U407,* $n = 18$; **49,** *S. multiflorum, U1946,* $n = 12$; **50,** *S. muscoideum, UC51.1355,* $n = 34$; **51–53,** *S. nanifolium:* **51,** *M6309,* $n = 26$; **52,** *U1499,* $n = 26 + 1B$; **53,** *U1913,* $n = 52$; **54,** *S. oaxacanum, UC54.418,* $n = 34$; **55,** *S. oteroi, U2160,* $n = 27$; **56–57,** *S. parvum,* subsp. *parvum:* **56,** *U1842,* $n = 32$; **57,** *M7652,* $n = 64$; **58,** *S. pentastamineum, T-Tis 7,* $n = 19$; **59–60,** *S. reptans;* **59,** *U2711,* $n = 34$; **60,** *M13381,* $n = 72$.

near Ciudad Guzman, Jalisco. Two accessions of the original collection from this population had $n = 12$ (Fig. 49), and this number also is basic to the polyploid series in *S. wrightii,* which is perhaps the species most closely related to *S. multiflorum.* A hybrid with *S. alamosanum* ($n = 18$) (*U1647* × *U2088*) showed relatively little chromosome pairing at metaphase I: 2–6 bivalents and multivalents plus 17–26 univalents (average 3.6 + 22.5) in 14 cells analyzed (3 + 24 in Fig. 6). A hybrid with *S. greggii* ($n = 26$) (*U1535* × *U2088*) produced very little stainable pollen, but chromosome pairing has not been analyzed. Attempted crosses with *S. diffusum, S. niveum, S. stelliforme, Pachyphytum hookeri,* and *Villadia* cf. *pringlei* were not successful.

Sedum muscoideum

Sedum muscoideum Rose of Oaxaca, as conceived here, has yellow flowers and tiny leaves that are imbricate and tightly appressed to the stem, measuring about 2 mm. long × 1.5 mm. wide × 1 mm. thick, and persisting on the stem after drying. A single collection of unknown origin in the wild had $n = 34$ (Fig. 50), also found in *S. oaxacanum* but not in the white-flowered *S. cupressoides* ($n = 30$, Fig. 14) with which it has been confused (*cf.* Clausen, 1959, p. 259). A similar plant was collected near Huautla in northern Oaxaca (Kimnach, 1982), but it has not yet flowered here.

Sedum nanifolium

Sedum nanifolium Fröderström was reduced to subspecific status under *S. parvum* by Clausen (1978), but it differs from that in its subshrubby habit, in its awl-shaped leaves that persist on the stem after drying, and in other ways (Clausen, 1981). Since its submergence into *S. parvum* seems a marginal case, since it already has its own name as a species, and since it differs significantly from *S. parvum* ssp. *parvum* in its chromosome numbers, it is treated separately as a species here. The species occurs on the drier interior slopes of the Sierra Madre Oriental in southeastern Coahuila and southern Nuevo Leon and probably into southwestern Tamaulipas. Eight collections had $n = 26$ (Fig. 51), three of them with one or more B-chromosomes (Fig. 52). Two other collections from the southern part of the range were tetraploids with $n = 52$ (Fig. 53). *Sedum parvum* ssp. *parvum,* ssp. *diminutum,* and ssp. *dendroides* all have $n = 32$–34 or near multiples. No crosses of *S. nanifolium* have been attempted.

Sedum niveum

Sedum niveum Davidson resembles *S. cockerellii* very closely, but it has elongate, creeping stems (Clausen, 1975). Plants from the San Bernardino and Santa Rosa Mountains of southern California reported previously (Uhl, 1972) have $n = 16$, as does one chromosome race of *S. cockerellii.* The same number has now been found in a plant from the New York Mountains, an isolated desert range about 200 km. to the northeast. Another collection from the Sierra San Pedro Martir of northern Baja California is octoploid ($n = 64$), as were others from there reported previously. Attempts to cross *S. niveum* with diploid *S. alamosanum, S. greggii* ($n = 33 + 6$), and *S. multiflorum* ($n = 12$) were unsuccessful.

Sedum oaxacanum

Sedum oaxacanum Rose has often been confused with other species, notably *S. australe,* but it has yellow flowers and its leaves are obovate (ca. 6 mm. long × 4 mm. wide × 2 mm. thick), not terete, and their white-scurfy surfaces when young are distinctive. I believe that Praeger's (1921) figures and descriptions are correct for this species, although Clausen (1946) considered them to be of *S. australe.* At any rate, the plants reported here as *S. oaxacanum* agree well with Praeger's interpretation. The type locality is in central Oaxaca, but the species also occurs in southern Puebla. One plant from Puebla had $n = 34$ (Fig. 54), as did two more of uncertain origin from the wild.

Sedum oteroi

Sedum oteroi Moran occurs in the Sierra Mixteca of northwestern Oaxaca. Like the species of Section (or Subgenus) Pachysedum, this diminutive species has lateral floral stems, but it differs in its racemose inflorescence and in other characters. Moran (1977) considered it to be taxonomically isolated, with no close relatives known. A plant of the type collection had $n = 27$ (Fig. 55), a number that is not known among the pachysedums.

Sedum parvum

Sedum parvum Hemsley, according to Clausen (1978, 1979, 1981), consists of five subspecies that range from very small soft herbs to diminutive shrubs, all with yellow flowers. Leaves are papillose and subterete, less flattened than in *S. greggii.* Since Clausen's subspecies *nanifolium* (1978) and *robertsianum* (1981) were named earlier as species, and since they are cytologically distinctive and differ from typical *S. parvum* in other ways, they are treated separately here as species. Subspecies *parvum* is a small herb native to the mountains of southwestern San Luis Potosi. Four collections had $n = 32$ (Fig. 56), $n = 32 + 2B$, $n =$ ca. 60, and $n = 64$ (Fig. 57). At metaphase I all of them had bivalent chromosomes that differ among themselves in size more than is generally seen in the Mexican sedums. Subspecies *diminutum* Clausen (1979) occurs in isolated desert mountains in western Coahuila and has $n = 34$, the chromosomes especially small but differing substantially in size. Subspecies *dendroides* Clausen (1978) has the form of a diminutive tree, with tuberous roots and erect woody stems up to 8 mm. thick and 20 cm. tall or more in cultivation, and petals erect for about 2 millimeters, then recurved outward. It differs so greatly from the low, soft subspecies *parvum* that I doubt the appropriateness of its assignment to the same species. Subspecies *dendroides* is known only from its type locality, high in the interior mountains of northern San Luis Potosi. A plant collected earlier from the type locality was tetraploid, with $n = 64$, probably.

Sedum pentastamineum

Sedum pentastamineum Clausen (1959) is similar to *S. longipes* in its trailing to repent habit, but it is smaller and has only five stamens. Two collections from about 40 km. apart on the lower southerly slopes of the Nevado de Toluca in the state of Mexico, including a clone of the type collection, both had $n = 19$ (Fig. 58). The same number is found also in *S. longipes*, which clearly is closely related. Two attempts to cross *S. pentastamineum* with *S. semiteres* were unsuccessful, as were also attempts with *S. alamosanum* and *S. greggii*.

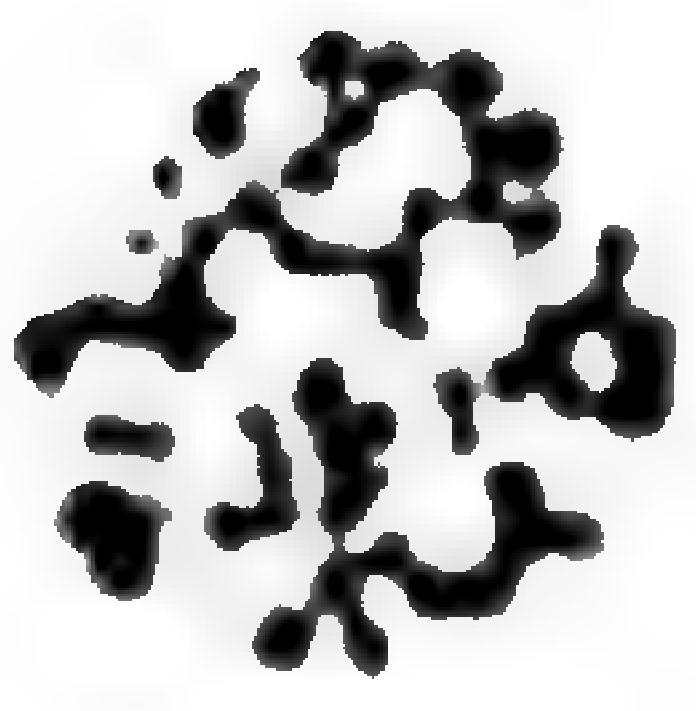
Sedum reptans

Sedum reptans Clausen (1978) typically has long trailing or pendent stems with many adventitious roots, elliptic-lanceolate leaves, and yellow flowers. A plant of the type clone, from south central San Luis Potosi, was apparently tetraploid, with $n = 72$, as was also another plant collected earlier from the same population (Fig. 60). However, another plant from central Queretaro, nearly 100 km. to the south southeast, had much shorter stems and $n = 34$ (Fig. 59); and a plant from cultivation of unknown origin in the wild had n = ca. 82. Subspecies *carinatifolium* Clausen (1981), with larger flowers and shorter and broader leaves keeled below, presents such a different appearance that its inclusion with *S. reptans* seems highly questionable. A plant of this subspecies collected earlier from the type locality in east central Queretaro only a few kilometers from the locality of the very different diploid cited above also differed from typical *S. reptans* in its chromosome number, having $n = 60$ (Fig. 61). Moreover, this plant is very tolerant of cold. At Ithaca, N.Y., it has survived many hard freezes all winter in the cold frame, where it flowers profusely in late spring, but it has never flowered here in the greenhouse.

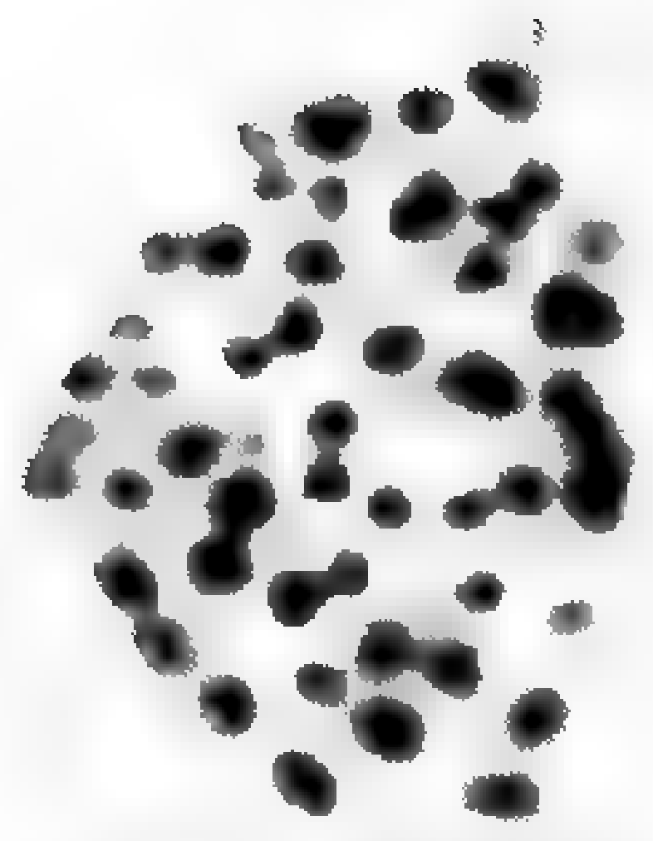
Tetraploid *Sedum reptans* from the type locality (*M13381*) has been crossed as pollen parent with diploid *Pachyphytum hookeri* (*M13349*, $n = 32$, Uhl and Moran, 1973) and *Graptopetalum fruticosum* (*U1398*, $n = 31$, Uhl, 1970). The resulting hybrids resemble the *S. reptans* pollen parent much more closely than they do their seed parents; and they both show about 36 bivalents and multivalents, plus about 20–30 univalents at metaphase I (Fig. 62, 63). These observations support the conclusion that *S. reptans* at its type locality is an autotetraploid whose 72 gametic chromosomes consist of two sets of 36 each. At meiosis in its hybrids the homologous chromosomes of these two sets pair preferentially with each other, while most or all of the chromosomes received from the diploid parent remain unpaired as univalents, or a few of them may find a homologous region in a chromosome of *S. reptans* and add themselves to that pair, creating a multivalent. The double dose of genetic information from *S. reptans* in these triploid hybrids accounts for their closer resemblance to that parent. Similar observations were made on triploid hybrids between autotetraploid *Echeveria secunda* (n = 30–32) and 22 diploid species of several different genera having chromosome numbers from $n = 12$ to $n = 34$ (Uhl, 1982b). Attempted crosses of tetraploid *S. reptans* (*M13381*) with several other tetraploids were all unsuccessful: *S. allantoides* ($n = 58$), *S. compactum* ($n = 60$), *S. versadense* ($n = 64$). Two attempts to hybridize diploid *S. reptans* ($n = 34$) also were unsuccessful.

Sedum rhodocarpum

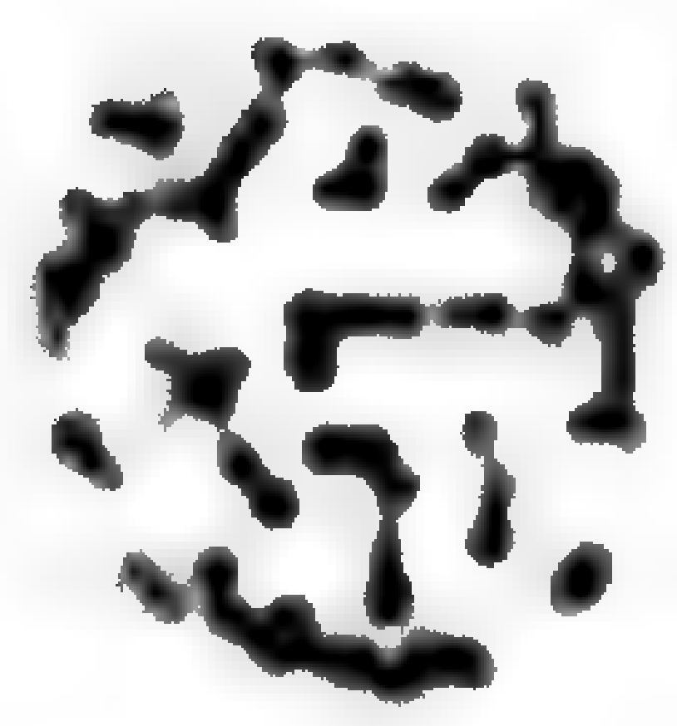
Sedum rhodocarpum Rose is the only Mexican species that bears broad leaves in whorls of three. Its typical form (ssp. *rhodocarpum*)



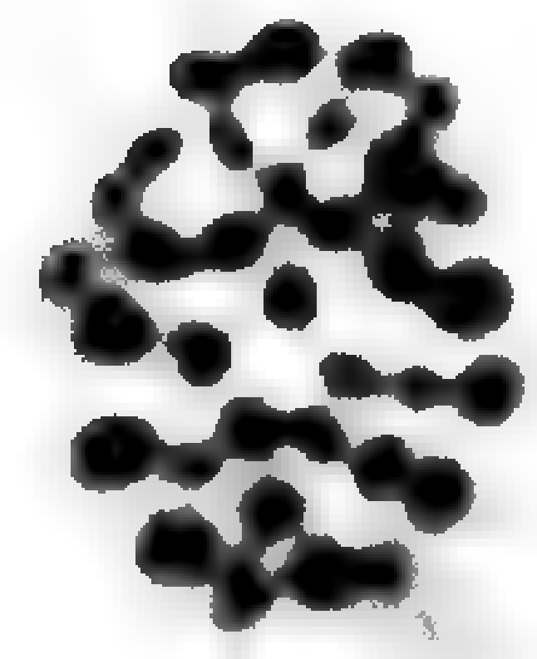
61



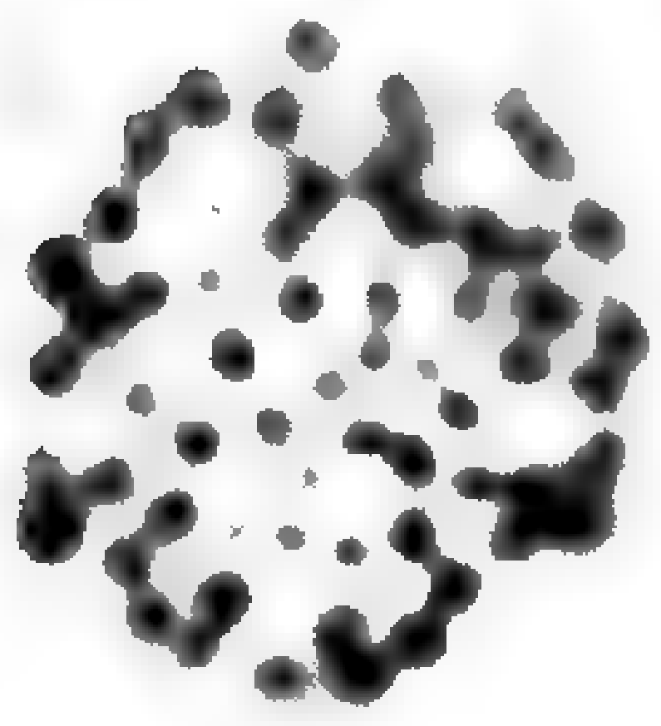
62



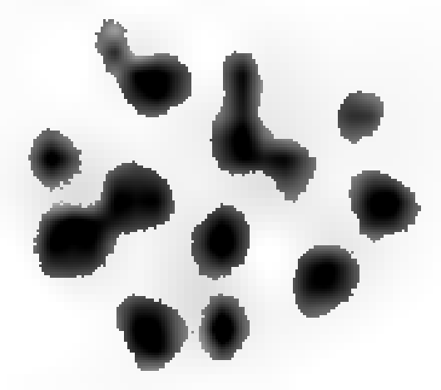
63



64

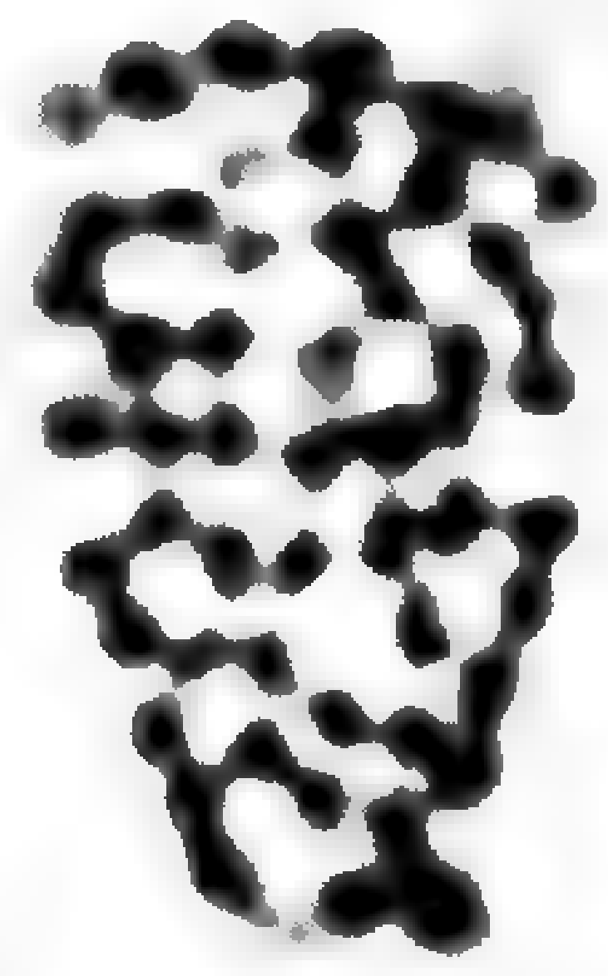


65

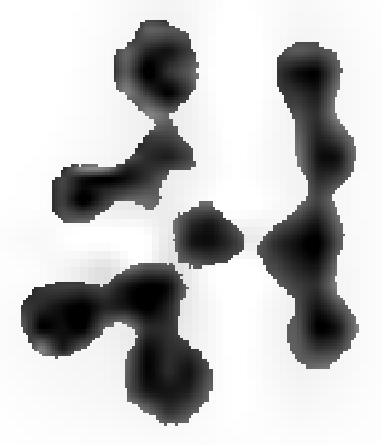


66

67

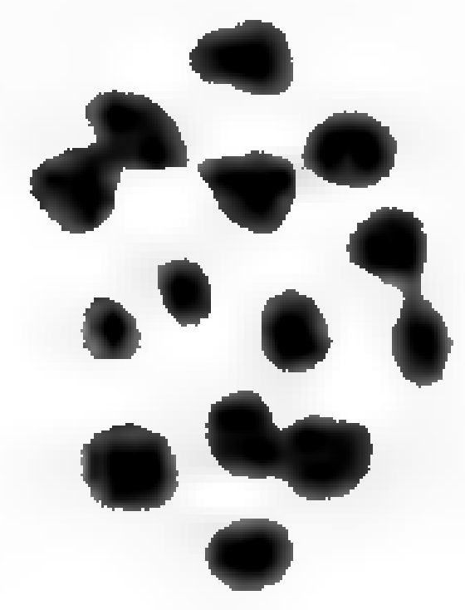


68

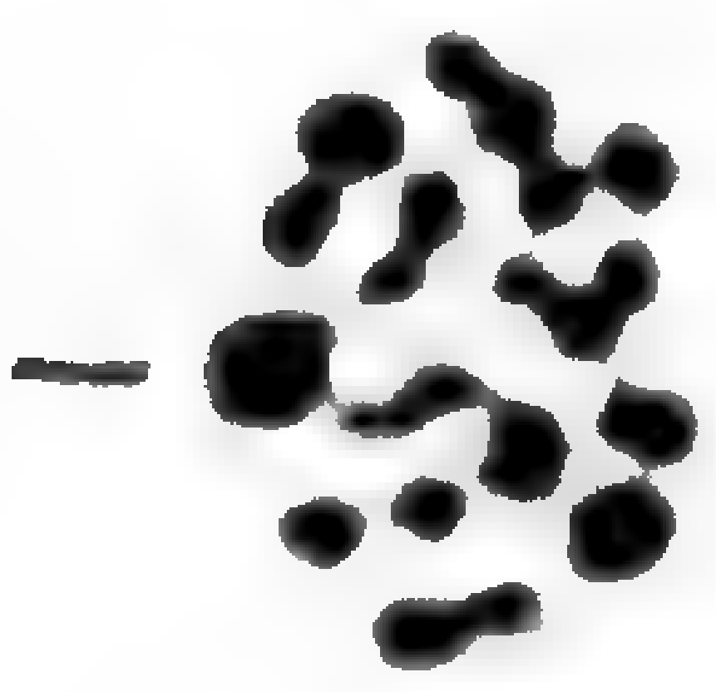


69

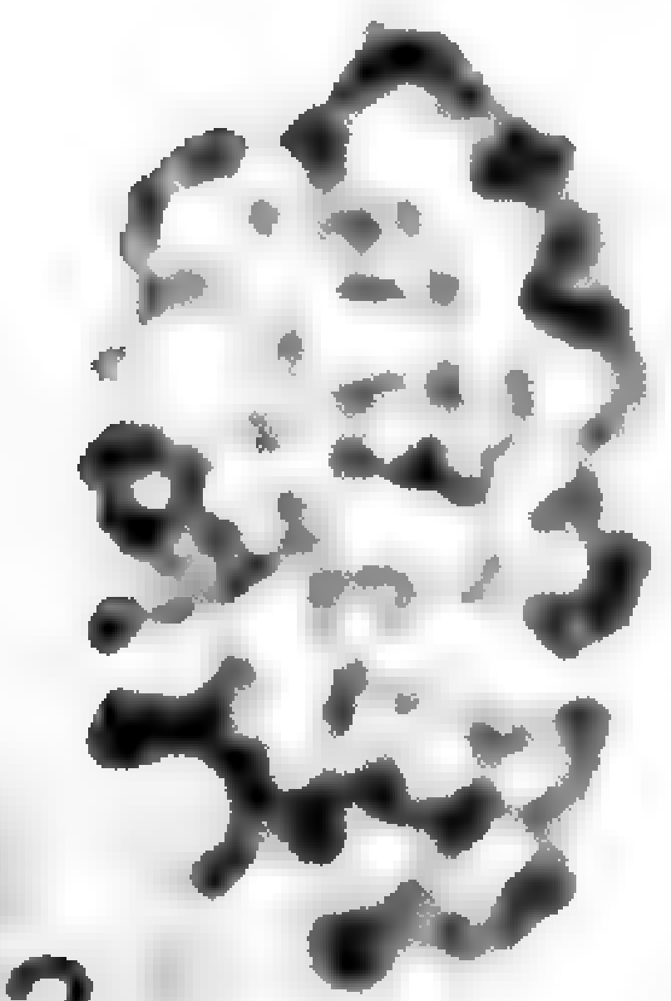
70



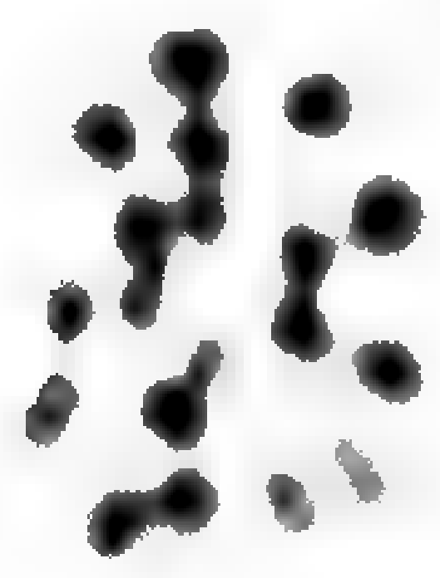
71



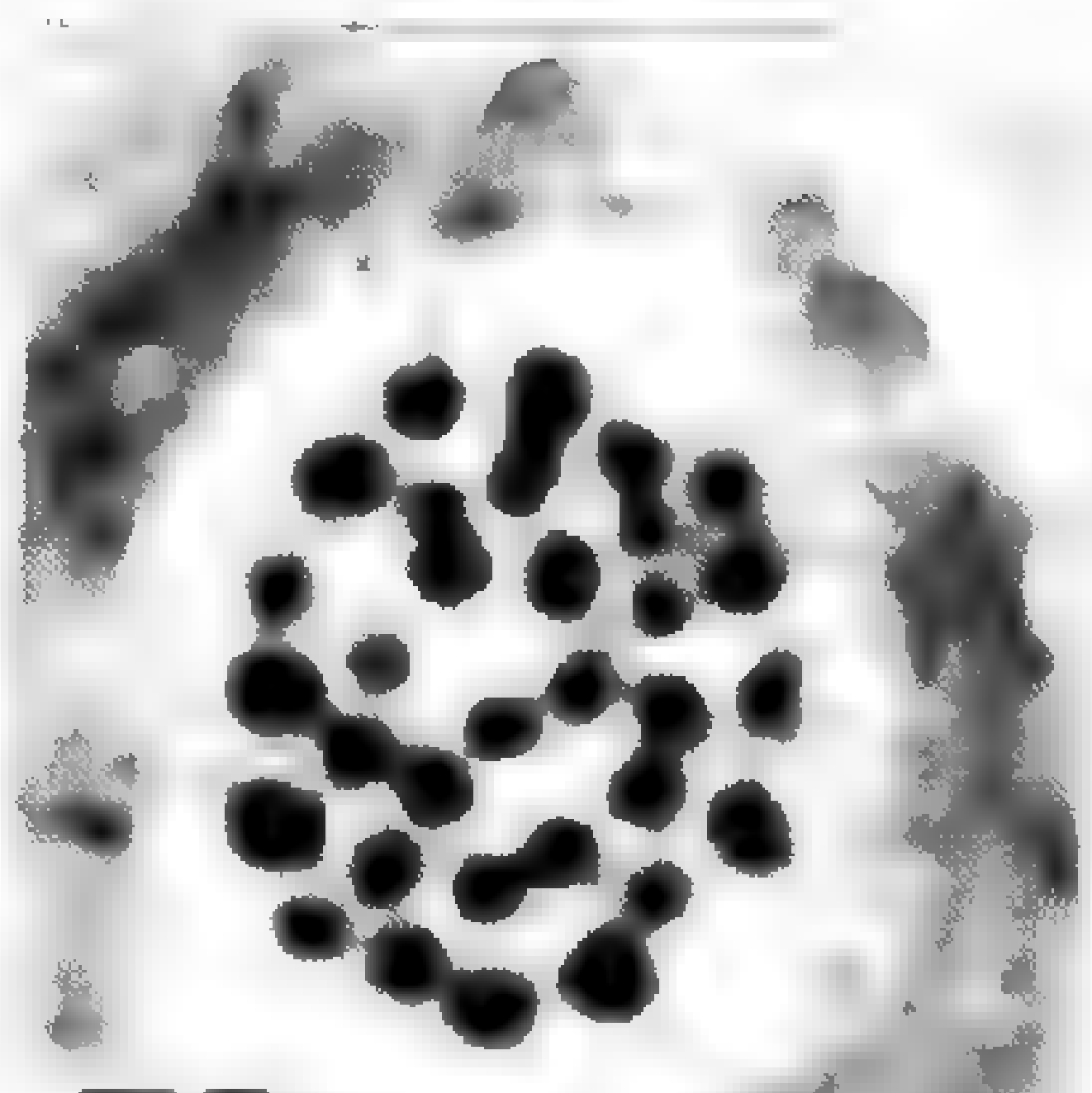
72



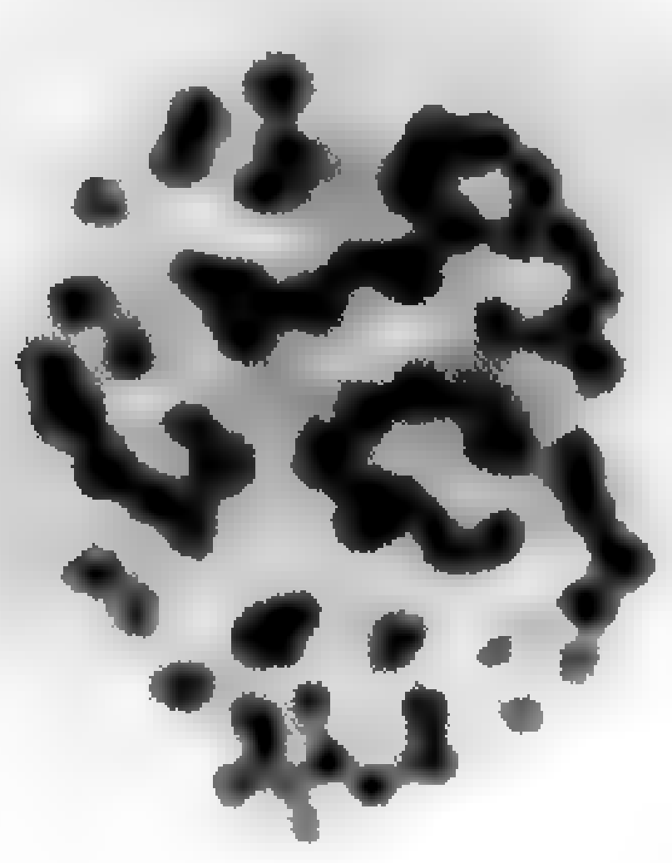
73



74

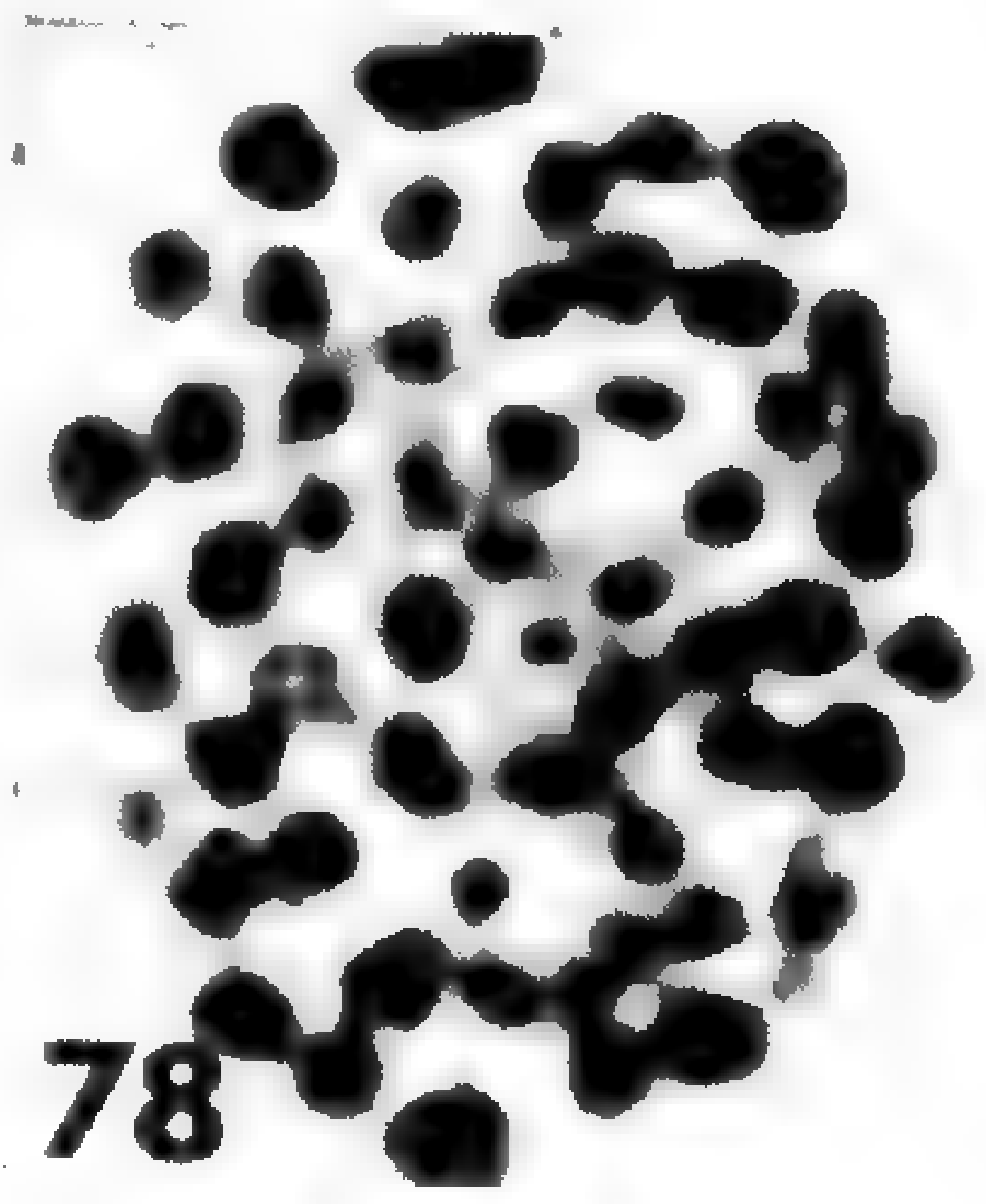


75

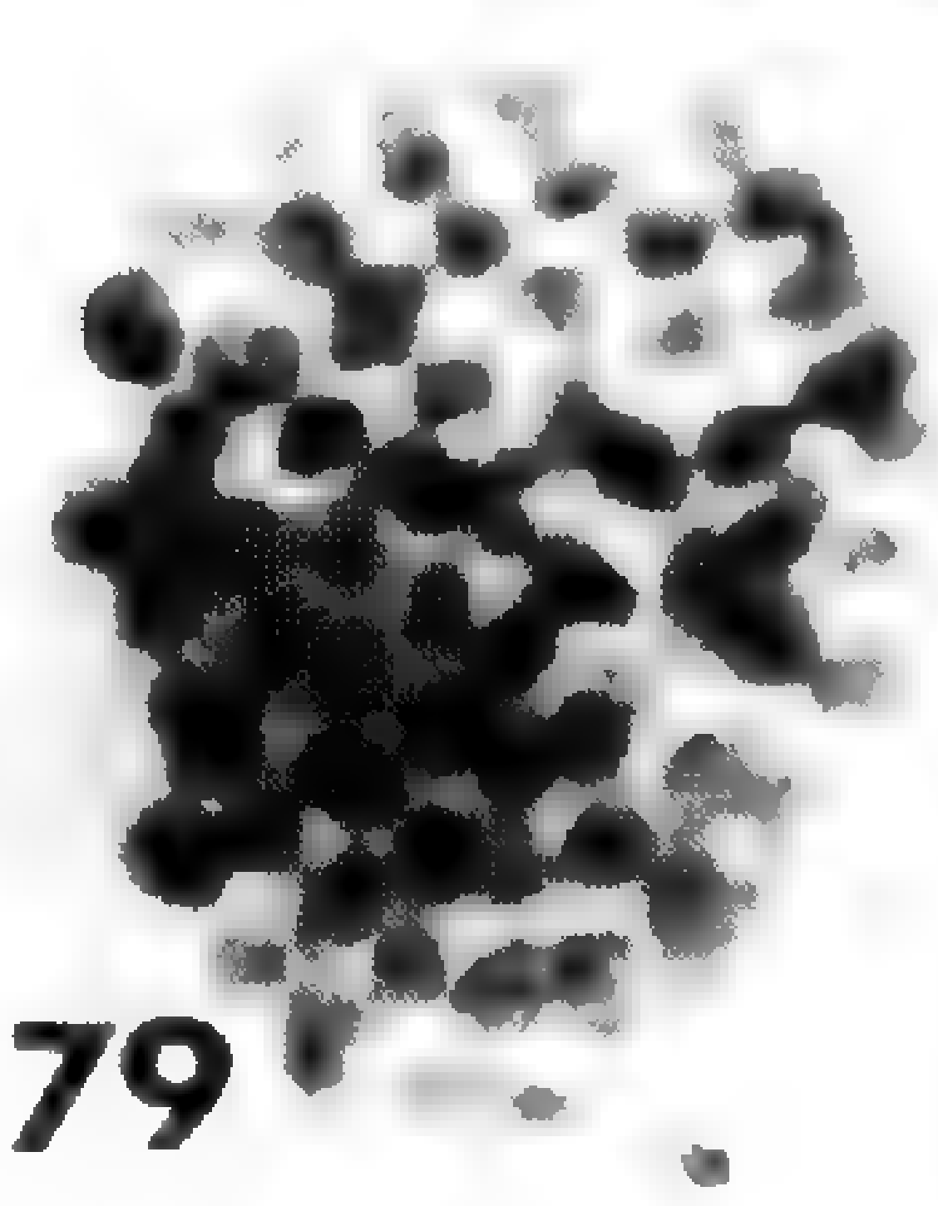


76

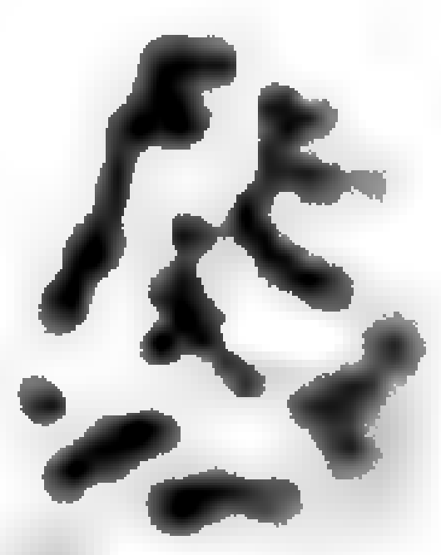
77



78



79



80

occurs in two disjunct areas on the eastern slopes of the Sierra Madre Oriental: near Monterrey and nearly 300 km. to the south in southern Tamaulipas (Clausen, 1981). Three collections, including one from the northern population and two from cultivation of uncertain origin, all had $n = 34$ (Fig. 64). Subspecies *edwardsii* Clausen (1981) is known only from an intermediate region at higher elevation. It differs in its conspicuously hairy stems, leaves, and floral parts, as well as in its tetraploidy. A clone of the type collection had $n = 62$ (Fig. 65), as did another plant from nearby and a third plant from a kilometer or so away. However, an earlier collection from the same area had $n = 64$ apparently. *Sedum ternatum* of the southeastern United States resembles *S. rhodocarpum* in bearing its broad leaves in whorls of three and was classified with it by Berger (1930), but it has $n = 8$, 16, and 24 (Baldwin, 1936). An attempted cross of *S. rhodocarpum* as pollen parent with *S. griseum* ($n = 26$) resulted in 70 seedlings, all selfs.

Sedum robertsianum

Sedum robertsianum E. J. Alexander resembles *S. parvum* and has been reduced to subspecific status there (Clausen, 1981). However, the cytological evidence obtained later argues strongly against this treatment, and it is retained as a species here. It is known only from the Big Bend region of west Texas, where it is the only species of *Sedum* that has yellow flowers. A topotype had $n = 14$ (Fig. 66),

---

Figures 61 80. Chromosomes of *Sedum* species and various hybrids in pollen mother cells at metaphase I unless otherwise indicated, all X2000. In some cells, univalents and/or B-chromosomes are indicated with thin lines, certain paired elements (bivalents and or multivalents) with thick lines. **61,** *S. reptans*, subsp. *carinatifolium*, *U2123*, $n = 60$; **62,** *Graptopetalum fruticosum* ($n = 31$) × *S. reptans* ($n = 72$), *U1398* × *M13381*, ca. 36 paired elements + 17 univalents in focus (mostly around margin of plate); **63,** *Pachyphytum hookeri* ($n = 32$) × *S. reptans* ($n = 72$), *M13349* × *M13381*, ca. 36 paired elements + 20 univalents in focus (mostly around margin of plate); **64–65,** *S. rhodocarpum*: **64,** subsp. *rhodocarpum*, *U487*, $n = 34$; **65,** subsp. *edwardsii*, *U2778A*, $n = 62$; **66,** *S. robertsianum*, *U2728*, $n = 14$; **67,** *S. semiteres*, *U2334*, $n = 19$; **68,** *S.* sp. aff. *semiteres*, *U2251*, $n = 54$; **69–73,** *S. stelliforme*: **69,** *U2337*, $n = 11$; **70,** *U2529*, $n = 13 + 3$; **71,** *U2246*, $n = 14$; **72,** *U2043*, 1 quadrivalent + 20 bivalents, equivalent to $n = 22$; **73,** *U2324*, $n =$ ca. 60; **74,** *S. trichromum*, *UC62.815*, $n = 19$; **75–77,** *S. versadense*: **75,** *M6377*, $n = 32$; **76,** *UC50.2283*, $n = 64$; **77,** subsp. *villadioides*, *U2662*, $n = 32$; **78–79,** *S. wrightii*: **78,** *U2148*, $n = 60$; **79,** **U2771,** $n = 72$; **80,** *S.* sp. nov., *U2410*, 31 elements (metaphase II).

with chromosomes all of about the same size and relatively large for the genus. Chromosomes of *S. parvum* (s. str.) are always much smaller and more numerous: $n = 32$, (Fig. 56) ca. 60 and 64 (Fig. 57) in subspecies *parvum*, $n = 34$ in subspecies *diminutum*, and $n = 64$ in subspecies *dendroides*, and they also differ substantially among themselves in size, an unusual characteristic in Mexican *Sedum*. Even allowing for the extraordinary cytological diversity that has been found in some Mexican species, *S. robertsianum* seems so different in its chromosomes from other collections cited here as *S. parvum* that its relationship to them must be quite distant. Hybrids might provide evidence of relationships and whether 32 gametic chromosomes in *S. parvum* represents tetraploidy, but no crosses have yet been attempted.

Sedum semiteres

Sedum semiteres Rose of the central Sierra Madre Occidental appears rather woody and resembles some species of Section Fruticisedum (e.g., *S. bourgaei*, $n = 29$, Uhl, 1980), but the stems die to the base after flowering and the plant continues the next year from small basal rosettes. It also resembles *S. lumholtzii*, but all surfaces (stems, leaves, and all floral parts) are papillose, not hairy. Three plants of the same original collection, possibly all the same clone, had $n = 19$ (Fig. 67), as does also *S. lumholtzii* (Fig. 41). A lone hybrid of *S. semiteres* with *S. greggii* ($n = 26$) (*U1535* × *U2334*) formed about 15 paired elements (bivalents plus multivalents) and 10 univalents at metaphase I in one cell, with other cells estimated to be about the same, and it produced no pollen. Eleven other attempted crosses, including one with *S. alamosanum*, yielded no progeny.

Another plant (*U2251*) was identified as *Sedum semiteres* (in herb) by R. T. Clausen, but it differs in having leaves up to 5 mm. broad and only 1 mm. thick, in its much less pronounced papillosity, and in other ways. It also differs in its polyploidy ($n = 54$, Fig. 68), with apparently a different basic chromosome number, and it may deserve recognition as a different species. Attempts to cross it with *S. compactum* and *Pachyphytum hookeri* were unsuccessful.

Sedum stelliforme

Sedum stelliforme S. Wats. differs from *S. alamosanum* and *S. mellitulum* in its smooth, not papillose, leaves and from *S. madrense* in its white or very pale, not deep pink, flowers. Generally its withered leaves remain attached to the stem for some time. In the northern part of its range, two plants from its type locality in southern Arizona had $n = 20$ + B-chromosomes (as did also a plant from southern Chihuahua). However, 14 plants from the White Mountains of east central Arizona and from the Black Range in southwestern New Mexico had $n = 12$ (Uhl, 1972), and these counts are supported by three more collections reported here. Eight additional collections reported here from the Sierra Madre Occidental of southwestern Chihuahua, northern Sinaloa and northwestern Durango were rather variable morphologically and very diverse cytologically, each with a different chromosome number: $n = 11$ (Fig. 69), 13 + 3 (Fig. 70), 14 (Fig. 71), 22 (Fig. 72), 24, 26, ca. 54 and ca. 60 (Fig. 73). The plant with $n = 22$ usually showed a quadrivalent at metaphase I, and all those with higher numbers also showed univalents and multivalents at metaphase I. The numbers reported for them represent counts from metaphase II and/or bivalent equivalents when these irregularities at metaphase I are allowed for.

Sedum stelliforme appears to consist of many isolated populations that are evolving very rapidly, with much restructuring of their genotypes, accompanied by many changes in chromosome number, both dysploid and polyploid. The extreme dysploidy here finds parallels in other widely distributed Mexican sedums, notably *S. moranense* (Uhl, 1983) and *S. jaliscanum* (Uhl, 1976b). Attempted crosses between *S. stelliforme* and 12 other species, including *S. alamosanum* and *S. cockerellii,* were unsuccessful.

Sedum trichromum

Sedum trichromum Clausen (1978) is named for the three colors of its petals: white at the base, pink in the middle, and green at the tips. It has only five stamems, like *S. pentastamineum* of central Mexico, but the latter differs in its slender, creeping, often pendulous habit and in its more conspicuous nectaries. *Sedum trichromum* is known from only two or possibly three localities 37 km. apart all at high elevation along the Durango-Mazatlan road in the Sierra Madre Occidental of western Durango. Clausen (1978), in making the type collection, could find only two other plants with it, and none remaining at the other localities. Three collections, representing all populations and including a clone of the type, all had $n = 19$ (Fig. 74), a number that is found also in *S. pentastamineum* (Fig. 58).

Clausen (1978) compared *Sedum trichromum* with *S. cockerellii* of northwestern Mexico and southwestern United States (n = 14–16, 29–32), which he then thought to be its closest relative, but the cytology offers no support at all to this. Later he reported (Clausen, 1981) that *S. trichromum* produced few seeds in cultivation and suggested that it might have originated through hybridization between an unspecified *Sedum* and *Echeveria*. This conclusion seems most unlikely to me, since meiosis in *S. trichromum* is completely normal in all three collections studied, and since nothing about it suggests any of the compromises in floral structure that I generally see in the many hybrids that I have made between *Sedum* and *Echeveria*. Attempted crosses with six other species, including *S. longipes* ($n = 19 + 1$) were unsuccessful.

Sedum versadense

Sedum versadense C. H. Thompson has finely hairy leaves and pinkish flowers. It is known mostly from Oaxaca, but it also occurs in the southwestern part of the state of Mexico, more than 200 km. to the northwest (Clausen, 1959). Two plants from northwestern Oaxaca had $n = 32$ (Fig. 75), as did another plant from cultivation. *Sedum chontalense* Alexander of southeastern Oaxaca differs only in minor ways from the typical form, and, following Clausen (1959), it is reduced to synonymy here. However, two plants of its type collection were tetraploids with $n = 64$ (Fig. 76). Variety *villadioides* Kimnach (1982) differs in its much narrower leaves and general *Villadia*-like aspect, but its flowers are identical. A plant of its type collection also had $n = 32$ (Fig. 77). Two attempts to cross diploid *S. versadense* with *S. greggii* were unsuccessful, as were also attempts of tetraploid *S. versadense* with *S. hintonii* ($n = 25$) and with six other tetraploids.

Sedum wrightii

Sedum wrightii A. Gray forms sessile rosettes with thick roots, usually pale green leaves, and white petals that are erect for the lower half or more and have a pungent odor (Clausen, 1975). The species ranges from southern New Mexico south and southeast across western Texas into isolated desert mountains of Coahuila and northern San Luis Potosi and to the northern Sierra Madre Oriental in Nuevo Leon and Tamaulipas. I have previously published chromosome counts and a map showing the distribution of diploid ($n = 12$), tetraploid, hexaploid, and octoploid collections of this species (Uhl, 1972). The 15 additional collections reported here supplement the earlier reports and also add 10- and 12-ploids to the list of polyploids known in *S. wrightii* (Fig. 78, 79). The higher polyploids ($8n$, $10n$, and $12n$) all occur in the southern part of its range. Clausen has recently described two new subspecies of *S. wrightii*, based chiefly on differences in size and numbers of flowers and seeds. Plants of the type clones of both subspecies *priscum* Clausen (1979) and subspecies *densiflorum* Clausen (1981) are diploid ($n = 12$), but at least the latter and also subspecies *wrightii* include polyploids also. These subspecies seem not to be clearly delimited, and they are not listed separately in Table 1. Clausen (1975) on the one hand (p. 682) classed *S. wrightii* in Section Cockerellia with *S. niveum* ($n = 16$ and 64) and *S. cockerellii* ($n = 14$–16 and tetraploids), but on the other hand stated (p. 211) that "*Sedum wrightii* really is not close to any other species." However, the more recently described *S. multiflorum* of southern Jalisco also has $n = 12$ and shares several other characters with *S. wrightii* and probably is its closest relative. Attempts to cross *S. wrightii* have been handicapped because it flowers in late summer and fall, when few other species are blooming. Reciprocal crosses with a species of *Lenophyllum* ($n = 33$) were unsuccessful, as was a cross with *S. trichromum*.

Sedum sp.

Sedum sp. A diminutive plant collect by Felipe Otero in the state of Mexico is clearly an undescribed species (*U2410*). It forms an acaulescent rosette reminiscent of a small *Graptopetalum* or *Echeveria*, then produces relatively long lateral flowering stems with yellow flowers typical of *Sedum*. It bears some resemblance to *S. oteroi* ($n = 27$), but its chromosome number is different ($n = 32$, prob; apparently $n = 31$ in Fig. 80). Its lateral inflorescence and its chromosome number are compatible with a conclusion that this species might be a diminutive member of section (or subgenus) Pachysedum (Uhl, 1978). A hybrid with *S. clavatum* ($n = 34$) of section Pachysedum (*U1566* × *U2410*) formed 31–32 paired elements and 0–4 univalents (average $31.7 + 1.2$) in 10 cells analyzed at metaphase I, with as many as three chromosome bridges at anaphase I. Quartets consisted of four spores of equal size, and 7.8% of pollen at anthesis was stainable. These observations, and especially the nearly complete chromosome pairing, are similar to those made for many other hybrids between two species of section Pachysedum (Uhl, 1978, and unpublished), and this is probably where this species should be assigned. Attempted crosses with three echeverias and two pachyphytums were unsuccessful.

DISCUSSION

The 39 species reported here are extraordinary for their cytological diversity, both among themselves and also within the more widely distributed species. About 38 different gametic chromosome numbers were found (ignoring univalents and B-chromosomes), ranging from $n = 11$ in one collection of *Sedum stelliforme* to $n =$ ca. 100 in a plant of *S.* cf. *australe;* and some other collections, probably odd-ploids, were so irregular at meiosis that their approximate numbers were not established. Both dysploidy and polyploidy are well represented, sometimes in the same species (e.g., *S. cockerellii, S. mellitulum, S. stelliforme*). As an extreme, *S. greggii* has at least six different chromosome numbers that are considered to be diploid ($n = 18 + 6$B through $n = 34$), probably the result of many rearrangements (translocations and inversions) of its basic genome (dysploidy), as well as two other numbers that are polyploid. *Sedum wrightii* has every even-numbered level of ploidy from diploid ($n = 12$) through 12-ploid ($n = 72$).

Of the 39 species reported here, 13 came only from cultivation or from only a single collection or population in the wild. Among the remaining 26 species, polyploidy is known in 17, dysploidy (including polyploids with different basic numbers) in 12, aneuploidy (defined here as unbalanced numbers of standard chromosomes) in 4, and B-chromosomes in 7. Only four species have the same chromosome number in all populations studied from the wild, and three of these (*S. grandipetalum, S. latifilamentum,* and *S. pentastamineum*) are represented by only two populations, the fourth (*S. trichromum*) by two populations, possibly three.

For these reasons, conclusions regarding relationships here based on chromosome numbers can be drawn only with great caution. Tabulation of the frequency of the various numbers shows some clusters, and some of these include species that resemble each other in other ways, as well as, often, some that seem not closely related. Thus, $n = 12$ was found in four species, all of them white-flowered: *Sedum wrightii* and *S. multiflorum* (which probably are indeed related), *S. stelliforme* (which also has $n = 11$, 13, 14 and higher), and also in the very distinctive *S. globuliflorum*. Five rather similar species, all again with white to pinkish flowers, have $n = 18$ and/or 19 (some of them also with polyploids): *S. alamosanum*, *S. diffusum*, *S. lumholtzii*, *S. mellitulum*, and *S. semiteres*, and a sixth species, *S. bellum* ($n = 36$) appears to be an autotetraploid based on 18. In addition, one collection of the yellow-flowered *S. greggii* had $n = 18 + 6B$ and thereby differed drastically from the many other collections of that species that were studied. A different pair of related species, *S. longipes* and *S. pentastamineum*, had $n = 19$, and this number is found also in *S. trichromum*.

Another cluster of nine species all have $n = 34$, although most of the species also include plants with other numbers, dysploid and/or polyploid. This number is so high as to suggest that it represents some sort of polyploidy, but none of these nine species seems closely related to anything with half or less this number of chromosomes. Hybrids have been produced with only two of these species (*S. greggii* and *S. grandipetalum*), but the appearance of these hybrids and the behavior of their chromosomes at meiosis are interpreted as indicating that, however these species may have originated in the past, they are effectively diploid now (*See below*). A similar conclusion has been reached from similar observations of species and hybrids of section Pachysedum, where all species but one have $n =$ 30 to 36 or a multiple, and where 11 species have $n = 34$ (Uhl, 1978). In addition, several species of other more or less woody sedums have $n = 34$ (Uhl, 1980): *S. obcordatum*, *S. palmeri*, and *S. torulosum* (these three designated as the "*S. palmeri* group"), *S. burrito*, and *S. furfuraceum*, again with no indication (other than the number itself) that $n = 34$ represents any kind of polyploidy.

Seven of the species with $n = 34$ (*S. grandipetalum*, *S. greggii*, *S. humifusum*, *S. muscoideum*, *S. oaxacanum*, *S. parvum*, and *S. reptans*) bear yellow flowers and resemble each other enough to suggest that most or all of them belong to the same natural group. The white-flowered *S. liebmannianum* ($n = 34$) and still other species that differ cytologically as dysploids: *S. cupressoides* ($n = 30$) and *S. nanifolium* ($n = 26$) also may be related.

Other than the species cited here that extend into the southwestern United States, the Mexican species of *Sedum* show no particular affinity in their chromosomes or otherwise with the species native farther north, most of which clearly have lower basic chromosome numbers. In fact, when all of North America is considered, the perennial species of *Sedum* show a pronounced trend toward higher chromosome numbers from north to south. Ignoring obvious polyploids, basic numbers of perennial sedums in the eastern United States are 6 (*S. nevii*), 8 (*S. ternatum*), 11 (*S. rosea*), 12 (*S. telephioides*), 14 (*S. glaucophyllum*), and 18 (*S. integrifolium*). In the western United States (not including those species that range south into Mexico), basic numbers are 7 (*S. rhodanthum*), 8 (*S. lanceolatum* and seven related species), 12 (*S. oreganum*), 15 (*S. spathulifolium*, *S. obtusatum* and five other species of section Gormania), and 18 (*S. integrifolium* again). Species native to the southwestern United States and ranging south into Mexico have basic numbers of 12 (*S. stelliforme* and *S. wrightii*), and 14–16 (*S. cockerellii* and *S. niveum*), and the most northerly populations of all of them are diploid. *Sedum robertsianum* (n = 14) of west Texas has been reduced to subspecific status under *S. parvum* (n = 32, 34, etc.) of northeastern Mexico (Clausen, 1981), but it is treated separately here.

Species of northern Mexico that do not extend as far north as the border have basic numbers of 18–19 (*S. alamosanum*, *S. diffusum*, and four others) or 30–32 (*S. craigii* and probably *S. suaveolens* of section Pachysedum). When all perennial Mexican species of *Sedum* are considered, those reported here as well as those reported previously (Uhl, 1978, 1980, 1983), those that are found from west-central Durango south and east across Mexico have basic numbers of 12 (only two species: *S. multiflorum* and *S. globuliflorum*), 15–16 (*S. tortuosum* and *S. tuberculatum*), 19–21 in four species (three reported here, plus *S. quevae*, or five species if *S. latifilamentum* is a *Sedum* and not a *Villadia*), 24 (*S. botteri*), and 26–35 in perhaps 16 species reported here plus about 37 other species of Section Pachysedum and other woody species reported previously.

Hybrids of many species of *Sedum* with the higher basic chromosome numbers (up to n = 34) give evidence (1) that none of their gametic chromosomes are able to pair at all with each other, and (2) that the chromosomes that they contribute to their hybrids are no more potent in determining the phenotypes of those hybrids than are other genomes that consist of far fewer chromosomes and that clearly must be considered diploid. These considerations, plus the normal behavior of the chromosomes and the absence of multivalents at their own meiosis, lead to a conclusion that most—but not all—species of Mexican *Sedum* having as many as 34 gametic chromosomes are effectively diploid now. The absence of any reasonably similar species having half or less their numbers of chromosomes that might be construed as ancestral species lends further support. It is possible, even probable, that these species arose as polyploids of some sort in the distant past. However, if that is true they have by now become so thoroughly diploidized, presumably by loss, mutation or suppression of duplicate genetic information, that only their high chromosome numbers offer any suggestion of their ancient polyploidy.

Mexican Crassulaceae in general and species of *Sedum* in particular usually occur as isolated populations, some consisting of only one or a few individuals. Typically they grow on cliffs and rocks, pioneer habitats that are of relatively short duration in terms of geological time. And they grow in an area that has been subjected to extensive tectonic activity, to volcanism in many regions, and doubtless also to severe changes in climate, especially during advances and retreats of the Pleistocene glaciers farther north as well as on some of the higher peaks in Mexico. Many species appear to lead a shifting, marginal existence, their populations fluctuating greatly in numbers, and with many colonizations and extinctions over relatively short periods of time.

The one or few individual(s) that serve as founder(s) or parent(s) of a new population are not necessarily themselves typical of their parental population, morphologically, physiologically, genetically, or in their chromosomes. Furthermore, these founders cannot be expected to carry the full range of genetic information and variability of the parental population with them into the new one. The new habitat may well differ somewhat from the old, and natural selection there may favor adaptations to a different range of environmental conditions. Random mutations in genes and/or in chromosome structure, if favorable or even if only neutral, can quickly become established in small new populations, and the whole series of processes and events is cumulative with each shift or new population. This description represents a model of a situation that would be expected to exhibit rapid evolution in physical appearance, in physiological adaptations, and in chromosomes (*cf.* Wright, 1982). The evidence presented here indicates very strongly that this is just what has been happening in the Mexican species of *Sedum*.

Table 1. **Chromosome Numbers**

Sedum alamosanum S. Watson

- *M18801* Baja California Sur. Sierra de las Palmas, SW of Santa Rosalia, 1000 m. 8 km. SSW of Rancho San Sebastian, Near 26° 57′N, 112° 26′W. R. Moran. $n = 18$.
- *U1647* Baja California Sur. Arroyo on N. side of Cerro Bareño, Sierra Giganta, W. of Loreto, 1050 m. A Carter & R. Moran 5329. $n = 18$.
- *UC53.113* Near topotype. Sonora. Cliffs on N. slope of Alamos Mt., ca. 1065 m. E. R. Blakely. $n = 18$.
- *U2682* Sonora. NE of the highest point, Sierra de Alamos, 1235 m. R. T. Clausen 80-1. $n = 18$.
- *C44-19* Chihuahua. R. T. Craig. $n = 18$ (Fig. 2).
- *U2685* Chihuahua. Arroyo Bacuseachi, W. of La Bufa on S. side of Barranca de Batopilas, ca. 1100 m. R. A. Bye Jr. 7320a. $n = 18$.
- *U2021, U2684* Chihuahua. Barranca del Cobre. K. Sabo. $n = 36$ (Fig. 3).
- *U2045, U2683* Chihuahua. Bottom of Cañon del Cobre of Rio Urique, Barranca de Bocaibo, 1240 m. Kimnach & Brandt 974. $n = 54$ (Fig. 4).
- *U2408* Coahuila. On limestone slopes of Cuesta Zozaya at W. end of Sierra de la Madera, ca. 75 km. WNW of Cuatrocienegas. 1500 m. Near 27° 15′N., 102° 42′W. J. Henrickson. $n = 17 + 1$ (Fig. 1).

Sedum australe Rose

- *UC58.854* T. MacDougall B-199. $n =$ ca. 100.

Sedum bellum Rose

- *U2648* Type collection. Durango. San Ramon mining camp, 129 km. W. of Durango City, E. Palmer in 1906, via J. N. Rose and N.Y. Bot. Garden. $n = 36$ (Fig. 8).

Sedum bellum hybrid

- *U1944* Cultivated. J. Marnier Lapostolle. HNT 23024, via R. Moran. 17-18 paired elements + 18-22 univalents (Fig. 9).

Sedum caducum Clausen

- *U2777* Tamaulipas. 19 km. SSW of Villa Hidalgo, 1210 m. R. T. Clausen 80-19. $n = 64$ (Fig. 10).
- *U2779* Isotype. Tamaulipas. Limestone in canyon 15 km. SW of Ciudad Victoria, 23° 38′N, 99° 12′W., 610 m. R. T. Clausen C7370. $n = 96$ (Fig. 11).
- *U204* Probably same locality. MacDougall-Alexander Expedition 1794, New York Botanical Garden. $n = 64$.

Sedum clavifolium Rose

- *U1762* State of Mexico. Cañada de Alcalican, SW slope of Iztaccihuatl, 3700 m. R. T. Clausen. 3 plants, all $n = 34$-38 irregular (Fig. 12).

Sedum cockerellii Britton

- *U2090* Arizona: Pima Co. Quinlan Mts. Small canyon above road, ca. 11 km. below Kitt Peak Observatory, ca. 1300 m. A. M. Phillips III. $n = 29$.
- *U2287* Arizona: Santa Cruz Co. Santa Rita Mts. Near Bathtub, Big Casa Blanca Canyon, 1500 m. T. R. Van Devender & S. F. Hale. $n = 14$.

U2296 Arizona: Cochise Co. Huachuca Mts. Pat Scott Canyon, above Ramsay Canyon. T. R. Van Devender & B. L. Everitt, via A. M. Phillips III. $n = 14$.

U2768 New Mexico: Sandoval Co. Jemez Mts. On granite, near Cuba, 2865 m. D. Demaree. $n = 16$.

U2729 Topotype. New Mexico: Santa Fe Co. Tuerto Mt., along old trail from Santa Fe to Pecos R., 2685 m. R. T. Clausen 62.233. $n = 16 + 2$ 4B.

U2766 Near Topotype of *S. wootoni* Britton. New Mexico. Doña Ana Co. NE slope of Organ Needle, Organ Mts., 2075 m. R. D. Worthington 5880. $n = 32$.

U2767 Texas: Jeff Davis Co. Davis Mts. 4.3 km. SE of top of Mt. Livermore, on crest of S. wall of Limpia Canyon, 2165 m. R. D. Worthington 6673. $n = 15$.

U2406 Texas: Jeff Davis Co. Davis Mts. N. slope of Spring Mt., 3 km. N. of McDonald Observatory. M. C. Johnston. $n = 15$.

U2247 Chihuahua. E. side of Rio Tonachic at Km. 54.5 on Mex. 16, 13 km. E. of Tomochic, 1980 m. $n = 15$.

U2245 Chihuahua. Km. 45 W. of La Junta on Mex. 16, 2070 m. $n = 15$.

U2765 Chihuahua. SW of dam on Rio Papagochic, SW of Guadalupe, 2125 m. R. T. Clausen 76 43. $n = 15$.

Sedum compactum Rose

U1509 Oaxaca. Tomellin Canyon. Coll. by Buchenau. Meyran 2717. $n = 60$ prob (Fig. 13).

Sedum cupressoides Hemsley

U2358 Puebla. Limestone S. of bridge at Km. 39.8 E. of Mex. 119, 5 km. W. of Tetela de Ocampo, 1770 m. $n = 30 + 1$B (Fig. 14).

M7773 Oaxaca. Sierra de Juarez. R. Moran. $n = 30$.

Sedum diffusum S. Watson

M18364 Chihuahua. Sierra Anahuac. C. Glass & R. Foster. $n = 19$.

U1922 Coahuila. Km. 40 on Mex. B-3, Monclova to Cuatrocienegas. J. & M. Bleck 068. $n = 19$ (Fig. 15).

C7595 Nuevo Leon. Mountainside below cave, Villa de Garcia, 1050 m. R. T. Clausen. $n = 57$.

U1368 Nuevo Leon. 1 km. below upper end of road to Chipinque Mesa, SW of Monterrey. $n = 19$.

C7569 Nuevo Leon. Canyon on W. side of Saddle Mt., SE of Monterrey, 1000 m. R. T. Clausen. $n = 19$.

C7363 Nuevo Leon. S. side of Huajuco Canyon, Villa Santiago. 25°25′, 100°08′W. R. T. Clausen & J. L. Edwards. $n = 19 + 1$ (Fig. 16).

C7544 Nuevo Leon. S. slope of La Boca Canyon, 3 km. E. of Villa Santiago, 650 m. R. T. Clausen. $n =$ ca. 19.

U2086 Nuevo Leon. 25 km. W. of Mex. 85 on road to Rayones, 640 m. M. Kimnach & Lyons 1398. $n = 19$.

49627 Cultivated, New York Botanical Garden. $n = 38$.

U2493, M3221, M7727a, C44-113. All cultivated. $n = 57$ (Fig. 17).

Sedum globuliflorum Clausen

U2643 Clonotype. Hidalgo. SW slope of Mount Cangando, 2 km. E. of Encarnación, 2600 m. 20°49′N, 99°20′W. R. T. Clausen 78 13 (7). $n = 12$ (Fig. 18).

Sedum grandipetalum Fröderström

U2074 Jalisco. Sierra de Minatlan. Above Haceraderos, 2300 m. F. Boutin & M. Kimnach 2970. $n = 34$.

U1755 Jalisco. NW slope of Nevado de Colima. Ravine 2 km. SSE of El Isote, 2500 m. R. T. Clausen. 2 plants, $n = 34$ (Fig. 19).

Sedum greggii Hemsley

U2675 Jalisco. Gorge of Los Guayabos Creek, E. of Ciudad Guzman. R. T. Clausen 77 19. $n = 30$ (Fig. 24).

U1535 San Luis Potosi. Canyon E. of road 16 km. N. of Ahualulco. $n = 26$ (Fig. 23).

U1491 San Luis Potosi. Bluff E. of Mex. 57, 1.1 km. S. of Rio Santa Maria. $n = 33$.

M13384 San Luis Potosi. Cerro Agujón, 40 km. SW of Rioverde. R. Moran. $n = 26$.

U2271 Guanajuato. Sierra de Guanajuato. 3 km. SW of Mesa San Jose, 2360 m. $n = 26 + 1$.

U2117, M14730. Guanajuato. Picachos de la Bufa, NE side of Guanajuato city, 2350 m. $n = 26$.

M14738. Guanajuato. Mesa de San Juan. R. Moran. $n = 24 + 1$ (Fig. 22).

U2676 Michoacan. S. side Rio Los Filtros, Cerro Azul, 23 km. SE of Morelia . R. T. Clausen. $n = 34$ (Fig. 27).

U2034 State of Mexico. 0.5 km. S. of Temascalcingo, along Rio Lerma. M. Kimnach 493. $n = 33 + 6$ (Fig. 26).

U1858 Queretaro. Canyon 2.6 km. N. of Pinal de Amoles, 2250 m. $n = 33$.

U2131 Queretaro. 7 km. S. of San Joaquin, 2250 m. $n = 33$.

UC50.1061 Hidalgo. Pan-American Hwy. (Mex. 85) near San Luis Potosi border. Coll. by Lefebure. $n = 33$.

U2342 Hidalgo. 4.4 km. S. of Durango at Km. 70.1 on Mex. 85, 2130 m. $n = 33$.

U2679 Hidalgo. Barranca de los Marmoles, 2300 m. 20°51′N., 99°14′W. R. T. Clausen C7532. $n = 34$.

M7807 Hidalgo. San Vicente, near same locality, 2315 m. R. Moran. $n = 33$.

U2677 Hidalgo. Near El Aguila Mine, 4 km. E. of Encarnación. 20°49′N., 99°18′W. R. T. Clausen 78 22. $n = 33$.

M7789 Hidalgo. Below El Carmen. R. Moran. $n = 33$.

U2680 Puebla. Canyon of Texcoco R., 1 km. NNW of Huauchinango, 1300 m. J. L. Edwards. Triploid.

U2354 Puebla. 7 km. W. of Aquixtla 2470 m. $n = 18 + 6B$ (Fig. 21).

U2678, U2681, UC52.1765 All cultivated. All $n = 33$ (Fig. 25).

U2792 Jalisco. Type collection of subspecies *angustifolium* Clausen. Volcan de Tequila. 2840 m. R. T. Clausen 77 15. $n = 74 \pm 4$, irregular.

U2791 Same locality, F. Boutin & M. Kimnach 3206. $n = 74 \pm 4$, irregular.

Sedum havardii Rose

U2702 Texas: Brewster Co. Big Bend National Park. N. slope of Casa Grande, 1860 m. R. T. Clausen 78 4 $n = 54$.

U2794 Texas: Brewster Co. Big Bend National Park. Just E. of summit, Emory Peak, 2320 m. R. T. Clausen 78 5. $n = 54$.

Sedum humifusum Rose

U1847 Guanajuato. Km. 19.5 E. of San Jose Iturbide on road to Tierrablanca, 1830 m. *n* = 68 (Fig. 34).

M14754 Queretaro. Santa Maria del Mexicano. R. Moran *n* = 35 (Fig. 33).

M14742 Hidalgo. 1.6 km. N. of Tecozautla, 1650 m. R. Moran. *n* = 34.

M14751 Hidalgo. Geysers, Tecozautla, 1550 m. R. Moran. *n* = 34 (Fig. 32).

U1478 Hidalgo. Presa Madero, 12 km. SW of Huichapan. *n* = 34.

UC61.593 Hidalgo. Beneath Puente de Tasquillo, 20 km. N. Ixmiquilpan, 1650 m. M. Kimnach & R. Moran 213. Triploid.

Sedum latifilamentum Clausen

U1855 Queretaro. Just S. of highway summit (Mex. 120), 8.4 km. S. of Pinal de Amoles, 2600 m. *n* = 20.

U2688 Clonotype. Hidalgo. Mount Cangando, 2 km. E. of Encarnación, 2490 m. R. T. Clausen C78–15. *n* = 20 (Fig. 35).

Sedum liebmannianum Hemsley

M6347 Puebla. 3 km. NW of Tepeaca, 2300 m. 18° 59′N, 97° 55′W. R. Moran. ca. 50 elements, very irregular.

U1551 Puebla. W. edge of Tepeaca at Km. 166.7 on Mex. 150. Ca. 18–25 elements, very irregular.

U2477 Puebla. 6 km. NW of Cañada Morelos, 2500 m. 68–80 elements, very irregular.

U1890 Puebla. 19 km. S. of Esperanza, 2680 m. ca. 20 elements, very irregular.

U2486 Puebla. 6.7 km. E. of Nicolas Bravo, 2620 m. *n* = 34.

U2023 Oaxaca. 12 km. on Tlaxiaco road SW of junction with Mex. 190. C. Glass & R. Foster 1352. *n* = 34 (Fig. 36).

U1907, U2380 Oaxaca. 11 km. NW of Yanhuitlan, 2375 m. ca. 39–46 elements, very irregular.

M6379 Oaxaca. 6 km. NW of Yanhuitlan, 2400 m. Near 17° 30′N, 97° 19′W. R. Moran. ca. 25 elements, very irregular (Fig. 37).

C200 Cultivated, New York Botanical Garden. *n* = 34–36.

Sedum longipes Rose

U1412 Michoacan. E. side of Puente Rio Turundeo, 8.4 km. N. of Tuxpan, 1830 m. *n* = 19 (Fig. 38).

M14775 State of Mexico. Barranca de Ahuatenca, near Chalma. R. Moran. *n* = 19.

Tep 7 Morelos. Topotype. Sierra de Tepoztlan, N. of Tepoztlan. R. T. Clausen. *n* = 20 (Fig. 40).

M10175 Morelos. Tepoztlan. R. Moran. *n* = 19 + 1 (Fig. 39).

SMO-Cu 2 Isotype of subsp. *rosulare* Clausen. Cultivated at Huauchinango, Puebla. *n* = 19.

Sedum lumholtzii Robinson & Fernald

UC68.144 Sinaloa. Cañon de Tarahunaus, below La Joya. D. Breedlove. *n* = 19 (Fig. 41).

Sedum madrense S. Watson

U2703 Chihuahua. Oteros R., 6 km. W. of Creel, 2270 m. R. T. Clausen 78–8. *n* = ca. 64.

Sedum mellitulum Rose

U2776 Sonora. 16 km. W. of Yecora. P. S. Martin. $n = 66 \pm 2$.

U2772 Chihuahua. 11 km. W. of Basaseachic along road from Yecora, 2440 m. L. J. Toolin 1342. $n = 95$ (Fig. 47).

U2579 Chihuahua. Yepachic. A. Lau 072. $n =$ ca. 84.

M23248 Chihuahua. Basaseachic Falls. R. Moran. $n = 80$–84 (Fig. 46).

M17272 Chihuahua. Cusarare Falls, S. of Creel. R. Reeves. $n = 50 \pm 1$ (Fig. 45).

U2042 Chihuahua. 3.7 km. S. of Basihuare on road from La Bufa to Creel, 2000 m. M. Kimnach & F. K. Brandt 971. $n = 18 + 1B$ (Fig. 43).

U2733 Chihuahua. 1.2 km. NE of Basihuare. R. Bye Jr. 8036. $n = 18$ (Fig. 42).

U2734 Chihuahua. 4 km. S. of Basihuare, 2100 m. R. T. Clausen 78-12. $n = 19$ (Fig. 44).

Sedum mexicanum Britton

U407, FL1418, S151 All cultivated. All $n = 18$ (Fig. 48).

Sedum millspaughii Hamet

U2585 Guatemala: Dept. Escuintla. 7 km. SW of Palin, 700 m. $n = 24$.

U843 Same locality. H. E. Moore Jr. $n = 24$.

Sedum multiflorum Clausen

1946, U2088 Jalisco. Canyon E. of Ciudad Guzman. Boutin & Brandt 2261. $n = 12$ (Fig. 49).

Sedum muscoideum Rose

UC51.1355 Cultivated, H. Johnson, $n = 34$ (Fig. 50).

Sedum nanifolium Fröderström

C7607 Coahuila. N. of Chorro Grande, 1600 m. 25°23′N., 100°48′W. R. T. Clausen. $n = 26$.

U1499 Coahuila. Puente Chorro #3, Chorro Canyon, Mex. 57 SE of Saltillo. $n = 26 + 1B$. (Fig. 52).

U2719 Coahuila. W. of El Chorro, upper end of Chorro Canyon. R. T. Clausen 78-3. $n = 26 + 3B$.

M6309 Coahuila. 5 km. N. of Puerto Flores, 1900 m. 25°18′N, 100°45′W. R. Moran. $n = 26$ (Fig. 51).

UC61.1196 Coahuila. Near Lirios. J. H. Strauss. $n = 26$.

U2463 Coahuila. Paso de Jame, 5 km. E. of Los Lirios, 2315 m. Near 25°23′N, 100°38′W. J. Henrickson 16882B. $n = 26$.

U2082 Nuevo Leon. Ca. 57 km. SE of Saltillo, Coah., 2135 m. M. Kimnach & Lyons 1489. $n = 26 + 4B$.

U1560 Nuevo Leon. 4 km. N. of Providencia, 68 km SE of Saltillo. $n = 52$.

U1913 Nuevo Leon. 26 km. N. of La Ascensión. $n = 52$ (Fig. 53).

U2718 Nuevo Leon. Cañada Zacatosa, 6 km. N. of La Escondida, 1730 m. 24°09′N., 99°55′W. R. T. Clausen 77-32. $n = 26$.

Sedum niveum Davidson

U2274 California: San Bernardino Co. New York Mts. Granitic ridge, N. of summit, 2200 m. J. Henrickson 14046. $n = 16$.

M21231 Baja California. Sierra San Pedro Martir. E. Vallecitos, 2480 m. R. Moran. $n =$ ca. 64.

Sedum oaxacanum Rose

M7723 Puebla. Cerro de la Yerba. R. Moran. n = ca. 34.

U1750, UC54.418 Cultivated. $n = 34$ (Fig. 54).

Sedum oteroi Moran

U2160 Oaxaca. Isotype. Sierra Mixteca, ca. 10 km. S. of San Miguel Aztatla, ca. 1900 m. Near 17°55′N, 97°23′W. F. Otero 17. $n = 27$ (Fig. 55).

Sedum parvum Hemsley

U1537 San Luis Potosi. Canyon 16 km. N. of Ahualulco. $n = 32 + 2B$.

M13373 San Luis Potosi. Sierra de Alvarez, 1.8 km. S and above Puerto Altamira. R. Moran & C. H. Uhl. $n = 60$ prob.

U1842 San Luis Potosi. Sierra de Alvarez, 0.4 km. E. of microwave relay station, 4 km. above Puerto Altamira, 2650 m. $n = 32$ (Fig. 56).

M7652 San Luis Potosi. Zaragoza. R. Moran. $n = 64$ (Fig. 57).

U2146 Topotype of subsp. *dendroides* Clausen. San Luis Potosi. 0.5 km. W. of Catorce, 2680 m. $n = 64$ prob.

U2699 Type collection of subsp. *diminutum* Clausen. Coahuila. Cañada La Hacienda, Sierra de la Madera, 1860 m. 27°03′N, 102°26′W. R. T. Clausen 78 7. $n = 34$.

Sedum pentastamineum Clausen

U2533 State of Mexico. Mex. 130, 15 km. NE of Temascaltepec, 2340 m. $n = 19$.

U2825 Clonotype. State of Mexico. Ravine of Tiscalatengo R., 4 km. NW of Villa Guerrero. R. T. Clausen plant 7. $n = 19$ (Fig. 58).

Sedum reptans Clausen

M13381 San Luis Potosi. Cerro Agujón, Sierra La Equiteria, 40 km. SW of Rioverde. 21°41′N, 100°03′W. R. Moran & C. H. Uhl. $n = 72$ (Fig. 60).

U2695 Type Collection. Same locality. R. T. Clausen 77-36. $n = 72$.

U2711 Queretaro. Vizarron. A. Lau 081. $n = 34$ (Fig. 59).

UC70.540 Cultivated. $n = 82 \pm 2$.

U2123 Topotype of subsp. *carinatifolium* Clausen. Queretaro. 16 km. NE of Vizarron on road to Maconi, 2165 m. $n = 60$ (Fig. 61).

Sedum rhodocarpum Rose

C7546 Nuevo Leon. La Boca Canyon, 3 km. E. of Villa Santiago, 650 m. 25°25′N, 100°08′W. R. T. Clausen. $n = 34$.

U487 Cultivated. $n = 34$ (Fig. 64).

21756 Cultivated, New York Botanical Garden, from J. N. Rose in 1904. $n = 34$.

U2778 Tamaulipas. Type collection of subsp. *edwardsii* Clausen. 26 km. SSW of Villa Hidalgo, 1820 m. R. T. Clausen 80 20D. Two plants, including the clonotype. $n = 62$ (Fig. 65).

U2784 Tamaulipas. 25 km. SSW of Villa Hidalgo. R. T. Clausen 80-20A. $n = 62$.

U2785 Tamaulipas. E. of mines at Dulces Nombres, Nuevo Leon, 1800 m. (probably same locality as the foregoing). J. L. Edwards. $n = 64$.

Sedum robertsianum Alexander

U2728 Texas: Brewster Co. Topotype. S. of Black Peak, Roberts Ranch, Del Norte Mts., 1260 m. R. T. Clausen 80 6. $n = 14$ (Fig. 66).

Sedum semiteres Rose

U2334 Durango. Canyon below Topia, 1160 m. M. Kimnach & H. Sanchez-Mejorada 1778. $n = 19$ (Fig. 67). (3 plants).

Sedum sp. aff. **semiteres**

U2251 Durango. Cliffs at Km. 190.8 on Mex. 40, 2.5 km. W. of Revolcaderos, 2040 m. $n = 54$ (Fig. 68).

Sedum stelliforme S. Watson

U2701, U2720 New Mexico: Grant Co. Gallinas Canyon, W. side of Black Range. R. T. Clausen 75 49 and 75 58. Both $n = 12$.

U2774 Chihuahua. Along road from San Juanito to Yecora, Sonora, 2135 m. L. J. Toolin & F. W. Reichenbacher 1325. $n = 24$.

U2246 Chihuahua. Km. 45.1 W. of La Junta on Mex. 16, 22.5 km. E. of Tomochic, 2070 m. $n = 14$ (Fig. 71).

U2732 Chihuahua. 1.8 km. S. of Basigochic toward Quirire, 2140 m. R. A. Bye, Jr. 7784. $n = 26$.

U2043 Chihuahua. 9.5 km. N. of Kirare on road to La Bufa Mine, 2285 m. M. Kimnach & F. K. Brandt 896. $n = 22$ (Fig. 72).

U2529 Sinaloa. 9.5 km. from San Vicente, Chih., on road to Tasajara, 2070 m. M. Kimnach & H. Sanchez-Mejorada 215. $n = 13 + 3$ (Fig. 70).

U2048 Chihuahua. 25.5 km. SW of Vergel on road to Guadalupe y Calvo, 2650 m. M. Kimnach & F. K. Brandt 1075. $n = 54 \pm 2$.

U2324 Durango. 11 km. W. of Escondida on road from Tepehuanes to Topia, 2470 m. M. Kimnach & H. Sanchez-Mejorada 1757. $n = 60 \pm 4$ (Fig. 73).

U2337 Durango. 13 km. W. of Los Altares on road from Topia to Santiago Papasquiaro, 2440 m. $n = 11$ (Fig. 69).

U2721 Cultivated. R. T. Clausen. $n = 12 + 2B$.

Sedum trichromum Clausen

U2395 Durango. Puerto Buenos Aires, 9 km. W. of La Ciudad, 2650 m. M. Kimnach 556. $n = 19$.

UC62.815 Durango. 8.4 km. NE of El Palmito, Sin., 2200 m. P. C. Hutchison 2487. $n = 19$ (Fig. 74).

U2786 Durango. Isotype. ca. 3 km. W. of Revolcaderos, 2070 m. Probably same locality as preceding. R. T. Clausen 76 33. $n = 19$.

Sedum versadense C. H. Thompson

U2576 Oaxaca. Huajuapan. A. Lau 056. $n = 32$.

M6377 Oaxaca. 23 km. SE of Huajuapan, 1850 m. Near 17°43′N, 97°38′W. R. Moran. $n = 32$ (Fig. 75).

58749 Cultivated. E. J. Alexander, New York Botanical Garden. $n = 32$.

U208, UC50.2283. Oaxaca. Type collection of *S. chontalense* Alexander. Above San Miguel Tenango, ca. 40 km. W. of Tehuantepec. T. MacDougall. $n = 64$ (Fig. 76).

U2662 Type collection of subsp. *villadioides* Kimnach. Oaxaca. 23 km. NE of Teotitlan del Camino on road to Huautla, 2135 m. J. Bauml & M. Kimnach 403. $n = 32$ (Fig. 77).

Sedum wrightii A. Gray

U2770 Clonotype of subsp. *priscum* Clausen. New Mexico: Otero Co. Silver Springs Canyon, Sacramento Mts., 8 km. NE of Cloudcroft, 2575 m. R. T. Clausen 75 83. $n = 12$.

U2764 Texas: El Paso Co. Franklin Mts. Canyon 0.6 km. SSE from top of N. Franklin Mt. R. D. Worthington 5578. $n = 24$.

U2773 Texas: Val Verde Co. Amistad Reservoir, Devils River. R. T. Clausen 70 142. $n = 36$.

U2409 Coahuila. Central valley of Sierra Santa Fe Del Pino. Near 28°06′N, 103°00′W. J. Henrickson. $n = 24$.

U2405 Coahuila. Sierra de la Madera. S. of Cañon Desiderio, 2750 m. Near 27°06′N, 102°32′W. J. Henrickson & B. Prigge 15290d. $n = 24$.

U2460 Coahuila. Sierra de la Madera. Cañon del Delgadito, 1980 m. Near 27°06′N, 102°27′W. J. Henrickson. $n = 12$.

U2775 Coahuila. S. of Cañada de la Enramada, Sierra de la Madera, 1800 m. R. T. Clausen 78 6. $n = 24 + 1$.

U2736 Clonotype of subspecies *densiflorum* Clausen. Coahuila. S. slope of Sierra Zapaliname, W. of El Chorro, 2500 m. 25°22′N, 100°49′W. R. T. Clausen 78 1. $n = 12$.

U2083 Coahuila. At end of short road S. from Mex. 40 at Nuevo Leon state line, NE of Saltillo, 1585 m. M. Kimnach & Lyons 1379. $n = 48$.

U2404 Nuevo Leon. Near top of cable lift to caves, Grutas de Garcia. J. Bauml. $n = 48$.

U2080. Nuevo Leon. 4 km. E. of Rayones, 915 m. M. Kimnach & Lyons 1425. $n = 60$ prob.

U2147 San Luis Potosi. W. of Catorce, 2680 m. $n = 60$.

U2148 San Luis Potosi. Above La Luz, 1.5 km. E. of tunnel to Catorce, 2560 m. $n = 60$ (Fig. 78).

U2735 Nuevo Leon. SE slope of Cerro El Viejo, near Zaragoza. R. T. Clausen 77 26. $n = 24$.

U2771 Tamaulipas. 15 km. SW of Ciudad Victoria, 1410 m. R. T. Clausen 80 23. $n = 72$ (Fig. 79).

Sedum sp. nov. (undescribed)

U2410 State of Mexico. 12 km. E. of Valle de Bravo Lake. F. Otero. $n = 32$ prob. (Fig. 80).

LITERATURE CITED

Baldwin, J. T., Jr. 1936. Polyploidy in *Sedum ternatum*. J. Hered. 27: 241 248.

Berger, A. 1930. Crassulaceae. *In:* Engler, A. Die Natürlichen Pflanzenfamilien, 2nd ed. 18a: 352 485.

Clausen, R. T. 1946. Nomenclatural changes and innovations in the Crassulaceae II. Jour. Cactus Succ. Soc. Am. 18: 74 77.

1950. Description of a *Sedum* from the Sierra Madre Oriental of Mexico. Jour. Cactus Succ. Soc. Am. 22: 86 89.

______. 1959. *Sedum* of the Trans-Mexican Volcanic Belt. Cornell Univ. Press, Ithaca, N.Y.

______. 1975. *Sedum* of North America North of the Mexican Plateau. Cornell Univ. Press, Ithaca, N.Y.

______. 1978. *Sedum*—seven Mexican perennial species. Bull. Torrey Bot. Club 105: 214-223.

______. 1979. *Sedum* in six areas of the Mexican cordilleran plateau. Bull. Torrey Bot. Club. 106: 205-216.

______. 1981. Variation of species of *Sedum* of the Mexican Cordilleran Plateau. Ithaca, N.Y.

______. 1984. *Sedum* (Crassulaceae) of the Mexican Cordilleran Plateau. Gentes Herbarum 12(3): 8-48.

FRÖDERSTRÖM, H. 1935. The genus *Sedum* L., part IV. Acta Horti Gotoburgensis 10: Appendix.

JACOBSEN, H. 1974. Lexicon of Succulent Plants. Blandford Press, London.

KIMNACH, M. 1982. *Sedum versadense* var. *villadioides* Kimn. var. nov. Journ. Cact. Succ. Soc. Am. 54: 206-208.

MORAN, R. 1977. *Sedum oteroi*, una nueva especie de Oaxaca, Mexico. Cact. y Sucul. Mex. 22: 51-54.

PRAEGER, R. L. 1921. An account of the genus *Sedum* as found in cultivation. J. Royal Hort. Soc. 46: 1-314.

ROSE, J. N. 1911. Studies of Mexican and Central American plants—no. 7. Contr. U.S. Nat. Herb. 13: 291-312.

SKOVSTED, A. 1934. Cytological studies in the tribe Saxifrageae. Dansk Bot. Arkiv 8: 1-52.

STANDLEY, P. C., AND J. A. STEYERMARK. 1946. Flora of Guatemala. Fieldiana 24, IV: 412-413.

TEERI, J. A. 1982. Carbon isotopes and the evolution of C_4 photosynthesis and Crassulacean acid metabolism. *In:* Nitecki, M. H. (ed.). Biochemical Aspects of Evolutionary Biology. University of Chicago Press, Chicago.

UHL, C. H. 1970. Chromosomes of *Graptopetalum* and *Thompsonella* (Crassulaceae). Amer. J. Bot. 57: 1115-1121.

______. 1972. Intraspecific variation in chromosomes of *Sedum* in the southwestern United States. Rhodora 74: 301-320.

______. 1976a. Chromosomes, hybrids and ploidy of *Sedum cremnophila* and *Echeveria linguifolia* (Crassulaceae). Amer. J. Bot. 63: 806-820.

______. 1976b. Chromosomes of Mexican *Sedum* I. Annual and biennial species. Rhodora 78: 629-640.

______. 1978. Chromosomes of Mexican *Sedum* II. Section Pachysedum. Rhodora 80: 491-512.

______. 1980. Chromosomes of Mexican *Sedum* III. Sections Centripetalia, Fruticisedum and other woody species. Rhodora 82: 377-402.

______. 1982a. The problem of ploidy in *Echeveria* (Crassulaceae) I. Diploidy in *E. ciliata*. Amer. J. Bot. 69: 843-854.

______. 1982b. The problem of ploidy in *Echeveria* (Crassulaceae) II. Tetraploidy in *E. secunda*. Amer. J. Bot. 69: 1497-1511.

———. 1983. Chromosomes of Mexican *Sedum* IV. Heteroploidy in *Sedum moranense*. Rhodora 85: 243–252.

———, and R. Moran. 1972. Chromosomes of Crassulaceae from Japan and South Korea. Cytologia 37: 59–81.

———, and ———. 1973. The chromosomes of *Pachyphytum* (Crassulaceae). Amer. J. Bot. 60: 648–656.

Wright, S. 1982. The shifting balance theory and macroevolution. Ann. Rev. Genetics 16: 1–19.

SECTION OF PLANT BIOLOGY
CORNELL UNIVERSITY
ITHACA, NEW YORK 14853

REDISCOVERY OF *TRIFOLIUM STOLONIFERUM* MUHL. EX A. EATON

Rodney L. Bartgis

ABSTRACT

Trifolium stoloniferum, the running buffalo clover, has apparently disappeared from most of its historical range and was considered to be possibly extinct. Two small extant populations have been recently found in West Virginia. Both populations are on disturbed floodplains, are threatened by human activity, and remain the only known extant populations. Circumstantial evidence suggests the disappearance of *Trifolium stoloniferum* is linked to the elimination of bison from its range.

Key Words: *Trifolium stoloniferum*, bison, clover, endangered species, West Virginia

Trifolium stoloniferum Muhl. ex A. Eaton, the running buffalo clover, is indigenous to the eastern United States, once occurring from eastern Kansas to central West Virginia (Brooks, 1983). In West Virginia it has been considered as "rare" (Clarkson et al., 1981), but only recently has the extent of its rarity become apparent. After reviewing herbarium specimens, consulting field botanists, and field-checking some historical records, Brooks (1983) could find no extant populations and suggested the species might be extinct. The U.S. Fish and Wildlife Service (1983) consequently placed the species under review for the federal Endangered and Threatened Species List, also noting the species was possibly extinct. My recent discovery of *T. stoloniferum* in the wild in West Virginia is discussed here.

There are three historical records of *Trifolium stoloniferum* from West Virginia. The oldest collection, from 1905 (*J. L. Sheldon 1640*, WVA), is from Marilla, Monongalia County. The site is now an urbanized area; the species was not found here during a 1984 search. The second record, collected in 1937 by Dr. and Mrs. H. A. Davis, is from the Cheat River, Preston County (Davis and Davis, pers. comm.). The species was not found here during recent searches (A. Cusick, E. Hutton, pers. comms.). In 1940, the species was collected from the Back Fork of Elk River, Webster County (*Davis and Davis 3748*, WVA). The two Davis and Davis collections were the only known post-1910 records of the species from throughout its range (Brooks, 1983).

Two populations of *Trifolium stoloniferum* have been discovered in West Virginia. On 2 June 1983, two plants were found along an off-road vehicle trail in a small floodplain forest in the New River Gorge, Fayette County, at an elevation of 240 m. (Figure 1). Both individuals were flowering and vigorously producing numerous stolons. In 1984, vehicle use of the trail had separated the stoloniferous shoots from the original parents, resulting in twenty-five less vigorous plants. Two plants were killed early in the year by vehicles; eleven other plants were severely damaged. Seven plants produced flowers at the site in 1984. Extensive searching in the Gorge in 1983 and 1984 revealed no additional plants. A voucher is deposited at WVA.

Associated species at the site in the New River Gorge include *Acer negundo, Betula nigra, Fagus grandifolia, Halesia carolina, Liriodendron tulipifera,* and *Platanus occidentalis* in the multiple-strata canopy. The shrub layer is largely *Lindera benzoin* with some *Rosa carolina;* herbaceous associates include *Alliaria officinalis, Aplectrum hyemale, Cardamine impatiens* and *Commelina communis. Lonicera japonica* and *Glechoma hederacea* are abundant throughout the floodplain; they spatially compete with *Trifolium stoloniferum* and appear to limit its spread. Flooding of the floodplain has apparently ceased following construction of the Hawks Nest Dam 0.8 km upstream.

On 7 June 1984, I visited the site of Davis and Davis' 1940 collection on the Back Fork of Elk River. Two vigorous plants were found at the margin of a field in an alluvial bottom at 470 m elevation. The field, dominated by *Dactylis glomerata* and *Festuca elatior,* is annually mowed but not pastured. Four other clovers were found at the Back Fork site: *Trifolium agrarium, T. hybridum, T. pratense,* and *T. repens.* No apparent hybrids were found. *Trifolium stoloniferum* retained its morphological distinctness as discussed by Brooks (1983), and bloomed earlier than the European native *T. repens* with which it is occasionally confused.

Presence of extant *Trifolium stoloniferum* populations in disturbed areas is not surprising. The species was originally a dominant species in bison-maintained grasslands of the Kentucky Bluegrass region; it may have been intimately adapted to conditions associated with bison (Campbell, 1984, unpublished ms., U. Ky., Lexington). In West Virginia, the historic Monongalia County and extant

Figure 1. One of two *Trifolium stoloniferum* plants discovered in the New River Gorge, West Virginia.

Fayette County records of *T. stoloniferum* are along known bison traces (Jakle, 1969); the Fayette County trace was used by bison moving between West Virginia's Greenbrier Valley and the Kentucky Bluegrass (McKeever and Frum, 1951). The extant Webster County population is in the immediate vicinity where bison were last recorded in West Virginia (McKeever and Frum, 1951). It appears plausible, therefore, that the range-wide disappearance of *T. stoloniferum* is tied to the elimination of the bison and their attendant disturbances from the lower Missouri and Ohio River drainages.

A search for the species throughout its range has recently been conducted, but no additional populations have been found (*see* Acknowledgments). Although it is possible that additional larger populations of *Trifolium stoloniferum* will be found, the species currently appears to be very close to extinction. In an attempt to increase the species' numbers, two plants were removed from the Fayette County population and are in a greenhouse at the University of Kentucky. At present, *T. stoloniferum* appears to be one of the rarest members of the North American flora.

ACKNOWLEDGMENTS

B. McDonald helped re-locate the Webster County population. J. Campbell and M. Medley started the greenhouse population. Information on recent searches for the species in other states was provided by the Indiana Heritage Program, Kentucky Heritage Program, Missouri Natural Heritage Inventory, and Ohio Natural Heritage Program. This study was funded by a grant from The Nature Conservancy.

LITERATURE CITED

Brooks, R. E. 1983. *Trifolium stoloniferum*, running buffalo clover: Description, distribution, and current status. Rhodora 85: 343–354.

Clarkson, R. B., D. K. Evans, R. Fortney, W. Grafton, and L. Rader. 1981. Rare and endangered vascular plant species in West Virginia. US Government Printing Office, Washington, DC.

Jakle, J. A. 1969. Salt on the Ohio Valley frontier, 1770–1820. Assoc. Am. Geogr. 59: 687–709.

McKeever, S., and W. Frum. 1951. A Survey of West Virginia Mammals. WV Dept. Natural Resources, Charleston, WV.

US Fish and Wildlife Service. 1983. Endangered and threatened species; supplement to review of plant taxa for listing; proposed rule. Federal Register 48: 53640-53670.

THE NATURE CONSERVANCY
1100 QUARRIER ST., ROOM 215
CHARLESTON, WV 25301

DISTRIBUTION OF *MERTENSIA MARITIMA* (BORAGINACEAE) AND SUBSPECIES OF *SAGINA NODOSA* (CARYOPHYLLACEAE) ON ISLANDS IN MACHIAS BAY, MAINE

Alan J. Lewis

ABSTRACT

Mertensia maritima and *Sagina nodosa* ssp. *nodosa* are uncommon in Maine. *S. nodosa* ssp. *borealis* is considered rare. The results of a survey of 13 islands in Machias Bay show seven previously unreported stations for *M. maritima* and five each for *S. nodosa* ssp. *nodosa* and *S. nodosa* ssp. *borealis*. Variability in the characteristics used to separate the two subspecies of *S. nodosa* was found.

Key Words: *Mertensia, Sagina,* island biogeography, Maine

Mertensia maritima (L.) Gray (Oysterleaf) and *Sagina nodosa* (L.) Fenzl. (Knotty Pearlwort) are two species whose range in the United States is restricted primarily to the Gulf of Maine. Olday et al. (1983), in a study of the distribution of these sub-arctic species on the Maine coast, reported the known occurrence of *M. maritima* at 30 stations and of *S. nodosa* at 14 stations. Distribution of the two subspecies of *S. nodosa* (ssp. *nodosa* and ssp. *borealis*) recognized by Crow (1978) was not recorded during recent field checks of the stations. This paper records previously unreported stations for *M. maritima* and the distribution of the two subspecies of *S. nodosa* on islands in Machias Bay.

During the summers of 1980–83, plant species occurring on 13 islands in Machias Bay (44°34′–39′N, 67°14′–25′W), Maine were recorded (Figure 1). *Mertensia maritima* was found growing on cobble beaches above the swash line on seven of the islands (Table 1). All populations found were vigorous and flowered during the growing season. Their distribution on the shore was restricted to lee sides of the islands or to coves protected from strong wave action.

Although not considered rare in Maine, *Mertensia maritima* is uncommon in its distribution along most of the coast. Olday et al. (1983) report that in a survey of 100 islands done for the Maine Critical Areas Program in western Maine, *M. maritima* was found on only four. The results of this survey indicate that in eastern Maine, where protected cobble beaches occur, *M. maritima* is a

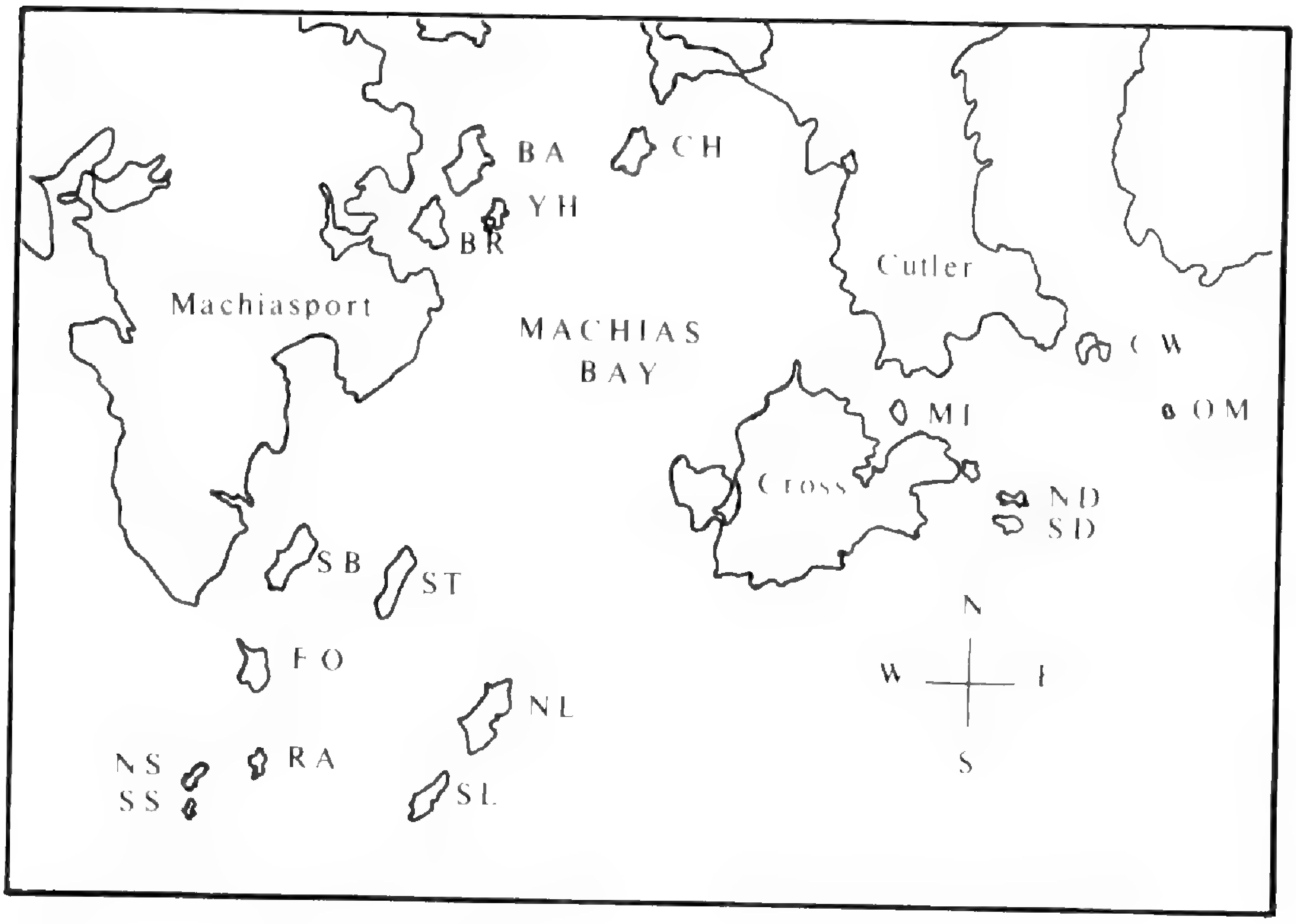


Figure 1. Islands in Machias Bay, Maine. BA—Bare, BR—Bar, CH—Chance, CW—Cape Wash, FO—Foster, MI—Mink, ND—North Double Head Shot, NL—North Libby, NS—North Scabby, OM—Old Man, RA—Ram, SB—Starboard, SD—South Double Head Shot, SL—South Libby, SS—South Scabby, ST—Stone, YH—Yellow Head.

common island species. The islands in Machias Bay on which it does not occur all appear to lack suitable habitat protected from strong wave action. Although *M. maritima* is listed for a few locations in Massachusetts, its primary distribution in the eastern United States is along the Maine Coast, where it has been reported from all coastal counties except Sagadahoc (Olday et al., 1983). With the seven additional stations recorded here, 20 of the 37 reported localities for *M. maritima* on the Maine coast occur in Washington County.

In his taxonomic revision of the genus *Sagina*, Crow (1978) recognized two subspecies of *Sagina nodosa:* ssp. *nodosa* and ssp. *borealis*. Of the two, ssp. *nodosa* is considered to be the more common. Ssp. *borealis* is listed as *rare* in Maine (Critical Areas Program, 1981), although no major attempt appears to have been made to determine its distribution and abundance. Olday et al. (1983) listed *Sagina nodosa* at 14 stations on the Maine coast. Six of the stations were previously unreported but, unfortunately, no determi-

Table 1. New Stations for *Mertensia maritima* and subspecies of *Sagina nodosa* on islands in Machias Bay.

	Taxon		
	Sagina nodosa		*Mertensia maritima*
Island	ssp. *nodosa*	ssp. *borealis*	
Yellowhead	X		
Ram	X		X
North Libby	X	X	
South Libby	X	X	X
North Scabby	X	X	X
South Scabby			X
North Double Headshot		X	
Foster		X	X
Chance			X
Cross			X

nations as to subspecies were made. Another six stations were identified on the basis of herbarium specimens labelled *S. nodosa* var. *nodosa.* Since Crow (1978) recognized var. *nodosa* as a synonym for ssp. *borealis,* it was assumed that the specimens were, in fact, ssp. *borealis.* The remaining two stations cited for *S. nodosa* were listed by Crow (1978) as ssp. *borealis;* he also listed a third station for ssp. *borealis* in Maine which was not cited by Olday et al. (1983). Crow (1978) also listed the most southerly station, which is in New Hampshire. The results of this survey reveal an additional five previously unreported stations for *Sagina nodosa* ssp. *borealis* (Table 1).

Sagina nodosa ssp. *nodosa* was reported by Crow (1978) to occur at 20 stations in Maine, three stations in Massachusetts and one station in New Hampshire. During the course of this survey, five new stations have been found for ssp. *nodosa* in Maine (Table 1). With the addition of the new stations found in this survey, there are thus at least 25 stations for *S. nodosa* ssp. *nodosa* and 14 stations for *S. nodosa* ssp. *borealis* in Maine. With the five new stations reported here, 12 out of the 14 reported localities for ssp. *borealis* in Maine occur in Washington County.

The populations of both subspecies were found on the windward sides of islands or on exposed rock outcrops. They grew in moist peat on the fringe of islands or in crevices on the rock outcrops. When found, there were generally numerous, vigorously growing individuals in the populations of each subspecies.

Sagina nodosa ssp. *borealis* has a more northerly distribution than *S. nodosa* ssp. *nodosa.* Olday et al. (1983) stated that little is known about the area of range overlap between the two subspecies, but Crow (1978) noted that ssp. *nodosa* is probably introduced. The results of this survey indicate that a range overlap occurs on islands in Machias Bay, with both subspecies growing on three of the seven islands supporting populations of *S. nodosa* (Table 1).

The primary characteristic used for identification of the two subspecies of *Sagina nodosa* is the distribution of pubescence on the stems, pedicels, calyx and basal leaves of the plant. In ssp. *nodosa,* the stems, uppermost portion of the pedicels and bases of the calyx are pubescent. The basal leaves usually bear glandular hairs, especially on the margins. In ssp. *borealis* the stems are glabrous or rarely weakly pubescent at the nodes, the pedicels are glabrous or pubescent on the uppermost portion, and the calyx is glabrous or pubescent at the base (Crow, 1978). The majority of Machias bay specimens examined were easily separated into the two subspecies groups on the basis of the above criteria. The amount of pubescence on the internodes and basal leaves of ssp. *nodosa* was, however, highly variable among individuals. Of 22 plants examined, pubescence on the internodes of 15 was readily apparent, but sparse; on five there was moderate pubescence, and on two the pubescence was dense. On nine of the plants, no glandular hairs were readily apparent on the margins of basal leaves. On the other thirteen plants, some hairs were found on leaf margins, although in most cases they were sparse. There was no apparent correlation between density of pubescence on the internodes and presence or absence of hairs on the margins of basal leaves. Crow (1978) stated that in Europe, "...where the ranges of the two taxa come together, intermediates are not infrequent." Since, as he also notes, *Sagina nodosa* is the strongest outcrosser in the genus, some of the variability in the Machias Bay specimens may be caused by cross-fertilization between the two subspecies.

Voucher specimens are filed at UMM.

ACKNOWLEDGMENTS

I thank Dr. Garrett E. Crow for aid in identification of the subspecies of *Sagina nodosa* and for comments on a first draft of this paper. I am appreciative of support provided for this work by the

University of Maine at Machias and for laboratory and field assistance provided by Deborah Webster-Pierce and Frank McGrady.

LITERATURE CITED

Critical Areas Program. 1981. Rare Vascular Plants of Maine. S. C. Gawler, ed. State Planning Office, Augusta.

Crow, G. E. 1978. A taxonomic revision of *Sagina* (Caryophyllaceae) in North America. Rhodora 80: 1–91.

Olday, F. C., S. C. Gawler, and B. St. John Vickery. 1983. Seven unusual sub-arctic plants of the Maine coast. Critical Areas Program planning report No. 78. State Planning Office, Augusta.

SCIENCE DIVISION
UNIVERSITY OF MAINE AT MACHIAS
O'BRIEN AVENUE
MACHIAS, MAINE 04654

NEW ENGLAND NOTE

ORNITHOGALUM NUTANS L. (LILIACEAE) IN CONNECTICUT

E. A. CHRISTENSON AND M. W. LEFOR

In May 1983, Ms. Margot Levy of New London, Connecticut, led us to a colony of an unfamiliar liliaceous species growing along the western side of the Mystic River in Groton, Connecticut, north of Interstate 95. There a well-established colony of approximately 50 individuals was found in late flower and early fruit. Flowers are white with a drab green stripe on the reverse of each tepal. The plants were growing along a roadside in full sun in sandy soil atop a stable riverbank. The closeness of this station to the riverbank makes it unlikely that the site was cultivated recently and it appears to be a naturalized population. Specimens collected are *Ornithogalum nutans* L., previously reported as escaped and naturalized from only as far north as New York (Fernald, 1950; Gleason and Cronquist, 1963). This is the first report of the species from Connecticut (*q.v.* Dowhan, 1979; Graves et al., 1910; Harger et al., 1930). *Ornithogalum nutans,* with its flowers in racemes and tepals 2.5 to 3.5 cm long, each with a broad greyish-green stripe on the reverse, differs from *O. umbellatum* L. with its flowers in umbels and its unmarked tepals 1 to 2 cm long.

An earlier collection at CONN has since been identified as *Ornithogalum nutans,* thus giving a second locality in the state.

SPECIMENS: **Groton, Ct.,** between River Road and the Mystic River, 20 May 1983, *E. A. Christenson, M. W. Lefor, et al. 842* (CONN!); **East Haddam, Ct.,** on side of road, 50′ north of intersection of Rte. 149 and Landing Hill Road, 25 Apr 1976, *D. Darrow 39* (CONN!); *D. Darrow 40* (US!); *D. Darrow 41* (NEBC!).

LITERATURE CITED

DOWHAN, J. J. 1979. Checklist of the Vascular Flora of Connecticut (Growing without Cultivation). Conn. State Geol. & Nat. Hist. Surv. Rep. Invs. No. 8. Hartford.

FERNALD, M. L. 1950. Gray's Manual of Botany. 8th ed., American Book Co. (Rev. 1970. Van Nostrand-Reinhold, N.Y.)

Gleason, H. A., and A. Cronquist. 1963. Manual of the Vascular Plants of the Northeastern United States and Adjacent Canada. Van Nostrand-Reinhold, N.Y.

Graves, C. B., et al. 1910. Catalogue of the Flowering Plants and Ferns of Connecticut. Conn. State Geol. & Nat. Hist. Surv. Bull., 14. Hartford.

Harger, E. B., et al. 1930. Supplement to a Checklist of the Flowering Plants and Ferns of Connecticut. Conn. State Geol. & Nat. Hist. Surv. Bull., 48. Hartford.

THE BOTANY SECTION, U-42
THE UNIVERSITY OF CONNECTICUT
STORRS, CONNECTICUT 06268

HISTORICAL NOTE

SEVERAL UNPUBLISHED ETHNOBOTANICAL NOTES OF RICHARD SPRUCE

RICHARD EVANS SCHULTES

The British botanical explorer, Richard Spruce, worked in various parts of the northwest Amazon of Brazil, Ecuador and Peru from 1851 to 1857—a period when the opportunity for ethnobotanical observations was perhaps at its height (Schultes, 1953). Spruce was deeply interested in ethnobotany, but his intense efforts to make representative collections of the floras of the region precluded his assembling as many data on aboriginal uses of plants as he otherwise might have been able to do (Schultes, 1983). Nevertheless, the few notes on native knowledge of the properties of plants are of extreme interest today, inasmuch as some of the uses which he reported in detail have died out.

The following several notes seem not to have been previously published. They are found in manuscripts and notebooks preserved in the Royal Botanical Gardens at Kew.

"*Ucu-úba* (= oil tree). *Myristica fatua* Sw. Caripe.

"Lofty tree with whorled brs. near apex. Fruit so oily as to burn with a clear light. A very fair wax said to be prepared from them. Ashes used with *Andiroba*-oil, or other greases for making vegetable soap. Ashes of *xiriuba* and skin of fruit of *cacao* used for same purpose."

"*Victoria amazonica*

"The Indian name *Auapé-Yaponna* is derived from *Auapé*, a small bird inhabiting the margins of rivers and often to be seen running on the surface of the leaves of the *Victoria*, which from their forms are aptly likened to a *yapona* or *mandiocca*-oven.

"This bird (called *Jacana* by the Portuguese) makes its nest in a patch of *Canna rana*—whether floating or stationary is immaterial to it, by bringing together tips of several blades of the canna and fastening them together on top of which it forms its nest.

"This bird is remarkable for its shining forehead; the name *Uaupés* is said to have been given to Indians of Caspari from the custom these Indians have of wiping their faces when perspiring with a certain leaf which renders them clean and shining, and suggests a resemblance to the bird *Auapé* or *Uaupé.*

"I have occasionally seen these Indians rub their faces with larger ls. of some *Melastoniae* (*Belluciae, Loreyae,* etc.) but they always told me that was not the proper kind, and that there was another leaf more effectual for removing impurities from the skin."

Hb. 2613 *Erisma-Japurá* sp.

"*Japurá* Freqt. on Rio No Uapés & Japurá.

"Fruit said to be ripe in May and June—size of a *castanha* and furnished with ears like a dog. It is pleasant eating both rare and roasted.

"The butter is thus prepared (according to better information—the resemblance to butter is very slight; its appearance is that of *Ambe* and taste peculiar. The extreme odor is never lost.) The kernels are rendered edible in this way: having been boiled from morning till night, they are well covered up in baskets and put into running water, where they remain 2 or 3 weeks. When at the end of this period they are opened out, they have a disagreeable stercoral odor. They are now beaten in a mortar until they form a mass having the consistence and appearance of very pale butter. To receive this, a large cylinder basket called a *Paricá* is made (. . . *Iriartia* sp.), 3–5 palms long by 1 in diam., and lined with leaves of *Pacora-sororoca* (*Heliconia* sp.). The basket of butter is now placed on a strap over the fire, where it is customary to put things that req. to be kept dry, and there the butter will remain good from 1 to 3 years.

"It is eaten with fish and game, being melted in the gravy along with the salt and *pimenta* (var. species of *Capsicum*) which are essential ingredients in the *molko* at a Brazilian table, whether the guests be white or red. It is said to be exc^{y}. tasty."

"Tarapoto, Peru

"*Iriartea ventricosa* Mart.

"The town of Tarapoto is modern and took its name from being built round a small lake whose margins were so studded with this palm that it was called *Tarapoto-cocha.*"

ACKNOWLEDGMENT

It is a pleasure to acknowledge the permission of the Director of the Royal Botanic Gardens, Kew, for permission to publish these ethnobotanical notes.

LITERATURE CITED

Schultes, R. E. 1953. Richard Spruce still lives. Northern Gardener 7: 20–27, 55–61, 87–93, 121–125; 1978. Reprinted in: Hort. Aliquando 3: 13–47.

———. 1983. Richard Spruce: an early ethnobotanist and explorer of the northwest Amazon and northern Andes. Journ. Ethnobiol. 3: 139–147.

BOTANICAL MUSEUM
HARVARD UNIVERSITY
CAMBRIDGE, MASS. 02138

BOOK REVIEW

Roger L. Williams. 1984. *Aven Nelson of Wyoming.* xii + 407 pp. Colorado Associated University Press, Boulder, Colo. 80309.

Ted Olson's "But these hills of Norway. He knew no more. He ploughed himself at last into a new land. Not so unlike his own. Making Wyoming richer with his bones" could hardly be appreciated by the average reader except perhaps in retrospect. But these lines, in a poetic way, epitomize the career of Aven Nelson. At once they signal the Norwegian origin, the immigrant influence and the pioneer spirit that were his earliest influences. From there he proceeded upon the least likely path to a position of botanical prominence in the United States and to some extent, the world. In the book, engaging accounts of an early life of dedication to nature and the teaching of natural history flow easily to a description of Nelson's early period as a freshly appointed faculty member of the newly created University of Wyoming, where he became Professor of Botany and Horticulture. Nelson took seriously both aspects of his appointment. His love of botany easily sustained his activities in that area but he did not neglect to contribute to horticulture in Wyoming. Again, in retrospect, it is hard for those not familiar with the situation to appreciate the almost complete lack of indigenous botany and horticulture in the frontier state of Wyoming at the turn of the nineteenth into the twentieth century. There was an awakening necessary and Nelson almost single-handedly brought it about.

Nelson was essentially a self-taught botanist. His background in the subject, from Missouri State Normal School at Kirksville, was minimal or possibly lacking entirely. But once his goals were defined at the University of Wyoming, outside his own professorial activities, he became an avid student of all those botanists available to him through correspondence or otherwise. One of the forceful and at the same time laudable aspects of Nelson's early career was that he was a seeker of knowledge. As a positive communicator, he siphoned from the whole botanical community a large measure of "know how" of the profession. A lesser man would have done far less.

The main thrust of Nelson's work on the Rocky Mountain Flora came during a period when P. A. Rydberg was at the height of his botanical activities on the same flora, and a little behind that of E.

L. Greene, who had not only the Rocky Mountain region as his baliwick but that of western North America in general. His first major consultant was E. L. Greene, from whom he received identifications and advice. At the same time, or shortly thereafter, he was in reciprocal communication with Rydberg. Also, during this time he was submitting specimens to B. L. Robinson and M. L. Fernald for their opinions. Since there were antagonisms individually between Greene, Rydberg, and Robinson, Nelson walked a tightrope to keep on reasonably good terms with all three. He was relatively quick to realize each of these well-established botanists had their own biases and that all were vulnerable to individual prejudices. Although he had cordial relationships with them and utilized their services intensively for more than ten years, eventually he was to turn away, to a large extent, from these influences and become a regular correspondent of John Merle Coulter, who published many of his contributions in the *Botanical Gazette*.

Coulter, who had published a *Manual of the Botany of the Rocky Mountain Region,* in 1885, recognized in Nelson a possible collaborator for a new edition, which by then was greatly needed. Clearly, the *New Manual of Botany of the Rocky Mountain Region,* by Coulter and Nelson, published in 1909, was largely the work of Nelson. However, he was forthright in acknowledging the superior editorial knowledge of the senior author. By then Nelson's field knowledge of Rocky Mountain plants was equal to, if not superior to, any other botanist, including Rydberg.

The "New Manual" signalled a break with the New York school: Britton, Rydberg, and Small et al., who followed the American Code of Botanical Nomenclature. Nelson's strength as a botanist, representing particularly those resident and working on the plants of the Rocky Mountain region, reached a zenith shortly after the publication of this important work. Long after, even after the publication of Rydberg's *Flora of the Rocky Mountains and Adjacent Plains* in 1917, Coulter and Nelson's book was still the trusted source reference on the plants of the area covered.

Nelson had a succession of students over a long period. Most proceeded only to the master's degree, if even that, under this tutelage, but many were funneled to prestigious institutions for their doctorates. The favorite destination for their formal training was the Missouri Botanical Garden in St. Louis, which really meant

Washington University as far as the doctorate was concerned. Jesse M. Greenman was the chief attraction in St. Louis and in many ways he was similar to Nelson in his relationships with students. Both men were firm in their beliefs, reasonably stringent as task-masters but, at the same time, conscientious and fatherly toward their students. Always they went the extra mile. Such students as Edwin Payson, George Goodman, Louis Williams, and Marion Ownbey followed this tradition. I myself might have followed the same path except that my interest at the time was more in the fungi than in the higher plants. William Penland and J. Francis Macbride went to Harvard, but the latter never finished his degree work. Other students took different routes: Leslie N. Godding, Leo Hanna and even his wife of later years, Ruth Ashton Nelson, to name only a few.

A significant segment of Aven Nelson's life was spent as President of the University of Wyoming. He never liked the assignment and got out of it as soon as he reasonably could but it did consume several years that left almost a complete void in his botanical activities. However, during his less than half-a-dozen years as President, his writing clearly revealed the general tenor of his philosophy, his values, and his intense commitment to scholarship. Picture a small, relatively new institution, going through the ailments of trying to become a university in an area where sympathies were indifferent. That was the milieu in which Nelson had to operate. He was a strong advocate of Wyoming University for Wyoming people and the best was none too good. In a large measure, he succeeded in putting the University on sound ground. The task was difficult and he was the first to admit such failures as he had with some of the politicians of the time. Wyoming University was fully dependent on funds from the state and many of the legislators, upon whom the funding depended, had stronger ties outside of Wyoming than within its borders. But his term of stewardship of the University was the most successful of any up to the time he terminated it by his unsolicited resignation.

There are many aspects of Nelson's life that are not generally known to botanists, even those somewhat familiar with his career. For example, he was the founder of the Colorado-Wyoming Academy of Science, which, for the first time, brought together the scientists of these two states for their common purposes. In his capacity as President-General of the honor society, Phi Kappa Phi, he traveled and spoke before many chapters during his four-year term. Nelson was the first botanist from the intermountain west to become President of the Botanical Society of America. Twice he attended botanical congresses in Europe, where he lent support to a compromise solution to the conflict between the American Code and the International Botanical Code of Nomenclature. His position with respect to these codes was somewhat ambivalent in his early years but in the end he was an advocate of the International Code. Nelson was a solid evolutionist who put his oar in whenever possible to keep such a "humiliating controversy" as the Scopes trial from raising its ugly head in the region where he had influence. Though strongly committed to evolutionary thought, he, like Asa Gray, was also religious. Between evolution and religion he found no conflict.

Without doubt, Aven Nelson's most important monument is the Rocky Mountain Herbarium. This is a first rate herbarium, representing the flora of the Rocky Mountains and the intervening high plateau country. Today it exceeds all other herbaria of the region in size and quality.

By skillfully blending the primary events of Nelson's life with those of his students and the primary concerns of systematic botany of the period, the author has produced a very readable and fascinating story. His sensitive handling of Nelson's relationships with E. L. Greene, P. A. Rydberg, B. L. Robinson, M. L. Fernald, J. M. Greenman, J. M. Coulter, C. E. Bessey, and many others, has provided important insights that are revealed for the first time. The botanical climate of the period is well-interpreted, even to the nuances that most botanists might have felt were incapable of being understood by a non-botanist. I enjoyed reading the book, not only for its content, but for the interest created by the author with his excellent style of presentation.

REED C. ROLLINS
GRAY HERBARIUM OF HARVARD UNIVERSITY
22 DIVINITY AVENUE
CAMBRIDGE, MA 02138

AN AWARD FOR THE SUPPORT OF BOTANICAL RESEARCH IN NEW ENGLAND, U.S.A.

Warren F. Lamboy has been selected to receive the first New England Botanical Club award in support of botanical research in New England for his proposal "A systematic study of *Aster* section *Biotia*." Mr. Lamboy, a Ph.D. candidate working with Dr. Almut G. Jones at the University of Illinois, Urbana-Champaign, will use the award to travel to New York and New England to observe the members of this group in the field and to collect material for crossing experiments and electrophoretic and cytological studies, and for statistical analysis.

The New England Botanical Club will again offer an award of $1,000 in support of botanical research to be conducted in the New England region during 1986. This award is being made to stimulate and encourage botanical research on the New England flora and to make possible visits to the New England region by those who would not otherwise be able to do so. The award will be given to the graduate student submitting the best research proposal dealing with field studies in systematic botany and plant ecology, but proposals for research in other areas of botany will also be considered. This award is not limited to graduate students at New England institutions, nor to members of the New England Botanical Club. Papers based on this research must acknowledge the NEBC's support, and it is encouraged that they be submitted to *Rhodora*, the Club's journal, for possible publication—subject to standard review processes.

Applicants should submit a proposal of no more than three double spaced pages, a budget (the budget will not affect the amount of the award), and their curriculum vitae. Two letters, one from the student's major professor, in support of the proposed research are also required. Proposals and supporting letters should be sent before 28 February 1986 to: Awards Committee, the New England Botanical Club, 22 Divinity Avenue, Cambridge, MA 02138. The recipient of the award will be notified by 30 April 1986.

NOTICE OF PUBLICATION

ANGELO, RAY. 1984. *Botanical Index to the Journal of Henry David Thoreau.* Gibbs M. Smith, Inc., Peregrine Smith Books (as part of the 15 volume set: *The Journal of Henry David Thoreau*) and *The Thoreau Quarterly* (as Volume 15). 203 pages.

The index includes all vascular plant references occurring in the *Journal* of Henry David Thoreau. References are translated into modern nomenclature with cross-references using modern scietific and common names. Clarification of the index translations is provided using 341 footnotes.

The first comprehensive account of Thoreau's botanical career is treated in an introductory essay entitled "Thoreau as Botanist". Compilation of the index spanned five years and was based in part on the author's study of the flora of Thoreau's hometown, Concord, Massachusetts.

Copies of the *Index* may be ordered by *Rhodora* subscribers for the reduced price of $12 from:

The Thoreau Quarterly
Department of Philosophy
University of Minnesota
224 Church St. SE
Minneapolis, MN 55455

Subscriptions to *The Thoreau Quarterly* may be obtained by U.S. subscribers for $12 per year by writing the same address.

Vol 87, No. 850, including pages 121-292, was issued April 30, 1985

INSTRUCTIONS TO CONTRIBUTORS TO RHODORA

Submission of a manuscript implies it is not being considered for publication simultaneously elsewhere, either in whole or in part.

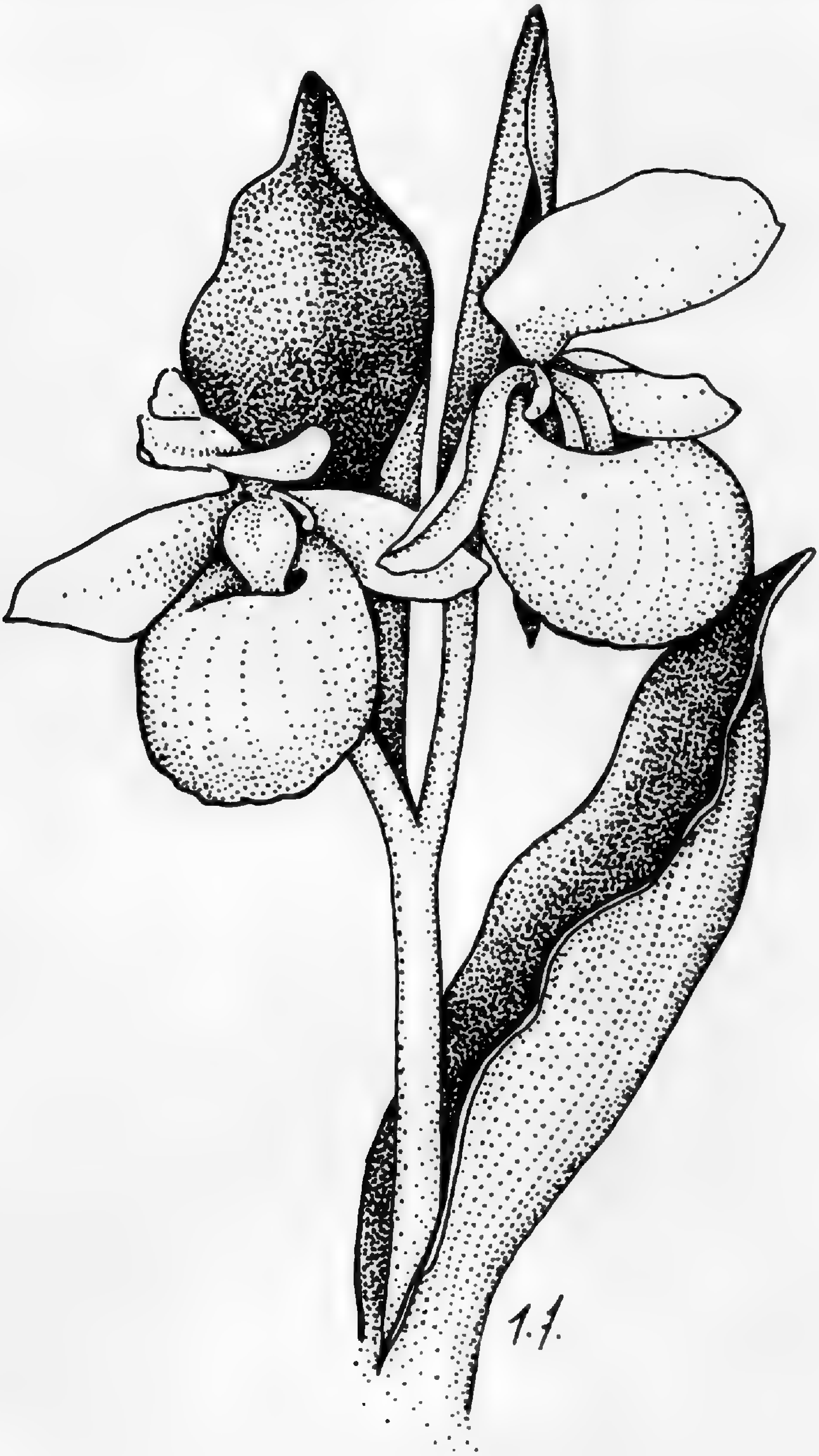
Manuscripts should be submitted in **triplicate** (an original and two xerographic copies) and *must be double-spaced* (at least 3/8 inch) **throughout** including footnotes, figure legends, and references. Please do not use corrasable bond. The list of legends for figures and maps should be provided on a separate page. Footnotes should be used sparingly. Do not indicate the style of type through the use of capitals or underscoring, particularly in the citation of specimens. Names of genera and species may be underlined to indicate italics in discussions. Specimen citations should be selected critically, especially for common species of broad distribution. Systematic revisions and similar papers should be prepared in the format of "A Monograph of the Genus Malvastrum", S. R. Hill, Rhodora 84: 1–83, 159–264, 317–409, 1982, particularly with reference to indentation of keys and synonyms. Designation of a new taxon should carry a **Latin diagnosis** (rather than a full Latin description), which sets forth succinctly just how the new taxon is distinguished from its congeners. Papers of a floristic nature should follow, as far as possible, the format of "Annotated list of the ferns and fern allies of Arkansas", W. Carl Taylor and Delzie Demaree, Rhodora 81: 503–548, 1979. For bibliographic citations, refer to the Botanico-Periodicum-Huntianum (B-P-H, 1968), which provides standardized abbreviations for journals originating before 1966. All abbreviations in the text should be followed by a period, except those for standard units of measure and direction (compass points). For standard abbreviations and for guidance in other matters of biological writing style, consult the *CBE Style Manual,* 5th ed. (original title: *Style Manual for Biological Journals*). In preparing figures (maps, charts, drawings, photos, etc.) please remember that the printed plate will be 4 × 6 inches; be sure that your illustrations are proportioned to reduce correctly, and indicate by blue pencil the intended limits of the figures. (Some "turn-page" figures with brief legends will be 3 1/2 × 6 in.) Magnification/reduction values given in text or figure legends should be calculated to reflect the actual printed size. An Abstract and a list of Key Words should be supplied at the beginning of each paper submitted, except for a very short article or note.

RHODORA **July 1985** **Vol. 87, No. 851**

CONTENTS

Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB



Vol. 87 October 1985 No. 852

The New England Botanical Club, Inc.

Botanical Museum, Oxford Street, Cambridge, Massachusetts 02138

Conducted and published for the Club, by
NORTON H. NICKERSON, Editor-in-Chief

RHODORA.—Published four times a year, in January, April, July, and October. A quarterly journal of botany, devoted primarily to the flora of North America. Price $20.00 per year, net, postpaid, in funds payable at par in the United States currency at Boston. Some back volumes and single copies are available. Information and prices will be furnished upon request. Subscriptions and orders for back issues (making all remittances payable to RHODORA) should be sent to RHODORA, Botanical Museum, Oxford Street, Cambridge, Mass. 02138. In order to receive the next number of RHODORA, changes of address must be received prior to the first day of January, April, July or October.

Scientific papers and notes relating to the plants of North America and floristically related aras will be considered by the editorial committee for publication. Articles concerned with systematic botany and cytotaxonomy in their broader implications are equally acceptable. Brevity is urged whenever possible in all papers. Short items will be published on otherwise blank end pages as soon as possible, even if they appear ahead of longer articles already accepted. All manuscripts should be submitted in TRIPLICATE AND MUST BE DOUBLE (AT LEAST 3/8 OF AN INCH) OR TRIPLE-SPACED THROUGHOUT. **Please conform to the style of recent issues of the journal. See "Instructions to Contributors to RHODORA" at the end of each issue. Extracted reprints, if ordered in advance, will be furnished at cost. RHODORA assesses modest page charges.**

Address manuscripts and proofs to:
Joan Y. Nickerson
Managing Editor, RHODORA
Phippen-LaCroix Herbarium, Dept. of Biology
Tufts University
Medford, Mass. 02155

Second Class Postage Paid at Boston, Mass.

PRINTED BY
THE LEXINGTON PRESS, INC.
LEXINGTON, MASSACHUSETTS

Cover illustration

Cypripedium reginae Walt., the Showy Lady's-slipper, was presumed until recently to be extirpated from New Hampshire; five sites for this exquisite orchid are now known.

Original artwork by Tess Feltes, Illustrator.

Rhodora
(ISSN 0035-4902)
JOURNAL OF THE
NEW ENGLAND BOTANICAL CLUB

Vol. 87 October 1985 No. 852

CHANGES IN THE POPULATION OF THE RARE AND ENDANGERED PLANT *POTENTILLA ROBBINSIANA* OAKES DURING THE PERIOD 1973 TO 1983

R. E. Graber and L. G. Brewer

ABSTRACT

The surviving trailside colony of *Potentilla robbinsiana* has declined in both number of reproducing plants (14.1%) and in area occupied (15.8%) during the period 1973–1983. Major causes of this mortality were hiker disturbance, drought, and frost heaving. Hiker impact has recently been reduced by increased regulation and the relocation of a short segment of the Appalachian Trail. Drought-caused mortality is largely limited to seedlings. Frost heaving is believed to be the most important current cause of mature plant mortality, especially in years of reduced snowfall. At the same time, frost heaving is believed to play a key role in slowing the invasion of other alpine plants, thus benefitting *P. robbinsiana*.

Key Words: *Potentilla robbinsiana*, rare and endangered species, autecology

INTRODUCTION

Potentilla robbinsiana has been classified as a species in danger of extinction (Cook, 1980). The plant now survives in a colony on Mt. Washington where its habitat is a barren alpine fellfield. There are reliable reports that the area occupied by *P. robbinsiana* has declined dramatically in recent decades. F. L. Steele (personal communication) has estimated that the Mt. Washington colony now grows on only about one-quarter of the area it occupied in the 1930's.

The discovery of a new colony of *P. robbinsiana* in the Green Mountains of Vermont was reported by Countryman (1980). A field check with Countryman and Crow has shown these plants to be *P.*

norvegica. A new (1984) unconfirmed finding of several *P. robbinsiana* plants in the White Mountains of New Hampshire has been reported by K. Kimball (personal communication).

A heavily travelled footpath, the Appalachian Trail, has brought large numbers of hikers through the fellfield for many years. It has been recognized that tramping by hikers was damaging the *Potentilla robbinsiana* habitat and destroying some plants (Graber, 1980). The trail has since been rerouted to the edge of the fellfield and a program instituted to keep people on the trail and out of the endangered plant's habitat (Taylor, 1982; Lanier and Hill, 1983). A long-term study was established to measure *P. robbinsiana* population changes. Information from this study will allow the monitoring of population trends and an evaluation of managerial decisions taken to protect the plant.

METHODS

To document changes in the *Potentilla robbinsiana* colony on Mt. Washington, all mature plants were counted in 1973. A mature plant was one with a leaf rosette diameter of at least 1.4 cm, the smallest size observed flowering. Baselines were established, and the mature plant population was counted in each of the four subplots A through D (Figure 1). The area occupied by *P. robbinsiana* was carefully mapped so that any shifts in the colony could be noted. During the next 10 years, the colony was visited at irregular intervals to observe general conditions and plant mortality. In 1983, the population was resurveyed and the number of mature plants in each square meter was recorded. In addition, percent plant cover was recorded on 28 randomly distributed square meter plots.

RESULTS AND DISCUSSION

Only 11.4 percent of the square meter units in the fellfield were occupied by *Potentilla robbinsiana* in 1973 (Graber, 1980). By 1983, the colony area had declined to 9.6 percent of the fellfield, a 15.8 percent reduction in area occupied (Figure 1). The plant's retreat was noticeable on the Appalachian Trail side of the colony and adjacent to a rock outcrop that defines, in part, the southeast boundary. The current boundaries of the plant colony, in both of these areas of decline, are defined by only a few scattered plants. Thus,

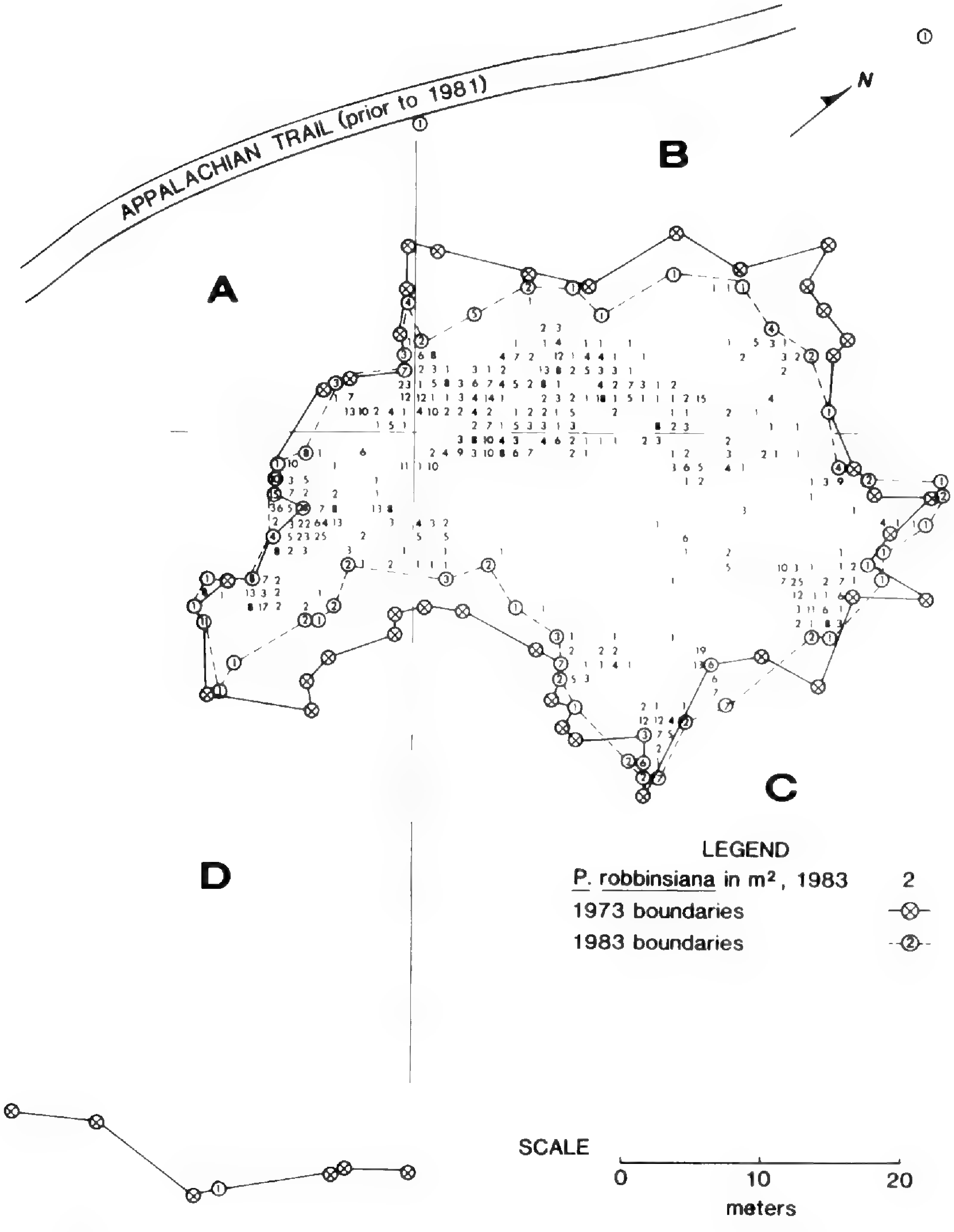


Figure 1. Peripheral plant locations in 1973 and 1983 and population distribution in 1983 of *Potentilla robbinsiana*.

even a small population loss in the future could cause a large decline in the area occupied by *P. robbinsiana.*

During the 10-year period, the total number of mature plants in the colony dropped from 1801 to 1547, a loss of 14.1 percent. This reduction was not uniformly distributed over the colony but concentrated in subplots A and B (Table 1) with respective losses of 37.6 and 20.0 percent. The two subplots on the south and east sides of the colony had small losses, 8.8 percent (C) and 7.6 percent (D). We cannot apportion these losses precisely, but we have made numerous informal observations of plant mortality and human disturbance on the fellfield during the past 10 years. We feel confident in making some general statements on causes of mortality.

Three major causes of *Potentilla robbinsiana* mortality were noted: human disturbance, drought, and frost heaving. The crushing of plants by hikers is not a serious problem except near the path; the plant no longer survives there. A more important effect of hiker traffic is the shifting and dislodging of the stony surface of the fellfield. The abrasion and churning caused by hikers' steps destroys the protected spaces between stones which often hold fine soil and organic matter. These sheltered niches are the nurseries for newly germinated *P. robbinsiana.* Once disturbed by footsteps, this essential soil is blown or washed away, thereby eliminating a part of the fellfield as suitable environment for seedling establishment. Thus as older *P. robbinsiana* die off, they are often not replaced; seedling mortality from this cause has its effects over a prolonged period. In a healthy population, mortality of mature plants must be at least balanced by the recruitment of juvenile plants. If replacement plants do not exist or occur in reduced numbers, the long-term trend wil be toward a declining population growing on a smaller area. It appears that a major part of the plant losses in subplot A and a smaller portion of the losses in subplots B, C, and D are related to hiker use of the fellfield. Before 1981, foot traffic was heavy and no formal program limited hiker use of this fragile area (Graber and Crow, 1982). This problem of negative hiker impact appears to be behind us now as comprehensive measures have been taken to reduce hiker trespass on the fellfield (Taylor, 1982; Lanier and Hill, 1983).

Drought is believed to be a serious cause of *Potentilla robbinsiana* seedling mortality. In the first growing season, more than half of the new seedlings die. This mortality was associated with periods

Table 1. Number of mature *Potentilla robbinsiana* in 1973 and 1983.

Item	Subplot A	Subplot B	Subplot C	Subplot D	Summary
1973	157	501	633	510	1801
1983	98	401	577	471	1547
# of plants lost	59	100	56	39	254
% of plants lost	37.58	19.96	8.847	7.65	14.10

of drought. After the first growing season, seedlings are less likely to be affected by drought because of their well-developed, deep root systems. Occasionally a mature plant which has been partially frost heaved will die of drought.

Frost heaving is the primary killer of established *Potentilla robbinsiana.* Most of the mature plant mortality that occurred in subplots B and C was due to this cause. Much of this loss took place on the north side of the colony where human traffic has been quite low. We observed plants of every size being frost heaved, but it was most common during the first few winters after germination. Frost heaving results from the formation of ice columns based on lenses at and just beneath the soil surface. The severity of a given heave depends upon the adequacy of the water supply and the temperature regime. During the autumn and spring, the fellfield soils freeze and thaw 60 or more times per year (Fowler, 1971). The characteristic mortality occurs when a *P. robbinsiana* is lifted by successive nightly heaves until the root system is fully exposed on the surface. This "heaved out" plant is soon blown away by the high winds typical of the fellfield habitat. Mortality from heaving is normally underestimated because the wind removes the direct evidence. A more noticeable damage is partial heaving, because these plants stay in place and are observable over an extended period. Some plants lifted only a few centimeters die from extensive damage to the fine root system, but more commonly the partially heaved *P. robbinsiana* survive one or more years.

The entire fellfield was not equally susceptible to frost heaving. The areas where frost was most active were characterized as follows: (1) the stony surface material was devoid of lichens; (2) there was fine textured soil at or near the surface; (3) there was ample moisture; and (4) the surface was level or gently sloping. The first characteristic, the absence of lichens, was an excellent indication of active

Table 2. Species and percentage cover of vegetation growing on the *Potentilla robbinsiana* habitat.

	Subplot				Weighted Mean
	A	B	C	D	
Number of quadrats	2	8	10	8	
Stony surface	43.50	66.40	31.72	45.40	46.20
Mineral soil	3.50	3.88	2.70	3.37	3.29
	47.00	70.28	34.42	48.77	49.49
Vascular Plants					
Diapensia lapponica	18.00	16.50	35.60	16.12	23.23
Salix uva-ursi	14.50	6.88	10.50	6.00	8.46
Vaccinium uliginosum	3.00	-	7.30	3.12	3.71
Empetrum nigrum	-		--	7.50	2.14
Arenaria groenlandica	--	1.25	.80	3.50	1.64
Rhododendron lapponicum	-	.50	2.55	1.88	1.59
Juncus trifidus	8.00	1.12	.20	.75	1.18
Carex bigelowii	2.50		1.05	.75	.98
Agrostis borealis	.50	1.06	.80	1.00	.91
Abies balsamea			---	3.12	.89
Loiseleuria procumbens	--	---	1.70	.63	.79
Solidago cutleri	3.50	.50	.60	.31	.70
Potentilla tridentata	.50	.12	.60	1.25	.64
Vaccinium vitis-idaea	--	---	.65	1.37	.62
Potentilla robbinsiana	.50	.31	.48	.75	.51
Geum peckii	---	---	.55	.75	.41
Campanula rotundifolia	-	.12	.15	.12	.18
Prenanthes boottii	---	.12	--	.31	.12
Lycopodium annotinum	---	---	.10	-	.04
Lichens	1.00	.62	1.50	.75	1.00
Mosses	1.00	.62	.45	1.25	.77

frost heaving. Lichens do not grow on the underside of stones, so if the stone is turned over frequently by frost, it remains lichen-free. The other characteristics relate to moisture supply, as water must be readily available to accommodate the considerable heaves that uproot *P. robbinsiana.* Much of the damage occurs in the spring when the plants are exposed to conditions conducive to frost heaving. In the winter of 1979–80, the snow accumulation was far below normal. During the period from November 1979 through March 1980, there was only 14% of the normal snow pack. The result was an extended period of frost heaving and unusually heavy mortality among mature *P. robbinsiana.*

The rigorous climate in the barren alpine fellfield, characterized by high winds and low temperatures coupled with severe frost heaving in the spring and autumn, creates a niche to which *Potentilla robbinsiana* is adapted. The growth habit of this plant with its stout caudex and low ground-hugging rosette of leaves is highly resistant to extremes of wind and temperature. Consequently, *P. robbinsiana* is better adapted to frost heaving than much of the alpine vegetation growing on or adjacent to the fellfield. During the autumn and spring, the dead *P. robbinsiana* leaves of the previous summer shade and mulch the base of the plant, reducing the likelihood of frost heaving. The stem of the plant is covered with a dense layer of persistent stipules which reduce the incidence of abrasion and serious injury when frost heaving does occur. The deep tap root provides good anchorage, reducing the probability of this plant being heaved. These morphological characteristics make *P. robbinsiana* fairly tolerant of frost heaving and give it a competitive advantage over most species on the fellfield.

Primary plant colonization has been completed in much of the alpine area of Mt. Washington since the glacial ice melt of 10,000–12,000 years ago (Bliss, 1963). An exception is the fellfield habitat of *Potentilla robbinsiana* where primary plant succession is still occurring. The average plant cover there is only 50.5% (Table 2). Severe frost heaving combined with high winds and a harsh climate have slowed the plant colonization process. Only those plants least affected by the environmental constraints have successfully invaded the fellfield. Examples include frost-tolerant species such as *Diapensia lapponica,* or those which when once established spread by vegetative means, such as *Salix uva-ursi, Vaccinium* *uliginosum, Juncus trifidus, Agrostis borealis,* and *Carex bigelowii.*

Frost heaving was most severe in subplot B where the *Potentilla robbinsiana* population depletion, in absolute numbers, was greatest. This subplot also had the lowest percentage of total plant cover (29.6%). In subplot C, which had a relatively low mortality of 8.8%, the plant cover percentage was much higher (65.1%).

The cause and effect relationship between total plant cover and *Potentilla robbinsiana* losses, due in part to frost heaving, is a key element in understanding the population dynamics in the fellfield. A higher percentage cover indicates a more stable environment, where conditions are less severe and the colonization process toward a closed plant community is proceeding. But *P. robbinsiana* does not compete well and suffers from crowding and shading by other plants. Even partial, noncompetitive shading by rock outcrops resulted in mortality to greenhouse-grown transplants established on Mt. Washington (Graber, unpublished). Thus, frost heaving, by retarding plant succession, is beneficial to *P. robbinsiana* even though the population experiences substantial losses in years of abnormally light snowfall. We believe that, ultimately, the *P. robbinsiana* niche will be altered and occupied by other better adapted species. The time frame for such a change is certainly many decades and more likely it will be centuries, but eventually other plants will probably displace *P. robbinsiana.*

LITERATURE CITED

BLISS, L. C. 1963. Alpine zone of the Presidential Range. L. C. Bliss, Edmonton, Canada.

COOK, R. S. 1980. Determination of *Potentilla robbinsiana* to be an endangered species with critical habitat. Federal Register 45(182): 61944–61947.

COUNTRYMAN, W. D. 1980. Vermont's endangered plants and the threats to their survival. Rhodora 82: 163–171.

FOWLER, B. K. 1971. The surficial geology of the Washington-Monroe colony. Appalachia 38(4): 148–163.

GRABER, R. E. 1980. The life history and ecology of *Potentilla robbinsiana.* Rhodora 82: 131–140.

———, AND G. E. CROW. 1982. Hiker traffic on and near the habitat of Robbins cinquefoil, an endangered plant species. New Hampshire Agric. Exp. Sta. Bull. 522. Durham.

Lanier, J. and B. J. Hill. 1983. Robbins cinquefoil *Potentilla robbinsiana* recovery plan. U.S.F.S. White Mountain National Forest, Laconia, NH.

Taylor, D. T. 1982. *Potentilla robbinsiana* education program and hiker survey. Appalachian Mountain Club, Research Department Publication, Boston, MA.

NORTHEASTERN FOREST EXPERIMENT STATION
L. C. WYMAN FORESTRY SCIENCES LABORATORY
DURHAM, NH 03824

A NEW LOCALITY FOR *TROLLIUS LAXUS* SALISB. SSP. *LAXUS* IN OHIO

JAMES K. BISSELL, BRIAN C. PARSONS, AND THOMAS A. YATES

In the spring of 1984 a new location for *Trollius laxus* Salisb. ssp. *laxus* (Kartesz and Kartesz, 1980), a member of the Ranunculaceae, was documented in Wayne Township, Ashtabula County, northeastern Ohio. The only other extant Ohio population of *Trollius laxus* ssp. *laxus* is in Boardman Township, Mahoning County, Ohio (Spooner et al., 1983) approximately forty miles south of the new site.

The Ashtabula County site contains approximately 400 plants in two disjunct populations within a 610 m span along the base of a creek valley wall. *Trollius* is locally common on lower valley slope spring heads and on the adjacent, level floodplain terrace. The swamp forest canopy where the *Trollius* plants grow is composed of widely spaced young trees with numerous openings occupied by swamp shrubs. The valley slope and uplands adjacent to the site are underlain by stratified glacial deposits. Fen springs and spring fed channels at the site have a pH of 7.7. Trees present on the swamp forest flats include: *Prunus serotina* Ehrh., *Populus tremuloides* Michx., *Ulmus americana* L., *Carya cordiformis* (Wang.) K. Koch, and *Acer rubrum* L. Most *Trollius laxus* ssp. *laxus* at the Ashtabula County site are growing in partial shade beneath shrub swamp canopies of *Alnus incana* (L.) Moench ssp. *rugosa* (DuRoi) Clausen. Less common shrubs associated with *Trollius* include: *Cornus sericea* L. ssp. *sericea, Rhamnus alnifolia* L'Herit., *Ribes americanum* Mill., *Carpinus caroliniana* Walt., *Viburnum trilobum* Marsh., and *Viburnum lentago* L. Herbs noted were: *Anemone quinquefolia* L., *Geranium maculatum* L., *Geum rivale* L., *Carex stricta* Lam., *Smilacina stellata* (L.) Desf., *Saxifraga pensylvanica* L., *Veratrum viride* Ait., *Aster puniceus* L., *Solidago patula* Muhl, and *Solidago rugosa* Ait.

A major break in the distribution of *Trollius laxus* ssp. *laxus* at the Ashtabula County site is a 7.7 ha mixed emergent marsh meadow, formerly inundated by a beaver pond. Occurrence of *Trollius* beneath swamp forest thickets of *Alnus incana* ssp. *rugosa* on both sides of the beaver marsh break strongly suggests that the *Trollius* population was larger before the area was flooded. Three hundred and seventy-eight plants are irregularly distributed across 0.3 ha of young swamp forest and shrub swamp on the north side of the marsh and 25 plants are restricted to 0.006 ha of young swamp forest and shrub swamp along the south side of the open beaver marsh. The two populations lie 488 m apart across the beaver marsh.

Plants of *Trollius laxus* ssp. *laxus* at the previously known Mahoning County site are growing beneath a swamp forest of *Quercus bicolor* Willd. (swamp oak) and *Fraxinus americana* L. var. *americana* (ash). *Ulmus rubra* Muhl. (slippery elm) occurs as dead stumps, having been eliminated as a competitive element in the canopy by Dutch Elm disease (Spooner, 1981). Dominant understory shrubs include: *Carpinus caroliniana* Walt., *Lindera benzoin* (L.) Blume, and *Ulmus rubra* Muhl. Dominant herbs at the Mahoning County site are: *Onoclea sensibilis* L., *Cinna arundinacea* L., and *Carex bromoides* Willd. Other herbs common at the Mahoning County site include: *Caltha palustris* L., *Geranium maculatum* L., *Saxifraga pensylvanica* L., *Ranunculus septentrionalis* Poir., *Symplocarpus foetidus* (L.) Nutt., *Mitella diphylla* L., and *Senecio aureus* L.

The Mahoning population contains 435 individuals in a relatively flat site containing numerous meandering small intermittent streams. Soils at the Mahoning County site are composed of recent alluvium with moderate to poor drainage and a pH range of 5.9 to 6.7 (Parsons and Yates, 1984).

Perhaps the greatest difference between the two sites lies in their water regimes. Spring heads and spring channels at the Ashtabula County site are perennial and arise from extensive deposits of glacial sands and gravels. In contrast the small streams flowing through the Mahoning County site are seasonal and arise from surficial runoff.

LITERATURE CITED

Kartesz, J. T. and R. Kartesz. 1980. A synonymized checklist of the vascular flora of the United States, Canada and Greenland. Volume II, Univ. North Carolina Press.

Parsons, B. C. and T. A. Yates. 1984. The cultural requirements of *Trollius laxus* Salisb. ssp. *laxus*. Report. The Holden Arboretum, Mentor, Ohio.

Spooner, D. M. 1981. Ohio Status of *Trollius laxus* ssp. *laxus*. Report. Ohio Department of Natural Resources, Columbus, Ohio.

———, A. W. Cusick, B. Andreas, and D. Anderson. 1983. Notes on Ohio vascular plants previously considered for listing as federally endangered or threatened species. Castanea 48(4): 250 258.

J. K. B.
CLEVELAND MUSEUM OF NATURAL HISTORY
WADE OVAL, UNIVERSITY CIRCLE
CLEVELAND, OHIO 44106

B. C. P. and T. A. Y.
THE HOLDEN ARBORETUM
SPERRY ROAD
MENTOR, OHIO 44060

INTRAGENERIC TAXONOMY OF *CAULOPHYLLUM* (BERBERIDACEAE)

HENRY LOCONTE AND WILL H. BLACKWELL

ABSTRACT

Patterns of morphological variation within the genus *Caulophyllum* are documented by principal components analysis, which supports the recognition of *C. giganteum* and *C. thalictroides* in eastern North America, and *C. robustum* in eastern Asia. The two North American species are sympatrically distributed and reproductively isolated by staggered flowering times. Analysis of mixed populations of *C. giganteum* and *C. thalictroides* from northern Ohio further demonstrates the morphological and phenological divergence between these two species.

Key Words: *Caulophyllum, C. giganteum, C. robustum, C. thalictroides*

The genus *Caulophyllum* was originally included in *Leontice s.l.* (Linnaeus, 1753). However, *Caulophyllum* species possess rhizomes, whereas *Leontice* species possess tubers; the two genera are also distinguishable by other characters. Modern treatments of *Caulophyllum* recognize from one to three species. This study supports the phenetic distinction of three *Caulophyllum* species, one of which is allopatric in eastern Asia, and two of which are sympatric in eastern North America. The two North American species are temporally reproductively isolated.

In 1803, Michaux described *Caulophyllum* from eastern North America as a monotypic genus, creating the binomial *C. thalictroides.* The disjunctive eastern North American – eastern Asian geographic range of *Caulophyllum* was noted by Gray (1859) in his recognition of the strong floristic relationships between the two regions. It is significant that eastern North America and eastern Asia share a large number of genera which are not found elsewhere (Li, 1952). Gray also proposed that species such as *C. thalictroides* are in fact identical in the two regions. However, Maximowicz (1859) distinguished the Asiatic plants as *C. robustum* on a morphological basis. The specific status of *C. robustum* has been supported by Kawano and Ihara (1967) who have shown it to be karyotypically distinguishable from *C. thalictroides.*

Most floristic treatments of eastern North America describe *Caulophyllum thalictroides* as a phenotypically variable species (Ernst, 1964). However, Farwell (1918) described *C. thalictroides* var. *giganteum* from Michigan. Farwell has been criticized for his taxonomic and nomenclatural judgment and many of his names have been ignored (McVaugh et al., 1953). Only the floras of Canada (Scoggan, 1978), Vermont (Seymour, 1969), and West Virginia (Core and Strausbaugh, 1978) mention *C. thalictroides* var. *giganteum.* This taxon was studied by Dore (1964) who suggested that it deserved specific ranking. We have elevated Farwell's variety to the status of species, as *C. giganteum* (Loconte and Blackwell, 1981).

MATERIALS AND METHODS

Data were collected from approximately 2,000 herbarium specimens from BGSU, BHO, BLH, BM, CINC, GE, IND, K, KE, KNK, KY, LE, MO, MU, MUHW, MUS, NCU, NY, OC, OS, PENN, PH, TENN, TI, US, WIS, and WSFA (Holmgren and Keuken, 1981). Additionally, specimens were collected from 30 populations of *Caulophyllum* in Ohio, New York, and Tennessee. A mass sample was made from mixed populations of *C. giganteum* and *C. thalictroides* in a forest on the east side of Rt. 23, 100 yards south of the Michigan state line, Sylvannia Twp., Lucas Co., Ohio.

The multivariate technique of principal components analysis was utilized by employing the NT-SYS program package (Rohlf et al., 1979). Two raw data sets were constructed. The first is geographical in scope and includes 96 OTUs (operational taxonomic units) of *Caulophyllum,* which were sampled to encompass the generic distribution. Ten characters of flowering specimens were utilized (Table 1). The second data set is populational in scope and includes 30 OTUs of *C. giganteum* and *C. thalictroides* from the mass sample, which were scored for 19 vegetative characters (Table 2). The characters were standardized, and a character by character correlation matrix was computed from which principal components were extracted.

RESULTS AND DISCUSSION

The first two principal components extracted from the geographical data set account for 45.4% and 22.7% of the variation (total of 68.1%). A bivariate plot of the two components shows three groups of OTUs that represent the three species of *Caulophyllum* (Figure 1). From left to right on component 1, there is an increase in stamen length, sepal length, pistil length, petal length, and the ratio of

Table 1. List of ten characters of flowering specimens used for geographical analysis of *Caulophyllum*.

1. Stem length; 2. Inflorescence length; 3. Number of flowers; 4. Floral bract length; 5. Sepal length; 6. Sepal length/width; 7. Petal length; 8. Stamen length; 9. Filament length/anther length; 10. Pistil length.

Table 2. List of nineteen vegetative characters used for populational analysis of *Caulophyllum*.

1a, b. Stem length to first leaf, to second leaf; 2a, b. Degree of compounding of first leaf, of second leaf; 3a, b. Primary petiolule length of first leaf, of second leaf; 4a, b. Secondary petiolule length of first leaf, of second leaf; 5. Tertiary petiolule length of first leaf; 6a, b. Leaflet length of first leaf, of second leaf; 7a, b. Leaflet width of first leaf, of second leaf; 8a, b. Leaflet sinus length of first leaf, of second leaf; 9. Terminal inflorescence length; 10. Number of flowers in terminal inflorescence; 11. Axillary inflorescence length; 12. Number of flowers in axillary inflorescence.

filament length to anther length (in order of decreasing value). These characters provide clear separation of *C. thalictroides* and *C. giganteum,* which have small and large floral appendages respectively. From bottom to top on component 2, there is an increase in inflorescence length, stem length, floral bract length, and the number of flowers (in order of decreasing value). These characters provide separation of *C. robustum* from both North American species, although one OTU of *C. robustum* does overlap the *C. thalictroides* cluster.

Of the three species of *Caulophyllum, C. robustrum* is geographically allopatric in eastern Asia. This species is found throughout Japan, as well as in China, the Korean peninsula, and extreme southeastern U.S.S.R. The two species of New World *Caulophyllum* are sympatrically distributed in eastern North America (Figure 2). The distribution of *C. thalictroides* encompasses most of the eastern united States and southeastern Canada, whereas *C. giganteum* is distributed in the Appalachian Mountain system and surrounding areas. Populations of *C. giganteum* are more common in the northern portion of its distribution and in the south this species is found north of the Smoky Mountains. Field work revealed no ecological isolation between these two species.

Gene flow between *Caulophyllum giganteum* and *C. thalictroides* is inhibited by a difference in flowering phenology (Figure 3). The large-flowered *C. giganteum* begins anthesis approximately two

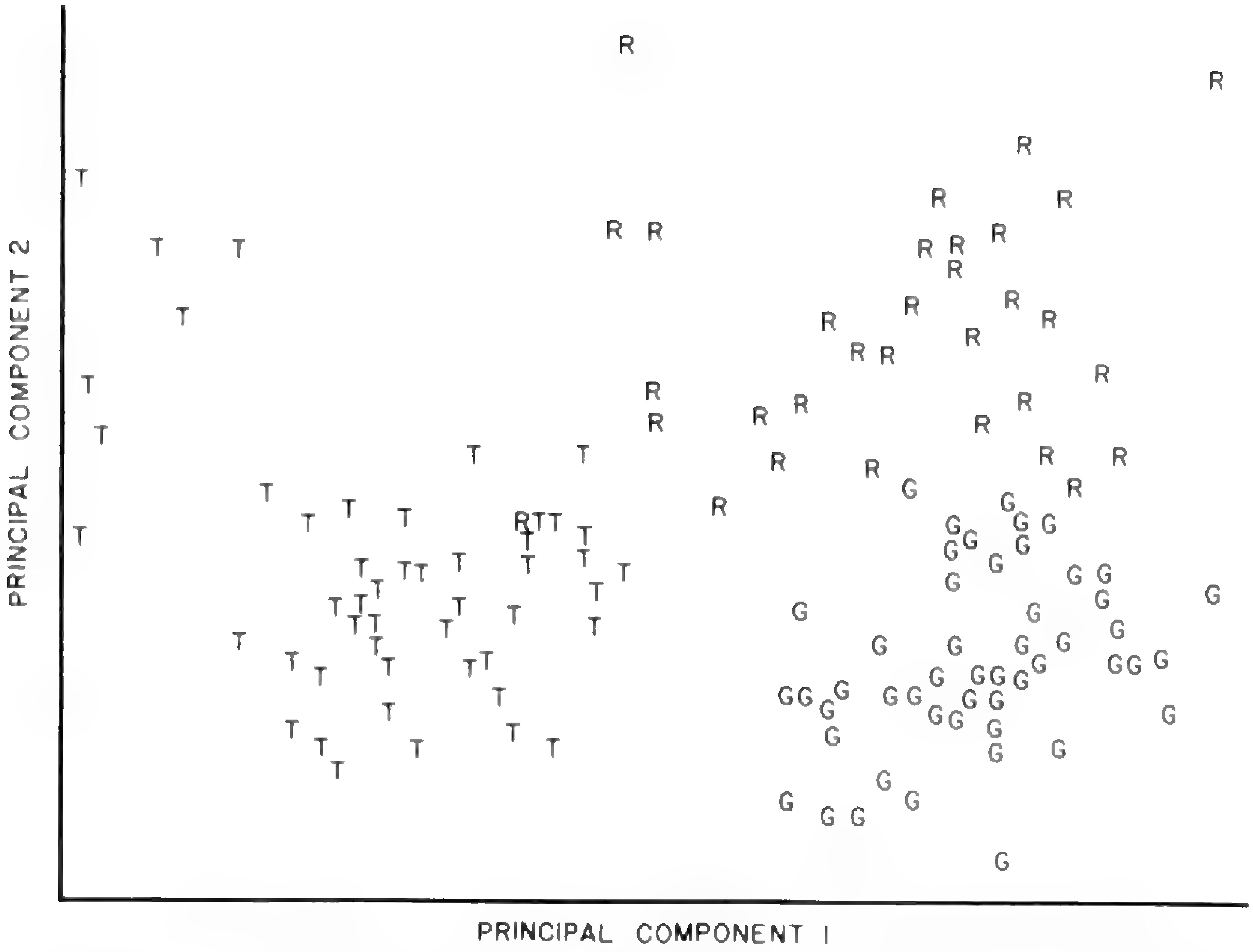


Figure 1. Bivariate plot of first two principal components in geographical analysis of *Caulophyllum*. **G** = *C. giganteum*, **R** = *C. robustum*, **T**= *C. thalictroides*.

weeks before sympatric *C. thalictroides*. The presence of few flowers per inflorescence enables *C. giganteum* to complete flowering before *C. thalictroides* has initiated flowering. The overlap of flowering times in Figure 3 is attributable to the regional extent of the states. For example, populations of *C. giganteum* from northern Ohio flower simultaneously with populations of *C. thalictroides* from southern Ohio. Temporal isolation was pronounced between all locally sympatric populations examined.

The first two principal components extracted from the populational data set account for 46.8% and 20.0% of the variation (total of 66.8%). A bivariate plot of the two components shows clear separation of *Caulophyllum giganteum* and *C. thalictroides* (Figure 4). From left to right on component 1 there is an increase in leaflet length of the second leaf, leaflet width of the first leaf, leaflet length of the first leaf, leaflet width of the second leaf, leaflet sinus length of the second leaf, primary petiolule length of the second leaf, leaflet sinus length of the first leaf, terminal inflorescence length, primary petiolule length of the first leaf, and a decrease in the degree of com-

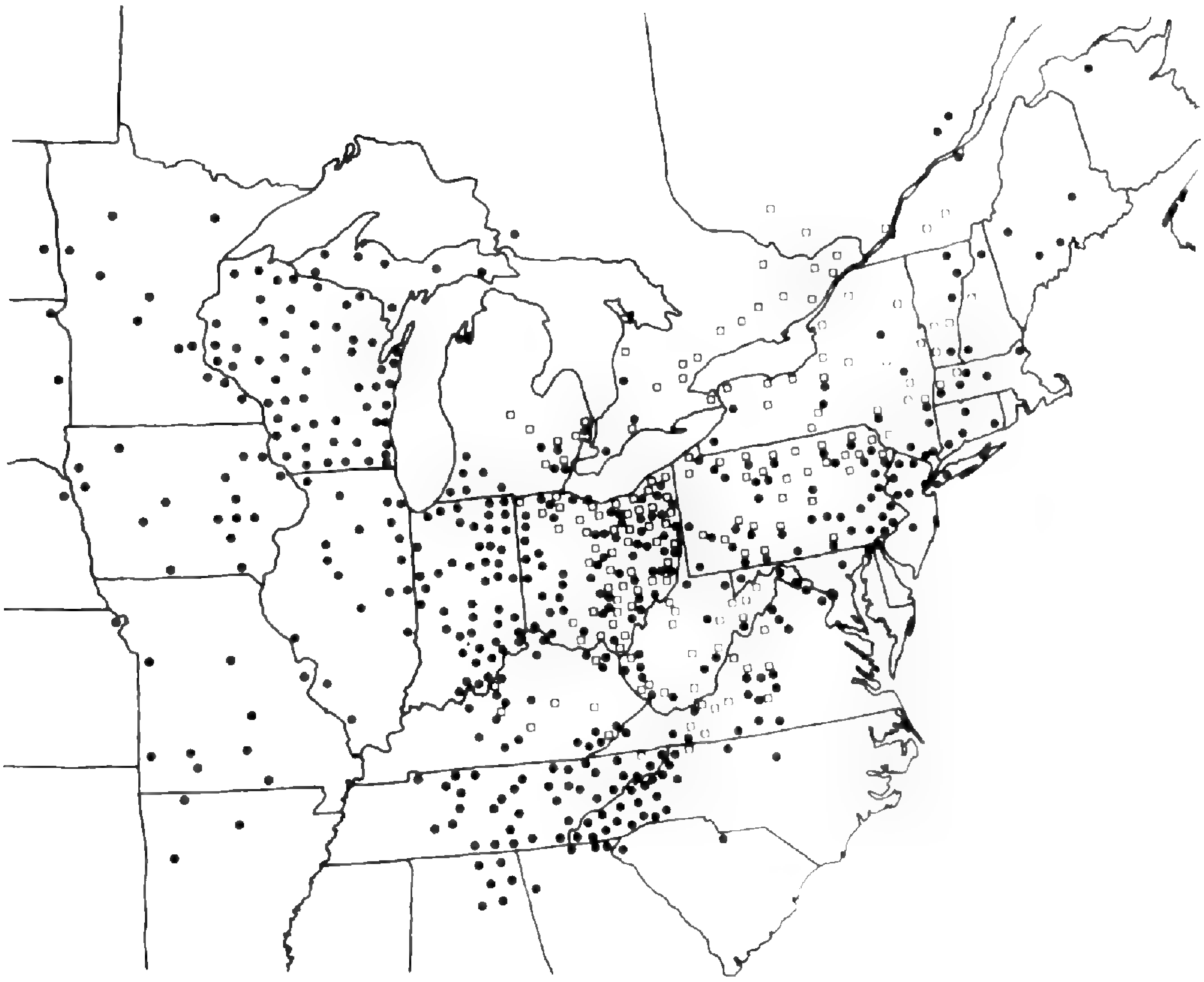


Figure 2. Geographical distribution of *Caulophyllum* in eastern North America. Symbols are county records. Squares = *C. giganteum*, circles = *C. thalictroides*.

pounding of the second leaf (in order of decreasing value). The morphological divergence of these two populations was correlated with a difference in flowering phenology. On the collection date of the mass sample, 11 May 1982, *C. giganteum* had completed flowering while *C. thalictroides* was in anthesis.

In conclusion, evidence supports recognition of three species in *Caulophyllum*. On a phenetic basis, *C. robustum* is more closely related to *C. thalictroides; C. giganteum* is the most phenetically distinct species of the genus. The Asiatic *C. robustum* is geographically allopatric. The two North American species of *Caulophyllum* are sympatrically distributed and reproductively isolated.

ACKNOWLEDGMENTS

This research was funded in part by a grant from the Ohio Biological Survey. We thank the aforementioned herbaria as well as Hardy Eshbaugh, James Estes, Dan Hough, Raymond Phillips, Gary Schnell, Gene Williamson, and Johann Wolf.

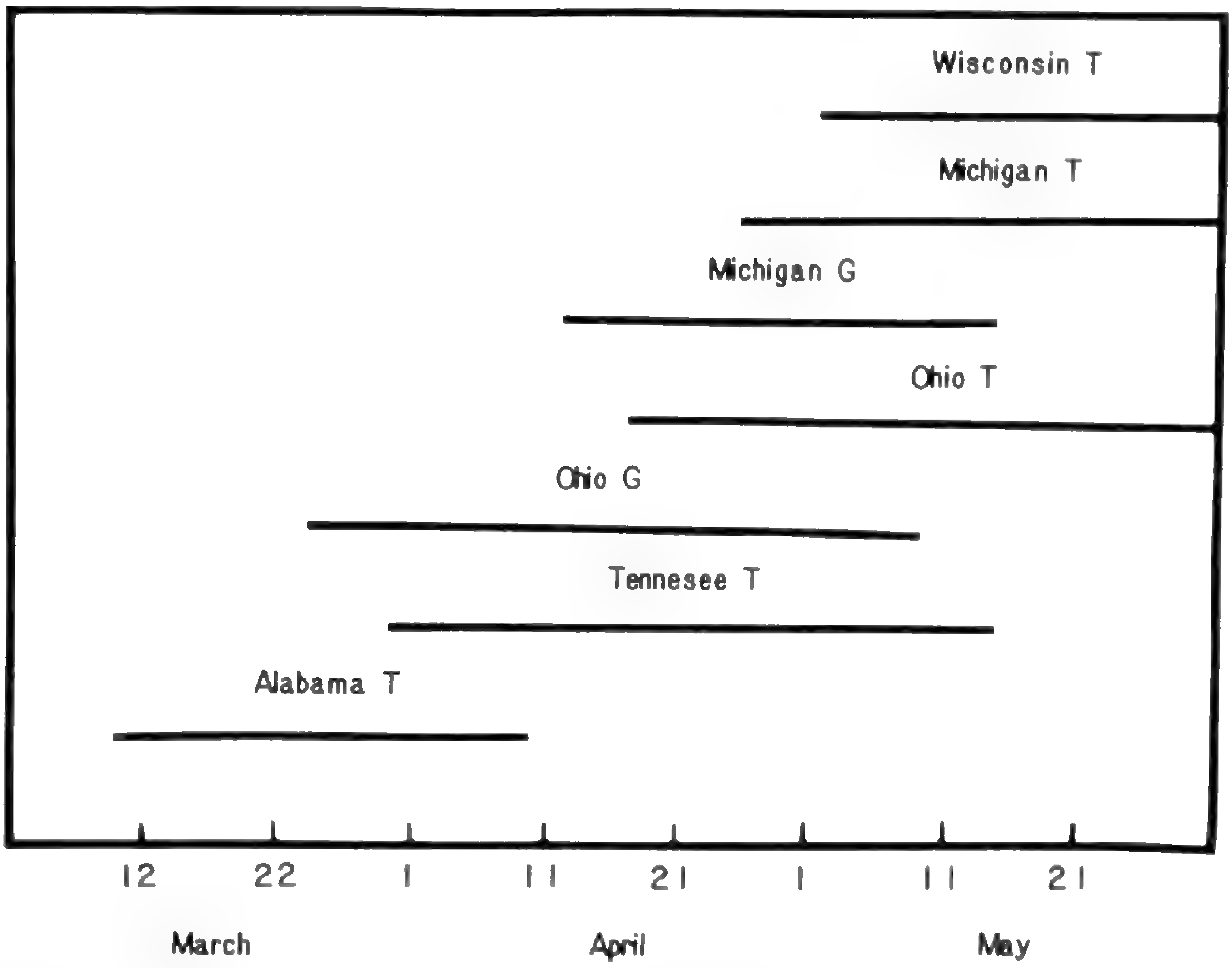


Figure 3. Flowering phenology of *Caulophyllum* in selected states of eastern United States. **G** = *C. giganteum*, **T** = *C. thalictroides*.

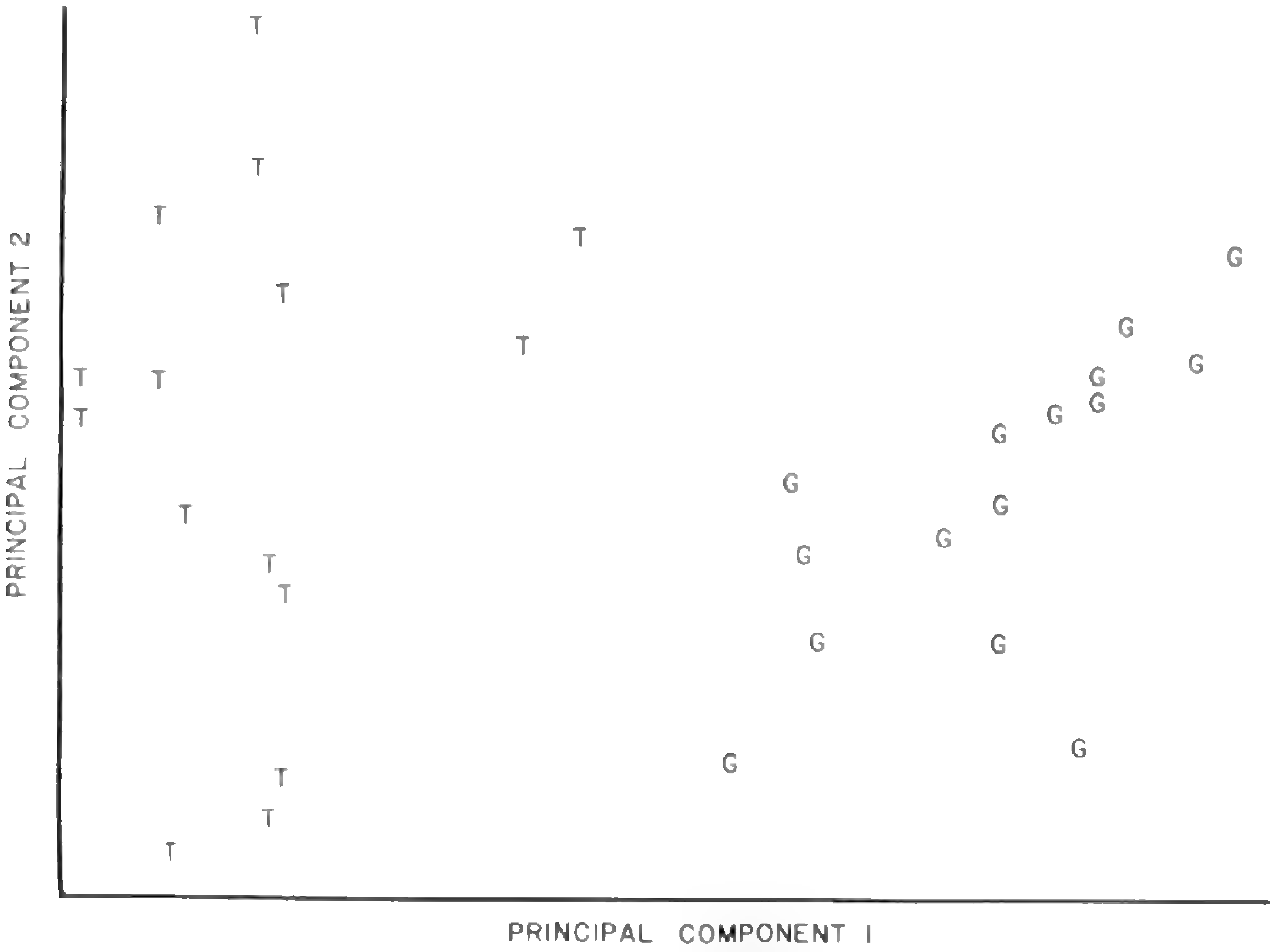


Figure 4. Bivariate plot of first two principal components in populational analysis of *Caulophyllum*. **G** = *C. giganteum*, **T** = *C. thalictroides*.

LITERATURE CITED

CORE, E. L. AND P. D. STRAUSBAUGH. 1978. Flora of West Virginia. Seneca Books Inc., Grantsville, WV.

DORE, W. G. 1964. Two kinds of blue cohosh. Ontario Nat. 2: 5–9.

ERNST, W. R. 1964. The genera of Berberidaceae, Lardizabalaceae, and Menispermaceae in the southeastern United States. J. Arnold Arbor. 45: 1–35.

FARWELL, O. A. 1918. Notes on the Michigan flora. Ann. Rep. Michigan Acad. Sci. 20: 178.

GRAY, A. 1859. Diagnostic characters of phanogamous plants, collected in Japan by Charles Wright, Botanist of the U.S. North Pacific Exploring Expedition, with observations upon the relations of the Japanese flora to that of North America, and of other parts of the northern temperate zone. Mem. Amer. Acad. Arts Sci. n.s. 6: 377–453.

HOLMGREN, P. K. AND W. KEUKEN. 1981. Index Herbariorum. Regnum Veg. 106.

KAWANO, S. AND M. IHARA. 1967. Chromosome morphology of *Caulophyllum robustum* and its systematic implications. J. Jap. Bot. 42: 129–135.

LI, H. 1952. Floristic relationships between eastern Asia and eastern North America. Trans. Amer. Phil. Soc. n.s. 42(2).

LINNAEUS, C. 1753. Species Plantarum. Facsimile edition, 1957. Ray Society, London.

LOCONTE, H. AND W. H. BLACKWELL. 1981. A new species of blue cohosh (*Caulophyllum,* Berberidaceae) in eastern North America. Phytologia 49: 483.

MAXIMOWICZ, C. J. 1859. Primitae Florae Amurensis. St. Petersbourg.

MCVAUGH, R., S. A. CAIN, AND D. J. HAGENAH. 1953. Farwelliana: an account of the life and botanical work of Oliver Atkins Farwell, 1867–1944. Bull. no. 34. Cranbrook Institute of Science, Bloomfield Hills, MI.

MICHAUX, A. 1803. Flora boreali-americana. Paris.

ROHLF, F. J., J. KISHPAUGH, AND D. KIRK. 1979. Numerical Taxonomy System of Multivariate Statistical Programs. Tech. Rep. State Univ. New York, Stony Brook, NY.

SCOGGAN, H. J. 1978. The Flora of Canada, Part 3. National Museums of Canada: Ottawa.

SEYMOUR, F. C. 1969. The Flora of Vermont. Bull. 60. Vermont Agr. Exp. Sta., Burlington.

H. L.
DEPARTMENT OF BOTANY AND MICROBIOLOGY
UNIVERSITY OF OKLAHOMA
NORMAN, OK 73019

W. H. B.
DEPARTMENT OF BOTANY
MIAMI UNIVERSITY
OXFORD, OH 45056

THE VEGETATION AND FLORA OF THE SEABROOK DUNES WITH SPECIAL REFERENCE TO RARE PLANTS[1]

DEBRA A. DUNLOP AND GARRETT E. CROW

ABSTRACT

The Seabrook Dunes, located in Seabrook, New Hampshire, represents the largest coastal sand dune remnant in the state. In 1982, a floristic inventory was conducted at this backdune community that documented 141 vascular plants. Special attention was given to nine rare species: *Artemisia caudata* and *Puccinellia paupercula* var. *alaskana,* rare; Ammophila breviligulata and *Salicornia bigelovii,* threatened; and *Hudsonia ericoides* ssp. *tomentosa* and *Salicornia virginica,* endangered. Three other endangered species, *Arenaria peploides* var. *robusta, Aristida tuberculosa* and *Cyperus grayii* occur in New Hampshire only at the Seabrook Dunes. The Seabrook Dune's populations of *Ammophila breviligulata, Hudsonia ericoides* and *Salicornia virginica* represent the most significant populations for these taxa in New Hampshire. The vegetation was described, mapped and classified into seven types: sunken forests, dunegrass, tall thickets, short shrub thickets, wet swales, salt marsh and drift-line.

Key Words: vascular plants, rare plants, dunes, New Hampshire

In the summer of 1982, a project was established to evaluate the plant species regarded as rare, threatened, or endangered along the coast of New Hampshire (Dunlop and Crow, 1983; 1985). As part of this project, special attention was directed at the Seabrook Dunes (Dunlop, et al., 1983). This paper provides a description and inventory of the dune vegetation and highlights those taxa considered rare in the state.

The coastline of New Hampshire represents a transitional zone between the sandy beaches and barrier beach islands of the South to Middle Atlantic states and the rocky coastline of Maine (Crow and Storks, 1980). In New Hampshire, dunes and salt marshes once extended from Seabrook to Hampton and intermittently northward.

A typical coastal dune system consists of a foredune, an interdune, and a backdune. The foredune ridge receives the greatest impact of coastal storms and few species are able to colonize it. Behind the foredune a more stable interdune of low undulating

---

[1] Scientific contribution 1293 from the New Hampshire Agricultural Experiment Station.

sands supports a more diversified flora. A backdune formation of higher dunes and deep hollows develops furthest from the beach and is characterized by shrub thickets and sunken forests. The dune ecosystem at nearby Plum Island, Massachusetts, represents the best-developed dune system north of Cape Cod (McDonnell, 1979).

PHYSICAL FEATURES

The backdune community at Seabrook (approximately 56 acres in the southeast corner of the Town of Seabrook) constitutes the largest coastal sand dune remnant in New Hampshire. Designated "The Sands" (USGS Hampton Quadrangle), the Seabrook dunes lie east of the extensive Seabrook salt marsh and the Blackwater River (Figures 1, 2). To the south the dunes are bordered by salt marsh, which separates the area from nearby commercial properties. The northern boundary, formed by salt marsh and Cross Beach Road, is periodically flooded by high storm tides. To the east, the dunes abut Route 1A.

METHODS

An inventory of the natural dune vegetation was divided into two parts: 1) a documentation of the dune's flora and 2) a description of the composition, structure, and distribution of the vegetation.

A systematic reconnaissance of the area was begun in May 1982, and the area was visited once each week through October 1982. Collections of all vascular plants were made and data on relative abundance and habitat were recorded in the field. Voucher specimens for all the species cited are deposited in NHA.

Aerial photographs were used to delineate all vegetated areas in the backdune. Subsequently, each unit of vegetation was inspected in the field. Dominant vascular species were estimated visually and observations were made on general physiognomy. We subjectively classified the vegetation into seven types based on the dominant vascular species and categories of physiognomy (i.e. trees, shrubs, and herbs).

VEGETATION TYPES OF THE SEABROOK DUNES

The seven vegetation types recognized for the Seabrook backdune community and adjacent salt marsh were: 1) sunken forests (SF); 2)

Figure 1. Aerial photograph of Seabrook Dunes. 1982. Photo courtesy of USDA-ASCS, Rockingham Co., NH.

Figure 2. Oblique aerial view of Seabrook Dunes, 1978. Photo by Garrett E. Crow.

dunegrass (DG); 3) tall thickets (TT); 4) short shrub thickets (ST); 5) wet swales (WS); 6) salt marsh (SM); and 7) driftline (DL).

The most conspicuous vegetation type is the sunken forest. These heavily wooded areas are in the deeper hollows between the highest dunes, and it is here that many trees reach their maximum height in the dune community. Surrounding these high dunes and sunken forests are low dunes where the dunegrass vegetation type predominates. Scattered among these low dunes are thickets of shrubs and small trees. Some thickets are dominated by shrubs less than 2 meters in height (short shrub thickets); others are dominated by trees over 2 meters in height (tall thickets). A number of wetland species are found in the isolated hollows of the low dunes; they form wet swales. Another vegetation type, salt marsh, is contiguous with the dune sands on all sides but the east. To the west, the boundary between the salt marsh and dunes is transitional. In these areas, the dunes are very low and are periodically inundated by high storm tides. These areas form a seventh vegetation type, the driftline. A description of the seven types follows, emphasizing the dominant species (cf. aerial photographs and vegetation map, Figures 1, 2, 3).

Sunken Forest

Four areas of sunken forests occur in the backdune. All are heavily wooded and dominated by a tall canopy of *Prunus serotina, Amelanchier stolonifera, Populus tremuloides, Acer rubrum* and occasionally *Pinus rigida*. The understory is dominated by *Lonicera morrowii, Berberis vulgaris, Toxicodendron radicans* and *Parthenocissus quinquefolia*. In addition, many herbs are common: *Aralia nudicaulis, Maianthemum canadense, Arenaria lateriflora,* and *Smilacina stellata. Myrica pensylvanica* and *Prunus maritima* are abundant in open areas along the fringes of the sunken forests.

Dunegrass

The vegetation of the low dunes is dominated by grasses and other low herbaceous plants; *Ammophila breviligulata* is the most abundant species. *Andropogon scoparius* and *Danthonia spicata* are common grasses in the southern portion of the backdune community. *Lathyrus japonicus, Lechea maritima, Polygonella articulata* and *Cyperus filiculmis* are common. *Solidago sempervirens* is abundant throughout and mats of *Hudsonia ericoides* ssp. *tomentosa* carpet large areas of the low dunes.

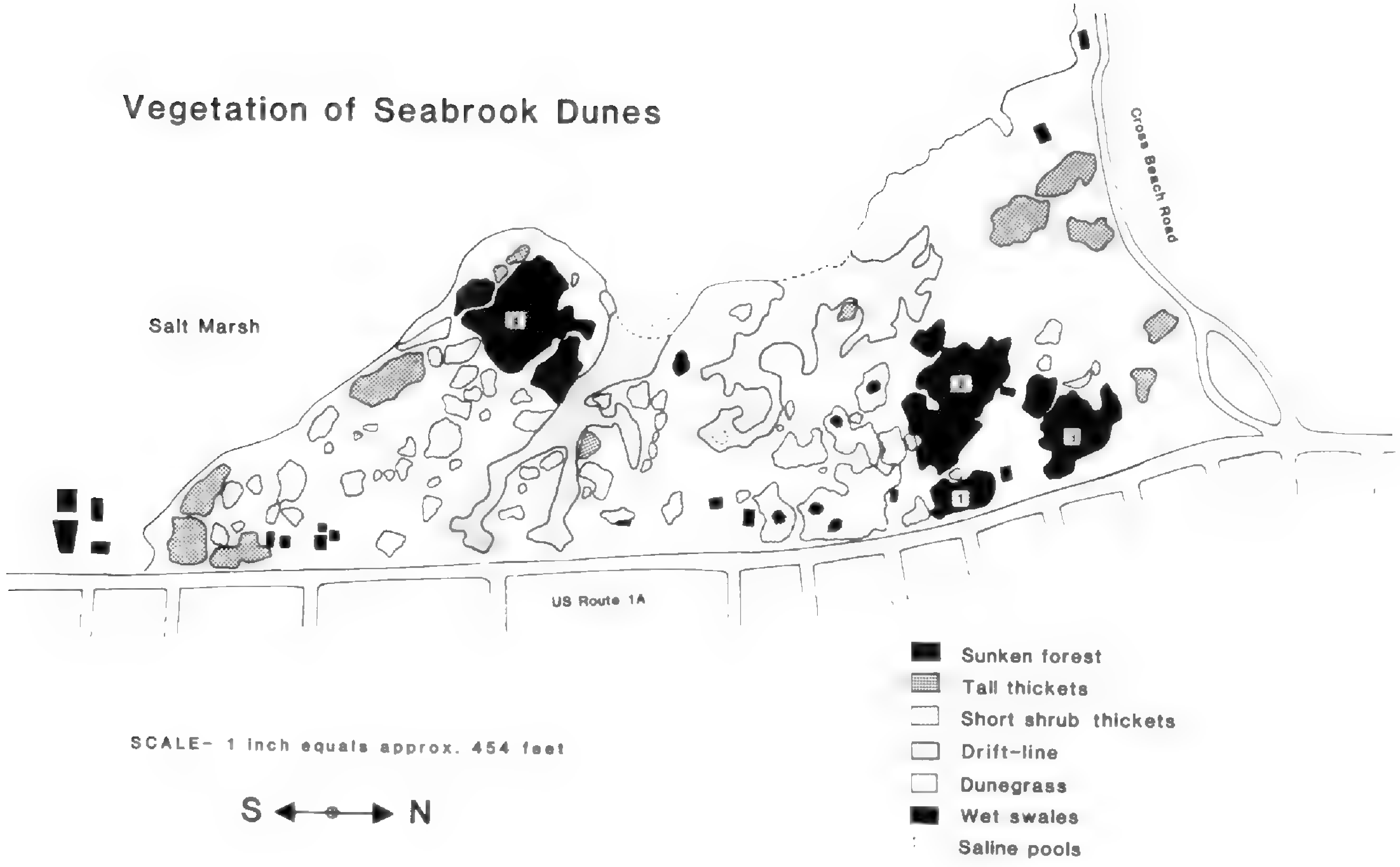


Figure 3. Vegetation of Seabrook Dunes.

Tall Thicket

Tall thickets are in the areas of stablized low dunes. Tall thickets contain species also present in the sunken forests, but differ from them in having smaller trees and a dense shrub layer. The canopy in the tall thickets varies but is most often composed of *Populus tremuloides, Prunus serotina, Amelanchier stolonifera,* and occasionally *Acer rubrum* and *Pinus rigida.* Other common species are *Amelanchier canadensis, Rosa virginiana, Parthenocissus quinquefolia, Berberis vulgaris, Viburnum recognitum* and *Toxicodendron radicans.*

Short Shrub Thicket

Short shrub thickets are widespread on protected slopes and hollows of the low dunes where *Myrica pensylvania* and *Prunus maritima* form extensive stands. Other common species are *Rosa virginiana, Achillea millefolium, Oenothera parviflora, Polygonum scandens* and *Toxicodendron radicans.*

Wet Swale

Wet swales of two kinds occur in the hollows of the low dunes. In one, *Vaccinium macrocarpon* forms dense mats; the other is dominated by *Juncus balticus.* Bordering each swale, *Aronia prunifolia, Ilex verticillata, Triadenum virginicum* and *Toxicodendron radicans* are common.

Salt Marsh

The high marsh bordering the backdune is dominated by the saltmarsh grass *Spartina patens,* among which commonly occur *Limonium carolinianum, Plantago maritima* and *Triglochin maritima.* Along the upper edge of the marsh *Juncus gerardi* and *Distichlis spicata* form dense stands with *Salicornia europaea, Suaeda linearis, S. maritima* and *S. richii.*

Driftline

Low areas between the salt marsh and backdune community are occasionally inundated by high storm tides, which as they subside leave behind large amounts of salt marsh detritus and debris. This line of debris forms the boundary between sites suitable for growth of dune grasses and other species more tolerant of salt. Few plants grow through these compact piles of debris, but along their seaward edges are *Spergularia marina* and thick stands of *Spartina patens. Limonium carolinianum* and *Puccinellia maritima* are also common.

FLORA OF SEABROOK DUNES

The following annotated list of vascular plants documents the flora of the Seabrook Dunes. Identifications were based primarily on Fernald (1950) and Gleason and Cronquist (1963). Rare species are marked with an asterisk and special notes on their abundance, distribution and vegetation type are included.

Ferns and Fern Allies

OSMUNDACEAE

Osmunda cinnamomea L.—Occasional; SF, WS.
Osmunda regalis L.—Occasional; SF.

ASPLENIACEAE

Onoclea sensibilis L.—Occasional; ST.

THELYPTERIDACEAE

Thelypteris palustris Schott—Uncommon; WS.

Gymnosperms

CUPRESSACEAE

Juniperus communis L.—Uncommon; TT.

PINACEAE

Pinus rigida L.—Uncommon; SF, TT.

Angiosperms

Dicots

ACERACEAE

Acer rubrum L.—Common; SF.

ANACARDIACEAE

Rhus copallina L.—Uncommon; SF.
Rhus typhina L.—Occasional; SF, TT.
Toxicodendron radicans (L.) Kuntze—Abundant; SF, TT, ST, DG.

AQUIFOLIACEAE

Ilex verticillata (L.) Gray—Occasional; WS, TT. Uncommon; SF.

ARALIACEAE

Aralia nudicaulis L.—Common; SF.

ASCLEPIADACEAE

Asclepias syriaca L.—Frequent; DG, SF.

ASTERACEAE

Achillea millefolium L.—Frequent; SF, DG, TT, ST.

Ambrosia artemisiifolia L.—Uncommon; DG.

**Artemisia caudata* Michx.—Uncommon in low dune areas with a few plants at the northern edge of Sunken Forest No. 2 and northern thicket; edge of abandoned building, now (1985) site of a new house.

Aster linariifolius L.—Occasional; DG.

Chrysanthemum leucanthemum L.—Occasional; edges of SF.

Erigeron canadensis L.—Occasional; roadsides.

Erechtites hieracifolia (L.) Raf.—Occasional; DG, TT, ST.

Gnaphalium obtusifolium L.—Occasional; DG.

Hieracium florentinum All.—Occasional; DG.

Hieracium pilosella L.—Uncommon; edge of SF.

Lactuca biennis (Moench) Fern.—Frequent; edges of SF, TT, ST, WS.

Solidago rugosa Ait.—Occasional; SF, TT, ST.

Solidago sempervirens L.—Common; DG, edges of SF, TT, ST.

BERBERIDACEAE

Berberis vulgaris L.—Common; SF.

BETULACEAE

Betula populifolia Marsh.—Rare; WS.

BRASSICACEAE

Barbarea vulgaris R. Br.—Occasional; along roadside.

Cakile edentula (Bigel.) Hook.—Common; DG, edges of TT, ST.

Sisymbrium altissimum L.—Common; edge of SF.

CAPRIFOLIACEAE

Lonicera ×bella Zabel—Common; SF.

Lonicera morrowi Gray—Common; SF, TT, ST.

Sambucus canadensis L.—Occasional; SF.

Viburnum recognitum Fern.—Common; SF, TT, ST, WS.

CARYOPHYLLACEAE

Arenaria lateriflora L.—Common; SF, WS.

**Arenaria peploides* L.—One plant at edge of interdune and salt marsh.

Lychnis alba L.—Occasional; roadside.

Silene antirrhina L.—Rare; DG.

Spergularia marina (L.) Griseb.—Common; SM.

CELASTRACEAE

Celastrus scandens L.—Uncommon; ST.

CHENOPODIACEAE

Atriplex glabriuscula Edmonston—Occasional; SM.

Atriplex patula L.—Common; SM.

Chenopodium album L.—Common; DG.

**Salicornia bigelovii* Torr.—Occasional: at north end of dunes in area indundated by very high tides. Few plants in open mud/sand patches.

Salicornia europaea L.—Common; SM.

**Salicornia virginica* L.—Locally abundant; in high marsh north of dunes and Cross Beach Road.

Suaeda linearis (Ell.) Moq.—Occasional; SM.

Suaeda maritima (L.) Dumort.—Occasional; SM.

Suaeda richii Fern.—Occasional; SM.

CISTACEAE

**Hudsonia ericoides* L. ssp. *tomentosa* (Nutt.) Nickerson & Skog—Common; on low dunes.

Lechea maritima Leggett—Common; DG.

CLETHRACEAE

Clethra alnifolia L.—Uncommon; SF.

CLUSIACEAE

Hypericum gentianoides (L.) BSP.—Occasional; along roadside.

Hypericum perforatum L.—Occasional; edges SF, TT, ST.

Triadenum virginicum (L.) Raf.—Occasional; WS.

ERICACEAE

Gaylussacia baccata (Wang.) K. Koch.—Common; TT.

Lyonia ligustrina (L.) DC.—Common; ST, TT.

Vaccinium corymbosum L.—Uncommon; SF.

Vaccinium macrocarpon Ait.—Abundant; WS.

EUPHORBIACEAE

Euphorbia esula L.—Occasional; SF, DG.

Euphorbia polygonifolia L.—Occasional; DG.

FABACEAE

Lathyrus japonicus Willd.—Occasional; DG.

Trifolium arvense L.—Common; SF.

Trifolium repens L.—Common; SF.

FAGACEAE

Quercus velutina Lam.—Occasional; SF.

LYTHRACEAE

Lythrum salicaria L.—Occasional; SF.

LAMIACEAE

Teucrium canadense L. *s. l.*—Common; SF.

MYRICACEAE

Comptonia peregrina (L.) Coult.—Occasional; SF.

Myrica pensylvanica Loisel.—Abundant; edge of SF, TT, ST.

ONAGRACEAE

Epilobium glandulosum Lehm.—Occasional; WS.

Oenothera parviflora L.—Common; DG, edge of SF.

PAPAVERACEAE

Chelidonium majus L.—Occasional; SF.

PLANTAGINACEAE

Plantago maritima L. ssp. *juncoides* (Lam.) Hult.—Common; SM.

PLUMBAGINACEAE

Limonium carolinianum (Walt.) Britt.—Common; SM.

POLYGONACEAE

Rumex acetosella L.—Frequent; SF, DG.

Polygonella articulata (L.) Meisn.—Common; DG.

Polygonum scandens L.—Frequent; TT, ST, edge of SF.

PRIMULACEAE

Lysimachia quadrifolia L.—Common; along roadside.

Trientalis borealis Raf.—Occasional; SF.

RHAMNACEAE

Rhamnus frangula L.—Occasional; SF.

ROSACEAE

Amelanchier canadensis (L.) Medic. Common; SF, TT, ST.

Amelanchier stolonifera Wieg.—Common; SF, TT.

Aronia arbutifolia (L.) Ell.—Occasional; SF, WS.

Aronia prunifolia Steud. —Common; SF, TT, ST, WS.

Crataegus chrysocarpa Ashe—Frequent; SF, TT.

Fragaria virginiana Duchesne—Local; in one ST.

Prunus maritima Marsh.—Abundant; SF, TT, ST.

Prunus pensylvanica L.—Uncommon; SF.

Prunus serotina Ehrh.—Common; SF, TT.

Prunus virginiana L.—Frequent; SF.

Rosa virginiana Mill.—Common; SF, TT, ST, DG.

Rubus allegheniensis Porter—Occasional; SF.

Rubus idaeus L. var. *strigosus* (Michx.) Maxim.—Occasional; SF.

Rubus occidentalis L.—Occasional; ST.
Spiraea latifolia (Ait.) Borkh.—Occasional; DG, WS, SF.
Spiraea tomentosa L.—Occasional; TT, ST.

RUBIACEAE

Galium aparine L.—Occasional; SF.
Houstonia caerulea L.—Uncommon; edge of SF.

SALICACEAE

Populus tremuloides Michx.—Common; SF, TT.

SAXIFRAGACEAE

Ribes hirtellum Michx.—Common; SF.

SCROPHULARIACEAE

Linaria canadensis (L.) Dumont Occasional; DG, along roadside.

SOLANACEAE

Solanum dulcamara L.—Frequent; SF.
Solanum nigrum L.—Uncommon; SF.

VITACEAE

Parthenocissus quinquefolia (L.) Planch.—Common; SF, TT, ST.
Vitis labrusca L.—Common; SF.
Vitis riparia Michx.—Uncommon; ST.

Monocots

CYPERACEAE

Carex silicea Olney—Occasional; DG, edge SF.
Carex pensylvanica Lam.—Abundant; SF, DG.
**Cyperus grayii* Torr.—Frequent; in low dunes.
Cyperus filiculmis Vahl—Common; DG.
Scirpus atrocinctus Fern.—Local; WS.

JUNCACEAE

Juncus balticus Willd.—Common; WS.
Juncus gerardi Loisel.—Abundant; SM.
Juncus greenei Oakes & Tuckerm.—Occasional; TT.
Juncus tenuis Willd.—Local; WS.

JUNCAGINACEAE

Triglochin maritima L.—Occasional; WS, DG.

LILIACEAE

Maianthemum canadense Desf.—Abundant; SF.
Polygonatum pubescens (Willd.) Pursh—Uncommon; SF.
Smilacina stellata (L.) Desf.—Common; SF, TT, ST.

POACEAE

Agrostis alba L.—Occasional; DG.

Agrostis scabra L.—Frequent; DG.

Agropyron repens (L.) Beauv.—Occasional; DG, ST.

**Ammophila breviligulata* Fern.—Abundant; low dunes.

Andropogon scoparius Michx.—Common; DG, edges of TT, SF.

**Aristida tuberculosa* Nutt.—Locally abundant; west side of Route 1A in dry sand, and in low dunes, especially in northern portion of study area.

Bromus tectorum L.—Common; SF, DG.

Calamagrostis canadensis (Michx.) Nutt.—Common; edge of SF.

Danthonia spicata (L.) Beauv.—Common; DG.

Digitaria ischaemum (Schreb.) Muhl.—Common; roadsides and around foundation of building.

Digitaria sanguinalis (L.) Scop.—Occasional; roadside and DG.

Distichlis spicata (L.) Greene—Common; SM.

Festuca ovina L.—Occasional; DG.

Festuca rubra L.—Frequent; edge SF.

Panicum lanuginosum Ell. var. *fasciculatum* (Torr.) Fern.—Occasional; DG.

Phleum pratense L.—Occasional; SF.

Poa pratensis L.—Occasional; SF.

Puccinellia maritima (Huds.) Parl.—Common; SM.

**Puccinellia paupercula* (Holm) Fern. & Weath. var. *alaskana* (Scribn. and Merr.) Fern. and Weath.—Occasional; edge of salt marsh.

Spartina alterniflora Loisel.—Common; SM.

Spartina patens (Ait.) Muhl.—Common; SM.

ENDANGERED SPECIES

Of the 398 vascular plant taxa regarded as rare in New Hampshire (Storks and Crow, 1978), 37 (9%) are coastal (including the Great Bay estuary); some are known only from a single town or one site (Crow and Storks, 1980). Of the 141 species found at the dunes, two are regarded as Rare, two are given Threatened status and five others are treated as Endangered (Crow and Storks, 1980):

Rare

Artemisia caudata

Puccinellia paupercula var. *alaskana*

Threatened
- *Ammophila breviligulata*
- *Salicornia bigelovii*

Endangered
- *Arenaria peploides* var. *robusta*
- *Aristida tuberculosa*
- *Cyperus grayii*
- *Hudsonia ericoides* ssp. *tomentosa*
- *Salicornia virginica*

Ammophila breviligulata

The Seabrook Dunes population of *Ammophila* represents the most significant (largest and best developed) in the state. This beach grass also occurs on the foredune at Seabrook Beach and in several sandy areas along the New Hampshire coast, especially along roadsides and near residential areas where the natural vegetation has managed to persist. Field work along the coast of New Hampshire in 1982 revealed that the assumed rarity of this species is probably a result of under-collection and that its status as a threatened species merits re-evalution.

Arenaria peploides var. *robusta*

The Seabrook Dunes site of *A. peploides* was originally discovered by Dr. Frank Richardson in 1973 (Breeding et al., 1974; Richardson, pers. comm.) This site consists of only one plant and represents the only known occurrence of this species in the state. The species appears to be declining in Massachusetts; it has not been collected on Plum Island since 1915 and may have been extirpated there (McDonnell, 1979).

Aristida tuberculosa

Aristida tuberculosa is locally abundant on the low dunes in the backdune community at Seabrook and along sandy roadsides at Seabrook Beach. This grass, restricted in New Hampshire to the Town of Seabrook, is also listed in the regional New England list of rare and endangered plants (Crow et al., 1981).

Artemisia caudata

Outside of the study area this composite is scattered along the New Hampshire coast in sandy sites such as on the foredune at Seabrook Beach.

Cyperus grayii

The Seabrook Dunes population of this sedge is highly significant since this species is restricted in New Hampshire to the Town of Seabrook. This species is also found on the foredune at Seabrook Beach.

Hudsonia ericoides ssp. *tomentosa*

Until the summer of 1982 when a small population of *Hudsonia ericoides* ssp. *tomentosa* was found in the Town of Rye, this taxon had only been documented from the Town of Seabrook and dunes near Ossipee Lake. In the Seabrook study area, it forms large mats on the low dunes where it is well adapted to shifting sands. McDonnell (1981) found that *Hudsonia* exhibited the greatest sensitivity to trampling of all the dune plants of Plum Island.

Puccinellia paupercula var. *alaskana*

This grass of saline sites occurs scattered on the salt marsh, particularly in the driftline area. It is sometimes difficult to distinguish this species from depauperate plants of *P. maritima.*

Salicornia bigelovii

This species is occasionally found on the New Hampshire coast in very saline pannes. At the Seabrook study site a few plants were found in a low area at the north end of the dunes. The assumed rarity of this species may be due in part to its inconspicuous habit.

Salicornia virginica

This larger, perennial species of *Salicornia* is known in New Hampshire from only two towns (Hampton Falls and Seabrook). Of the three New Hampshire populations, the population at the Seabrook Dunes is the largest (albeit still rather small).

SUMMARY

In New Hampshire the coastal sand dune habitat appears once to have been more extensive and widespread than it is now. Presently, native sand dune species have patchy distributions and persist along roadsides, among residential buildings and on the foredunes at Seabrook and Hampton Beach State Park. Hence, the Seabrook Dunes represents the largest remnant sand dune habitat of the New Hampshire coast. These dunes harbor two rare, two threatened and five endangered plant taxa. Of these nine rarities, three species have populations at the Seabrook Dunes considered the most significant in the state.

ACKNOWLEDGMENTS

We thank T. J. Bertrand for help with field and herbarium work. We also thank I. Storks Cotter, M. J. McDonnell, T. D. Lee and C. T. Philbrick for comments on an earlier draft of the manuscript. This project was funded by the Department of Commerce, NOAA, Office of Ocean and Coastal Resource Management through the New Hampshire Office of State Planning.

LITERATURE CITED

Breeding, C. H. J., F. D. Richardson, and S. A. Pilgrim. 1974. Soil survey of New Hampshire tidal marshes. New Hampshire Agric. Exp. Sta. Res. Rep. 40.

Crow, G. E., W. D. Countryman, G. L. Church, L. M. Eastman, C. B. Hellquist, L. J. Mehrhoff, and I. M. Storks. 1981. Rare and endangered vascular plant species in New England. Rhodora 83: 259–299.

______, and I. M. Storks. 1980. Rare and endangered plants of New Hampshire: a phytogeographical viewpoint. Rhodora 82: 173–189.

Dunlop, D. A. and G. E. Crow 1983. Coastal Endangered Plant Inventory. A report on the rare and endangered plant species of the coastal zone of New Hampshire. (Includes maps). The State of New Hampshire Office of State Planning, Concord, New Hampshire. (Report).

______, and G. E. Crow. 1985. Rare Plants of Coastal New Hampshire. Rhodora 87: 478–501.

______, G. E. Crow, and T. J. Bertrand. 1983. Coastal Endangered Plant Inventory. A report on the Seabrook Dunes, its vegetation and flora. New Hampshire Office of State Planning. Concord, New Hampshire. (Report).

Fernald, M. L. 1950. Gray's Manual of Botany. 8th ed. Corrected printing, 1970. D. Van Nostrand Co., New York.

Gleason, H. A. and A. Cronquist. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. D. Van Nostrand Co., New York.

McDonnell, M. J. 1979. The flora of Plum Island, Essex County, Massachusetts. New Hampshire Agric. Exp. Stat. Bull. 513.

______. 1981. Trampling effects on coastal dune vegetation in the Parker River National Wildlife Refuge, Massachusetts, USA. Biol. Conserv. 21: 289–301.

Storks, I. M. and G. E. Crow. 1978. Rare and endangered vascular plant species in New Hampshire. The New England Botanical Club in cooperation with the U.S. Fish and Wildlife Service [Region 5, Newton Corner, MA].

DEPARTMENT OF BOTANY AND PLANT PATHOLOGY
NESMITH HALL
UNIVERSITY OF NEW HAMPSHIRE
DURHAM, N.H. 03824

RARE PLANTS OF COASTAL NEW HAMPSHIRE[1]

Debra A. Dunlop and Garrett E. Crow

ABSTRACT

An inventory was made in the summer of 1982 of 42 vascular plant species previously identified as rare, threatened, or endangered in the coastal regions of seven New Hampshire towns. Field work was conducted to confirm historical records and investigate appropriate habitats for new sites. Of the 42 species, 14 are considered *rare,* 11 *threatened,* 13 *endangered* and 4 are believed to be extirpated from this area. Forty-eight new sites are reported, 12 of which are new town records.

Key Words: Rare plants, coastal plants, New Hampshire flora

In the summer of 1982, a two-part project was established to develop baseline data on coastal New Hampshire resources, particularly with respect to vascular plants regarded as rare, threatened, or endangered. One part of this project focused on the natural dune vegetation of the Seabrook dunes, with special recognition given to those plant species considered rare for the state (Dunlop et al., 1983). This paper summarizes the results of the second part (Dunlop and Crow, 1983), and focuses on the rare vascular plant species in the coastal regions of seven New Hampshire towns.

In 1978, 398 vascular plant taxa were determined by Storks and Crow (1978) as sufficiently rare in New Hampshire to warrant their protection through habitat preservation. The majority of the plants included on New Hampshire's rare plant list reflected documentation of populations in fewer than ten towns, with 60% of them known from four or fewer towns and 36% known from only one or two towns in the entire state. The criteria used in that study were largely based on guidelines developed by the Natural Areas Criteria Committee of the New England Botanical Club (Countryman, 1972; Countryman et al., 1981). Special consideration was given to taxa which then appeared to be on the decline with respect to the number of documented localities, to plants of specialized or vulnerable habitats, to plants that occur here disjunct from their normal geographical range, and to endemics. Further attention was given to plants such as ferns and orchids that were likely to be exploited because of particularly appealing features.

---

[1] Scientific contribution 1297 from the New Hampshire Agricultural Experiment Station.

Later, Crow and Storks (1980) identified areas of New Hampshire that seemed to have high concentrations of rare plants. Nine percent of the state's rare flora was chiefly restricted to the coastal area (including the Great Bay estuary). Since the coastal region in New Hampshire has experienced continued pressure from development interests, the irreversible impact on our rare flora is a major concern.

In this study we investigated populations of 42 species; of these, 14 are regarded as rare, 11 threatened, 13 endangered, and 4 are now believed to be extirpated from the state. For the purposes of this study, the coastal area was defined as the region below the 20′ contour line on the USGS topographical maps in the seven coastal towns (New Castle, Portsmouth, Rye, North Hampton, Hampton, Hampton Falls and Seabrook). This area includes a wide range of habitats such as sand dunes and interdune swales, brackish ponds and tidal creeks, and salt marshes, as well as ecotones at their margins and moist woods on some salt marsh islands.

A list which provided information on historical sites for rare plants in each coastal town was generated based both on previous work of Storks and Crow (1978) and on a computerized data base of rare plants at NHA. This list included specimen records from regional herbaria and label data such as site, habitat and collection date. During the period from May to October 1982, a search was made to re-locate each historical site with a known location (except those reported from the Isles of Shoals). However, many of the older records lacked specific locality data an could not be located and verified. Additional field work was carried out to locate new sites for each species by examining appropriate habitats in the coastal area.

An alphabetical tabulation of the species considered rare, threatened, endangered or extirpated in the coastal area follows. For each town, historical sites and new locations are listed (north to south). First, unverifiable historical sites (those lacking locality data) are listed for the record; these are followed by historical sites with specific locations. When a historical site was verified, the most recent documentation of that population is given. When a search failed to re-locate the historical population, it is indicated as "plants not re-located" and the date of the most recent collection is cited. Forty-eight new sites are listed; 12 of these are new town records and are so indicated.

Locality maps are available at NHA and at the New Hampshire Office of State Planning.

Concern for exploitation of these plant populations was carefully considered before a decision was made to publish locality data. Species presented here do not appear to be vulnerable to such exploitation. Site information is provided with the possibility that it will be useful for future phytogeographical, ecological and floristic studies by establishing a baseline against which future work in the area can be measured.

ACKNOWLEDGMENTS

We thank T. J. Bertrand for assistance in the field and C. M. Straus for providing information and directing us to sites for *Iris prismatica* and *Iva fructescens*. We are grateful to T. D. Lee and C. M. Straus for their helpful comments on an earlier draft of this manuscript. This project was funded by the Department of Commerce, NOAA, Office of Ocean and Coastal Resource Management through the New Hampshire Office of State Planning.

RARE, THREATENED, AND ENDANGERED PLANTS OF COASTAL NEW HAMPSHIRE

State Status: R = rare; T = threatened; E = endangered; Ex = believed to be extirpated in the state.

Status	Town	Site	Date	Comments
R	*Agalinis maritima* (Raf.) Raf.			
	Portsmouth	Sagamore Creek	12 Oct 1961	
			19 Aug 1982	Verifies 12 Oct 1961 record
	Rye	Rye Harbor	31 Aug 1982	New town record
	Hampton Falls	Unspecified	8 Sep 1916	
	Seabrook	Hunt's Island	17 Aug 1982	New site
		Hunt's Island Creek	17 Aug 1982	New site
		Beckman's Island	26 Aug 1982	New site
		Mill Creek	26 Aug 1982	New site
		Shepherd Brook	10 Aug 1982	New town record
T	*Ammophila breviligulata* Fern.			
	Note: with 10 new sites, status as "threatened" may warrant re-evaluation			
	New Castle	Unspecified	19 Aug 1901	
		New Castle Commons	7 Jul 1982	New site
	Rye	Rye Beach	13 Aug 1886	Plants not re-located
		Wallis Sands	22 Jul 1982	New site
		Awcomin Marsh	31 Aug 1982	New site

		North Straw Point	31 Aug 1982	New site
		Jenness Beach	22 Jul 1982	New site
		Eel Pond	19 Aug 1982	New site
	North Hampton	Little River Swamp	19 Aug 1982	New town record
	Hampton	Unspecified	Aug 1876	
		North Plaice Cove	19 Aug 1982	New site
		Bicentennial Park	31 Aug 1982	New site
		Hampton State Beach	1895	
			10 Oct 1903	
			1 Jul 1982	Verifies 1895 and 1903 records
	Seabrook	Hampton Harbor	25 Aug 1982	New site
		Seabrook Dunes	13 Oct 1977	
			15 Aug 1982	Largest state population Verifies 1977 record
E	*Arenaria peploides* Gray			
	Seabrook	Seabrook Dunes	1973	
			7 Oct 1982	Verifies 1973 record Only one plant found
E	*Aristida tuberculosa* Nutt.			
	Note: also listed on the New England List (Crow et al., 1981)			
	Seabrook	Seabrook Beach	17 Sep 1958	
			15 Aug 1982	Verifies 1958 record
		Seabrook Dunes	13 Oct 1977	
			15 Aug 1982	Verifies 13 Oct 1977 record

Status	Town	Site	Date	Comments
R	*Artemisia caudata* Michx.			
	Rye	Unspecified	14 Nov 1957	
		Wallis Sands	25 Aug 1949	Plants not re-located
		East Route 1A	19 Aug 1982	New site
	North Hampton	Little Boars Head	31 Aug 1982	New site
		Little River Swamp	19 Aug 1982	New town record
	Hampton	Unspecified	Aug 1876	
		Unspecified	31 Aug 1902	
		N. Plaice Cove	19 Aug 1982	New site
		Hampton State Beach	1 Jul 1982	New site
	Hampton Falls	Unspecified	22 Sep 1901	
		Railroad Embankment	10 Sep 1916	
			10 Aug 1982	May verify 10 Sep 1916 record
	Seabrook	Seabrook Beach	9 Sep 1958	
			1 Jul 1982	Verifies Sep 1958 record
		Seabrook Dunes	15 Aug 1982	New site
E	*Cardamine bulbosa* (Schreb.) BSP.			
	Hampton Falls	Unspecified	28 May 1915	
	Seabrook	Unspecified	Jun 1896	
		John Lowell's	1896	Plants not re-located

R	*Celtis occidentalis* L.			
	Note: species approaches northern limit in New Hampshire			
	Seabrook	Hunt's Island	14 Aug 1972	
			29 Jun 1982	Verifies 14 Aug 1972 record Two trees found
R	*Cenchrus longispinus* (Hack.) Fern.			
	Seabrook	Seabrook Beach	17 Sep 1958	Plants not re-located
R	*Chamaecyparis thyoides* (L.) BSP.			
	Note: species approaches northern limit in New Hampshire and coastal Maine			
	Rye	Unspecified	26 Jun 1922	
		Unspecified	8 Nov 1948	
		Rye Beach	10 Nov 1948	*See* Burke Pond site
		Fairhill Swamp	24 Sep 1979	
			15 Jun 1982	Verifies 24 Sep 1979 record Only 10 live trees
		Burke Pond	22 Jul 1982	May verify 1948 Rye Beach site.
	Hampton	Unspecified	no date	
E	*Chenopodium rubrum* L.			
	Rye	Rye Beach	no date	Plants not re-located
E	*Cirsium horridulum* Michx.			
	Rye	Unspecified	14 Jun 1903	
	Hampton Falls	Taylor River	3 Aug 1982	New site

Status	Town	Site	Date	Comments
	Seabrook	The Rocks	22 Jun 1982	New town record
E	*Cyperus grayii* Torr.			
	Seabrook	Unspecified	no date	
		Seabrook Dunes	13 Oct 1977	
			15 Aug 1982	Verifies 13 Oct 1977 record
Ex	*Diplachne maritima* Bickn. syn. = *Leptochloa fasicularis* (Lam.) Gray var. *maritima* (Bickn.) Gl.			
	Seabrook	John Brown's	Sep 1902	Plants not re-located
R	*Eleocharis parvula* (R. & S.) Link			
	Rye	Rye Beach	8 Aug 1886	Plants not re-located
	Hampton	Unspecified	22 Sep 1901	
	Seabrook	Unspecified	Aug 1896	
E	*Eleocharis halophila* Fern.			
	Rye	Star Island	14 Jun 1952	
Ex	*Elymus mollis* Trin.			
	Rye	Isles of Shoals	Aug 1885	
R	*Gentiana crinita* Frol.			
	North Hampton	Unspecified	14 Oct 1968	

	Hampton	Unspecified	9 Sep 1902	
	Hampton Falls	Unspecified	8 Sep 1960	
E	*Hudsonia ericoides* L. ssp. *tomentosa* (Nutt.) Nickerson & Skog			
	Rye	Eel Pond	19 Aug 1982	New town record
	Hampton	Unspecified	no date	
		Unspecified	Jul 1896	
	Seabrook	Seabrook Beach	1 Jul 1982	New site
		Seabrook Dunes	13 Oct 1977	
			15 Aug 1982	Verifies 13 Oct 1977 record
R	*Iris prismatica* Pursh			
	Rye	Unspecified	28 Jun 1944	
		Marsh Pond Rd.	24 Jun 1982	New site
		Wallis Sands Marsh	13 Jul 1982	New site
		Rye North Beach	13 Jul 1982	New site
	Hampton	Unspecified	Aug 1876	
		Rte. 1 Interchange	29 Jun 1982	New site
	Hampton Falls	Taylor River	3 Aug 1982	New site
T	*Isoetes engelmannii* A. Br.			
	Seabrook	Unspecified	Aug 1896	
R	*Iva frutescens* L. var. *oraria* (Bartlett) Fern. & Griscom			
	Portsmouth	Unspecified	8 Jan 1949	
		Pleasant Point	11 Aug 1982	New site

Status	Town	Site	Date	Comments
T	*Lemna trisulca* L.			
	Hampton/ Hampton Falls (Town Line)	Taylor River	21 Aug 1971	
			21 Sep 1982	Verifies 21 Aug 1971 record
T	*Lycopodium inundatum* L. var. *bigelovii* Tuckerm.			
	Seabrook	Unspecified	Sep 1895	
R	*Lycopus rubellus* Moench			
	Hampton Falls	Unspecified	8 Sep 1916	
T	*Mikania scandens* (L.) Willd.			
	Hampton Falls	Hampton Falls River	15 Sep 1960	Plants not re-located
T	*Platanthera flava* (L.) Lindl. var. *herbiola* (R. Br.) Luer			
	syn = *Habenaria flava* (L.) R. Br. var. *herbiola* (R. Br.) Ames and Correll			
	Hampton Falls	Unspecified	12 Jul 1896	
T	*Polygala cruciata* L. var. *aquilonia* Fern. and Schub.			
	Rye	Unspecified	27 Aug 1917	
	Hampton	Unspecified	Aug 1876	
		Unspecified	1896	
	Seabrook	Unspecified	Sep 1898	

T	*Polygonum prolificum* (Small) Robins.			
	Rye	Rye Beach	16 Aug 1886	Plants not re-located
		Rye Harbor	3 Aug 1959	Plants not re-located
	Hampton Falls	Unspecified	22 Sep 1901	
		Unspecified	8 Sep 1916	
	Seabrook	Mill Creek	26 Aug 1982	New town record
E	*Polygonum robustius* (Small) Fern.			
	Hampton	Unspecified	31 Aug 1902	
		Unspecified	8 Sep 1960	
R	*Potamogeton pectinatus* L.			
	Rye	Unspecified	10 Aug 1886	
	Hampton	Unspecified	15 Jul 1911	
T	*Potentilla pectinata* Raf.			
	Rye	Unspecified	Jul 1911	
		Star Island	2 Jul 1967	
	Hampton	Unspecified	15 Jul 1911	
R	*Puccinellia paupercula* (Holm) Fern. & Weath. var. *alaskana* (Schribn. & Merr.) Fern. & Weath.			
	Portsmouth	Unspecified	no date	
	Rye	Unspecified	no date	
	Seabrook	Unspecified	Sep 1978	
		Seabrook Dunes	15 Aug 1982	New site

Status	Town	Site	Date	Comments
E	*Rumex pallidus* Bigel.			
	Rye	Star Island	5 Jul 1967	
	North Hampton	Little Boars Head	14 Aug 1886	Plants not re-located
	Hampton	Hampton Beach	5 Oct 1901	Plants not re-located
Ex	*Sagina nodosa* (L.) Fenzl ssp. *nodosa*			
	Rye	Isles of Shoals	no date	
T	*Salicornia bigelovii* Torr.			
	Portsmouth	Sagamore Creek	10 Jul 1973	
			27 Jul 1982	Verifies 10 Jul 1973 record
	Rye	Little Harbor	19 Sep 1901	Plants not re-located
		Rye Harbor	3 Oct 1959	Plants not re-located
	Hampton Falls	Unspecified	8 Sep 1916	
		Hampton Falls River	17 Aug 1982	New site
	Seabrook	Unspecified	1931	
		Brown's River	14 Aug 1972	
			10 Jun 1982	May verify 14 Aug 1972 record
		Hunt's Island Creek	17 Aug 1982	New site
		Seabrook Dunes	7 Sep 1966	
			15 Aug 1982	Verifies 7 Sep 1966 record
E	*Salicornia virginica* L.			
	Hampton	Unspecified	Aug 1876	

	Hampton Falls	Hampton Falls River	10 Aug 1982	New town record
	Seabrook	Unspecified	7 Sep 1966	
		Brown's River	17 Aug 1982	New site
		Seabrook Dunes	17 Sep 1958	
			14 Sep 1982	May verify 17 Sep 1958 record
R	*Sparganium eurycarpum* Engelm.			
	New Castle	New Castle Commons	7 Jul 1982	New town record
	Rye	Parson Road	24 Jun 1982	New town record
		Burke Pond	22 Jul 1982	New site
	Hampton	Unspecified	no date	
R	*Spartina caespitosa* (A. A. Eaton) Fern.			
	Hampton Falls	Unspecified	26 Aug 1896	
		John Brown's	29 Sep 1896	
	Seabrook	Unspecified	Aug 1896	
		Unspecified	21 Aug 1952	
E	*Sporobolus cryptandrus* (Torr.) Gray			
	Rye	Eel Pond	31 Aug 1982	New town record
	North Hampton	Little Boars Head	31 Aug 1886	
			31 Aug 1982	Verifies 31 Aug 1886 record
		Little River Swamp	31 Aug 1982	New site
	Hampton	N. Plaice Cove	31 Aug 1982	New site
		Bicentennial Park	31 Aug 1982	New site
		Hampton Beach	20 Sep 1898	

Status	Town	Site	Date	Comments
			26 Aug 1982	Verifies 20 Sep 1898 record
		S. Hampton Harbor	26 Aug 1982	New site
	Seabrook	Bound Rock	26 Aug 1982	New town record
Ex	*Triplasis purpurea* (Walt.) Chapm.			
	Rye	Little Harbor	19 Sep 1901	Plants not re-located.
E	*Triosteum aurantiacum* Bickn.			
	Seabrook	The Rocks	3 Jun 1972	
			22 Jun 1982	Verifies 3 Jun 1972 record
		Hunt's Island	29 Jun 1982	New site
T	*Woodwardia areolata* (L.) Moore			
	Rye	Rye Beach	1 Sep 1886	Plants not re-located
	Seabrook	Unspecified	14 Sep 1896	

LITERATURE CITED

Countryman, W. D. 1972. Guidelines and criteria for the evaluation of natural areas. Natural Areas Criteria Committee of the New England Botanical Club, Inc. Cambridge, MA.

———, J. J. Dowhan, and L. E. Morse. 1981. Regional coordination of rare plant information synthesis by the New England Botanical Club. pp. 123–131 *In:* L. E. Morse and M. S. Henifin, Eds. Rare Plant Conservation: Geographical Data Organization. N. Y. Bot. Gard., Bronx, NY.

Crow, G. E., and I. M. Storks. 1980. Rare and endangered plants of New Hampshire: a phytogeographical viewpoint. Rhodora 82: 173–189.

———, W. D. Countryman, G. L. Church, L. M. Eastman, C. B. Hellquist, L. J. Mehrhoff, and I. M. Storks. 1981. Rare and endangered vascular plant species in New England. Rhodora. 83: 259–299.

Dunlop, D. A., and G. E. Crow. 1983. Coastal Endangered Plant Inventory. A report on the rare and endangered plant species of the Coastal Zone of New Hampshire. (Includes maps.) The State of New Hampshire Office of State Planning, Concord, NH. (Report).

———, ———, and T. J. Bertrand. 1983. Coastal endangered plant inventory. A report on the Seabrook Dunes, its vegetation and flora. The State of New Hampshire Office of State Planning, Concord, NH. (Report).

Storks, I. M., and G. E. Crow. 1978. Rare and endangered vascular plant species in New Hampshire. Prepared by the New England Botanical Club in cooperation with the U.S. Fish and Wildlife Service [Region 5, Newton Corner, MA].

DEPARTMENT OF BOTANY AND PLANT PATHOLOGY
UNIVERSITY OF NEW HAMPSHIRE
NESMITH HALL
DURHAM, NEW HAMPSHIRE 03824

THE INTRODUCTION AND SPREAD OF *VERONICA BECCABUNGA* (SCROPHULARIACEAE) IN EASTERN NORTH AMERICA

Donald H. Les and Ronald L. Stuckey

ABSTRACT

Veronica beccabunga L., indigenous to Eurasia, was introduced into North America toward the latter part of the nineteenth century. Originally confined to the East Coast of the United States, the range of the species has expanded to include seven states and two Canadian provinces. Historical evidence implicates ballast disposal in the initial introduction of the species, although multiple introductions may have occurred. Compared with other non-indigenous aquatic plants, the spread of *V. beccabunga* has been slower and less conspicuous. Interspecific competition with the native flora may have kept the progress of the species in check. The presently known distribution of *V. beccabunga* is mapped for North America. The species is dispersed mainly by plant fragments dislodged during periods of high water flow.

Key Words: *Veronica beccabunga*, European Brooklime, introduced aquatic, dispersal, North America

The European Brooklime, *Veronica beccabunga* L. (Scrophulariaceae), is one of about 12 aquatic species constituting section *Beccabunga* Dumort. of the genus (Cook, et al., 1974; Ozturk & Fischer, 1982). According to Smith (1823), the curious epithet "beccabunga" is derived from the German "Bach-pungen," Bach ("beck") meaning "rivulet" in English and referring to the usual habitat of the species. Fischer (1981) recognized three allopatric Eurasian subspecies of *V. beccabunga* [ssp. *beccabunga*, ssp. *abscondita* M. A. Fischer, and ssp. *muscosa* (Korsh.) A. Jelen], each occurring within a well-defined geographical region. *Veronica beccabunga* (Figure 1) is widespread in Europe (Pennell, 1921) where it commonly inhabits upper stream reaches of various substrate compositions (Haslam, 1978). Prior to 1870, European Brooklime (hereinafter E. Brooklime) was not known to occur in North America. The closely related native species *Veronica americana* (Raf.) Schwein., however, is as widespread in North America as *V. beccabunga* is in Europe (Pennell, 1921).

Specimens of *Veronica beccabunga* collected in New Jersey by Schrenk in 1876 provide the earliest evidence of the species in North America. Since that time, collections of E. Brooklime have been made throughout many parts of the eastern United States and

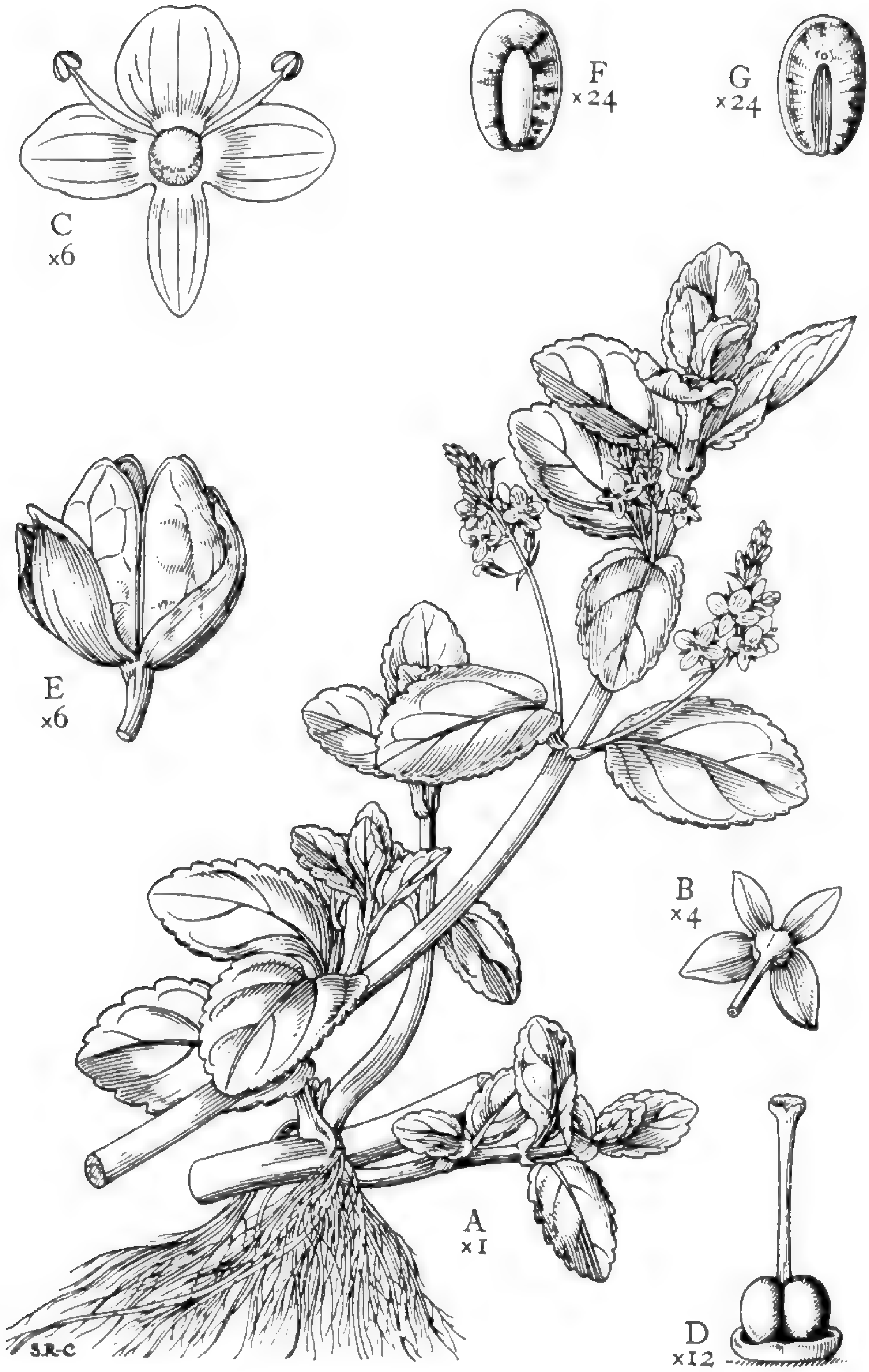


Figure 1. Habit of *Veronica beccabunga* L. **A.** lower and upper parts of a flowering stem an internode and two branches cut out; **B.** calyx; **C.** corolla and stamens; **D.** gynoecium and disc; **E.** fruit; **F–G.** seed in two views. Figure and caption from Ross-Craig (1979); used with permission from Bell and Hyman, Ltd.

Canada. In 1982, the authors collected specimens of *V. beccabunga* at several localities in central Ohio; these specimens constituted the first state records of the species known at that time. Discovery of these new localities indicates that the range of E. Brooklime in North America is continuing to expand. This discovery provided the impetus for us to investigate further the distributional history of this species in North America.

MIGRATORY PATTERNS

Pennell (1921) listed *Veronica beccabunga* as occurring only in Quebec, New York, and New Jersey. Later works by Pennell (1935), Muenscher (1944), Groh (1946), Dore and Gillett (1955), Voss (1957), and Rosseau (1968) included additional records of the species in Ontario, Michigan, Pennsylvania and West Virginia. Mason (1957), Stodola (1967), and Sellers (pers. comm.) have recorded E. Brooklime (subsp. *beccabunga*) on the West Coast of North America (California and British Columbia), but these localities will not be considered in detail here. Using published reports as a guide, a list of the presently known localities for *V. beccabunga* was compiled. Voucher specimens for most sites reported in the literature were located in several regional herbaria (ALBC, CU, DAO, HAM, MICH, MO, NY, NYS, OS, PENN, PH) and constitute the sites listed on our maps. The verified localities were arranged chronologically (*see* Appendix) and then mapped for three time periods based upon dates of collection: 1) specimens collected before 1900, 2) specimens collected 1900–1940, and 3) specimens collected 1940–1985 (Figure 2). This technique provides an interpretation of the spread of the species in terms of time (years elapsed between new collection sites) and degree (number of new sites per time interval). The resulting pattern (Figure 2) is one of a general northward and westward movement from a point of origin near the harbor district of New York City. Similar patterns have been observed for several other foreign aquatic and wetland species such as *Lythrum salicaria, Lycopus europaeus,* and *Rorippa sylvestris* (Stuckey, 1966; Stuckey, 1980; Stuckey & Phillips, 1970). In the case of *V. beccabunga,* however, the spread has not been nearly as rapid or as conspicuous as that noted for "weedy" species such as *Lythrum salicaria.* Unlike many foreign aquatic weeds, *V. beccabunga* does not do well in lentic environments, but requres colder, more oxygen-rich waters of streams, brooks, and springs (Aichele, 1976; Stodola, 1967).

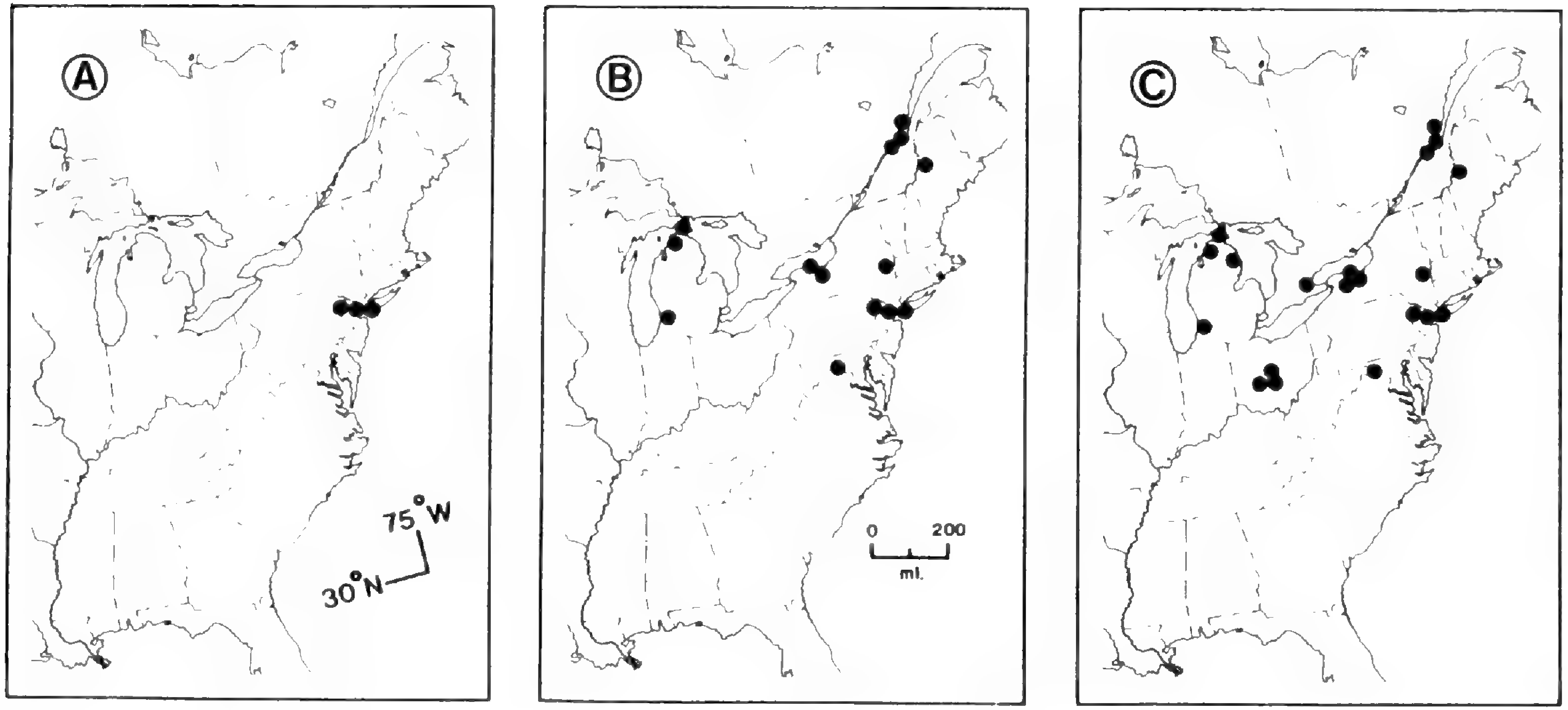


Figure 2. The distribution of *Veronica beccabunga* in eastern North America during three consecutive time intervals. **A.** distribution before 1900; **B.** distribution from 1900–1940; **C.** distribution from 1940–1985. Vouchers for mapped sites are listed in Appendix.

The slower migration of E. Brooklime may be due to its affinity for undisturbed habitats where native species such as *Veronica americana* are already established. Because both *V. americana* and *V. beccabunga* are essentially equivalent ecologically (Marie-Victorin, 1935), it would be difficult for E. Brooklime to become established under such circumstances. Our finding of *V. beccabunga* in two localities of undisturbed vegetation in Ohio supports this hypothesis; in both of these areas *V. americana* does not occur. Furthermore, *V. beccabunga* was found at three sites within Clark and Delaware counties, Ohio in which *V. americana* is not known to occur. (*See* map of *V. americana* in Bentz & Cooperrider, 1978.) The absence of the native species presumably opened a vacant niche in which invading plants of E. Brooklime could become established. It would be informative to carry out experiments to determine which of these two species is the better competitor for newly opened habitats, and whether there are differences in their relative dispersal efficiency. Observations regarding habitats occupied by *V. beccabunga* were made by Groh (1946, p. 47) who remarked, "like its nearest American ally, *V. amèricana* Schwein., it [*V. beccabunga*] is confined mostly to ditches and muddy shores where it is of little account as a weed." However, the species has been noted as weedy in Ontario by Dore and Gillett (1955, p. 82) who reported it to be "choking Hopple Creek" near Wales. If habitat competition is indeed a factor regulating the migration of E. Brooklime, then one would expect its progress to be as slow as our maps indicate. However, opportunistic establishment could eventually expand the range of *V. beccabunga* to equal that of *V. americana* (map in Muenscher, 1944, p. 318). Such has been the case with *V. anagallis-aquatica,* another non-indigenous Eurasian species (map in Muenscher, 1944, p. 318).

POSSIBLE MEANS AND SITES OF INTRODUCTION

Although the name *Veronica beccabunga* appears in several older manuals (e.g., Pursh, 1814), these records refer to *V. americana,* which was not regarded as distinct taxonomically from the European plants until 1830. The earliest records of bona fide *V. beccabunga* are from the East Coast of the United States (*see* Appendix). Propagules were probably first brought into this region in ship ballast as it was disposed of at ports. This method has been implicated in the introduction of *Lycopus europaeus* into North America (Stuckey & Phillips, 1970). Evidence for a similar introduction of E. Brooklime is an early specimen [Schrenk, s.n. (NY)] collected in 1880 from a ballast site in New York. Brown (1879) discovered plants of *V. beccabunga* in such disposal sites in New York which had (p. 355) "undoubtedly sprung from seeds introduced with ballast." He also indicated that the species was not known to him previously as growing wild in the country.

Brown's (1879) account contained valuable information regarding the importance of ballast disposal as a method of plant introduction. He stated (p. 353) "Never before ... has so much [foreign vegetation] been brought to this country [USA] during the same period as in the past two years [1878–79]." He further commented (p. 353) "... on Gowanus Creek [the site where he first discovered *V. beccabunga*], vessels have for many months past been discharging [ballast] without cessation, night and day." The fact that the oldest collections of E. Brooklime were made within a 100 mile radius of Long Island, New York attests to the likelihood that ballast disposal was responsible for the earliest introduction of the species into North America.

Although plants and seeds of *Veronica beccabunga* were likely to have been dispersed to different sites from the New York City area, some populations of the species may have been established independently. A possibility exists that plants were brought in from Europe with fish stocks and carelessly discarded into watercourses. Muenscher (1944, p. 318) noted that in the United States, *V. beccabunga* occurs locally "... in spring-fed ponds about fish hatcheries," and Bursche (1971, p. 78) reported that E. Brooklime is "specially valued in trout streams" in Europe. Fish hatcheries were responsible for much of the early spread of another aquatic plant, *Potamogeton crispus*, in North America (Stuckey, 1979).

Voss (1957, p. 29) related information noted on a specimen of *Veronica beccabunga* collected in Emmet Co., Michigan suggesting yet another means by which the species could have spread: "Its location ... is possibly due to seed having been washed in from Lake Michigan, but more likely to having been brought to the Tannery with hides." In any case, hides brought to that tannery would have originated in North America, and contaminating seeds would have effected dispersal of populations already established in the region.

There is also a possibility that whole plants were intentionally brought to North America for use in home aquaria. This explanation is reasonable in light of Muhlberg's (1982, p. 191) comments that "*V.[eronica] beccabunga* has often been used in cold-water aquaria, particularly in early days of aquarium plant cultivation." Because such introductions usually result from the careless disposal of specimens, actual incidents are very difficult to document. We have been unable to find evidence that any introductions of E.Brooklime occurred via this route.

We are not certain, therefore, whether the present distribution of E. Brooklime in North America is the result of one or of multiple introductions. Although there is fairly good documentation that the initial introduction of the species occurred around Long Island, New York by seeds disposed of in ballast, whole plants brought in with fish hatchery stocks may have been responsible for establishing some of the other sites at which the plant was subsequently found. The presence of disjunct populations on the Pacific Coast also indicates the likelihood of multiple introductions because of the relatively great distance (over 1700 miles) separating the eastern and western North American populations.

GEOGRAPHICAL ORIGIN OF NORTH AMERICAN POPULATIONS

In Eurasia, *Veronica beccabunga* is comprised of three vicarious subspecies, a factor which enabled us to trace the geographical origin of plants introduced into North America. Manfred Fischer (1981) and G. Fischer (1981) detailed these distributions, which we summarize as follows: subspecies *muscosa*—Asia, mainly east of Iran; subspecies *abscondita*—Mediterranean and Transcaucasian region; subspecies *beccabunga*—Europe and northwest Turkey. Brown (1879) noted that ballast-introduced species were most often natives of Europe (Britain and Germany) or the Mediterranean region. Specimens of *V. beccabunga* collected in British Columbia, New Jersey, Ohio, Pennsylvania, and Quebec were identified as subspecies *beccabunga* (by Roger Sellers, University of Oklahoma), placing the origin of our plants in Europe rather than in the Mediterranean region where supspecies *abscondita* occurs. Other subspecies of *V. beccabunga* have not yet been found in North America.

It may also be possible to use cytological data to assist in pinpointing actual sites of origin for North American plants. In contrast to the native *Veronica americana* which is tetraploid, *V. beccabunga* is usually diploid with the exception of several tetraploid populations of subspecies *beccabunga* in the northern part of its range (Ozturk & Fischer, 1982). It would be informative to determine whether North American plants are diploid or tetraploid cytotypes. Such data might better clarify the region from which these plants originally came.

METHODS OF DISPERSAL

Little information has been published on the biology of *Veronica beccabunga*; in particular, its reproductive biology is not well known. The species is perennial and produces globose, flattened fruits in axillary racemes (Pennell, 1921). Two avenues of dispersal are possible, by seed or by entire plants. Van der Pijl (1982) includes *Veronica* with ombrohydrocharous (rain-wash) dispersed species and suggests that in *V. beccabunga* this method of dispersal may be enhanced by hygrochasy (capsule dehiscence in humid atmospheres). Although these factors may function to promote short-distance dispersal along stream banks, it is unlikely that long-distance dispersal occurs by actual water transport. The seeds of E. Brooklime are not buoyant (Guppy, 1906), and in most *Veronica* species they sink within one minute in fresh water (Praeger, 1913). Although the dynamics of seed movement in flowing waters have not been studied in detail, it is not likely that in *V. beccabunga* seed transport occurs over very great distances. Guppy (1906) observed that seeds of *V. beccabunga* were not represented in floating river drift as were those of characteristically water-dispersed species. In the Index to Ridley (1930), *V. beccabunga* is cited as an example of dispersal by adhesion. Guppy (1906) found that seeds of E. Brooklime form a mucilaginous coating when exposed to water, a feature not occurring in other species of the genus that he examined. The formation of mucilaginous seeds in E. Brooklime is circumstantial evidence for dispersal by adhesion.

Ridley (1930) referred to *Veronica beccabunga* as an example of a water-dispersed plant of riparian habitats that produces nonbuoyant seeds. He accounted for the abundance of E. Brooklime along watercourses by its ability to grow rapidly from detached branches when stranded on river banks. Ridley observed this form of dispersal in *V. beccabunga* in various English river systems. Plants of *V. beccabunga* are tolerant to drying apparently because of their ability to produce terrestrial forms along shores and other drying habitats (Stodola, 1967). Haslam (1978) remarked that *V. beccabunga* is a species characteristically uprooted during storm damage, and possesses the ability to recover quickly from such events. *Veronica* species can also exploit temporary habitats of silt deposition along stream banks where coarse substrates ordinarily prevent plant establishment (Haslam, 1978).

CONCLUSIONS

Veronica beccabunga was introduced into eastern North America near New York City in the late nineteenth century as a result of ballast disposal. The species spread westward through the dispersal of seeds and plant fragments. Separate introductions of plants from contaminated fish hatchery stocks may also have influenced the present distribution of the species. The rate by which E. Brooklime has spread in North America is slow in comparison to that of other non-indigenous aquatic plants and has probably been governed by competition with native plant species. Plants introduced into North America originated in Europe and belong to subspecies *beccabunga*. *Veronica beccabunga* is dispersed along rivers as fragments broken off from plants during storms or other periods of rapid current flow. Although the spread of E. Brooklime has not been as aggressive as that characteristic of weedy species, its distribution deserves further observation.

ACKNOWLEDGMENTS

We thank Roger Sellers for identifying our collections at OS and for supplying us with helpful information. We also extend our thanks to Daniel Crawford and Wayne Elisens who made useful comments on an early draft of the manuscript and to James Pringle who brought certain distributional information to our attention. We appreciate the assistance of the curators of herbaria from which we examined specimens and welcome reports of any records that may have been overlooked in the course of this study.

LITERATURE CITED

AICHELE, D. 1976. Wild Flowers. Cathay Books, London.

BENTZ, G. D., AND T. S. COOPERRIDER. 1978. The Scrophulariaceae subfamily *Rhinanthoideae* of Ohio. Castanea 43: 145–154.

BROWN, A. 1879. Ballast plants in New York City and its vicinity. Bull. Torrey Bot. Club 6: 353–360.

BURSCHE, E. M. 1971. A Handbook of Water Plants. Frederick Warne & Co. Ltd., London.

COOK, C. D. K., B. J. GUT, E. M. RIX, J. SCHNELLER, AND M. SEITZ. 1974. Water Plants of the World. Dr. W. Junk b.v., The Hague, The Netherlands.

DORE, W. G., AND J. M. GILLETT. 1955. Botanical Survey of the St. Lawrence Seaway Area in Ontario. Botany & Plant Pathology Division, Science Service, Canada Dept. of Agriculture, Ottawa.

FISCHER, G. 1981. Distribution patterns of *Veronica* species in the Balkan Peninsula. *In:* V. I. Velcev & S. I. Kozuharov, Eds., Mapping the Flora of the Balkan Peninsula. Publishing House of the Bulgarian Academy of Sciences, Sofia.

FISCHER, M. A. 1981. *Veronica* section *Beccabunga,* pp. 145–165. *In:* K. H. Richinger, Ed., Flora Iranica, vol 147. Akad. Druck- und Verlagsanstelt, Graz.

GROH, H. 1946. Canadian weed survey, third annual report.

GUPPY, H. B. 1906. Observations of a Naturalist in the Pacific Between 1896 and 1899. Vol. 2: Plant Dispersal. Macmillan & Co., Ltd., London.

HASLAM, S. M. 1978. River Plants. Cambridge University Press, Cambridge.

MARIE-VICTORIN, FR. 1935. Flora Laurentienne. Imprimerie de la Salle, Montreal.

MASON, H. L. 1957. A Flora of the Marshes of California. University of California Press, Berkeley.

MUENSCHER, W. C. 1944. Aquatic Plants of the United States. Comstock Pub. Co., Ithaca, New York.

MUHLBERG, H. 1982. The Complete Guide to Water Plants. EP Publishing Ltd., Germany.

OZTURK, A., AND M. A. FISCHER. 1982. Karyosystematics of *Veronica* section *Beccabunga* (Scrophulariaceae) with special reference to the taxa in Turkey. Pl. Syst. and Evol. 140: 307–319.

PENNELL, F. W. 1921. "Veronica" in North and South America. Rhodora 23: 1–22; 29–41.

———. 1935. The Scrophulariaceae of eastern temperate North America. Philadelphia Acad. Sci. Monogr. 1: 1–650.

PRAEGER, R. L. 1913. On the buoyancy of the seeds of some Brittanic plants. The Sci. Proc. Roy. Dublin Soc., ser. B. 14: 13–62.

PURSH, F. 1814. [1813]. Flora Americae Septentrionalis. 2 vols. White, Cochrane & Co., London.

RIDLEY, H. N. 1930. The Dispersal of Plants Throughout the World. L. Reeve & Co., Ltd., Ashford, Kent.

ROSS-CRAIG, S. 1979. Drawings of British Plants. Vol. 6 Scrophulariaceae. Bell & Hyman Ltd., London.

Rosseau, C. 1968. Histoire, habitat, et distribution de 220 plantes introduites au Quebec. Naturaliste Canad. 95: 49–169.

Smith, J. E. 1823. The English Flora, Vol. 1, 2nd ed. Longman, Rees, Orme, Brown & Green, London.

Stodola, J. 1967. Encyclopedia of Water Plants. T. F. H. Publications, Inc., Neptune City, New Jersey.

Stuckey, R. L. 1966. The distribution of *Rorippa sylvestris* (Cruciferae) in North America. Sida 2: 361–376.

———. 1979. Distributional history of *Potamogeton crispus* (Curly Pondweed) in North America. Bartonia 46: 22–42.

———. 1980. Distributional history of *Lythrum salicaria* (Purple Loosetrife) in North America. Bartonia 47: 3–20.

———, and W. L. Phillips. 1970. Distributional history of *Lycopus europaeus* (European Water-Horehound) in North America. Rhodora 72: 351–369.

Van der Pijl, L. 1982. Principles of Dispersal in Higher Plants, 3rd ed. Springer-Verlag, Berlin.

Voss, E. G. 1957. New records of vascular plants from the Douglas Lake region (Emmet and Cheboygan Counties), Michigan. Pap. Michigan Acad. Sci., Arts, and Letters. 42: 3–34.

DEPARTMENT OF BOTANY
THE OHIO STATE UNIVERSITY
COLUMBUS, OH 43210

APPENDIX

A chronology of collections of *Veronica beccabunga* made in eastern North America from 1876–1985

Collections prior to 1900

NEW JERSEY: Hudson Co.: Bergen Tunnel, Aug., 1876. *Schrenk s.n.* (NY). NEW YORK: Kings Co.: A. Brown *In:* Torr. Club Bull. 6: 358. 1879 (actual specimen not seen). NEW YORK: Hunter's Point, L[ong] I[sland] (ballast), 17 July, 1880, *Schrenk s.n.* (MO). PENNSYLVANIA: Northampton Co.: In cold, shaded rivulets on the shore of the Delaware, 1 mi. above Easton, 5 Oct., 1891, *Porter s.n.* (NY).

Collections from 1900 to 1940

QUEBEC: wet ground, St. Lawrence River, 10 July, 1905, *Churchill 72* (MO). NEW YORK: Monroe Co.: Irondequoit, wet meadow, Sept., 1915, *Baxter s.n.* (NY). NEW YORK: Monroe Co.: Irondequoit, wet meadows, 5 Sept., 1916, *Baxter 13* (NYS). NEW YORK: Monroe Co.: moist fields near Rochester, Oct. 10, 1916, *Baxter s.n.* (NYS). NEW YORK: Monroe Co.: Densmore Creek, Sept., 1917, *Baxter s.n.* (NYS). QUEBEC: Greves intercotidales de Beauport, 8 Aug., 1922, *Rolland 16204* (NY). MICHIGAN: Emmet Co.: Tannery Creek where it empties into Little Traverse Bay, 1924, *Fallass s.n.* (ALBC). QUEBEC: Murray Bay [La Malbaie], 1929, *Groh s.n.* (DAO). WEST VIRGINIA: Jefferson Co.: Harper's Ferry, 20 Aug., 1931, *Core s.n.* (NY). QUEBEC: Quebec Co.: Sillery, lieux sourceux au pied des caps, 30 July, 1933, *Marie-Victorin, et al. 45243* (PH). QUEBEC: 1934, *Groh s.n.* (DAO). MICHIGAN: Mackinac Co.: in shallow water, beach of Lake Huron, Mackinac Island, 28 July, 1935, *Gleason s.n.* (MICH, NY). NEW YORK: Rensselaer Co.: springy bank N. of Rennselaer, 4 Sept., 1936, *House 24065* (NY). MAINE: Somerset Co.: in muddy place on trickle from cold spring roadside north of Macomber, Aug. 31, 1937, *True 4462* (PENN). MICHIGAN: Kent Co.: Crooked Lake, Grattan Twp. sec. 20, 18 May, 1939. *Marcelline 1351* (MICH).

Collections from 1940 to 1985

NEW YORK: Livingston Co.: in spring brook, Caledonia, 13 June, 1942, *Muenscher, et al. 20472* (CU). ONTARIO: Wentworth Co.: S. area 20, trampled bank of canal at bridge [Royal Botanic Gardens, Dundas], 7 Aug., 1954, *Tamsalu 5120* (HAM). MICHIGAN: Alcona Co.: T27N, R9E, sec. 24, 12 July, 1958, *Gehring s.n.* (MICH). OHIO: Clark Co.: Moorefield Twp., SE 1/4 sec. 5, uncommon along creek in floating mats; ca. 10 miles NE of Springfield at the intersection of St. Rt. 4 and Mumper Rd. (169), 24 October, 1970, *Roberts 902* (OS). QUEBEC: Quebec Co.: Lorretteville, Rang St-Jacques, sur escarpement de la riviere pres du blvd Honore Mercier, 16 June, 1971, *Perras 71-156* (OS). OHIO: Franklin Co.: infrequent on mudflat of small island in Olentangy River just SE of Fawcett Center, 29 Oct., 1982, *Les 331* (OS). OHIO: Franklin Co.: infrequent in low depression between bicycle path and west bank of Olentangy River, just north of Bethel Rd., 31 Oct., 1982, *Les 332* (OS). OHIO: Franklin Co.: infrequent in low depressions and along muddy banks of Olentangy River, due east of lake in Antrim Park, 3 Nov., 1982, *Les 333 & Stuckey s.n.* (OS). OHIO: Clark Co.: Prairie Rd. fen, SE of intersection of old SR-4 and Prairie Rd., 15 Oct., 1983, *Les 350* (os). OHIO: Delaware Co.: Blue Limestone Park, Delaware, occasional in spring flowing through park, 26 Feb., 1984, *Les 354* (os).

CHROMOSOME NUMBER DETERMINATIONS IN FAM. COMPOSITAE TRIBE ASTEREAE

JOHN C. SEMPLE

ABSTRACT

The chromosome numbers of 245 individuals representing 145 taxa as well as hybrids from 21 genera are reported. The sample includes taxa with chromosomal base numbers of $x = 4$, 5, 6, 8 and 9. The following numbers are first reports for the taxa: *Aster chilensis* Nees, $2n =$ ca. 96; *A. gormanii* Piper, $2n = 9_{II}$; *A. ledophyllus* var. *covillei* (Greene) Cronq., $2n = 9_{II}$; *A. perelegans* Nels. & Macbr., $2n = 9_{II}$; *A. radulinus* Gray, $2n = 18$. Supernumerary chromosomes were found in *Aster prenanthoides* T. & G., *Erigeron inornatus* Gray var. *inornatus, Gutierrezia sarothrae* (Pursh) Britt. & Rusby, *Haplopappus venetus* (H.B.K.) Blake, *Lessingia nemaclada* Greene, and *Macheranthera commixta* Greene.

Key Words: Compositae, Astereae, chromosome numbers

INTRODUCTION

General cytological trends in the Tribe Astereae of the Fam. Compositae have been discussed by Raven et al. (1959), Turner et al. (1961), Solbrig et al. (1964), Anderson et al. (1974), Grau (1977) and Semple (1981). The tribe is recognized to consist of one large group of genera with an ancestral base number of $x = 9$ and a second group of taxa with $x = 6$, 5, 4 or 3. The origins of the latter taxa are viewed as polyphyletic and derived by some workers, while they are viewed as primitive and potentially ancestral to the former group by others. The data needed to clarify the cytological history of the tribe is not yet available. The counts listed below do not support or refute any of the theories that have been put forward during the past 25 years. Names used reflect my views on tribal history which have been outlined previously (Semple, 1981).

The chromosome number determinations listed below are being reported for the first time. Most are confirmations of previously published reports. The counts are being reported so that the information will be available to those doing biosystematic research on specific taxa. Strother (1972) has noted the need for large numbers of reports of chromosome numbers in biosystematic studies.

MATERIALS AND METHODS

Meiotic counts were made from pollen parent cells (PPC's) fixed in the field in Carnoy's Fixative 3:1 (absolute EtOH: glacial acetic acid) and then stored in 70% EtOH under refrigeration until examined. Anthers containing PPC's were dissected out of florets and squashed in 1% acetic orcein stain. Counts were made from freshly prepared slides using a Zeiss RA Standard Microscope with phase contrast optics.

Mitotic counts were made from root tip cells obtained from either seedlings or transplanted rootstocks following Semple (1978). Counts were made from freshly prepared slides as above.

Vouchers for all counts are deposited in WAT. Loran C. Anderson and Lowell Urbatch assisted in identifying collections of *Chrysothamnus, Ericameria,* and *Macronema*; Guy Nesom confirmed identifications of collections of *Erigeron*; Geraldine Allen assisted in identifying collections of some western $x = 8$ species of *Aster.*

RESULTS AND DISCUSSION

Chromosome number determinations from 245 collections representing 145 taxa as well as hybrids from 21 genera of the Tribe Astereae (Fam. Compositae) are listed in Table 1 below alphabetically by genus and species. About half the counts are from individuals of the genus *Aster.* The following are first reports for the taxa listed: *Aster chilensis,* $2n =$ ca. 96; *A. gormanii,* $2n = 9_{II}$; *A. ledophyllus* var. *covillei,* $2n = 9_{II}$; *A. perelegans,* $2n = 9_{II}$; *A. radulinus,* $2n = 18$.

Supernumerary chromosomes were found in the following taxa: *Aster prenanthoides* ($x = 8$), *Erigeron inornatus* var. *inornatus* ($x = 9$), *Gutierrezia sarothrae* ($x = 4$), *Haplopappus venetus* ($x = 6$), *Lessingia nemaclada* ($x = 5$), and *Macheranthera commixta* ($x = 4$). Supernumerary chromosomes varied in size from small 0.5 μm dots to larger chromosomes 1–2 μm long. They were present in taxa in both the large $x = 9$ group and the lower base number group(s) in the tribe.

Collections not otherwise indicated are those of J. and B. Semple (*S & S*). Key to other collectors: *Br* = Brammall; *Bt* = L. Brouillet; *Ch* = J. Chmielewski; *K* = R. Keir; *R* = G. Ringius; *S* = J. Semple.

Table 1. Alphabetical list of chromosome number determinations

Aster ascendens Lindl. $2n = 52$. U.S.A. **Colorado.** Teller Co.: Florissant, *S & Bt 7247.* **Montana.** Wheatland Co.: W of Shawmut, *S & Bt 6996.*

A. acuminatus Ait. $2n = 18$. CANADA. **Nova Scotia.** Halifax Co.: Sheet Harbour, *S & K 4803.* U.S.A. **Maine.** Franklin Co.: ME-16, rest area by Carrabassett River, *S. & K 4626.* **Vermont.** Addison Co.: W of Hancock, *S. 6893.*

A. anomalus Engelm. $2n = 16$. U.S.A. **Missouri.** Callaway Co.: W of New Bloomfield, *S & Ch 5302.*

A. ×*blakei* (Porter) House. $2n = 18$. CANADA. **Nova Scotia.** Digby Co.: Digby Neck, Midway Lake, *S. & K 4869.*

A. azureus Lindl. $2n = 32$. U.S.A. **Nebraska.** Nemaha Co.: W of Auburn, *S & Bt 7357.*

A. bracteolatus Nutt. $2n = 16$. U.S.A. **Washington.** Klickitat Co.: Klickitat, *S & Bt 7086;* Skamania Co.: along Cook-Underwood Rd, *S & Bt 7103;* Yakima Co.: US-12 2.4 mi E of Clear Creek Rd, *S & Bt 7077.*

A. aff. *bracteolatus* Nutt. $2n = 16$. U.S.A. **Idaho.** Boise Co.: W of Lowman, *S & Bt 7063.*

A. chilensis Nees. $2n = 48$. U.S.A. **Oregon.** Coos Co.: N of Coaledo, *S & Bt 7128;* Lincoln Co.: N of Newport, *S & Bt 7121.* $2n =$ ca. 96. U.S.A. **Washington.** Pacific Co.: Raymond, *S & Bt 7110.*

A. conspicuus Lindl. $2n =$ ca. 108. U.S.A. **Idaho.** Boundary Co.: N of Naples, *S & Bt 4379.* $2n =$ ca. 122. CANADA. **British Columbia.** S of Moyie, *S & Bt 4375.* U.S.A. **Montana.** Broadwater Co.: E of Townsend, near Carl Creek Trail, *S & Bt 7010.*

A. cordifolius L. $2n = 16$. U.S.A. **Maine.** Franklin Co.: ME-16 rest area by Carrabasett River, *S & K 4627.* $2n = 32$. **New York.** Dutchess Co.: Taconic Parkway at Putnam County line, *S 6830.*

A. ciliolatus Lindl. $2n = 48$. U.S.A. **Michigan.** Delta Co.: Garden Corners, *S & Ch 5020.*

A. divaricatus L. $2n = 18$. U.S.A. **Massachusetts.** Worcester Co.: Harvard, *S 6868.* **New York.** Broome Co.: E of Binghamton, *S 6802.* **Pennsylvania.** Fulton Co.: E of Amaranth, *S & Ch 5865.* **Vermont.** Addison Co.: W of Hancock, *S 6895;* Windham Co.: W side of Hogback Mtn, *S & K 4953.*

A. drummondii Torr. & Gray var. *drummondii.* $2n = 16$. U.S.A. **Kansas.** Miami Co.: NE of Beagle, *S & Ch 5255.* $2n = 32$. U.S.A. **Illinois.** Adams Co.: Bluff Hall, *S & Bt 7371 & 7372;* Cook Co.: Northbrook, *S & Bt 6930.*

A. dumosus L. $2n = 16$. U.S.A. **Florida.** Lake Co.: FL-46 at Wekiwa River, *5342;* Pasco Co.: US-301 N of county line, *5414.*

A. dumosus L. var. *strictior* Torr. & Gray. $2n = 32$. U.S.A. **New York.** Suffolk Co.: E of Centre Moriches, *S 6855.*

A. engelmannii A. Gray. $2n = 9_{II}$. U.S.A. **Washington.** Yakima Co.: Clear Lake Rd. near US-12, *S & Bt 7074.*

A. exilis Ell. $2n = 10$. U.S.A. **Alabama.** Marengo Co.: Demopolis, *S & Ch 6362.*

A. foliaceus Lindl. $2n = 16$. U.S.A. **Montana.** Broadwater Co.: E of Townsend near Carl Creek Trail, *S & Bt 7009.* **Wyoming.** Carbon Co.: W of Ryan Park R. S., *S & Bt 7236.* Johnson Co.: Powder River Pass, *S & Bt 4454.* $2n = 32$. U.S.A. **Washington.** Lewis Co.: White Pass, *S & Bt 7073.* $2n = 48$. U.S.A. **Oregon.** Clackamas Co.: US-24, 2.1 mi S of OR-35, *S & Bt 7098.* $2n = 64$. U.S.A. **Idaho.** Boise Co.: W of Lawman, *S & Bt 7062;* Lehmi Co.: NW of Carmen, Stormy Peak Rd, *S & Bt 7037.* **Montana.** Beaverhead Co.: Chief Joseph Pass, *S & Bt 7025;* 2.6 mi E of Wise River, *S & Bt 7015;* 5.8 mi E of Wise River, *S & Bt 7020.* **Oregon.** Deschutes Co.: W of Bend, *S & Bt 7192;* Hood River Co.: Bennett Pass, *S & Bt 7092.* **Wyoming.** Carbon Co.: SE of Saratoga, *S & Bt 7230.* $2n = 80$. U.S.A. **Colorado.** Routt Co.: SE of Steamboat Springs, *5774;* Summit Co.: Arapahoe Basin Ski Area, *6565.* $2n =$ ca. 96. U.S.A. **Wyoming.** Teton Co.: Teton Pass, *S & Bt 7212.*

A. glaucodes Torr. & Gray $2n = 9_{\mathrm{II}}$ U.S.A. **Colorado.** Montezuma Co.: SE of Cortez, *5523.* **Wyoming.** Teton Co.: W of Teton Pass, *S & Bt 7211.*

A. gormanii (Piper) Blake. $2n = 9_{\mathrm{II}}$ U.S.A. **Oregon.** Marion Co.: Sardine Mtn. W of Detroit, *S & Bt 7176.*

A. hesperius Gray. $2n = 64$. U.S.A. **Colorado.** El Paso Co.: NW of Manitou Springs, *S & Bt 7270.* **Oregon.** Sherman Co.: The Dalles, W of the dam, *S & Bt 7084.*

A. integrifolius Nutt. $2n = 18$. U.S.A. **Wyoming.** Teton Co.: WY-22 at Trail Creek Campground, *S & Bt 7202.*

A. jessicae Piper. $2n = 40_{\mathrm{II}}$ U.S.A. **Washington.** Whitman Co.: Pullman, *S & Bt 7070.*

A. laevis L. var. *laevis.* $2n = 48$. U.S.A. **Colorado.** El Paso Co.: Manitou Springs, *S & Bt 7273, 7276.* **New York.** Broome Co.: W of Windsor, *6811.* Suffolk Co.: Mattituck, *S 6860.* **North Dakota.** Barnes Co.: Valley City, *S & Bt 6957;* Stark Co.: E of Gladstone, *S & Bt 6969.* **Wisconsin.** Jackson Co.: SE of Milton, *S & Bt 6940.*

A. lanceolatus Willd. $2n = 64$. CANADA. **Ontario.** Cochrane Dist.: Timmins, Porcupine Lake. *Brunton 4712.* U.S.A. **New York.** Dutchess Co.: Taconic State Parkway by Miller Hill Rd, *S 6836.*

A. lateriflorus (L.) Britt. $2n = 16$. U.S.A. **Michigan.** Delta Co.: E of Bark River, *S & Ch 5029.* $2n = 32$. U.S.A. **Wisconsin.** Crawford Co.: S of Prairie du Chien, *S & Ch 5184.*

A. ledophyllus A. Gray var. *covillei* (Greene) Cronq. $2n = 9_{\mathrm{II}}$ U.S.A. **Oregon.** Lane Co.: 3.2 mi W of McKenzie Pass, *S & Bt 7172.*

A. ledophyllus A. Gray var. *ledophyllus.* $2n = 9_{\mathrm{II}}$ U.S.A. **Oregon.** Hood River Co.: Bennett Pass, *S & Bt 7093;* Mt. Hood Meadows Ski Area, *S & Bt 7101;* Marion Co.: Sardine Mtn. near Detroit, *S & Bt 7174.*

A. linariifolius L. $2n = 9_{\mathrm{II}}$ U.S.A. **South Carolina.** Berkeley Co.: SE of Alvin, *S & Ch 6129.*

A. aff. *longifolius* Lam. $2n = 64$. CANADA. **Ontario.** Cochrane Dist.: Kesagami Prov. Park, mouth of Kesagami River, *Brunton 4677.*

A. macrophyllus L. $2n = 72$. CANADA. **Ontario.** Kenora Dist.: E of Kenora, *6727;* Thunder Bay Dist.: W of Shebandowan, *S & Bt 4119.*

A. meritus A. Nels. $2n = 36$. U.S.A. **Montana.** Carbon Co.: S of Red Lodge, *S & Bt 4430.* **Wyoming.** Johnson Co.: Powder River Pass, *S & Bt 4453;* Rock Co.: N of Beartooth Pass, *S & Bt 4438.*

A. modestus Lindl. $2n = 18$. CANADA. **Alberta.** W of Entwistle, *S & Bt 4294.* U.S.A. **Idaho.** Lemhi Co.: N of Gibbonsville, Twin Creek Campground, *S & Bt 7026.* **Montana.** Broadwater Co.: E of Townsend near Carl Creek Trail. *S & Bt 7008.* **Oregon.** Clackamas Co.: US-24 2.1 mi S of OR-35, *S & Bt 7097;* Douglas Co.: Diamond Lake, *S & Bt 7157;* N of Union Creek, *S & Bt 7154;* Linn Co.: OR-22 just E of Twin Meadows Rd. W of Marion Lake, *S & Bt 7173.* **Washington.** Lewis Co.: White Pass, *S & Bt 7071.*

A. nemoralis Ait. $2n = 18$. CANADA. **Nova Scotia.** Queens Co.: W of Summerville, *S & K 4839.*

A. novi-belgii L. $2n = 48$. CANADA. **New Brunswick.** Northumberland Co.: E of Loggieville, *S & K 4695.*

A. occidentalis (Nutt.) Torr. & Gray $2n = 16$. U.S.A. **Oregon.** Douglas Co.: OR-230 9.7 mi N of OR-62, *S & Bt 7153.* **Washington.** Yakima Co.: Clear Lake Rd., S of US-12, *S & Bt 7076.* $2n = 32$. U.S.A. **Oregon.** Douglas Co.: Diamond Lake, *S & Bt 7158A;* Jackson Co.: W of Butte Falls, *S & Bt 7140;* Linn Co.: Santiam Pass, *S & Bt 7190.* $2n = 64$. U.S.A. **Idaho.** Blaine Co.; US-20 3.6 mi W of ID-75, *S & Bt 7199.* **Oregon.** Lane Co.: Blue River, *S & Bt 7165.*

A. ontarionis Wieg. $2n = 32$. U.S.A. **Minnesota.** Washington Co.: Pt. Douglas, *S & Ch 5084.*

A. oregonensis (Nutt.) Cronq. $2n = 9_{\mathrm{II}}$ U.S.A. **California.** Shasta Co.; E of Buckhorn Summit, *5699.* $2n = 18$. U.S.A. **Oregon.** Lane Co.: Nemrod, *S & Bt 7164.*

A. paternus Cronq. $2n = 18$. U.S.A. **North Carolina.** Harnett Co.: at Moore Co. line, SE of Cameron, *S & Ch 6071.*

A. perelegans Nels. & Macbr. $2n = 9_{\mathrm{II}}$ U.S.A. **Idaho.** Blaine Co.: Galena Summit, *S & Bt 7056.*

A. praealtus Poir. var. *angustior* Wieg. $2n = 64$. U.S.A. **New York.** Nassau Co.: East Norwich, *6843.*

A. praealtus Poir. var. *praealtus.* $2n = 32$. U.S.A. **Iowa.** Keokuk Co.: E of Richland, *S. & Ch 5216.* **Kansas.** Anderson Co.: S of Greeley, *S. & Ch 5261.* **Missouri.** Callaway Co.: N of Auxvasse, *S & Ch 5309.* **Nebraska.** Holt Co.: Willow Swamp Creek, *S & Bt 4495.*

A. prenanthoides Torr. & Gray. $2n = 32 + 2$ supernumeraries. U.S.A. **New York.** Steuben Co.: N of Lindley. *Ch & Hart 261.*

A. puniceus L. $2n = 16$. CANADA. **Nova Scotia.** Digby Co.: Digby Neck, E of Tiddville, *S & K 4874.* **Ontario.** Cochrane Dist.: Kesagami Prov. Park, E shore Newnham Bay. *Brunton 4622.* U.S.A. **Maine.** Washington Co.: SW of Calais, *S & K 4903.*

A. radulinus A. Gray. $2n = 18$. U.S.A. **Oregon.** Douglas Co.: NW of Drew, *S & Bt 7146;* Klamath Co.: W of Summit, NE of Fish Lake,, *S & Bt 7134.* **Washington.** Yakima Co.: Clear Lake Rd near US-12, *S & Bt 7075;* US-12, 2.4 mi E of Clear Lake Rd, *S & Bt 7079.*

A. scopulorum A. Gray. $2n = 18$. U.S.A. **Oregon.** Marion Co.: Sardine Mt., W of Detroit, *S & Bt 7177.*

A. simmondsii Small. $2n = 32_{\mathrm{II}}$. U.S.A. **Florida.** Broward Co.: W of Deerfield Beach, S of Loxahatchee Reserve, *5360.* $2n = 64$. U.S.A. **Florida.** Collier Co.: S of Immokalee, *5398.*

A. sibiricus L. $2n = 18$. CANADA. **Alberta.** W of Hinton, E of Jasper Nat'l Park, *S & Bt 4320.*

A. solidagineus Michx. $2n = 18$. U.S.A. **New York.** Suffolk Co.: E of Center Moriches, *6856*. **North Carolina.** Sampson Co.: NE of Clinton, *S & Ch 6029.*

A. subspicatus Nees. $2n = 48$. U.S.A. **Oregon.** Tillamook Co.: Cape Lookout Park, *S & Bt 7116 & 7117.*

A. subulatus Michx. $2n = 5_{II}$. U.S.A. **Maryland.** Queens Anne Co.: N of Grasonville, *S & R 7630.* $2n = 10_{II}$ U.S.A. **Florida.** Collier Co.: Immokalee, *5401.*

A. tenuifolius L. $2n = 10$. U.S.A. **Florida.** Lee Co.: Sanibel Island, behind Bowman Beach, *7504.*

A. tortifolius Michx. $2n = 18$. U.S.A. **North Carolina.** Wayne Co.: E of Grantham, *S & Ch 6022.*

A. tradescanti L. $2n = 16$. CANADA. **New Brunswick.** Charlotte Co.: Lake Utopia, *S & K 4900.*

A. turbinellus Lindl. $2n = 96$. U.S.A. **Missouri.** Callaway Co.: W of New Bloomfield, *S & Ch 5301.*

A. umbellatus Mill. $2n = 18$. CANADA. **Quebec.** Fountainbleau, *S & K 4601.*

A. undulatus L. $2n = 32$. U.S.A. **Massachusetts.** Franklin Co.: W of Riverside, *S 6876.*

Benitoa occidentalis (Hall) Keck. $2n = 5_{II}$. U.S.A. **California.** Fresno Co.: W of Coalinga, *5651.*

Boltonia asteroides (L.) L'Her. $2n =$ ca. 36. U.S.A. **Nebraska.** Jefferson Co.: US-136, 3 mi W of county line, *S & Bt 7348.*

Chrysopsis gossypina (Michx.) Ell. subsp. *gossypina.* $2n = 18$. U.S.A. **Georgia.** Wayne Co.: N of Jessup, 7558.

C. linearifolia Semple subsp. *dressii* Semple. $2n = 10$. U.S.A. **Florida.** Brevard Co.: Allenhurst, 7531.

C. scabrella Torr. & Gray. $2n = 10$. U.S.A. **Florida.** Brevard Co.: S of Titusville, *7529;* Osceola Co.: S of Narcoossee, *7476.*

Chrysothamnus greenei (Gray) Greene susbp. *filifolius* (Rydb.) Hall. & Clem. $2n = 9_{II}$. U.S.A. **Colorado.** Chaffee Co.: S of Poncho Springs, *5463.*

C. parryi (Gray) Greene subsp. *parryi.* $2n = 9_{II}$. U.S.A. **Colorado.** Saquache Co.: Pancho Pass, *5473.*

Corethrogyne filaginifolia (Hook. & Arn) Nutt. var. *virgata* (Benth.) A. Gray. $2n = 5_{II}$. U.S.A. **California.** Los Angeles Co.: N of La Canada, *5496;* San Pedro, Pt. Fermin, *5619;* Riverside Co.: W of Lake Elsinore, *5586;* San Diego Co.: E of Live Oak, *5571, 5577.*

C. leucophylla (Lindl.) Jeps. $2n = 5_{II}$. U.S.A. **California.** Monterey Co.: S of Carmel Highlands, *5659.*

C. linifolia (Hall) Ferris. $2n = 5_{II}$. U.S.A. **California.** San Diego Co.: Del Mar, near Torrey Pines Park, *5582.*

Ericameria arborescens (Gray) Greene. $2n = 9_{II}$. U.S.A. **California.** San Diego Co.: I-8 and Pine Valley Rd, *5578.*

E. parishii (Greene) Blake. $2n = 9_{II}$. U.S.A. **California.** Los Angeles Co.: N of La Canada, *5593.*

Erigeron aequifolius Hall. $2n = 18$. U.S.A. **California.** Tulare Co.: N of Stoney Creek, *5644.*

E. coulteri Porter. $2n = 18$. U.S.A. **Colorado.** Summit Co.: S of Loveland Pass, *6573.*

E. divergens Torr. & Gray. $2n = 18_{II}$. U.S.A. **Oregon.** Deschutes Co.: E of Bend, W of Horse Ridge Summit, *S & Bt 7193.*

E. divergens Torr. & Gray var. *cinereus* A. Gray. $2n = 18_{II}$. U.S.A. **Colorado.** La Plata Co.: W of Durango, *5514.*

E. foliosus Nutt. $2n = 9_{II}$. U.S.A. **California.** Los Angeles Co.: NE of La Canada, *5605.*

E. inornatus (Gray) Gray var. *inornatus.* $2n = 18$. U.S.A. **California.** Siskiyou Co.: Mt. Shasta, *5711.* $2n = 18 + 0\text{–}5$ supernumeraries. U.S.A. **California.** Tahema Co.: E of Morgan Summitt, *5705.*

E. ochroleucus Nutt. $2n = 54$. U.S.A. **Wyoming.** Niobrara Co.: N of Lusk, *6628.*

E. pumilus Nutt. subsp. *intermedius* Cronquist. $2n = 9_{II}$. U.S.A. **Idaho.** Custer Co.: N of Challis, *S & Bt 7040.* S of Clayton, *S & Bt 7048.*

E. quercifolius Lam. $2n = 9_{II}$. U.S.A. **Florida.** Lee Co.: Sanibel Is., W of Sanibel, *7498.*

E. simplex Greene. $2n = 18$. U.S.A. **Colorado.** Summit Co.: Loveland Pass, *6579.*

E. speciosus (Lindl.) DC. $2n = 18$. U.S.A. **Idaho.** Blaine Co.: Galena summit, *S & Bt 7054;* Lemhi Co.: N of Gibbonsville, *S & Bt 7030.* **Wyoming.** Teton Co.: Teton Pass, *S & Bt 7214;* WY-22 near Coal Creek near state line, *S & Bt 7208.*

E. strigosus Muhl. $2n = 36$. U.S.A. **Idaho.** Nez Perce Co.: near Arrow, *S & Bt 4397.*

Euthamia graminifolia (L.) Nutt. $2n = 18$. U.S.A. **Maine.** Waldo Co.: E of Belmont, *S & K 4920.*

E. occidentalis Nutt. $2n = 18$. U.S.A. **Oregon.** Deschutes Co.: W of Redmond, *S & Bt 7191.* **Utah.** Juab Co.: W of Nephi, *5756.*

Grindelia squarrosa (Pursh) Dunal (variety undetermined). $2n = 6_{II}$. U.S.A. **Nevada.** Eureka Co.: US-50 at Hwy-20, *5735.*

G. squarrosa (Pursh) Dunal var. *nuda* (Wood) A. Gray. $2n = 6_{II}$. U.S.A. **Colorado.** El Paso Co.: S of Colorado Springs, *5458.*

G. squarrosa (Pursh) Dunal var. *squarrosa.* $2n = 12$. U.S.A. **Idaho.** Idaho Co.: E of Kooskia, *S & Bt 4401.*

Gutierrezia sarothrae (Pursh) Britt. & Rusby. $2n = 4_{II}$. U.S.A. **Colorado.** El Paso Co.: Colorado Springs, *5444.* $2n = 8_{II} + 3_{I}$ supernumerary. **California.** San Diego Co.: E of Live Oak, *5572.*

Haplopappus (*Isocoma*) *annuus* (Rydb.) Cory. $2n = 12$. U.S.A. **Colorado.** Pueblo Co.: E of Avondale, *S & Bt 7285.*

H. (*Prionopsis*) ciliatus (Nutt.) DC. $2n = 12$. U.S.A. **Oklahoma.** Cotton Co.: W of Randlett, *S & Ch 6465.* **Texas.** Potter Co.: SE of Ady, *S & Ch 6475.*

H. (*Pyrrocoma*) *carthamoides* (Hook.) A. Gray. $2n = 12 +$ supernumeraries. **Washington.** Yakima Co.: S of Tieton River, near Lost Lake S of US-12, *S & Bt 7080.*

H. (*Hazardia*) *squarrosus* Hook. & Arn. subsp. *squarrosus.* $2n =$ ca. 5_{II}. U.S.A. **California.** Monterey Co.: S of Carmel Highlands, *5660.*

H. (*Isocoma*) *venetus* (H.B.K.) Blake. $2n = 6_{II}$. U.S.A. **California.** Orange Co.: CA-74 W of county line, *5589.* $2n = 6_{II}$. + 1_{I} supernumerary. U.S.A. **California.** San Diego Co.: near Lakeside, *5584.* $2n = 12_{II}$. U.S.A. **California.** Los Angeles Co.: San Pedro, W of Point Fermin, *5620;* San Diego Co.: W of Ramona, *5583.*

Heterotheca camporum (Greene) Shinners var. *glandulissimum* Semple. $2n = 36$. U.S.A. **Tennessee.** Bradley Co.: Cleveland, *5331.*

H. canescens (DC.) Shinners. $2n = 9_{II}$. U.S.A. **Kansas.** Barber Co.: US-160, 5 mi E of county line, *S & Br 2728.*

H. echioides (Benth.) Shinners. $2n = 9_{II}$. U.S.A. **California.** Fresno Co.: N of Priest Valley, *5653.*

H. fastigiata (Greene) Harms. $2n = 9_{II}$. U.S.A. **California.** Los Angeles Co.: N of La Canada, *5598.*

H. grandiflora Nutt. $2n = 9_{II}$. U.S.A. **California.** Santa Cruz Co.: W of Scotts Valley, *5669.*

H. horrida (Rydb.) Harms. $2n = 9_{II}$. U.S.A. **Colorado.** Chaffee Co.: S of Poncha Springs, *5465.*

H. latifolia Buckley. $2n = 9_{II}$. U.S.A. **Oklahoma.** Pittsburg Co.: W of Dow, *S & Br 2745.*

H. oregona (Nutt.) Shinners. $2n = 9_{II}$. U.S.A. **California.** Tehama Co.: 23 mi E of Red Bluff, *5701.*

H. stenophylla (Gray) Shinners. $2n = 18_{II}$. U.S.A. **Kansas.** Gray Co.: W of Dodge City, *S & Br 2725.*

H. subaxillaris (Lam.) Britt. & Rusby. $2n = 9_{II}$. U.S.A. **North Carolina.** Harnett Co.: Benson, *Canne 645.*

H. villosa (Pursh) Shinners var. *villosa.* $2n = 9_{II}$. U.S.A. **Colorado.** La Plata Co.: W of Durango, *5513.*

Lessingia nemaclada Greene. $2n = 5_{II} + 1_{I}$ supernumerary. U.S.A. **California.** Humbolt Co.: S of Mad River Park, *5692.*

Leucelene ericoides (Torr.) Greene $2n = 16_{II}$. U.S.A. **Arizona.** Navajo Co.: SW of Kayenta, W of Marsh Pass, *5532.*

Macheranthera bigelovii (Gray) Greene. $2n = 8$. U.S.A. **Colorado.** Larimer Co.: S of Estes Park, *5831.*

M. canescens (Pursh) A. Gray. $2n = 4_{II}$. U.S.A. **Arizona.** Coconino Co.: N of Parks, *5548.* $2n = 8$. U.S.A. **California.** Siskiyou Co.: Mt. Shasta, 4380′ el, *5710.*

M. commixta Greene. $2n = 8$. U.S.A. **Montana.** Silver Bow Co.: SE of Butte, *S & Bt 4421.* $2n = 8 + 2$ supernumeraries. U.S.A. **Montana.** Carbon Co.: S of Bridger, *S & Bt 4440.*

M. gracilis (Nutt.) Shinners. $1_{II} + 1$ multivalent. U.S.A. **Arizona.** Coconino Co.: S of Tusayan, *5534.*

M. grindelioides (Nutt.) Shinners. $2n =$ ca. 8_{II}. U.S.A. **Wyoming.** Albany Co.: E of Centennial, *S & Bt 7243.*

M. pinnatifida (Hook.) Shinners. $2n = 4_{II}$. U.S.A. **North Dakota.** Morton Co.: Sweet Briar Lake rest area on I-94, *S & Bt 6966.*

M. tanacetifolia (H.B.K.) Nees. $2n = 4_{II}$. U.S.A. **Colorado.** Chaffee Co.: S of Poncha Springs, *5464.*

Macronema filiforme Nels. & Macbryde. $2n = 9_{II}$. U.S.A. **California.** Siskiyou Co.: S of Mt. Shasta City, *5709.*

M. greenei (Gray) Greene. $2n = 9_{II}$. U.S.A. **Washington.** Klickitat Co.: Baldy Peak, *S & Bt 7107.*

M. suffruticosa Nutt. $2n = 9_{II}$. U.S.A. **Nevada.** White Pine Co.: Wheeler Peak, *5751.*

Pityopsis adenolepis (Fern.) Semple. $2n = 18$. U.S.A. **Georgia.** Johnson Co.: W of Wrightsville, *S, Bt & Canne 4041.*

P. graminifolia (Michx.) Nutt. var. *graminifolia.* $2n = 36$. U.S.A. **Florida.** Collier Co.: Immokalee, *5400.*

P. graminifolia (Michx.) Nutt. var. *microcephala* (Small) Semple. $2n = 18$. U.S.A. **Florida.** Bradford Co.: FL-100 NW of county line, *S, Bt & Canne 4001.*

Solidago arguta Ait. $2n = 18$. U.S.A. **Pennsylvania.** York Co.: E of Sunnyburn, *S & R 7614.*

S. altissima L. $2n = 54$. U.S.A. **Illinois.** Livingston Co.: E of Forrest, *S & Bt 7387.* **Kansas.** Osborne Co.: S of Osborne, *S & Bt 7327.* **Missouri.** Atchison Co.: W of Rock Port, *S & Bt 7362.* **Nebraska.** Johnson Co.: SW of Crab Orchard, *S & Bt 7353.*

S. caesia L. $2n = 18$. U.S.A. **Indiana.** Porter Co.: US-12 at IND-49, *S & Bt 4525.*

S. californica Nutt. $2n = 9_{II}$. U.S.A. **California.** Los Angeles Co.: below Kratka Ridge, *5610;* Santa Cruz Co.: NW of Saratoga in mountains, *5671.*

S. canadensis L. var. *canadensis.* $2n = 18$. U.S.A. **Illinois.** Adams Co.: Bluff Hall, *S & Bt 7367.*

S. canadensis L. aff. var. *salebrosa* (Piper) Cronq. $2n = 18$. U.S.A. **Oregon.** Douglas Co.: Diamond Lake, *S & Bt 7160.*

S. fistulosa Mill. $2n = 18$. U.S.A. **Delaware.** Sussex Co.: S of Rehoboth, Indian River Bay, *S & R 7649.*

S. gigantea Ait. $2n = 54$. U.S.A. **Colorado.** El Paso Co.: Manitou Springs, *S & Bt 7269.*

S. gilvocanescens (Rydb.) Smyth. $2n = 18$. U.S.A. **Montana.** Dawson Co.: E of Fallon, *S & Bt 6978.* $2n = 18_{II}$. U.S.A. **Kansas.** Pawnee Co.: W of Garfield, *S & Bt 7306.* $2n = 36$. U.S.A. **Montana.** Wheatland Co.: W of Shawmut, *S & Bt 6997.*

S. hispida Muhl. $2n = 18$. CANADA. **Ontario.** Kenora Dist.: Nestor Falls, *S & Bt 4142.*

S. leavenworthii Torr. & Gray. $2n = 9_{II}$. U.S.A. **Florida.** Osceola Co.: Yeehaw Junction, *5356.*

S. lepida DC. $2n = 54$. U.S.A. **Washington.** Klickitat Co.: Klickitat, *S & Bt 7088, 7089.*

S. mollis Bartl. $2n = 18_{II}$. U.S.A. **Kansas.** Ford Co.: W of Dodge City, *S & Bt 7296;* E of Bellefont, *S & Bt 7304.* $2n = 27_{II}$. U.S.A. **Montana.** Rosebud Co.: SE of Vananda, *S & Bt 6984.*

S. missouriensis Nutt. $2n = 18_{II}$. U.S.A. **Colorado.** La Plata Co.: W of Durango, *5517.*

S. multiradiata Ait. $2n = 36$. U.S.A. **Wyoming.** Teton Co.: W of Teton Pass, *S & Bt 7215;* W of Togwatee Pass, *S & Bt 7222.*

S. nemoralis Ait. var. *nemoralis.* $2n = 18$. U.S.A. **Georgia.** Monroe Co.: E of Forsyth, *5332.*

S. parryi (Gray) Greene. $2n = 18$. U.S.A. **Colorado.** Clear Creek Co.: E of Berthoud Pass, *5802.*

S. riddellii Frank. $2n = 9_{II}$. U.S.A. **Wisconsin.** Jefferson Co.: N of Whitewater, *S & Bt 6935.*

S. sempervirens L. $2n = 9_{II}$. U.S.A. **Florida.** Collier Co.: S of Jerome, *5394;* Manatee Co.: Terra Ciea, edge of bay, *S 5409.*

S. sparsiflora A. Gray. $2n = 9_{II}$. U.S.A. **Arizona.** Coconino Co.: N of Parks, *5547.*

S. uliginosa Nutt. $2n = 18$. U.S.A. **Michigan.** Delta Co.: Garden Corners, *S & Ch 5021.*

Townsendia grandiflora Nutt. $2n = 9_{II}$. U.S.A. **Colorado.** El Paso Co.: S of Colorado Springs, *5457.*

Virgulus adnatus (Nutt.) Reveal & Keener. $2n = 20$. U.S.A. **Florida.** Flagler Co.: N of Bunnell, *7538.*

V. concolor (L.) Reveal & Keener. $2n = 8$. U.S.A. **Florida.** Wakulla Co.: S of Sopchoppy, *7431.* **Georgia.** Charlton Co.: Folkston, *7553.*

V. ericoides (L.) Reveal & Keener. $2n = 10$. CANADA. **Manitoba.** SE of Lenore. *4192;* N. of Ridgeville, 6703.

V. walteri (Alex.) Reveal & Keener. $2n = 20$. U.S.A. **Florida.** Osceola Co.: S of Narcoossee, *7478.*

ACKNOWLEDGMENTS

This work was supported by Natural Sciences and Engineering Research Council of Canada Operating Grants to the author. Drs. Allen, Anderson, Nesom, and Urbatsch are thanked for their assistance in identifying collections. The following people are thanked for their assistance on field trips and for material provided for study: R. Brammall, L. Brouillet, D. Brunton, J. Canne, J. Chmielewski, Calvin Hart, Chris Hart, R. Keir, G. Ringius, and B. Semple.

LITERATURE CITED

ANDERSON, L., D. KYHOS, T. MOSQUIN, A. POWELL AND P. RAVEN. 1974. Chromosome numbers in Compositae. IX. *Haplopappus* and other Astereae. Amer. J. Bot. 61: 665–671.

GRAU, J. 1977. Astereae-systematic treatment. *In:* Heywood, V. H., J. B. Harborne and B. L. Turner, Eds. The Biology and Chemistry of the Compositae. Academic Press. London.

RAVEN, P. H., O. T. SOLBRIG, D. W. KYHOS, AND R. SNOW. 1959. Chromosome numbers in Compositae. I. Astereae. Amer. J. Bot. 47: 124–132.

SEMPLE, J. C. 1978. The cytogeography of *Aster pilosus* (Compositae): Ontario and the adjacent United States. Canad. J. Bot. 56: 1274–1279.

———. 1981. A revision of the goldenaster genus *Chrysopsis* (Nutt.) Ell. nom. cons. Rhodora 83: 323–384.

Solbrig, O. T., L. C. Anderson, D. W. Kyhos, P. H. Raven, and L. Rudenberg. 1964. Chromosome numbers in Compositae. V. Astereae II. Amer. J. Bot. 51: 513–519.

Strother, J. 1972. Chromosome studies in western North American Compositae. Amer. J. Bot. 59: 242–247.

Turner, B. L., W. L. Ellison and R. M. King. 1961. Chromosome numbers in the Compositae. IV. North American species with phylogenetic interpretations. Amer. J. Bot. 48: 216–233.

DEPARTMENT OF BIOLOGY
UNIVERSITY OF WATERLOO
WATERLOO, ONTARIO
CANADA N2L 3G1

THE STATUS AND IDENTITY OF *CAREX* ×*CAESARIENSIS* (CYPERACEAE)

A. A. REZNICEK AND P. M. CATLING

ABSTRACT

Carex ×*caesariensis* was previously hypothesized to be a *C. trichocarpa* × *C. walteriana* hybrid, and has been variously treated as a species, as a hybrid, or has not been recognized at all in floras covering northeastern North America. Scatter diagrams and discriminant analysis suggest that it is a *C. trichocarpa* × *C. lanuginosa* hybrid. The diagnostic character combination includes perigynia with relatively short beaks (1.3–2.1 mm) and relatively short teeth (0.7–1.3 mm), elongate true sterile culms with nodes, and sheaths red-tinged at the apex and red-dotted on the inner band. Described originally from New Jersey, *C.* ×*caesariensis* is newly reported from Pennsylvania.

Key Words: *Carex*, *Carex* ×*caesariensis*, Cyperaceae, hybrid, New Jersey, Pennsylvania

INTRODUCTION

Carex ×*caesariensis* was described by K. K. Mackenzie (1935) (*pro sp.*) from specimens collected near Laurel Springs, New Jersey. It has been hypothesized to be a hybrid of *C. trichocarpa* Schk. in section *Paludosae* and *C. walteriana* L. H. Bailey in section *Carex* (*Hirtae*) (Gleason, 1952; Gleason and Cronquist, 1963) and has only been reported from the type locality. Authors of northeastern North American and local floras have recognized it variously as a species, as a hybrid, or have not recognized it at all. The present study was undertaken to determine whether the suggested parentage was likely, whether hybrid status was reasonable, and which features of the taxon are most diagnostic.

METHODS

Since *Carex* ×*caesariensis* possessed several features known otherwise only in *C. trichocarpa* in the North American *Carex* flora, *C. trichocarpa* was postulated with confidence to be one of the parents. A list of possibilities for the other parent was prepared based on extrapolation from the morphology of *C. caesariensis* and *C. trichocarpa.* This choosing was done using the methodology and criteria outlined in Humphries (1983) and Wagner (1980, 1983). An attempt was made to find *C.* ×*caesariensis* at its type locality and elsewhere, to gather evidence of hybridization. Specimens from many herbaria (CAN, DAO, F, GH, IND, MICH, MO, MSC, ND, NY, PH, SIU, TRT, TRTE, UC, UMO, and US) were examined and measurements were recorded for a variety of characters from material of *C.* ×*caesariensis,* possible parents, and other taxa resembling the hybrid. Variation was assessed in two-dimensional scatter diagrams.

The lack of living colonies and the very few known collections of *Carex* ×*caesariensis* precluded analyses based on population samples. Therefore, a discriminant analysis (using the S.R.S. Program 5015-Canonical Analysis) was performed as the final step in determining the likely parentage of *Carex* ×*caesariensis.* This analysis employed 11 characters: widest leaf (mm), no. of crossveins/cm of leaf surface (lower 1/3 of leaf), no. of prickle-hairs on 5 mm of leaf margin, spike thickness (mm), perigynium length (mm), perigynium width (mm), beak length (mm), tooth length (mm), no. of hairs/0.25 mm^2 perigynium surface, height of apex of uppermost sheath of sterile shoot (cm), and length of longest awn on pistillate scales (mm) (raw data available from authors). Three groups comprising 38 OTUs were used: 15 *C. lanuginosa,* 13 *C. walteriana,* and 10 *C. trichocarpa,* each group represented by specimens from throughout the range of the species. Specimens of *C.* ×*caesariensis* were plotted on the first two discriminant axes using the derived discriminant formula.

RESULTS AND DISCUSSION

The hybrid status of *Carex* ×*caesariensis* was strongly suggested by its rarity (only 2 stations represented in the herbaria searched) and by its sterility (mature achenes being empty).

The combination of elongate, true sterile culms and sheaths red-tinged at the mouth possessed by *Carex* ×*caesariensis* confirms that *C. trichocarpa* is one of its parents. *Carex trichocarpa* is the only species of subgenus *Carex* in New Jersey with true sterile culms, and the glabrous, reddish (but not red-dotted), thickened apex to the inner band of the sheath is unique in the eastern North American *Carex* flora. Mackenzie (correspondence to B. Long dated Nov. 27, 1921 and filed with holotype at NY) and Gleason (1952) proposed that *C. walteriana* was the other parent. *Carex walteriana* is a common species in New Jersey, but examination of the type locality and specimens of *C.* ×*caesariensis* raised the following doubts about this parentage: (1) the type locality was a swale along a small river, in a bottomland site, whereas *Carex walteriana* is a species of wet, acid swamps and bogs; (2) the perigynia of *C.* ×*caesariensis* are about as pubescent as *C. trichocarpa* suggesting that the unknown parent probably has pubescent perigynia, yet the perigynia of *C. walteriana* are glabrous or nearly so; (3) the leaves of *C.* ×*caesariensis* are quite narrow, up to 4.6 mm wide, whereas the leaves of *C. trichocarpa* are up to ca. 11 mm wide and those of *C. walteriana* are up to ca. 10 mm wide, so that a hybrid involving these two taxa would probably have leaves up to ca. 10 mm wide; (4) the fertile culms of *C.* ×*caesariensis* are reddish at base, more or less fibrillose, and have bladeless sheaths at base, but the fertile culms of *C. walteriana* are not (or barely) reddened at base, not fibrillose, and have marcescent remains of leaves at base. Also, a recently discovered collection from Northampton County, Pennsylvania (*Schaeffer 22877,* PH!) that is referable to *C.* ×*caesariensis* is from beyond the geographical distribution of *C. walteriana.* By extrapolation from the characters by which *C.* ×*caesariensis* differs from *C. trichocarpa,* the other parent must be a medium sized, rhizomatous *Carex* with smaller, pubescent perigynia with shorter beaks and beak teeth than those of *C. trichocarpa.* Also, its leaves should be less than 4.6 mm wide and have sheaths with a copiously red-dotted inner band.

Two species occurring in the vicinity of the type locality fit the description above: *Carex lanuginosa* and *C. vestita* Willd., both in section *Carex* (*Hirtae*). *Carex vestita* has an unusual, friable, hyaline, obscurely toothed apex to the beak and a mostly solitary staminate spike with a short peduncle 2–20 mm long. None of these features is discernible in *C.* ×*caesariensis.* Furthermore, *C. vestita* occurs in drier, upland sites. We reject it as a possible parent. This rejection leaves either *C. walteriana* or *C. lanuginosa* as the unknown parent.

In a diagram plotting perigynium length versus beak length (Figure 1) *Carex* ×*caesariensis* is clearly in an intermediate position between *C. trichocarpa* and *C. lanuginosa.* A similar result is shown by Figure 2, where perigynium length is compared to leaf width for the same species. A scatter plot from a 2-dimensional discriminant analysis based on 11 characters (Figure 3) shows *C. trichocarpa, C.*

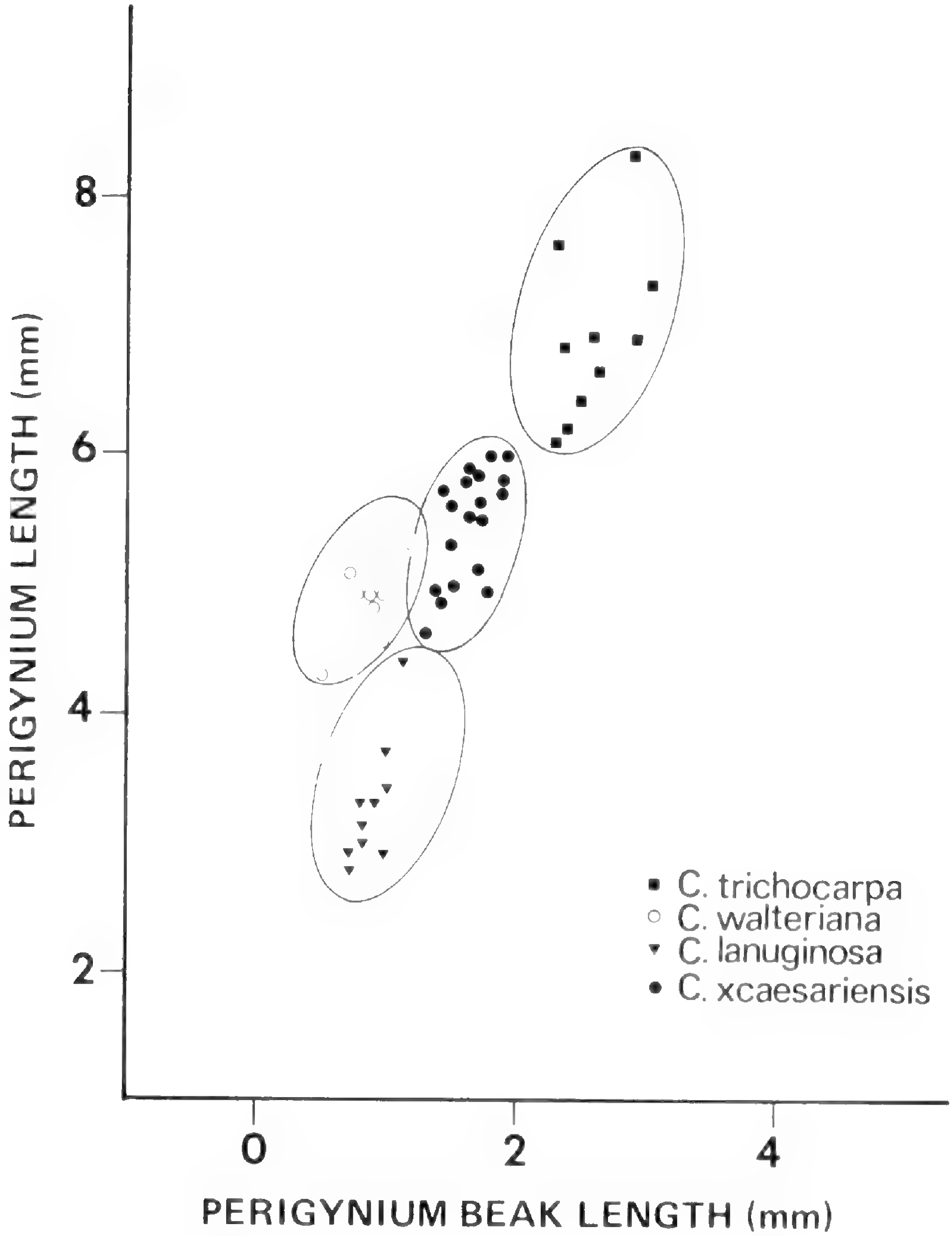


Figure 1. Perigynium length (mm) plotted against beak length (mm) for *Carex trichocarpa*, *C. lanuginosa*, *C. walteriana*, and *C.* ×*caesariensis*. Ovals are merely an aid to visualizing groupings of symbols and have no statistical significance.

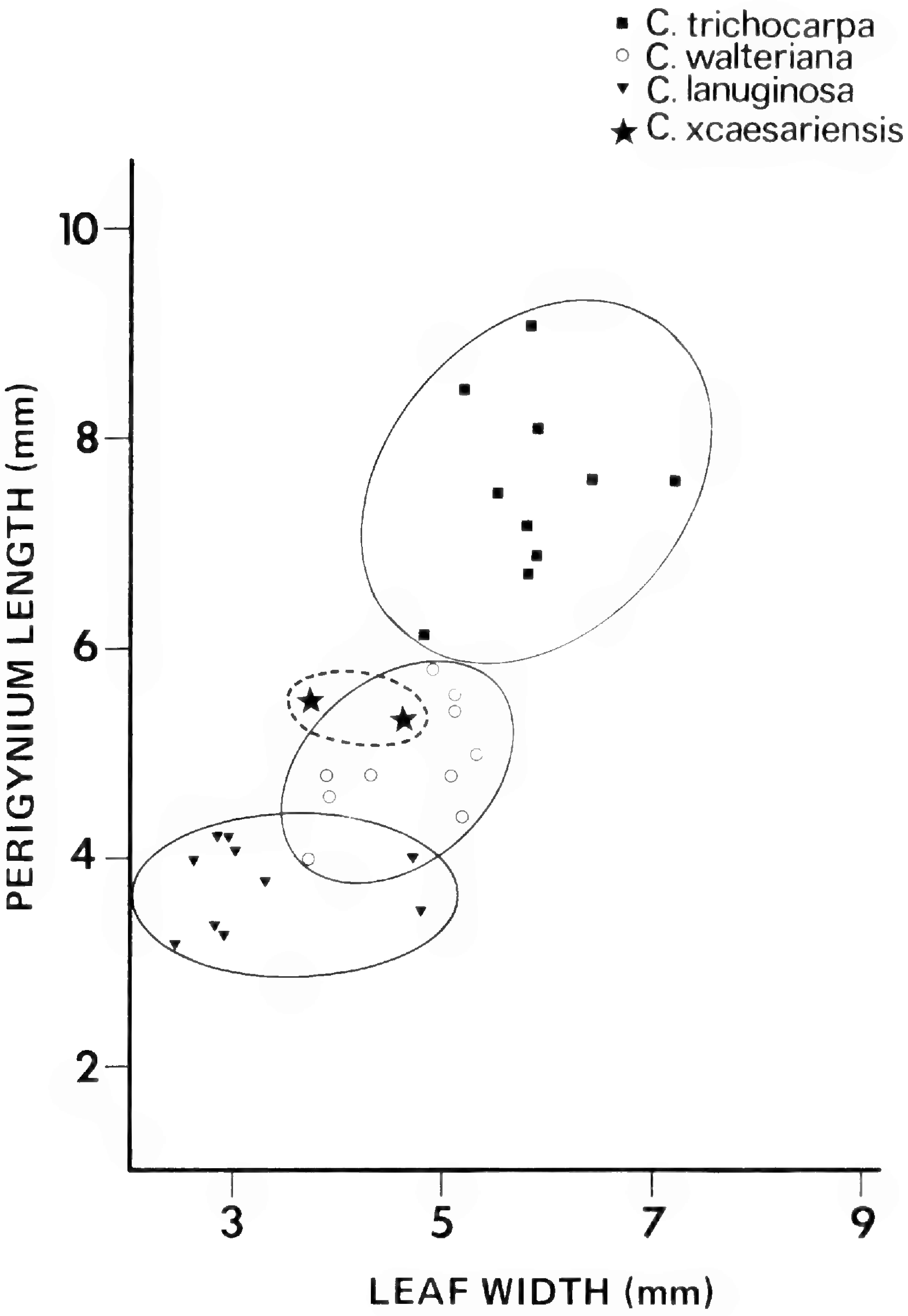


Figure 2. Perigynium length (mm) plotted against leaf width (mm) for *Carex trichocarpa*, *C. lanuginosa*, *C. walteriana*, and *C. ×caesariensis*. Ovals are merely an aid to visualizing groupings of symbols and have no statistical significance.

lanuginosa, and *C. walteriana* as three clearly resolved groups. Using the derived discriminant formula to determine the coordinates for an isotype and a topotype of *C.* ×*caesariensis,* we find that they are placed unequivocally between *C. lanuginosa* and *C. trichocarpa* (Figure 3). No affinity to the cluster representing *C. walteriana* is apparent. Although attempts to re-discover the hybrid have been in vain both at the type locality and elsewhere, the hypothesized parentage, *C. lanuginosa* × *C. trichocarpa,* seems well founded.

The characteristic perigynia of *Carex trichocarpa, C. lanuginosa,* and *C.* ×*caesariensis* are shown in Figure 4, which illustrates clearly the intermediacy of *C.* ×*caesariensis.* A more complete description than has been previously available is provided below along with specimen citations.

Carex ×**caesariensis** Mackenzie (*pro sp.*), N. Am. Fl. 18: 440. 1935. TYPE: NEW JERSEY, Camden County, swale, north branch Timber Creek, ca. 1 mi. W.S.W. Laurel Springs, June 15, 1920, *Bayard Long 23212* (HOLOTYPE: NY!; ISOTYPES: GH!, MICH!, PH!).

Plants colonial, rhizomes long creeping, 1.7–4.5 mm thick. Fertile culms 60–80 cm tall, lateral, with reddish bladeless sheaths at base, more or less fibrillose. Leaves 3–5 per fertile culm, equally distributed, the larger blades 30–45 cm long, 2–4.2 mm wide, plicate, antrorsely scabrous-margined; sheaths usually covering nodes, tight, glabrous, 4–13 cm long; inner band of sheath hyaline to pale stramineous, red-dotted, red-tinged at the concave, thickened mouth; ligule 2.3–4.2 mm long, ovate. Sterile culms 108–114 cm tall, blades 23–55 cm long, 3.5–4.6 mm wide, ligules ca. 3–4 mm, height of uppermost sheath apex 56–66 cm. Infructescence 15–37 cm long; pistillate spikes 2–3, sessile or the lower on a peduncle up to 8 cm long, 2.2–3.9 cm long, 5.5–9.5 mm wide, 35–50-flowered; lowermost bract with blade 23–42 cm long, 2.2–3.9 mm wide, sheathless or with a short sheath up to 4.2 cm long, the upper bracts much reduced. Staminate spikes 2–3, above pistillate; terminal spike 2.6–4.5 cm long, 2.1–3.7 mm wide, ca. 70–100-flowered; lateral staminate spikes smaller than terminal one, 1.2–3.4 cm long, bractless or with a short bract up to 5.5 cm long. Pistillate scales stramineous, often with a castaneous to purple margin distally 3(5)-veined, ovate, 2.2–5.9 mm long, 1.3–1.9 mm wide, prolonged into a scabrous awn 0.3–2.9 mm long. Staminate scales stramineous, castaneous to purple tinged above, 3-veined, narrowly obovate, ca. 3.8–5.2 mm long, 1.6–2.3

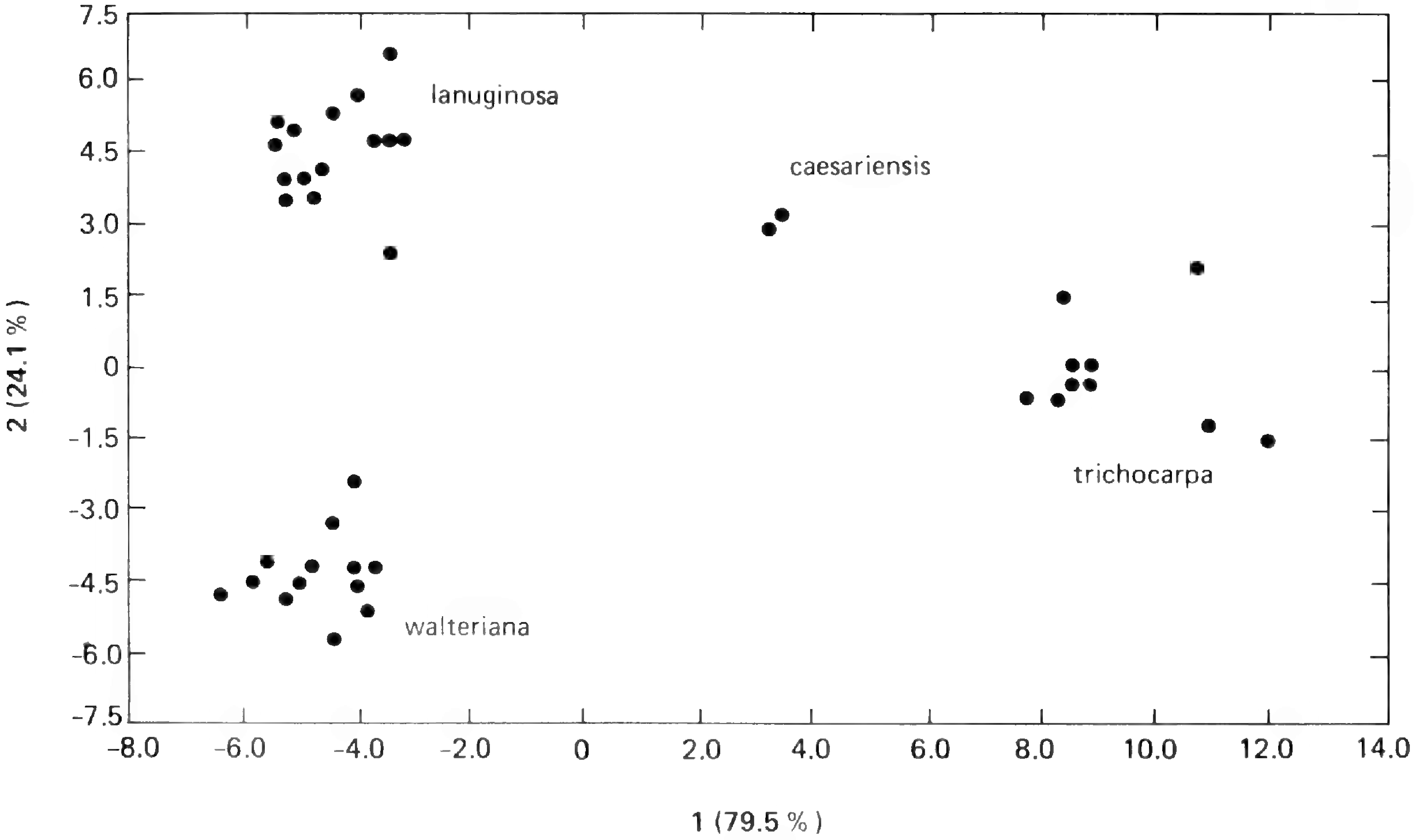


Figure 3. Discriminant plot of *Carex trichocarpa*, *C. lanuginosa*, and *C. walteriana* with an isotype and topotype of *C. ×caesariensis* plotted using coordinates calculated with the derived discriminant formula.

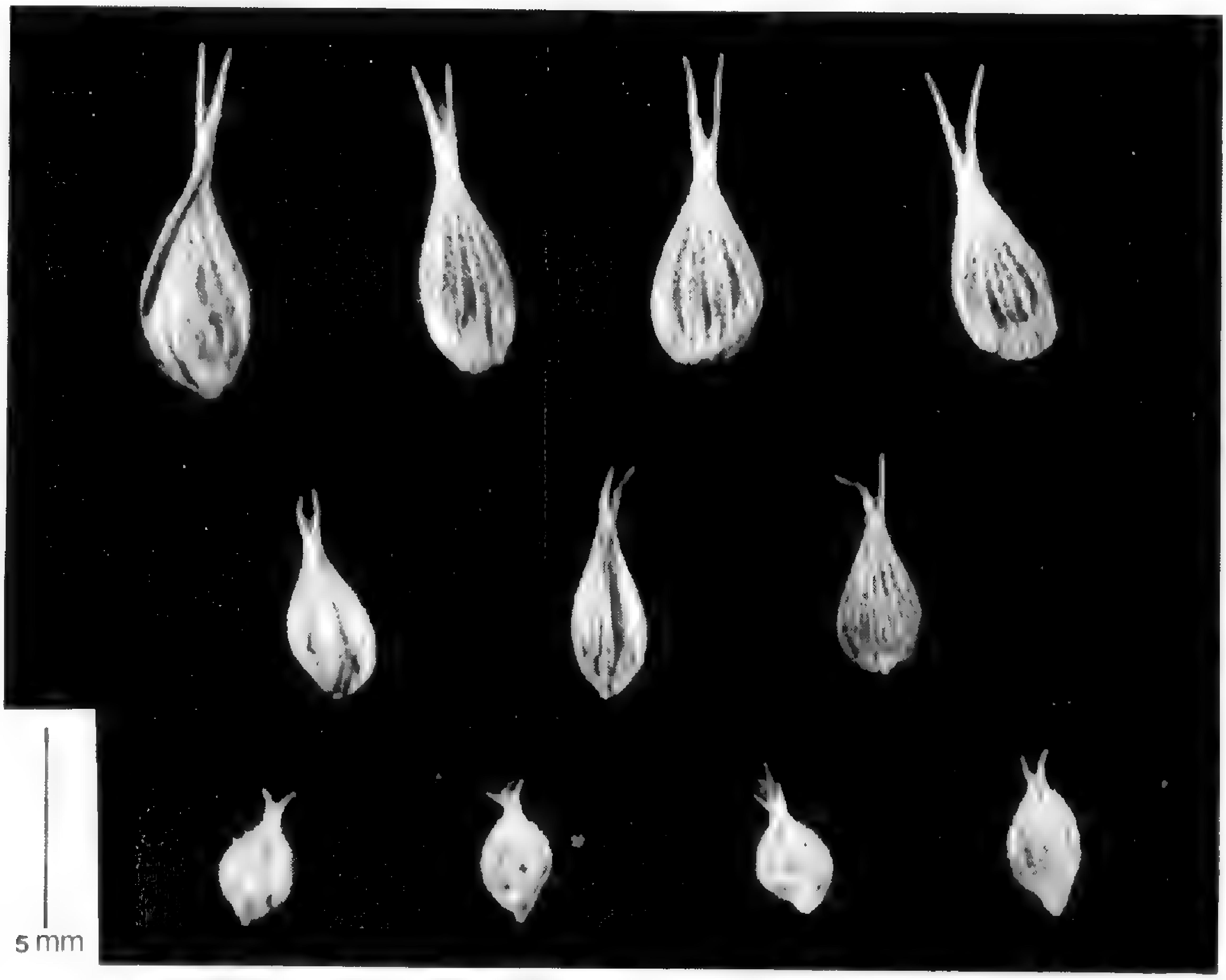


Figure 4. Perigynia of *Carex trichocarpa* (top), *C.* ×*caesariensis* (middle), and *C. lanuginosa* (bottom).

mm wide, ciliate on upper margin, acute to scabrous-acuminate or short-prolonged into an awn up to 1.1 mm long. Perigynia ascending to spreading, yellowish to brown when mature, moderately pubescent, narrowly ovoid, 4.3–6.1 mm long, 1.4–2.4 mm wide, ± strongly 12–18-veined, tapering into a bidentate beak; beaks 1.3–2.1 mm long; teeth 0.7–1.3 mm long. Achenes very rarely developing and apparently never filled with endosperm, pale brown, broadly trigonous with convex sides, obovate in outline, ca. 1.8–2.3 mm long, 1.4–1.7 mm wide. Styles indurate in lower third, brittle and shrivelled above, straight or slightly contorted just above achene, breaking close to achene; stigmas 3. Anthers 3, 2.1–2.8 mm long; pollen malformed and collapsed.

ADDITIONAL COLLECTIONS EXAMINED. UNITED STATES. **New Jersey.** Camden Co., swale, north branch Timber Creek, ca. 1 mi. W.S.W. Laurel Springs, July 11, 1922, *Bayard Long 26083* (GH!, MICH!, SIU!). **Pennsylvania:** Northampton Co., 1 mile W. of Portland, June 26, 1946, *R. L. Schaeffer, Jr. 22877* (PH!).

Carex ×*caesariensis* is evidently a rarely formed hybrid. It has not been collected for nearly 40 years and careful search for it at a number of sites where both putative parents occur has been unsuccessful. Undoubtedly, the confusion surrounding this intersectional hybrid has resulted from the difficulty in deducing the very dissimilar parents.

LITERATURE CITED

Gleason, H. A. 1952. Illustrated Flora of the Northeastern United States and Adjacent Canada. New York Bot. Gard. New York. 3 vols.

———, and A. Cronquist. 1963. Manual of the Vascular Plants of Northeastern North America and Adjacent Canada. Van Nostrand Reinhold Co. New York.

Humphries, C. J. 1983. Primary data in Hybrid Analysis. *In:* Advances in Cladistics, vol. 2, Eds. Platnick, N. I. & V. A. Funk. Columbia Univ. Press. New York.

Mackenzie, K. K. 1935. Cyperaceae-Cariceae. N. Am. Fl. 18: 169 478.

Wagner, W. H. Jr. 1980. Origin and philosophy of the groundplan divergence method of cladistics. Syst. Bot. 5: 173–193.

———. 1983. Reticulistics: The recognition of hybrids and their role in cladistics and classification. *In:* Advances in Cladistics vol. 2, Eds. Platnick, N. I. & V. A. Funk. Columbia Univ. Press. New York.

A. A. R.
UNIVERSITY OF MICHIGAN HERBARIUM
NORTH UNIVERSITY BLDG.
ANN ARBOR, MICHIGAN 48109

P. M. C.
BIOSYSTEMATICS RESEARCH INSTITUTE
AGRICULTURE CANADA
WM. SAUNDERS BLDG., C. E. F.
OTTAWA, ONTARIO K1A 0C6

CYPERUS FLAVICOMUS, THE CORRECT NAME FOR *CYPERUS ALBOMARGINATUS*

GORDON C. TUCKER[1]

ABSTRACT

The correct name for *Cyperus albomarginatus*, a pantropical and warm-temperate sedge, is shown to be *C. flavicomus* Michaux.

Key Words: *Cyperus albomarginatus, C. flavicomus*, Cyperaceae

The species commonly known as *Cyperus albomarginatus* Mart. & Schrad. is pantropical and warm temperate. In North America, it extends along the coastal plain and piedmont from Florida to New York and westward to New Mexico (Fernald, 1950). It also occurs on the Pacific coast of Mexico and Central America (Tucker, 1983); in South America from eastern Brazil to Ecuador and Paraguay; and in the Old World tropics (Kükenthal, 1935–36). The species is readily identified by its widely spaced, non-overlapping scales with their prominent hyaline borders, to which the epithet "*albomarginatus*" refers (Tucker, 1983).

In most twentieth century floristic works the authority given for *Cyperus albomarginatus* is "Mart. & Schrad. *ex* Nees" or simply "Mart. & Schrad." However, the actual name published by Nees in *Flora Brasiliensis* in 1842 was *Pycreus albomarginatus* Mart. & Schrad. *ex* Nees; *C. albomarginatus* was merely a manuscript name given in synonymy there, and hence not validly published (ICBN, Art. 34.1d). The combination *Cyperus albomarginatus* was first validly published twelve years later by Steudel (Syn. cyp. 10, 1854). Fernald (1950), Gleason and Cronquist (1962) and Radford et al. (1967) have treated this species as *C. albomarginatus*. However, in nineteenth century manuals, e.g., Chapman (1860), and early twentieth century works, e.g., Britton and Brown (1901) and Robinson and Fernald (1908), the name applied to this species was *C. flavicomus* Michx. The change in name used seems to have been the result of publication of Kükenthal's worldwide monograph of *Cyperus* in *Das Pflanzenreich* (1935–36). There, Kükenthal treated this species

---

[1] Present address: Biological Survey, New York State Museum, The State Education Department, Albany, New York 12230.

as *C. albomarginatus* Martius & Schrad. *ex* Nees, while placing the older name, *C. flavicomus* Michx., in the synonymy of the common eastern North American species, *C. strigosus* L. Through the courtesy of the Muséum National d'Histoire Naturelle, Paris, I was able to examine a photograph of the type of *C. flavicomus* Michx. This type can also be seen on the IDC microfiche edition of the Michaux herbarium. Apparently, Kükenthal never saw the type of *C. flavicomus,* for it is clearly a plant of the species currently referred to as *C. albomarginatus.* Thus the oldest name for the species is *C. flavicomus* Michx., with the following synonymy:

Cyperus flavicomus Michx., Fl. bor.-amer. 1: 27. 1803.—Type: U.S.A., "Carolina," 1786–96, *Michaux s.n.* (Holotype: P, not seen; photo: DUKE!, IDC microfiche Herb. Michaux!).

C. flavicomus Vahl, Enum. pl. 2: 360. 1805. Type: U.S.A. South Carolina, *Bosc s.n.* (Holotype: C!), *nom. superfl.*

Pycreus albomarginatus Mart. & Schrad. *ex* Nees *in* Mart., Fl. bras. 2(1): 9. 1842. Type: BRAZIL, Prov. Piauí, *Martius s.n.* (Holotype: M!).

P. sabulosus Mart. & Schrad. *ex* Nees *in* Mart., Fl. bras. 2(1): 10. 1842. Type: BRAZIL, Prov. Rio Nigri, juxta lacum di Coari, *Martius s.n.* (Lectotype, here designated: M!).

C. albomarginatus (Mart. & Schrad. *ex* Nees *in* Mart.) Steud., Syn. cyp. 10. 1854.

C. sabulosus (Mart. & Schrad. *ex* Nees *in* Mart.) Steud., Syn. cyp. 10. 1854.

C. albomarginatus var. *sabulosus* (Mart. & Schrad. *ex* Nees *in* Mart.) Kükenth., Pflanzenreich IV(20): 361. 1936.

C. albomarginatus var. *pachyanthemos* Kükenth., Pflanzenreich IV(20): 361. Type: PARAGUAY. Itacurubí, *Rojas 2286A* (Holotype: B).

Uttal (1984) in his summary of Michaux's type localities, followed Kükenthal's and Fernald's usage in treating *Cyperus flavicomus* as a synonym of *C. strigosus.* Uttal gave the spelling as "*flavicornus,*" while the epithet was spelled "*flavicomus*" both in *Flora boreali-americana* and on the label of Michaux's type. [L. J. Uttal (pers. comm.) has acknowledged that his spelling "*flavicornus*" was an error of transliteration, not caught in proofreading, and that in his original handwritten notes the spelling was indeed "*flavicomus.*" Editor.]

Hooper and Raynal (1969) treated *Cyperus albomarginatus* as a synonym of the earlier name, *C. macrostachyos* Lam. (Tabl. encycl. 1: 147, 1791). They indicated that they did not see the type of *C. albomarginatus.* Examination of a photograph of the type of *C. macrostachyos* ("ex Africa," Herb. Lamarck, P), shows it to be strikingly different from *C. flavicomus* Michx. (= *C. albomargina-*

tus), notably in its long spikelets with 60 to 70 closely imbricate scales; *C. flavicomus* has only 6 to 24 scales per spikelet. Another distinctive characteristic of *C. flavicomus* is its spreading, non-overlapping scales (Kükenthal, 1935–36; Fernald, 1950; Tucker, 1983). Thus, the type of *C. macrostachyos* Lam. clearly does not belong in the same species as *C. flavicomus.* It seems best identified with the Indian-Asian *C. puncticulatus* var. *quinquagintiflorus* C. B. Clarke, sensu Kükenthal (1935–36). Such disposition of *C. macrostachyos* is supported by Kunth (1837), who also treated *C. macrostachyos* as a variety of *C. punticulatus.*

ACKNOWLEDGMENTS

I thank Dr. N. Hallé of the Muséum National d'Histoire Naturelle, Paris, for sending negatives of types from the herbaria of Michaux and Lamarck; Prof. Robert L. Wilbur for nomenclatural advice; the staff of Gray Herbarium Library for providing access to literature; and the curators of C and M for sending specimens.

LITERATURE CITED

Britton, N. L. and A. Brown. 1901. Manual of the Flora of the Northern States and Canada. Holt and Co., New York.

Chapman, A. W. 1860. Flora of the Southern United States. Ivison, Phinney, New York.

Fernald, M. L. 1950. Gray's Manual of Botany, 8th ed. American Book Co., New York.

Gleason, H. A. and A. Cronquist. 1962. Manual of Vascular Plants. Van Nostrand, New York.

Hooper, S. and J. Raynal. 1969. New species and names in African *Pycreus* P.-Beauv. (Cyperaceae). Kew Bull. 23: 313–314.

Kükenthal, G. 1935–36. *Cyperus. In:* A. Engler & L. Diels, Eds., Das Pflanzenreich IV(20). Engelmann-Cramer, Stuttgart.

Kunth, C. S. 1837. Enumeratio plantarum: Cyperacearum. J. G. Cotta, Stuttgart.

Radford, A. E., H. E. Ahles, and C. R. Bell. 1967. Manual of the Vascular Flora of the Carolinas. Univ. N. Carolina Press, Chapel Hill.

Robinson, B. L. and M. L. Fernald. 1908. Gray's Manual of Botany, 7th ed. American Book Co., New York.

Tucker, G. C. 1983. Taxonomy of *Cyperus* (Cyperaceae) in Costa Rica and Panama. Syst. Bot. Monogr. 2: 1–85.

Uttal, L. J. 1984. The Type Localities of the *Flora boreali-americana* of André Michaux. Rhodora 86: 1–66.

DEPARTMENT OF BOTANY
DUKE UNIVERSITY
DURHAM, NORTH CAROLINA 27706

CAREX JAMESII IN MINNESOTA WITH PHYTOGEOGRAPHICAL NOTES ON THE GENUS

Gerald A. Wheeler

ABSTRACT

Carex jamesii Schwein. is reported new to Minnesota. The *Carex* flora of the state now stands at 143 species. The area where carices from four floristic provinces intermingle is illustrated and discussed as to its apparent relationship to *Carex jamesii* and other areas of floristic transition in the Great Lakes region.

Key Words: *Carex jamesii,* new record, phytogeography, area of transition, Minnesota.

CAREX JAMESII IN MINNESOTA

In 1984 Wheeler and Ownbey reported 142 species of *Carex* native to Minnesota and discussed the phytogeographical and ecological status of the genus in the state. A sedge was discovered at Beaver Creek Valley State Park in Houston County in May 1984 that appeared vegetatively to be *Carex jamesii,* based on its cinnamon-brown sheaths and relatively narrow leaves. This tentative assignment was confirmed in June of that year when mature fruiting material became available. Also in June a second station for this taxon was discovered at Forestville State Park in Fillmore County. This species has been previously reported from Wisconsin (Hartley, 1966; Zimmerman, 1976) and Iowa (Mackenzie, 1931–1935) but not from Minnesota.

At Beaver Creek Valley State Park, several cespitose clumps of *Carex jamesii* were observed near the base of a steep, moist, east-facing wooded slope overlooking Beaver Creek. Several other clumps were observed slightly higher up on the slope, and a few plants were observed in a deep ravine nearby. This species grows in association with species richness indicators such as *Allium tricoccum, Claytonia virginica, Dicentra cucullaria, Hepatica acutiloba,* and *Hydrophyllum virginianum.* Other carices growing in proximity to *C. jamesii* are indicated in Table 1.

At Forestville State Park, approximately 48 km west of Beaver Creek Valley State Park, *Carex jamesii* was discovered in a rich sugar maple - basswood forest situated high above the east bank of the South Branch Root River. The plants occur primarily on the

Table 1. *Carex* species occurring on wooded slopes at three State Parks in southern Minnesota. [1) Beaver Creek Valley State Park, Houston County; 2) Forestville State Park, Fillmore County; 3) Kilen Woods State Park, Jackson County.]

	Park Distance Relationships		
		290 km	
	W	- - - - - - - - - -	E
	← 242 km	↓	48 km →
	State Parks		
Species	3	2	1
C. arctata Boott (m; very rare)	-	-	+
C. laxiculmis Schwein. (M, B) var. *copulata* (Bailey) Fern.	-	-	+*
C. jamesii Schwein. (m, B)	-	+**	+**
C. oligocarpa Willd. (M, B)	-	+*	+*
C. woodii Dew. (m, B)	-	+	+
C. gracillima Schwein. (M)	-	+*	+
C. hirtifolia Mack. (M, B)	-	+*	+*
C. normalis Mack. (M, b)	-	+	+
C. cephalophora Willd. (T)	-	+	+
C. deweyana Schwein. (M, b)	-	+	+
C. hitchcockiana Dew. (M, b)	-	+*	-
C. albursina Sheldon (M, B)	+	+*	+*
C. sparganioides Willd. (M, B)	+	+*	+*
C. pedunculata Willd. (M, b)	+	+	+*
C. cephaloidea (Dew.) Dew. (M, b)	+	+	+
C. amphibola Steud. (m, B) var. *turgida* Fern.	+	+*	+*
C. convoluta Mack. (M, B)	+	+*	+*
C. blanda Dew. (t, M, B)	+	+*	+*
C. pensylvanica Lam. (T, M, b)	+	+*	+*
C. eburnea Boott (T)	+	+	+
C. peckii Howe (t, M, b)	+	+	+
C. sprengelii Spreng. (t, M, b)	+	+	+
C. assiniboinensis W. Boott (B)	+	-	-

*Sedge growing within 3 m of *C. jamesii* at a particular site
**Sedge of major concern

+ = observed
- = not observed

T = occurring at or near the top of steeply-wooded slopes
t = only rarely occurring in these locations
M = occurring near the middle region of steeply-wooded slopes
m = only rarely occurring in these locations
B = occurring at or near the base of steeply-wooded slopes
b = only rarely occurring in these locations

slopes of deep ravines, and on a few slopes it is the dominant species in the field layer. Some plants were also observed near the western edge of the woodland, just before the terrain drops precipitously to the river floor. As at Beaver Creek Valley State Park, the species here grows in association with a fairly diverse ground flora, including several other carices (Table 1).

A search for *Carex jamesii* was also conducted at Kilen Woods State Park (Jackson County), 242 km west of Forestville State Park, but was without success. Several other carices that grow in eastern woodlands were not observed at this site and are presumed absent (Table 1). On the other hand, *C. assiniboinensis* while growing in some abundance in Kilen Woods, was not observed at either of the two eastern localities. All *Carex* species observed on wooded slopes at the three sites mentioned above are listed in Table 1.

Carex jamesii appears to be rare in Minnesota; the bluffs in extreme southeastern Minnesota provide the habitats for the northwesternmost stations of this species in North America (Fernald, 1950; Gleason and Cronquist, 1963; McGregor et al., 1977; Scoggan, 1978). Figure 1 shows the distribution of *C. jamesii* in Minnesota, Wisconsin, and Iowa. Specimens at MIN, WIS, IA, and ISC (Holmgren et al., 1981) were utilized in preparation of the maps. All collection numbers cited are my own; all specimens cited are in MIN.

SPECIMENS EXAMINED: Fillmore Co.: Forestville State Park, rich sugar maple-basswood forest overlooking South Branch Root River (east bank), T102N, R12W, Sec. 13, *8297, 8366.* Houston Co.: Beaver Creek Valley State Park, near base of a steep, east-facing wooded slope overlooking Beaver Creek, T102N, R6W, Sec. 8, *8208, 8391.*

PHYTOGEOGRAPHICAL NOTES

Wheeler and Ownbey (1984) illustrated nine areas of *Carex* affiliation in Minnesota and noted that Area 4 (shaded portion of Minnesota, Figure 2) is characterized by an intermingling of carices from four floristic provinces which converge in the state. In general, carices associated with the Grassland (e.g., *C. eleocharis, C. praegracilis,* and *C. obtusata*) and Prairie-Forest (e.g., *C. blanda, C. convoluta,* and *C. eburnea*) floristic provinces have their major occurrences to the south and west of this area, whereas sedges of the Northern Conifer province (e.g., *C. chordorrhiza, C. gynocrates,* and *C. vaginata*) and the Northern Hardwoods province (e.g., *C.*

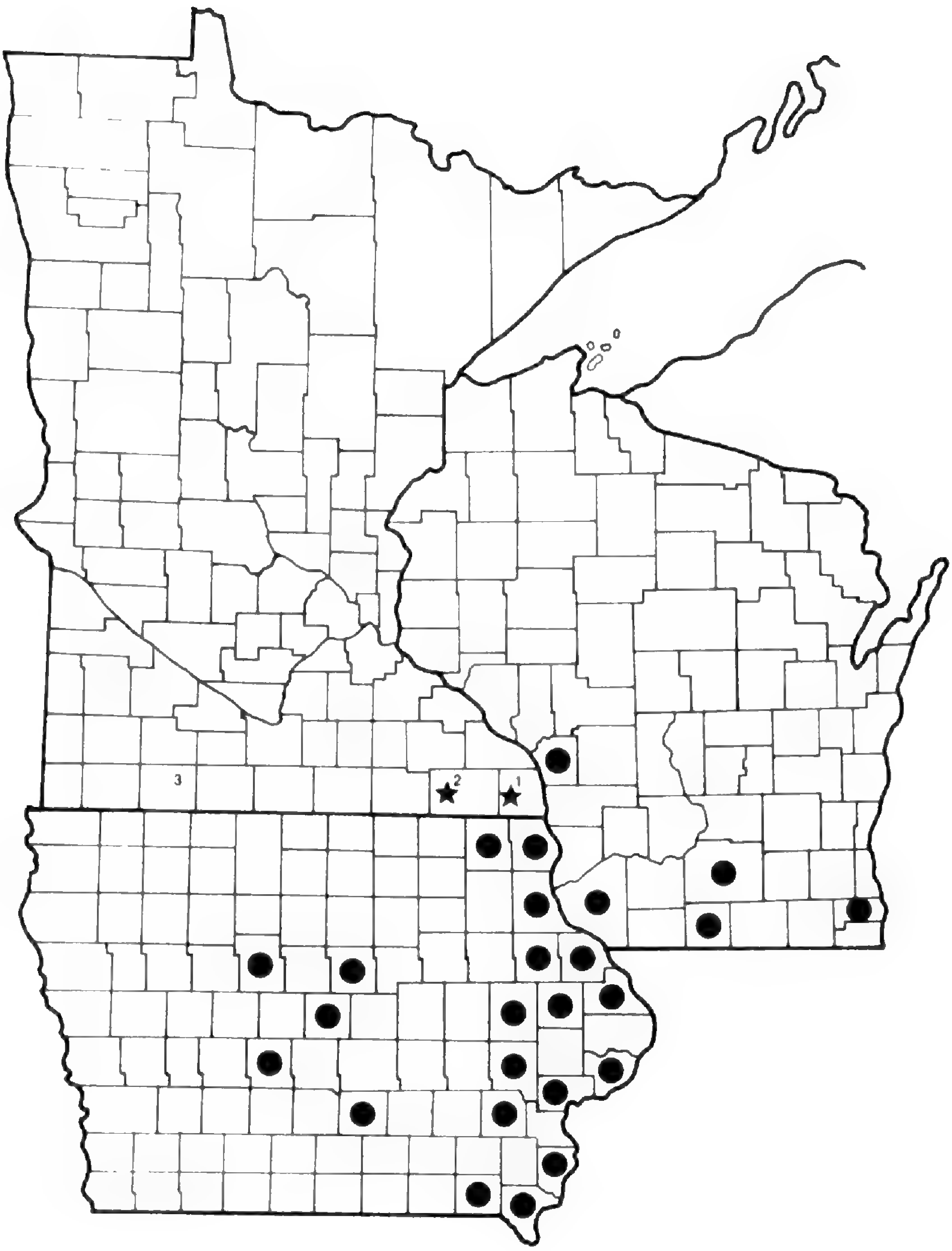


Figure 1. Distribution of *Carex jamesii* in Minnesota, Wisconsin, and Iowa. Stars indicate specific localities; dots indicate county records. Sites are: **1)** Beaver Creek Valley State Park (Houston Co.); **2)** Forestville State Park (Fillmore Co.); **3)** Kilen Woods State Park (Jackson Co.).

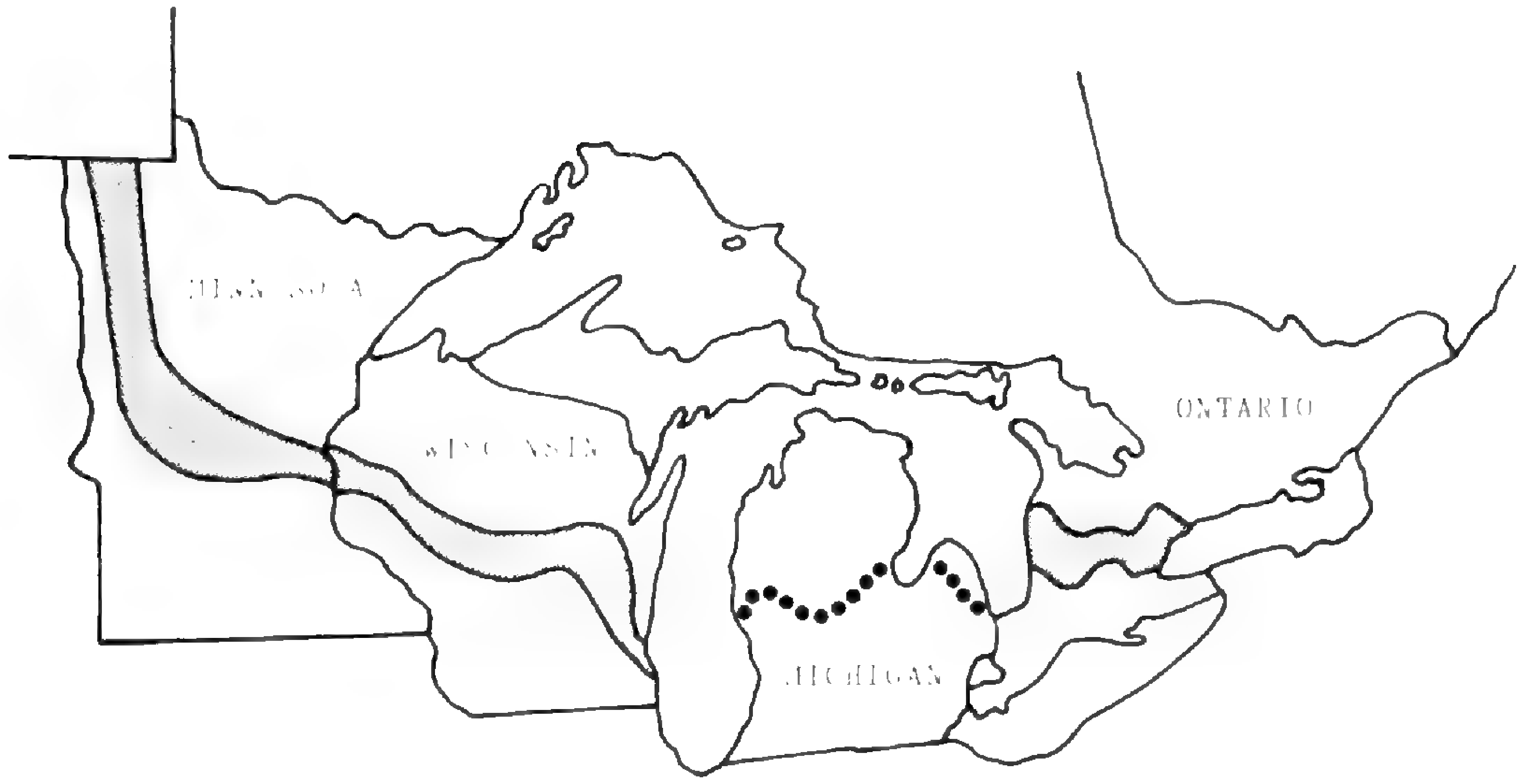


Figure 2. Areas of floristic transition in Minnesota (Wheeler and Ownbey, 1984, Area 4 in Fig. 3: p. 156), Wisconsin (Curtis, 1959, Fig. 5: p. 20), Michigan (McCann, 1979, Fig. 11: p. 21), and Ontario (Thaler and Plowright, 1973, slightly modified from Fig. 4: p. 1773). Further explanation in the text.

gynandra, C. leptonervia, and *C. ormostachya*) have their major occurrences to the north and east of it.

Of the 143 *Carex* species occurring in Minnesota, 61 occur primarily to the north and east of Area 4, while 48 occur primarily to the south and west of it. Many of these carices display reasonably well-defined range boundaries in the state (Wheeler and Ownbey, 1984). The remaining 34 carices have either ubiquitous distributions in Minnesota or insufficient information with which to categorize them.

One of the best known floristic boundaries has been mapped in Wisconsin by Curtis (1959); it is suggested here that Area 4 represents an extension (albeit probably a rough approximation) of this boundary zone across Minnesota. Some supporting evidence for this hypothesis is that (1) the eastern extremity of Area 4 is closely congruent with the area in which the tension zone in Wisconsin meets the Minnesota border, (2) the northwestern extremity of this area corresponds closely to the boundary between the Northern Conifer province and the Grassland province in Manitoba (Gleason and Cronquist, 1964; Cushing, 1965), and (3) ongoing work by the author and others demonstrates that the range boundaries of 280 vascular species (representing 63 families) occurring in the western and southern portions of the state form a band of concentration that lies clearly within this area. It is suspected, however, that the shape of this zone will change, probably appreciably so, when the entire Minnesota flora is taken into account.

The position of the above-mentioned floristic boundary in the Great Lakes region, as presently understood, is illustrated in Figure 2. The transition zone in Minnesota represents an area where carices from four floristic provinces intermingle. The area of transition in Wisconsin is Curtis' (1959) tension zone, based on the range boundaries of 182 species in 12 families or orders. The dotted line drawn through the lower peninsula of Michigan in Figure 2 represents the center of the tension zone as determined by McCann (M.A. thesis, West. Mich. Univ., Kalamazoo, 1979), based on a zone allegiance study of 649 vascular taxa. Because she did not illustrate a boundary zone per se, but presented several figures indicating range limits of northern and southern plants in the state, I have not tried to interpret the data further. The area of transition in Ontario is based on a canonical correlation analysis of 100 vascular species by Thaler and Plowright (1973). It should also be noted that slightly different shaped zones were produced by these workers when they utilized zone allegiance and principal components analyses. The clearest trend, however, emerged from the canonical correlation analysis (Thaler and Plowright, 1973); the position of this zone interestingly corresponds closely to the boundary zone obtained earlier by Fox and Soper (1954), who utilized range limits data.

ACKNOWLEDGMENTS

The writer thanks Gerald B. Ownbey and Eville Gorham, as well as two anonymous reviewers, for reading and criticizing an earlier draft of the manuscript.

LITERATURE CITED

Curtis, J. T. 1959. The Vegetation of Wisconsin. University of Wisconsin Press, Madison.

Cushing, E. J. 1965. Problems in the Quaternary phytoegeography of the Great

Lakes region. *In:* H. W. Wright, Jr. and D. G. Frey (Eds.). The Quarternary of the United States. Princeton University Press, Princeton, New Jersey. 403 416.

FERNALD, M. L. 1950. Gray's Manual of Botany. 8th ed. American Book Co., New York.

FOX, W. S., AND J. H. SOPER. 1954. The distribution of some trees and shrubs of the Carolinian zone of southern Ontario. Part III. Trans. R. Can. Inst. 30: 99 130.

GLEASON, H. A., AND A. CRONQUIST. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Van Nostrand Reinhold Co., New York.

———, AND ———. 1964. The Natural Geography of Plants. Columbia University Press, New York.

HARTLEY, T. G. 1966. The flora of the "Driftless Area." Univ. Iowa Stud. Nat. Hist. 21: 1-174.

HOLMGREN, P. K., W. KEUKEN, AND E. K. SCHOFIELD. 1981. Index Herbariorum, Ed. 7. Regnum Veg. 106: 1-452.

MACKENZIE, K. K. 1931-1935. Cariceae. *In:* North American Flora 18: (1 7), 1-478. New York Botanical Garden, New York. Parts 1 3, 1931; 4 7, 1935.

MCGREGOR, R. L., T. M. BARKLEY, ET AL. 1977. Atlas of the Flora of the Great Plains. Iowa State University Press, Ames.

SCOGGAN, H. J. 1978. The Flora of Canada. Part 2. Nat'l Mus. Canad. Publ. Bot. 7.

THALER, G. R., AND R. C. PLOWRIGHT. 1973. An examination of the floristic zone concept with special reference to the northern limit of the Carolinian zone in southern Ontario. Canad. J. Bot. 51: 1765-1789.

WHEELER, G. A., AND G. B. OWNBEY. 1984. Annotated list of Minnesota Carices, with phytogeographical and ecological notes. Rhodora 86: 151 231.

ZIMMERMAN, J. H. 1976. *Carex. In:* N. C. Fassett. Spring Flora of Wisconsin. 4th ed., revised by O. S. Thomson. University of Wisconsin Press, Madison. p. 32 70.

DEPARTMENT OF BOTANY
UNIVERSITY OF MINNESOTA
ST. PAUL, MN 55108

ON THE ANCESTRY OF *BETULA CORDIFOLIA* REGEL

STEPHEN F. MAYER[1] AND DAVID J. SCHIMPF

ABSTRACT

Betula alleghaniensis, *B. cordifilia*, and *B. papyrifera* from the Lake Superior region of Minnesota were compared morphologically in order to infer whether *B. cordifolia* is likely to be a hybrid of the other two species. Multivariate distance relationships based on 11 characters from leaves, pistillate catkins, or fruits suggested that such a hybrid status for *B. cordifolia* is unlikely. Chromosome counts from the literature are also inconsistent with this hypothesized hybrid ancestry.

Key Words: *Betula*, inferred hybridization, Minnesota

INTRODUCTION

The most recent evidence supporting specific status for *Betula cordifolia* Regel came from Brittain and Grant (1965b, 1967), who countered the conclusion by Fernald (1945) that heart-leaved birch is a variety of *B. papyrifera* Marsh. These authors did not address the suggestion by Gleason (1952) that heart-leaved birch is probably a fertile hybrid of *B. alleghaniensis* Britton and *B. papyrifera*. We present morphological evidence from *Betula* in Minnesota and chromosome counts from the literature that are inconsistent with Gleason's hypothesis.

MATERIALS AND METHODS

Twigs that included both leaves and mature fruiting catkins were collected from *Betula cordifolia* in Lake and Cook Counties and from *B. alleghaniensis* and *B. papyrifera* in St. Louis, Lake, and Cook Counties, Minnesota. Material was obtained with the aid of an extensible pruning shear or a shotgun. All individuals sampled grew within 20 km of Lake Superior. We also used specimens from the same zone that were already in the Olga Lakela Herbarium (DUL).

For each individual, data consisted of means from five leaves, five catkin bracts, five samaras and, where possible, five catkins. Most leaves used were attached to short shoots. Characters assessed for

---

[1] Present address: RR 3, Box 105, Greenfield, IN 46140

leaves were number of serrations/side, number of lateral veins/side, a/m ratio (Brayshaw, 1966) and shape of the base of the blade. Characters assessed for fruiting catkins were catkin length exclusive of the peduncle, bract length, bract shape, samara length, samara width exclusive of the wings, length/width of samara less wings, and style length. These characters statistically distinguished *Betula cordifolia* from *B. papyrifera* in eastern Canada (Brittain and Grant, 1965b, 1967) as well as in northeastern Minnesota (Mayer, 1983, M.S. thesis, Univ. of Minn., Duluth).

Each character was scaled from 0 to 1 and used to obtain a hybrid distance diagram after the method of Wells (1980). This procedure involves plotting each individual at the intersection of its Euclidean multivariate distances from two points representing the extremes for all characters in the hypothesized parents. If non-distinguishing characters have been excluded, an individual plotted at a point between those of the hypothesized parent taxa would be strongly suspected to be a hybrid. An individual plotted at a point far from intermediate is unlikely to be a hybrid of the hypothesized parent taxa.

RESULTS AND DISCUSSION

Even though *Betula cordifolia* is intermediate between *B. alleghaniensis* and *B. papyrifera* in number of lateral veins, samara length and width, samara length/width, and bract length, the hybrid distance diagram (Figure 1) indicates that it is not intermediate in an overall morphological sense. Essentially all of the *B. cordifolia* individuals lie beyond the semicircle that just encloses the hypothesized parent taxa, indicating that they have many characters that are more extreme than those of the hypothesized parents in the direction that is opposite from an intermediate. Those individuals beyond the outer semicircle are more extreme in the direction opposite from intermediate than the most extreme values represented by the reference points Bae and Bpe. This situation suggests that it is quite unlikely that *B. cordifolia* is a fertile hybrid of *B. alleghaniensis* and *B. papyrifera. Betula cordifolia* lies farther from *B. papyrifera* than from *B. alleghaniensis* in Figure 1; this spacing probably derives from use of characters that distinguish the first two species in particular. We do not see this choice as biasing the results, as these same characters also distinguish *B. alleghaniensis* from the other two species satisfactorily.

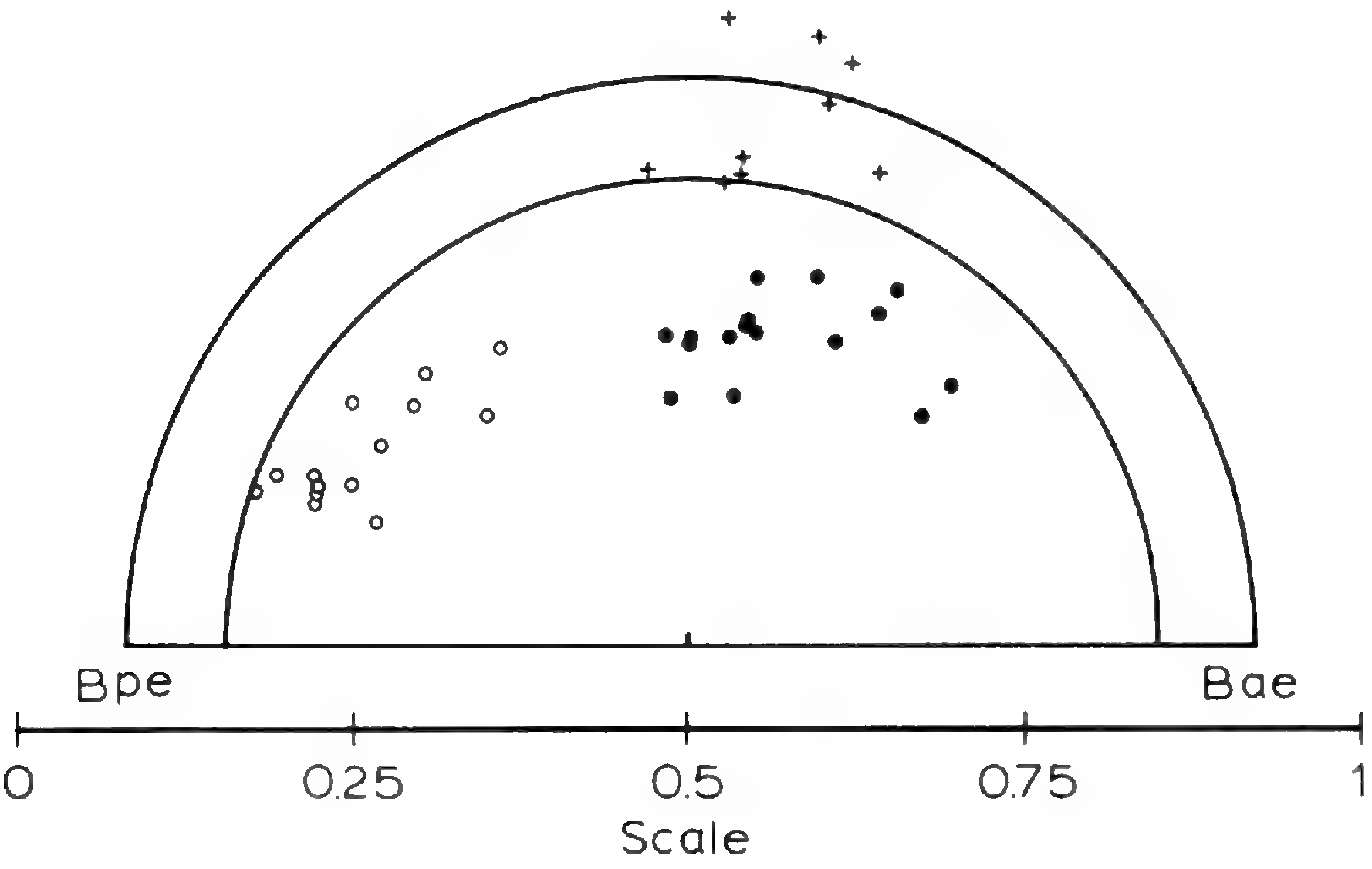


Figure 1. Hybrid distance diagram. Individuals of *Betula papyrifera* (open circles), *B. alleghaniensis* (solid circles), and *B. cordifolia* (crosses) are plotted at the intersections of their multivariate distances from the *B. papyrifera* extreme (Bpe) and the *B. alleghaniensis* extreme (Bae). Inner semicircle encloses the variation exhibited by individuals of the hypothesized parent species. Outer semicircle encloses the maximum variation possible in the hypothesized parents, as represented by the extreme values observed for each character. Scale shows the Euclidean multivariate distance between Bpe and Bae.

Chromosome counts from the literature are also inconsistent with the ancestry hypothesized by Gleason (1952). Brittain and Grant (1965b, 1967, 1969) reported somatic numbers of 28, rarely 42 or 56, for *Betula cordifolia*. The typical number for *B. papyrifera* in eastern North America is 70, sometimes 84, and rarely 56 (Brittain and Grant, 1965a, 1967, 1969). The only number reported for *B. alleghaniensis* of which we are aware is 84 (VaLanne, 1972; Löve, 1982).

ACKNOWLEDGMENTS

We thank Terry Wiens, Sigma Xi, and the Minnesota Department of Natural Resources for their contributions to this study.

LITERATURE CITED

Brayshaw, T. C. 1966. What are the blue birches? Canad. Field-Nat. 80: 187–194.

Brittain, W. H., and W. F. Grant. 1965a. Observations on Canadian birch (*Betula*) collections at the Morgan Arboretum. I. *B. papyrifera* in eastern Canada. Canad. Field-Nat. 79: 189–197.

———, and ———. 1965b. Observations on Canadian birch (*Betula*) collections at the Morgan Arboretum. II. *B. papyrifera* var. *cordifolia*. Canad. Field-Nat. 79: 253–257.

———, and ———. 1967. Observations on Canadian birch (*Betula*) collections at the Morgan Arboretum. V. *B. papyrifera* and *B. cordifolia* from eastern Canada. Canad. Field-Nat. 81: 251–262.

———, and ———. 1969. Observations on Canadian birch (*Betula*) collections at the Morgan Arboretum. VIII. *Betula* from Grand Manan Island, New Brunswick. Canad. Field-Nat. 83: 361–383.

Fernald, M. L. 1945. Some North American Corylaceae (Betulaceae). I. Notes on *Betula* in eastern North America. Rhodora 47: 303–329.

Gleason, H. A. 1952. The new Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada. New York Botanical Garden, New York.

Löve, A. 1982. IOPB chromosome number reports LXXIV. Taxon 31: 119–128.

VaLanne, T. 1972. Colchicine effects and colchicine-induced polyploidy in *Betula*. Ann. Acad. Scient. Fenn. Ser. A. 191: 1–28.

Wells, H. 1980. Distance coefficients as a hybridization index: an example using *Mimulus longiflorus* and *M. flemingii* (Scrophulariaceae) from Santa Cruz Island, California. Taxon 29: 53–65.

DEPARTMENT OF BIOLOGY
UNIVERSITY OF MINNESOTA
DULUTH, MINNESOTA 55812

A RECONSIDERATION OF *GOMPHONEMA ANGUSTATUM* VAR. *SARCOPHAGUS* (GREG.) GRUN.

Louis L. Lipsey, Jr.

ABSTRACT

The diatom *Gomphonema angustatum* var. *sarcophagus* (Greg.) Grun. is reduced to synonymy and the description of the nominate variety emended.

Key Words: diatom, *Gomphonema*, Wisconsin

Rabenhorst in 1864 combined *Sphenella angustata* of Kützing (1844) under the name *Gomphonema angustatum*. Grunow (*in* Van Heurck, 1880) later reduced *Gomphonema sarcophagus* of Gregory (1856) to a variety of *G. angustatum*. Traditionally, *G. angustatum* (Kütz.) Rabh. var. *angustatum* and *G. angustatum* var *sarcophagus* (Greg.) Grun. have been distinguished from one another on the basis of the shape of their valves and the number of striae per 10 μm (Hustedt, 1930; Patrick & Reimer, 1975). The latter authors stated that valves of the nominate variety are characteristically lanceolate or almost linear in outline with protracted, somewhat rostrate, apices and that the striae count is 9–12 per 10 μm. Valves of variety *sarcophagus* on the other hand are described as being linear in outline with rostrate apices, and the striae count is typically 7–8 per 10 μm at the center of the valve, becoming 10–11 per 10 μm toward the apices.

In the course of a recent investigation on the freshwater diatoms of the northeastern glacial lake district of Wisconsin (Lipsey, Ph.D. dissertation, Southern Illinois University, 1982), an interesting collection on 16 August 1979 from Bearskin Lake (T 37/38 N*, R 6/7 E), Oneida County, yielded diatom frustules of *Gomphonema angustatum* with dissimilar valves (A.G.C. slide #54262). Epivalves were routinely characteristic of *G. angustatum* var. *angustatum* (Figure 1A) and hypovalves of *G. angustatum* var. *sarcophagus* (Figure 1B). Based on these observations it is apparent that Grunow's (1880) var. *sarcophagus* is not a distinct variety but is

---

*Based on Wisconsin Department of Transportation Division of Highways north-central zone coordinate numbering system.

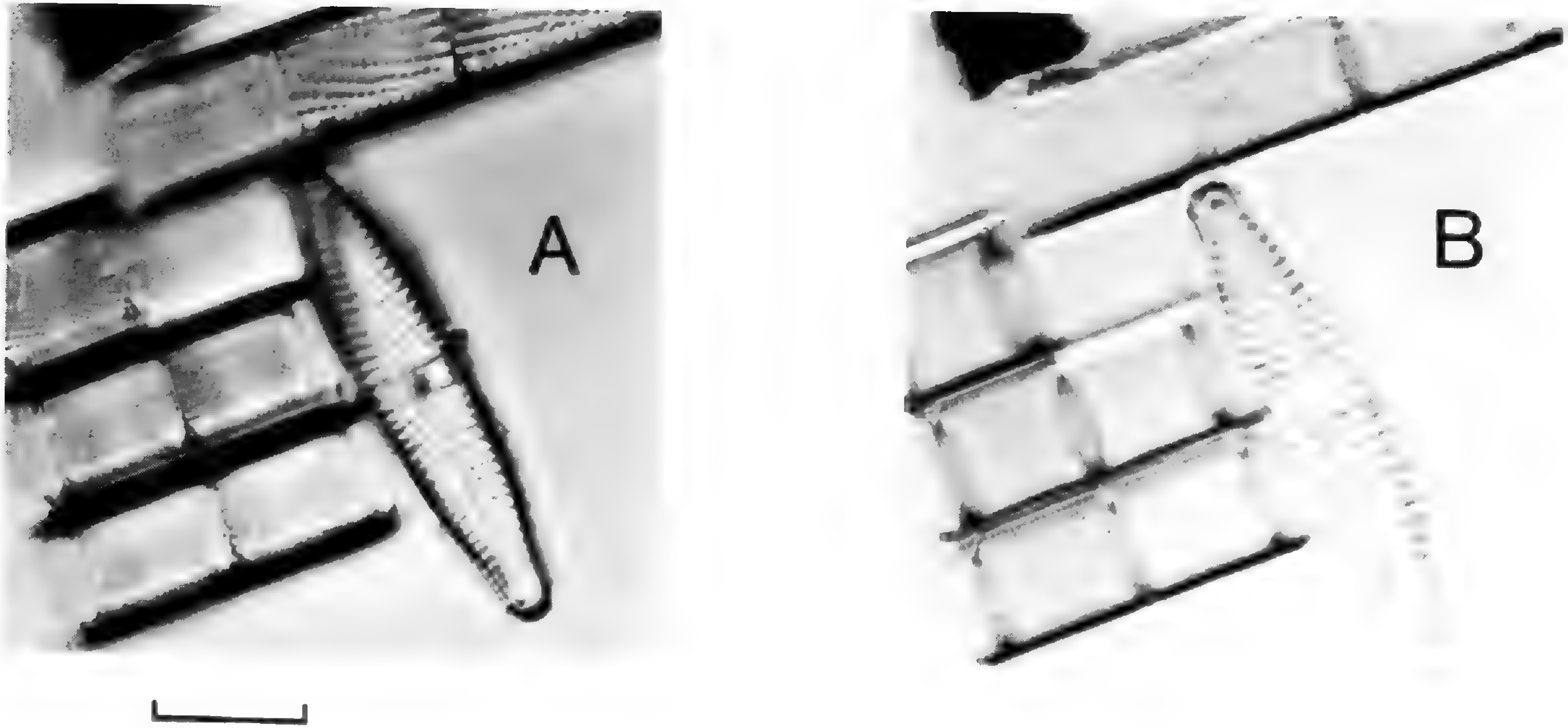


Figure 1. An epivalve (**A**) and a hypovalve (**B**) of *Gomphonema angustatum* from Bearskin Lake, Oneida County, Wisconsin. Scale bar equals 10 μm. (Photograph taken from A.G.C. slide #54262, which is currently housed in the Diatom Herbarium at the Philadelphia Academy of Science.)

merely one extreme of the normal range of variation of the nominate variety. *Gomphonema angustatum* var. *sarcophagus,* therefore, should be reduced to synonymy and the description of *G. angustatum* var. *angustatum* emended:

Gomphonema angustatum (Kütz.) Rabh. var. **angustatum**

Sphenella angustata Kütz., Bacill., p. 83, pl. 8, fig. 4. 1844.
Gomphonema angustatum (Kütz.) Rabh., Fl. Europaea Alg., sect. 1, p. 283. 1864.
Gomphonema sarcophagus Greg., Quart. J. Micr. Sci., 4: 13, pl. 1, fig. 42. 1856.
Gomphonema angustatum var. *sarcophagus* (Greg.) Grun. *in* V. H., Syn. Diat. Belgiqúe, pl. 25, fig. 2. 1880

Emended description: Valves linear to lanceolate, with slight transverse asymmetry, 12–47* μm long and 5–9 μm wide, with rounded, usually subrostrate to rostrate, apices; striae indistinctly punctate, radiate, often shortened about the central region, 6*–12 per 10 μm; axial area narrowly linear, with an indistinct to slightly orbicular central area containing an isolated stigma; raphe branches distinct.

Patrick & Reimer (1975) questioned the validity of the known varieties of *Gomphonema angustatum,* and mentioned that *G. angustatum* may be closely related to some varieties of *G. parvulum* Kütz., whose morphological variability has already been considered (Lowe, 1972; Wallace & Patrick, 1950). Future investigations may further resolve the affinities which exist between these species and other closely related taxa.

LITERATURE CITED

GREGORY, W. 1856. Notice of some new species of British freshwater Diatomaceae. Quart. J. Micros. Sci. 4: 1–14.

HUSTEDT, F. 1930. Bacillariophyta. *In:* A. Pascher. Die Süsswasser-Flora Mitteleuropas. Heft 10. Jena, G. Fischer.

KÜTZING, F. T. 1844. Die kieselschaligen Bacillarien oder Diatomeen. Bearbeitet von Dr. Friedrich Traugott Kützing ... Nordhausen, Kohne. (with 30 plates).

LOWE, R. L. 1972. Diatom population dynamics in a central Iowa drainage ditch. Iowa State J. Res. 47: 7–59.

PATRICK, R., AND C. W. REIMER. 1975. The Diatoms of the United States Exclusive of Alaska and Hawaii. Vol. 2, part 1, Entomoneidaceae, Cymbellaceae, Gomphonemaceae, Epithemiaceae. Acad. Nat. Sci. Phil., Monogr. No. 13.

---

*Denotes measurements observed from Wisconsin specimens.

RABENHORST, L. 1864. Flora Europaea Algarum Aquae Dulcis et Submarinae. Section 1, Algas diatomaceae complectens. Lipsiae, Apud Eduardum Kummerum.

VAN HEURCK, H. F. 1880–1885. Synopsis des Diatomées de Belgiqúe, Atlas et texte. Anvers. (with 132 plates).

WALLACE, J. H., AND R. PATRICK. 1950. A consideration of *Gomphonema parvulum* Kütz. Butler Univ. Bot. Stud. 9: 227–234.

507 OAK AVE.
AURORA, IL 60506

BASICLADIA VIVIPARA NORMANDIN & TAFT (CLADOPHORALES) IN ILLINOIS

LOUIS L. LIPSEY, JR.

ABSTRACT

The epizoic alga *Basicladia vivipara* is reported from Cook County, Illinois. Observations with regard to its growth and general morphology are compared to the type description.

Key Words: *Basicladia*, Cladophorales, Illinois

There have been few citings of *Basicladia vivipara* in North America since it was originally discovered by Normandin & Taft (1959) at Put-in-Bay, Ohio. Unlike other species of *Basicladia* whose growth is more or less restricted to the carapace of turtles, *B. vivipara* Normandin & Taft is unique in that its habitat is restricted to snail shells.

Basicladia vivipara Normandin & Taft was found on July 28, 1984 in an unnamed irrigation pond at the Evanston Country Club, Cook County, Illinois epizoic upon the shell of the snail *Stagnicola walkeriana* F. C. Baker. Several light green tufts were observed measuring up to two centimeters in length (Figure 1). In general, individual coenocytes were longer and broader at the base (300–700 μm × 34–70 μm) than toward the apex (210–368 μm × 24–30μm).

Normandin & Taft's (1959) observations revealed that apical cells of *Basicladia vivipara* were characteristically larger in diameter than basal cells. Also, they noted that cell length typically shortened toward the apex, resulting in a distinctive club-like filament. However, measurements from Cook County filaments appear to contradict these observations. Filaments and individual coenocytes were distinctly longer and broader at the base than toward the apices. Perhaps the differences in growth can be attributed to different hosts. For example, Normandin & Taft (1959) found *B. vivipara* growing on the snail *Viviparus malleatus* Reeve. Additional studies should be conducted to determine the relationship between differential hosts and morphological variability of this taxon.

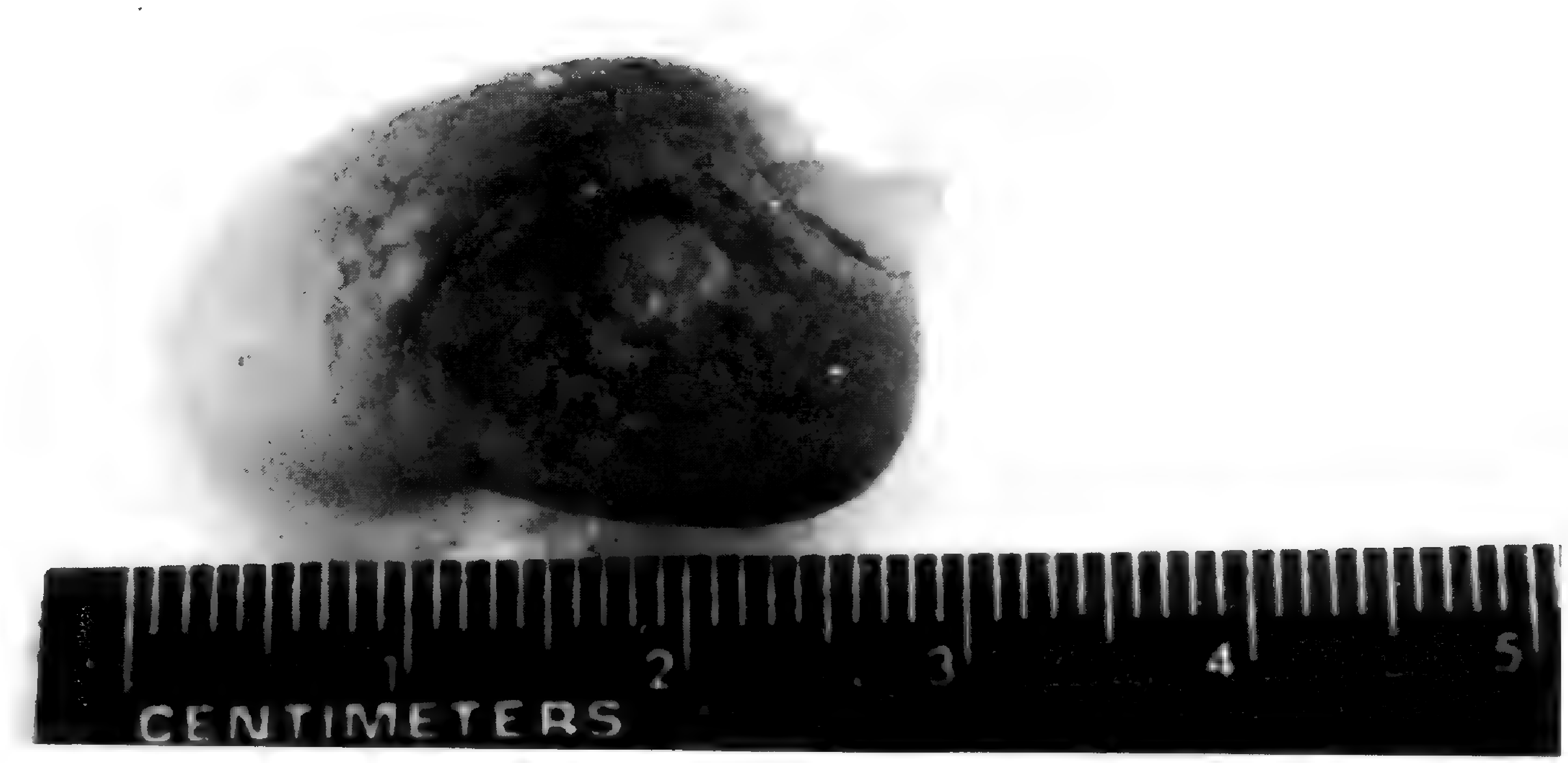


Figure 1. *Stagnicola walkeriana* Reeve with tufts of *Basicladia vivipara* Normandin & Taft.

LITERATURE CITED

NORMANDIN, R. F. & C. E. TAFT. 1959. A new species of *Basicladia* from the snail *Viviparus malleatus* Reeve. Ohio J. Sci. 59: 58–62.

507 OAK AVE.
AURORA, IL 60506

ADDITIONAL CHROMOSOME NUMBERS IN *TITHONIA* (COMPOSITAE)

JOHN C. LA DUKE AND TIM REMPLE

As part of a revision of the genus *Tithonia,* La Duke (1982) published chromosome numbers for all the taxa. Not all of the bud material collected was analyzed at that time, and additional counts have now been made. The staining and squashing methods followed standard techniques (Snow, 1963; Stuessy, 1971; Jackson, 1973). Chromosome counts for all populations were $n = 17$. This number is consistent with previous reports.

Tithonia brachypappa B. L. Robinson. **México.** San Luis Potosi: 10–20 mi W of Ciudad Valles on rte. 86, *Stuessy & Gardner 4038* (OS).

T. diversifolia (Hemsl.) A. Gray. **Guatemala.** Alta Verapaz: .5 mi NE of San Pedro Carchá on rd. to Sebol, *Jansen & Harriman 526* (OS). **Honduras.** Morazan: ca. 18 mi S of Tegucigalpa on rte. 1, *Stuessy & Gardner 4424* (OS). **México.** Chiapas: 2 mi W of Cascadael Aquacero on rte. 190, *La Duke et al. 512* (OS); 2 mi NW of Pinolas Rosas on rd. to Teopisca, *Stuessy & Gardner 4424* (OS). **Panama.** Cocle: 14.4 mi N of junct. Pan-Am. hwy. and rd. to El Valle, *Stuessy & Gardner 4529* (OS).

T. longiradiata (Bertol.) S. F. Blake. **México.** Chiapas: km 70, hwy. 190, *Jansen & Harriman 511* (OS). **Nicaragua.** Matagalpa: 2.5 mi down from Hotel Maria de Ostuma, *Jansen & Harriman 559* (OS).

T. rotundifolia (Miller) S. F. Blake. **Costa Rica.** Alajuela: on freeway near Grecia, *Stuessy & Gardner 4468* (OS). **El. Salvador.** Ahuachapan: 5 mi SE of Hachadura on rte. CA-2, *Stuessy & Gardner 4565* (OS); La Libertad: ca. 13 mi W of La Libertad on rte. CA-2, *Stuessy & Gardner 4564* (OS). **Guatemala.** Escuintla: .1 mi N of intersection of El Naranjo on CA-9, *La Duke et al. 528* (OS). **Honduras.** Comayagua: ca. 15 mi SE of Siguatepeque on rte. 1, *Stuessy & Gardner 4417* (OS). **México.** Guerrero: ca. 29 mi S of Chilpancingo *Funk & Rico 2844* (GFND, OS), SE edge of Cacahuamilpa on rte. 55 toward Taxco, *Stuessy & Gardner 4204* (OS); Jalisco: W limits of Jalostotitan on rte. 80, *Stuessy & Gardner 4093* (OS); Michoacan: 1.9 mi W of rd. to

Gómez Farias on hwy 15, *La Duke et al. 479* (GFND, OS). **Nicaragua.** Matalgapa: 27.6 mi S of Sébaco on rte. 1, *Stuessy & Gardner 4553* (OS).

T. tubaeformis (Jacq.) Cass. **México.** Nayarit: 1.3 mi E of rd. to La Labor on hwy. 15, *La Duke et al. 389* (OS); Puebla: 1.6 mi N of intersection of hwy. 190 on hwy. 160, *La Duke et al. 397* (OS).

LITERATURE CITED

La Duke, J. C. 1982. Revision of *Tithonia.* Rhodora 84: 453–522.

Jackson, R. C. 1973. Chromosomal evolution in *Haplopappus gracilis:* a centric transposition race. Evolution 27: 243–256.

Snow, R. 1963. Alcoholic hydrochloric acid-carmine as a stain for chromosomes in squash preparations. Stain. Tech. 38: 9–13.

Stuessy, T. F. 1971. Systematic relationships in white-rayed species of *Melampodium* (Compositae). Brittonia 23: 177–190.

J. L.
DEPARTMENT OF BIOLOGY
UNIVERSITY OF NORTH DAKOTA
GRAND FORKS, ND 58202

T. R.
MEDICAL SCHOOL
UNIVERSITY OF MINNESOTA
MINNEAPOLIS, MN 55455

HISTORICAL NOTES

TYPIFICATION OF THE HAWAIIAN PLANTS DESCRIBED BY ASA GRAY FROM THE WILKES EXPEDITION COLLECTIONS, AND AN ENUMERATION OF THE OTHER HAWAIIAN COLLECTIONS

HAWAIIAN PLANT STUDIES 54

Harold St. John

Asa Gray was requested by Capt. Charles Wilkes to report on the foreign plant collections gathered on the United States Exploring Expedition on their world tour from 1838 to 1842, mostly by Charles Pickering and W. D. Brackenridge. In 1854 Gray published (Gray, 1854) a first volume on the botany, and for this the atlas with the plates followed in 1857. Dissatisfied with the treatment given him by Commander Wilkes, who directed the publication of the scientific volumes, Gray withheld the manuscript of his second volume. From it he extracted the descriptions of the new species, and published them (1852–1862) in the Proceedings of the American Academy of Arts and Sciences, of which he was an editor. His original manuscript, which is more extensive than the material published, is in the library of GH at Harvard University.

The type method was not then in use. When Gray described a new species or variety from a single specimen, this specimen, in one herbarium (usually US), automatically becomes the holotype. These holotypes are enumerated here. In the few instances when there are more than one sheet of the new taxon in US, each is here listed by its sheet number.

These publications were important in making known many species from the Pacific islands, including ones from Hawaii. The first, and usually the best set of these collections was returned by Gray, and deposited in Washington, and now is in US. The second set, nearly complete, but in many parts fragmentary, was kept by Gray, and now is in GH. Other duplicates, few in number, are in other herbaria, NY, P, etc.

When Gray based a new taxon on two or more collections, often from different localities, it is necessary now to select a lectotype (International Code of Botanical Nomenclature, 1978, Art. 7.5.)

Several monographers of Hawaiian plants have already designated the lectotypes within their genera. These plants are here listed, with the references to their places of publication. For the remaining ones, lectotypes are here designated. In preparation for these choices, the Wilkes Expedition collections in US and in GH were examined.

Enumerated herein also are the Hawaiian records of older species included by Gray in his reports. The arrangement of the plants here followed is the same as that in Gray's book and articles; numbers at the left are page numbers. Insertions by the author are in brackets.

Wilkes Expedition Botany, Vol. 15, 1854
(Gray, 1854–1857.)

RANUNCULACEAE

10. *Ranunculus Hawaiiensis* Gray. "Hawaii, also collected by Douglas." (Lectotype: "Hawaii, water runs," US). (Isotype: Wilkes Expedition, GH) marked "type" by L. Benson, but he did not publish his choice.

11. *Ranunculus Mauiensis* Gray. "Mountains of West Maui." (Holotype: US).

11. var. β "mountains, Kauai." This taxon has remained unnamed.

MENISPERMACEAE

39. *Nephroica Ferrandiana* (Gaud.) Miers [= *Cocculus Ferrandianus* Gaud.], "Oahu, Kaala Mountains [= Waianae Mts.], behind Honolulu; Hawaii, District of Puna; and Waimea, Hawaii; Kauai, also in the mountains."

CRUCIFERAE

50. *Cardamine hirsuta* L., "Hawaii, in the district of Waimea, &c."

63. *Lepidium Owahiense* Cham & Schlecht. [= *o-waihiense*], "coast of Oahu, and Hawaii."

CAPPARIDACEAE

65. *Cleome Sandwicensis* Gray, "Oahu, on the coast near Honolulu. Also gathered by Lay and Collie, Barclay, and

Meyen." Not now in either US or GH. The collection from "hills of Woahu [= Oahu], July 1837, Barclay" (Lectotype: BM).

VIOLACEAE

85. *Viola Kauaensis* Gray, "On the mountains of Kauai, with *Drosera longifolia"* (Holotype: US).
86. *Viola Chamissoniana* Ging., "Oahu, on the Kaala Mountains, and in the vicinity of Wailuka [= Wailuku]."
93. *Isodendrion pyrifolium* Gray, "Oahu, wooded portion of the Kaala Mountains" (Holotype: US; isotype: GH).
95. *Isodendrion longifolium* Gray, "Kaala Mountains, Oahu" (Holotype: US; isotype: GH). *See* St. John, Pacif. Sci. 6: 245, 1952.
96. *Isodendrion laurifolium* Gray, Oahu, Kaala Mountains, "with the preceding species" (Holotype: US; isotype: GH).

DROSERACEAE

100. *Drosera longifolia* L., Kauai, mountains, "from a marsh on the table land."

CARYOPHYLLACEAE

109. *Silene struthioloides* Gray, "Hawaii, Mouna [= Mauna] Loa and Mouna Kea, in the region of *Edwardsia;* near the crater of Lua Pele "(Lectotype: US); "also in the district of Waimea." Vars. α and β: "The two forms apparently grow in the same stations."
111. *Silene lanceolata* Gray. "Kauai, mountains" (Lectotype: US); "also on Maui" [a sterile specimen]. Sherff (Amer. J. Bot. 33: 501, 1946) discussed these specimens, but did not designate a lectotype.
133. *Schiedea Hookeri* Gray, "Sandwich Islands, Menzies" (Holotype: K); it is listed by Sherff (Brittonia 5: 329, 1945).
135. *Schiedea spergulina* Gray, "On the mountains of Kauai" (Holotype: US; isotype: P). It is listed by Sherff (Brittonia 5: 327, 1945).
137. *Schiedea Nuttallii* Hook., "Oahu, on rocks near Honolulu; where it was also collected by Nuttall; and recently by B.

Seemann on the cruise of the Herald; also in the mountains of the west side of Maui?" [this specimen sterile].

138. *Schiedea diffusa* Gray, "Hawaii, in the forests of Mouna [= Mauna] Kea, and Mouna Loa; also on west side of the island of Maui" (Lectotype: US), designated by Sherff (Brittonia 5: 315, 1945). (Isolectotype: GH).

PORTULACACEAE

140. *Portulaca villosa* Cham., "Oahu, on Diamond Hill [= Diamond Head], and on the plains near Ewa."

141. *Portulaca sclerocarpa* Gray, "Hawaii, district of Waimea" (Lectotype: US); "also (?) on sand hills, Maui."

MALVACEAE

161. *Sida fallax* Walp.," Oahu; on Diamond Hill, &c., near Honolulu. Also gathered on Oahu by Lay and Collie, Nuttall, Guadichaud, &c." Gray also included an unnamed var β.

162. *Sida Diellii* Gray, "Hawaii, Port Byron [= Hilo], Rev. J. Diell" (Lectotype: US); "on the coast southwest of the Crater Lua Pele [= Kilauea], and Port Byron [= Hilo], Rev. J. Diell."

163. *Sida sertum* Nutt. ex Gray, "Oahu, on the mountains behind Honolulu" (Lectotype: US). "(Also gathered by Lay and Collie, Nuttall, Diell)."

164. *Sida Meyeniana* Walp., "Oahu, near Honolulu; also gathered by Lay and Collie, Macrae, Meyen, Gaudichaud, Barclay, &c."

168. *Abutilon incanum* Don, "Oahu, on Diamond Hill; likewise on the coast near Honolulu. Also gathered by Chamisso, Macrae, and Nuttall."

174. *Hibiscus Youngianus* Gaud., "Oahu, in the marshes near Honolulu."

175. *Hibiscus Brackenridgei* Gray, "Maui, on the mountains in the west division." Lectotype designated by Roe (Pacif. Sci. 15: 9, 1961).

176. *Hibiscus Arnottianus* Gray, "Oahu, on the Kaala Mountains behind Honolulu" (Lectotype: US). "where it was also gathered by Macrae, Lay and Collie, Diell, Barclay, &c. (Byron's Bay [Hilo Bay], Hawaii, Macrae, Diell)." Roe

(Pacif. Sci. 15: 26–30, 1961) considered the white-flowered plant typical, but did not definitely designate a lectotype.

178. *Paritium tiliaceum* A. Juss. [= *Hibiscus tiliaceus* L.], "Sandwich Islands."

STERCULIACEAE

189. *Waltheria americana* L., [= *W. indica* L.], "Hawaii, and Oahu, on the coast."

190. *Waltheria pyrolaefolia* Gray [= *W. indica* L.], "Maui, sand hills near Wailuku." (Holotype: US; isotype: GH). This taxon was typified, and reduced to synonomy by St. John (Phytologia 33: 92, 1976).

ELAEOCARPACEAE

205. *Elaeocarpus bifidus* H. & A., "Oahu, Kaala Mountains, behind Honolulu; Also by Macrae, Lay and Collie, Nuttall, &c."

THEACEAE

209. *Eurya ? sandwicensis* Gray, "Oahu, on the mountains behind town of Honolulu, 1840" [Wm. Rich] (Lectotype: GH; isolectoype: NY); "Hawaii, in forests on the side of Mouna Kea." The specimen at US lacks locality data. In his monograph, Kobuski (Journ. Arn. Arb. 16: 349, 1935) listed the Oahu collection by Rich in GH and NY as the type. It needed a lectotype, and this designation cannot be in two places. The Gray Herbarium sheet is here chosen as the lectotype.

PITTOSPORACEAE

229. *Pittosporum glabrum* H. & A., "Oahu, on the Kaala Mountains, and behind Honolulu."

231. *Pittosporum terminalioides* Planch. ex Gray, "Hawaii, Mouna Loa, at 7,000 feet elevation; on the coast S. E. of the crater of Lua Pele [= Kilauea] and Puna" (Lectotype: US); "Oahu." This taxon was discussed by Sherff (Field Mus. Nat. Hist., Bot Ser. 22: 514–517, 1942) but he failed to choose a lectotype. Gray also had three unnamed varieties.

232. *Pittosporum confertiflorum* Gray, "at the base of the crater Haleakala, east division of Maui" (Holotype: US; isotype: GH). Listed by Sherff (Field Mus. Nat. Hist. Bot. Ser. 22: 554, 1942).

SAPINDACEAE

260. *Dodonaea viscosa* L., "Sandwich Islands; several different forms. On the coast of Hawaii and on the mountains behind Honolulu, Oahu collected; at the latter locality the [probably abnormal] form with elongated styles, some of them 5 or 6 lines in length! Similar specimens were gathered at Oahu by Guadichaud, in the Voyage of the Bonite."

261. *Dodonaea spathulata* Sm., "Hawaii, on the mountains near the Crater Lua Pele [= Kilauea], and on Mouna Loa, at the elevation of 8,000 feet. Mountains of Maui, in the eastern side, (a narrow-leaved variety)."

261. *Dodonaea eriocarpa* Sm., "Hawaii, District of Waimea."

RHAMNACEAE

283. *Gouania vitifolia* Gray, "Oahu, on dry hills in the District of Waianai [= Waianae]." Holotype indicated by St. John (Pacif. Sci. 23: 513, 1969).

284. *Gouania ? orbicularis* Walp. [= *G. Meyenii* Steud.], "Oahu, in dry and rocky situations near Waianai."

CELASTRACEAE

291. *Perrottetia sandwicensis* Gray, "Oahu, on the mountains behind Honolulu" (Lectotype: US); "also Hawaii, along the margin of forests." The sheets in US and GH bear only the locality "Sandwich Islands." According to a note on the ticket of Gaudichaud's specimen, this shrub is called "Oraye" or "Olaye" by the Hawaiians.

AQUIFOLIACEAE

296. *Byronia sandwicensis* Endl. [= *Ilex anomala* H. & A.], "Oahu, Kaala Mountains; Hawaii, forests on Mouna Kea; and near the Crater of Lua Pele [= Kilauea]. Also gathered by Macrae, Lay and Collie, &c."

GERANIACEAE

311. *Geranium multiflorum* Gray, "Hawaii, Maui, and Kauai. Hawaii, specimen a single branch" (Holotype: US).
312. *Geranium cuneatum* Hook., var. *α Menziesii* Gray, Hawaii, Aleala, a small form."
312. var. *β hypoleucum* Gray, "Hawaii, Mouna Loa, a common shrub from the crater of Lua Pele [= Kilauea] to the elevation of 8,000 feet" (Lectotype: US); "mountains of Maui, a very small form, without flowers."
312. var. *γ hololeucum* Gray, "Hawaii, Mouna Kea" (Lectotype: US), "also Mouna Loa, abundant through the region of *Edwardsia,* E. part of Maui on banks of the crater Haleakala."
314. *Geranium ovatifolium* Gray [= *G. multiflorum* Gray, var. *ovatifolium* (Gray) Fosb.], "Maui, East division, on the north bank of the crater Haleakala" (Lectotype: GH), selected by Fosberg, (Bishop Mus., Occas. Papers 16(15): 340, 1942). The specimen so labeled in US is the var. *canum* Hbd.
315. *Geranium arboreum* Gray, "Maui, Eastern part near the upper border of the forest, at about the elevation of 6,000 feet" (Holotype: US).

OXALIDACEAE

320. *Oxalis corniculata* L. "Oahu, and Hawaii."
321. *Oxalis Martiana* Zucc., "Hawaii, Hilo." The specimen was marked by Brackenridge as not indigenous.

ZYGOPHYLLACEAE

325. *Tribulus cistoides* L., "Oahu, near Honolulu, doubtless introduced from South America." It is now considered indigenous.

RUTACEAE

340. *Pelea clusiaefolia* Gray, "Oahu, mountains behind Hololulu" (Lectotype: US). The first collection, (USEE, Oahu) was cited by Stone (Phanerog. Monogr. 3: 138, 1969) and listed as the type, thus effectively choosing it as the lectotype. Oahu, "where it was also gathered by Macrae, Lay and Collie, Gaudichaud, &c., and this was also *Clusia sessilis*

sensu H. & A., Beechey Voyage, non Forst. Hawaii, District of Puna, and on the margin of the Bullock Plain, Mouna Kea" [US; this latter specimen was made the holotype of *P. Pickeringii* St. John (Lloydia 7: 266, 1944)]. There were also two unnamed variations, from Kaala, and Mouna Kea.

343. *Pelea auriculaefolia* Gray [= *Pelea clusiaefolia* Gray, var. *auriculaefolia* (Gray) Stone, (Phanerog. Monogr. 3: 155, 1969)], "Hawaii, Mouna Kea, forests on flank of," (US). The holotype was listed by Stone (Monogr. Phanerog. 3: 156, 1969).

343. *Pelea oblongifolia* Gray, "Hawaii, in the district of Puna at an elevation of 800 or 1,000 feet near the Lua Pele Crater" (Lectotype: US); "also found in the margins of Bullock Plains, Mouna Kea, Kauai? (foliage only), Mountains behind Honolulu." Stone (Monogr. Phanerog. 3: 81, 1969) chose the Lua Pele [= Kilauea] collection as the type, thus unintentially, but effectively, making it the lectotype. The Bullock Plains specimen is sterile.

344. *Pelea rotundifolia* Gray. "Oahu, mountains behind Honolulu" (Holotype: US).

345. *Pelea Sandwicensis* (H. & A.) Gray, "Oahu, mountains behind Honolulu; Maui; Oahu, where it was also gathered by Gaudichaud, Macrae; Oahu, Lay & Collie" (Holotype: K).

346. *Pelea volcanica* Gray, "Hawaii, Mouna Kea, in forests near Bullock Plains, etc." (Holotype: US).

350. *Melicope cinerea* Gray [= *Pelea cinerea* (Gray) Hbd., Fl. Haw. Is. 68, 1888], "Oahu, Kaala Mountains, in the district of Waianae, in a ravine" (Holotype: US), listed by Stone (Phanerog. Monogr. 3: 51, 1969).

351. *Melicope barbigera* Gray [= *Pelea barbigera* (Gray) Hbd., Fl. Haw. Is. 70, 1888], "Kauai, on the mountains" (Holotype: US).

352. *Melicope spathulata* Gray [= *Platydesma spathulata* (Gray) Stone, (Journ. Arn. Arb. 43: 416, 1962)], "Kauai, on the mountains" (Holotype: US).

353. *Melicope elliptica* Gray [= *Pelea elliptica* (Gray) Hbd., Fl. Haw. Is. 69, 1888], "Oahu, Kaala Mts., district of Waianae" (Holotype: US).

354. *Melicope grandifolia* Gray [= *Platydesma spathulata* (Gray) Stone, Madrono 16: 165, 1962], "Hawaii, in the forests of Mouna Kea" (Holotype: US).

354. *Zanthoxylum Kauaense* Gray, "Kauai, on the mountains" (Holotype: US).

ANACARDIACEAE

369. *Rhus Sandwicensis* Gray, "Oahu, in the mountains behind Honolulu (where it was collected by the Rev. J. Diehl)" (Lectotype: US), "and in the forests near Hilo, Hawaii, (Byron's Bay [= Hilo], Hawaii), Macrae; Oahu, Gaudichaud."

LEGUMINOSAE

403. *Indigofera anil* L., "Oahu, on the hills behind Honolulu." This taxon is probably *I. suffruticosa* Mill.

407. *Tephrosia piscatoria* Pers. [= *T. purpurea* (L.) Pers.]. "Sandwich Islands."

408. *Agati grandiflora* Pers. [= *Sesbania grandiflora* (L.) Poir.], "Oahu, cultivated, but not naturalized."

409. *Agati tomentosa* (H. & A.) Gray [= *Sesbania tomentosa* H. & A., Bot. Beechey Voy. 286, 1838], "Oahu, District of Waianae; Hawaii, coast east of Lua Pele [= Kilauea]. Also collected, principally on Oahu, by Lay and Collie, Douglas, Gaudichaud, Nuttall, &c." The holotype was published as from Acapulco, Mexico, Lay & Collie (K). This was certainly erroneous, as the species occurs only in the Hawaiian Islands.

420. *Vicia Menziesii* Spreng., "Hawaii, in forests of Mouna Kea; also by Macrae; it was discovered by Menzies at the upper edge of the forest on Mouna Loa."

433. *Desmodium Sandwicense* E. Meyer [= *D. uncinatum* (Jacq.) DC., an introduced weed], "Oahu, on the hills behind Honolulu; Also gathered by Seemann."

439. *Dioclea violacea* Mart., "Hawaii, on the coast near Hilo; also Kauai; probably introduced, as it is a native of Brazil." The Hawaiian plant is now classed as *D. Wilsonii* Standl.

441. *Canavalia galeata* Gaud., "Oahu, near the coast at Waianae; also on Kauai." [The Kauai plant is probably *C. kauaiensis* Sauer].

442. *Mucuna gigantea* DC., "Hawaii, district of Puna, at a watering place near Kaimo. Introduced?"

443. *Mucuna urens* DC., "Hawaii, district of Waimea, near the coast, probably introduced."

444. *Erythrina monosperma* Gaud. (non Lam.) [= *E. sandwicensis* Deg., Fl. Haw. 169c: 12/5/32], "Oahu, in the Kaala Mountains, district of Waianae." The holotype is "In insulis Sandwicensibus, (Alt. 350–400 hex.), Gaudichaud (P)."

446. *Strongylodon ruber* Vogel, "Oahu, on the Kaala Mountains, behind Honolulu; Hawaii, in forest on the side of Mouna Loa. (Also gathered by Chamisso, Macrae, Diehl, Barclay, Nuttall, &c.)"

449. *Phaseolus rostratus* Wallr. [= *Phaseolus adenanthus* G. F. W. Mey.], "Oahu, on Diamond Hill [= Diamond Head], probably introduced."

450. *Vigna Oahuensis* Vogel, "Oahu, on the Kaala Mountains, where it was also collected by Chamisso, Douglas, &c.; Kauai, Maui."

451. *Vigna Sandwicensis* Gray, "Hawaii, on Mouna Loa six miles from the crater of Lua Pele [= Kilauea]" (Lectotype: US); "Kauai, on the mountains; Maui, on the mountains in the western division of the island."

452. *Vigna lutea* (Sw.) Gray [= V. marina (Burm.) Merr.], "Oahu, on the shores; Maui, on the mountains of the western part."

453. *Lablab vulgaris* Savi [= *Lablab purpureus* (L.) Sweet], "Sandwich Islands, introduced and partially naturalized."

453. *Cajanus indicus* Spreng. [= *C. Cajan* (L.) Millsp.], "Sandwich Islands, cultivated, introduced and partially naturalized."

459. *Edwardsia chrysophylla* Salisb. [= *Sophora chrysophylla* (Salisb.) Seem., in Fl. Vit. 66, 1865], "Hawaii, Mouna Kea, occupying a zone reaching to an elevation of 11,000 feet; and Mouna Loa, above the Crater Lua Pele [= Kilauea]; also on the mountains of Kauai, and east Maui, on the banks of the crater of Haleakala."

461. *Guillandina Bonduc* Ait. [= *Caesalpina Bonduc* (L.) Roxb.], "Sandwich Islands." There is also an unnamed var. β.

463. *Cassia Guadichaudii* H. & A., "Oahu, mountains behind Honolulu; also gathered by Gaudichaud, Lay & Collie, Nuttall, &c."

480. *Acacia Koa* Gray, "Oahu, mountains behind Honolulu" (Lectotype: K, chosen by St. John (Pacif. Sci. 33: 358, 1979);

"Hawaii, side of Mouna Loa; and Mouna Kea" Isolectotypes: GH, US). In US there are two sheets labeled only "Sandwich Islands". One sheet (no. 62,797) bears a stem, phyllodia, and flowers; the other (No. 62,798) bears a stem, phyllodia, and one pod. Pedley (Queensland Herbarium Contrib. 18: 7, 1975) cited as syntypes, "Oahu, on the mountains behind Honolulu" (Isotype: K), and "on the sides of Mouna Loa and Mouna Kea" (Syntypes: K). This treatment is not satisfactory typification. Since the species was based on several collections, one must be made the lectotype. Because it has island data, the Oahu collection (K) was chosen as the lectotype.

ROSACEAE

498. *Acaena exigua* Gray, "Kauai, on the table-land in the mountains, in a marsh" (Holotype: US).

500. *Fragaria Chilensis* Ehr. [= *F. chiloensis* (L.) Duch.], "Hawaii, in moist places on the edges of the crater Lua Pele [= Kilauea]; on Mouna Kea; and in the district of Waimea, specimens were gathered in the bullock pit in which the unfortunate Douglas lost his life. Also on the mountains of Maui."

504. *Rubus Hawaiiensis* Gray, "Hawaii, in the forest and the Bullock Plains on Mouna Loa" (Lectotype: GH). "Mouna Kea, where it was discovered by Menzies." It is not present in US which has only var. β, a sheet without island data.

505. *Rubus Macraei* Gray, "Hawaii, Mouna Kea" (Lectotype: US, sheet 42,449), "where it was first collected by Mr. Macrae; east Maui, on the banks of crater Haleakala."

507. *Osteomeles anthyllidifolia* (Sm.) Lindl., "Oahu, on the plains near Ewa, and the coast near Pearl River; Hawaii, in the district of Waimea, and on Mouna Loa. Found by all collectors since the islands were first botanized by Nelson, in Cook's last voyage."

MYRTACEAE

510. *Eugenia malaccensis* L., "Sandwich Islands, cultivated and introduced, Pickering."

519. *Eugenia Sandwicensis* Gray, "Oahu, on the mountains behind Honolulu both forms" (Lectotype: US, chosen by K. A. Wilson, Pacif. Sci. 11: 168, 1957). Degener (Fl. Haw. 273, 6/15/62) almost typifies it, by listing this same specimen as the type locality, but he does not select it as a lectotype, and does not mention the herbarium in which it is placed. On Oahu: "also gathered by Gaudichaud, Macrae, &c.; Kauai; foliage only." Gray also had an unnamed var. β.

550. *Psidium guajava* L., "Sandwich Islands, introduced."

560. *Metrosideros lutea* Gray, "Hawaii, vicinity of Hilo." This single sheet (US, no. 47,897) is the holotype. The synonyms are *Nani*(*a*) *lutea* (Gray) Heller, (Minn. Bot. Stud. 1: 867, 1897) and *M. polymorpha* Gaud. var. ϵ Hbd. (Fl. Haw. Is. 126, 1888). This species was not included in recent general studies of the genus. It has not been critically studied.

561. *Metrosideros rugosa* Gray, "Oahu, on the mountains behind Honolulu" (Holotype: GH). Added in pencil on the sheet is "Eastern end of Oahu, heights of Niu and Wailupe. Also gathered by Guadichaud on the Bonite Voyage."

562. *Metrosideros polymorpha* Gaud., "Oahu, in the mountains behind Honolulu. Gathered by all collectors from Nelson, in Cook's third voyage, and Menzies, to the present time." Gray also had five unnamed varieties.

564. *Metrosideros macropus* H. & A., "Oahu, on the mountains behind Honolulu. Also gathered by Macrae, Lay & Collie, Gaudichaud, Seemann."

LYTHRACEAE

606. *Lythrum maritimum* HBK., "Oahu, on the coast near Honolulu; Hawaii, in the district of Waimea."

ONAGRACEAE

619. *Jussiaea octofila* DC. [= *Ludwigia octovalvis* (Jacq.) Raven], "Oahu, fide Walpers." "A glabrous variety likewise occurs in the Sandwich Islands."

GUNNERACEAE

629. *Gunnera petaloidea* Gaud., "West Maui, on face of high mural precipices."

629. var. *kauaense* Gray [= *G. kauaiensis* Rock in Forbes, Bishop Mus., Occas. Papers 9(5): 3-4, pl. 1, 1930], "Kauai" (Holotype: US).

CARICACEAE

640. *Carica Papaya* L., "Sandwich Islands, cultivated, where the fruit of the *Papau* is a favorite esculent."

CUCURBITACEAE

650. *Sicyos pachycarpus* H. & A., "Oahu, Kaala Mts., district of Waianae, (also found by Lay and Collie, Gaudichaud, &c.). Maui, on the mountains of western part of that island."

651. *Sicyos macrophyllus* Gray, "Hawaii, in the forest of Mouna Kea, towards their upper margin" (Holotype: US).

653. *Sicyos cucumerinus* Gray, "Hawaii, Mouna Kea, upper part of the forests" (Holotype: US). Gray also had two unnamed vaieties.

SAXIFRAGACEAE

683. *Broussaisia arguta* Gaud., "Oahu, common on the mountains behind Honolulu."

685. *Broussaisia pellucida* Gaud. [= *B. arguta* Gaud., var. *pellucida* (Gaud.) Fosb., Bishop Mus., Occas. Papers 15(4): 59, 1939].

UMBELLIFERAE

705. *Sanicula Sandwicensis* Gray, "East Maui, on the mountains; Hawaii: on Mouna Loa, at the elevation of 8,000 feet" (Lectotype (St. John, in press): US].

ARALIACEAE

719. *Hedera Gaudichaudi* DC. [= *Cheirodendron trigynum* (Gaud.) Heller], "Hawaii, in forests at the base of Mouna Loa and Mouna Kea; Oahu, on Kaala Mts.; (first collected by Menzies)."

720. *Hedera platyphylla* (H. & A.) Gray [= *Cheirodendron platyphyllum* (H. & A.) Seem.], "Oahu, on the mountains behind

Honolulu at the elevation of 2,000 feet. Also gathered by Gaudichaud in the voyage of the Bonite."

724. *Reynoldsia Sandwicensis* Gray, "Oahu, in a ravine near Waianae" (Holotype: GH). Sherff (Bot. Leafl. 6: 10, 1952) selected this specimen as the lectotype, but this selection can be interpreted as indicating placement of the holotype.

726. *Gastonia Oahuensis* Gray [= *Tetraplasandra oahuensis* (Gray) Harms, in Engler & Prantl, Pflanzenfam. III, 8: 30, 1898], "Oahu, on mountains behind Honolulu, at the elevation of 2,000 feet; Hawaii, in the district of Puna," (Lectotype: US) designated by Sherff (Fieldiana Bot. 29(2): 66, 1955).

728. *Tetraplasandra Hawaiensis* Gray, "Hawaii, in the district of Puna" (Holotype: US), so indicated by Sherff (Fieldiana Bot. 29(2): 66, 1955).

Species Published by Gray in Proc. Amer. Acad. Arts 2: 159 160, 1852 (Gray, 1852a); 323–325 (Gray, 1852b).

COMPOSITAE

160. *Argyroxiphium macrocephalum* Gray, "Maui, at the base of high crater." It is present in US, but the best specimen is in GH, hence the latter is here chosen as the lectotype.

160. *Wilkesia Gymnoxiphium* Gray, "Kauai, in montibus" (Holotype: US). As to the validity of the genus *Wilkesia, see* St. John (Bishop Mus., Occas. Papers 24(8): 134–137, 1971).

VIOLACEAE

324. *Isodendrion pyrifolium* Gray, "Oahu, Kaala Mountains" (Holotype: US), so indicated by St. John (Pacif. Sci. 6: 247, 1952).

324. *Isodendrion longifolium* Gray, "Kaala Mountains, Oahu, Sandwich Islands" (Holotype: US), designated by St. John (Pacif. Sci. 6: 236, 1952).

324. *Isodendrion laurifolium* Gray, "Oahu, Kaala Mountains" (Holotype: US), so indicated by St. John (Pacif. Sci. 6: 233, 1952.)

Species Published by Gray in Proc. Amer. Acad. Arts. 3: 48–54, 127–129, (1857) = 1853 (Gray, 1853)

RUTACEAE

50. *Pelea auriculaefolia* Gray [= *P. clusiaefolia* Gray ssp. *dumosa* (Rock) Stone var. *auriculaefolia* (Gray) Stone, Phanerog. Monogr. 3: 155, 1969], "Hawaii, Mouna Kea" (Holotype: US).
50. *Pelea oblongifolia* Gray, "Hawaii, Lua Pele Crater, Puna District, 800–1000 feet elevation" (Holotype: US), though Stone called it the lectotype (Phanerog. Monogr. 3: 81, 1969).
50. *Pelea Sandwicensis* (H. & A.) Gray [= *Brunellia Sandwicensis* H. & A.], "mountains, Lay & Collie" (Holotype: K).
50. *Pelea volcanica* Gray, "Sandwicenses" (Holotype: US), indicated by Stone (Phanerog. Monogr. 3: 85, 1969).

CUCURBITACEAE

54. *Sicyos macrophyllus* Gray, "Sandwich Islands" (Holotype: US).
54. *Sicyos cucumerinus* Gray, "Sandwich Islands, Hawaii" (Holotype: US). Gray also had two unnamed varieties.

ARALIACEAE

129. *Reynoldsia Sandwicensis* Gray, "Sandwich Islands" (Holotype: GH).
129. *Tetraplasandra Hawaiiensis* Gray, "Hawaii, Sandwich Islands" (Holotype: US).

Species Published by Gray in Proc. Amer. Acad. Arts 4: 33–50 (1860) = 1858; 306–318, (1860) = 1859 (Gray, 1858); 319–324 (Gray, 1859a); 326–327 (Gray, 1859b).

RUBIACEAE

36. *Bobea elatior* Gaud., "Oahu, Sandwich Islands."
36. *Bobea brevipes* Gray [= *B. elatior* Gaud. var. *brevipes* (Gray) Hbd., Fl. Haw. Is. 173, 1888], "Oahu, Sandwich Islands" (Holotype: US).
38. *Chomelia ? Sandwicensis* Gray [= *Bobea sandwicensis* (Gray) Hbd., Fl. Haw. Is. 174, 1888], "Oahu, Sandwich Islands" (Holotype: US).

43. *Straussia Kaduana* (C. & S.) Gray [= *Psychotria kaduana* (C. & S.) Fosb., Bishop Mus., Occas. Papers 23: 43, 1962; (*Coffea kaduana* C. & S.), "Oahu."

43. *Straussia Mariniana* (C. & S.) Gray [= *Psychotria Mariniana* (C. & S.) Fosb., Bishop Mus., Occas. Papers 23: 43, 265, 1962; *Coffea Mariniana* C. & S.], "Oahu."

43. *Straussia Hawaiensis* Gray [= *Psychotria hawaiensis* (Gray) Fosb., as *P. hawaiiensis,* Bishop Mus., Occas. Papers 23: 43, 1962], "Sandwich Islands" (Holotype: US), so indicated by Sohmer (Lyonia 1: 176, 180, 1977).

48. *Coprosma rhynchocarpa* Gray, "Hawaii, Sandwich Islands," (Holotype: US), here indicated, "gathered also by Nelson, Macrae, and Gaudichaud." In Gray's manuscript (GH), it is stated "Puna and Waimea, and near the crater Lua Pele [= Kilauea]."

48. *Coprosma longifolia* Gray, "Sandwich Islands" (Holotype: US, sheet 42,341), so indicated by Oliver (Bishop Mus. Bull. 132: 177, 1935); "also gathered by Gaudichaud."

48. *Coprosma foliosa* Gray, "Sandwich Islands" (Holotype: US, sheet 42,340), so indicated by Oliver, (Bishop Mus. Bull. 132: 167, 1935); "where it was also gathered by Gaudichaud, Nuttall, and Seemann."

49. *Coprosma pubens* Gray, "Sandwich Islands" (Holotype: US), so indicated by Oliver (Bishop Mus. Bull. 132: 171, 1935). Gray in his manuscript (GH), stated the locality as: "Hawaii, forest and high bullock plains on Mouna Kea."

49. var. *Kauensis* Gray, "Sandwich Islands, Kauai" (Holotype: US, sheet 42,351). Gray in his manuscript (GH) stated: "mountains of Kauai."

49. *Coprosma Menziesii* Gray, "Hawaii" (Holotype: US, sheet 42,342), mentioned by Oliver (Bishop Mus. Bull. 132: 160, 1935). "Collected by Menzies, Macrae, Gaudichaud, and Douglas." Gray in his manuscript (GH) said, "Hawaii, Puna and Waimea." He also had two unnamed varieties.

49. *Coprosma ernodeoides* Gray, "Hawaii, Sandwich Islands" (Holotype: US, sheet 42,338), indicated by Oliver, (Bishop Mus. Bull. 132: 31, 1935). "Collected by Menzies, &c." Gray in his manuscript (GH) wrote: "Hawaii, lava plains and near Crater Lua Pele [= Kilauea]."

310. *Gouldia Sandwicensis* Gray, based on *Kadua affinis* C. & S. [= *Gouldia terminalis* (H. & A.) Hbd., var. *coriacea* (H. & A.) Fosb., Bishop Mus. Bull. 147: 47, 1937]. Gray also cited var. *terminalis* (H. & A.) Gray; and var. *hirtella* Gray, the latter without diagnosis.

317. *Kadua parvula* Gray [= *Hedyotis parvula* (Gray) Fosb., Bishop Mus. Bull. 174: 54, 1943], "Sandwich Islands, Oahu" (Holotype: US).

318. *Kadua petiolata* Gray, "Oahu, Sandwich Islands." According to Fosberg (Bishop Mus. Bull. 174: 73, 79, 81, 1943), the syntypes are in part *Hedyotis acuminata* (C. & S.) Steud., and in part its forma *Grayana* Fosb.

318. var. *ovalifolia* Gray [= *Hedyotis acuminata* (C. & S.) Steud., f. *ovalifolia* (Gray) Fosb., Bishop Mus. Bull. 174: 87, 1943], "Maui, Sandwich Islands" (Holotype: US).

318. *Kadua grandis* Gray [= *Hedyotis acuminata* (C. & S.) Steud., f. *grandis* (Gray) Fosb., Bishop Mus. Bull. 174: 90, 1943], "Oahu, Sandwich Islands, 1840" (Lectotype: US). The other collection, from Oahu, a syntype, is *H. acuminata* f. *alicarpa* Fosb.

LOGANIACEAE

322. *Labordea tinifolia* Gray, "Sandwich Islands, in Kauai, Maui, Oahu, Hawaii, and Maui. Coll. Expl. Exped., and coll. Remy" (GH), the latter the lectotype, chosen by Sherff (Field Mus. Nat. Hist, Bot. 17: 531, 1939).

323. *Labordea fagraeoidea* Gaud., "Hawaii."

323. *Labordea sessilis* Gray [= *Labordea fagraeoidea* Gaud., var. *sessilis* (Gray) Sherff, Amer. J. Bot. 25: 587, 1939], "Oahu, 1840" (Holotype: US).

SANTALACEAE

326. *Santalum Freycinetianum* Gaud., "Sandwich Islands, Oahu-Hawaii."

327. var. *latifolium* Wawra [= *Santalum haleakalae* Hbd.], "Maui and Hawaii." The Maui specimen needs investigation.

327. *Santalum ellipticum* Gaud. "Sandwich Islands."

327. *Santalum pyrularium* Gray, "Kauai, Sandwich Islands" (Holotype: GH), selected by Skottsberg, (Bishop Mus. Bull. 43: 48, 1927).

Species Published by Gray in the Proc. Amer. Acad. Arts 5: 114–146 (Gray, 1862a), 146–152 (Gray, 1862b).

COMPOSITAE

118. Vittadinia humilis Gray [= *Tetramolopium humile* (Gray) Hbd., Fl. Haw. Is. 198, 1888], "Sandwich Islands, on the mountains of Hawaii, and Maui." (Lectotype: US). Sherff (Bishop Mus. Bull. 135: 7, 1935) listed the type as, "on the mountains of Hawaii and Maui."

119. *Vittadinia tenerrima* (Less.) Gray [= *Tetramolopium tenerrimum* (Less.) Nees, Gen. Sp. Aster 202, 1833], "Oahu, Chamisso, Macrae."

119. *Vittadinia Remyi* Gray [= *Tetramolopium Remyi* (Gray) Hbd., Fl. Haw. Is. 197, 1888], "Maui, Remy 239" (Holotype: GH).

119. *Vittadinia Chamissonis* (Less.) Gray [= *Tetramolopium lepidotum* (Less.) Sherff, Bot. Gaz. 95: 500, 1934, Bishop Mus. Bull. 135: 14, 1935]. "Kaala Mountains of Oahu, U. S. Explor. Exped. 1840; 1816–17, A. von Chamisso" (Holotype: B).

119. var. ? *arbuscula* Gray [= *Tetramolopium arbusculum* (Gray) Sherff, Bot. Gaz. 95: 502, 1934; Bishop Mus. Bull. 135: 17, 1935], "Maui, 1840, in the great crater of the eastern part of Maui [= Haleakala]," (Holotype: US), "Sandwich Islands, on the mountains of Oahu, 1840".

120. *Vittadinia consanguinea* Gray [= *Tetramolopium consanguineum* (Gray) Hbd., Fl. Haw. Is. 199, 1888], "Sandwich Islands, on Hawaii and the mountains of Kauai", 1840, Kauai (Lectotype: US) selected by Sherff (Bishop Mus. Bull. 135: 19, 1935). He removed the Hawaii plant as var. *leptophyllum* Sherff (Bot. Gaz. 95: 502, 1934).

120. *Vittadinia arenaria* Gray [= *Tetramolopium arenarium* (Gray) Hbd., Fl. Haw. Is. 199, 1888], "Sandwich Islands, on the sand hills of Maui, in the district of Waimea, Hawaii, 1840."

The Maui specimen (US) was chosen as lectotype by Sherff, (Bishop Mus. Bull. 135: 20, 1935).

120. *Vittadinia conyzoides* Gray [= *Tetramolopium conyzoides* (Gray) Hbd., Fl. Haw. Is. 200, 1888], "Sandwich Islands, on the sand hills of Maui" (Holotype: US).

125. *Coreopsis Mauiensis* Gray [= *Bidens mauiensis* (Gray) Sherff, Field Mus. Nat. Hist. Bot. 16: 157, 1937], "Sandwich Islands, Maui, on sandy or dry hills near the coast" (Holotype: GH).

126. *Coreopsis macrocarpa* Gray, [= *Bidens macrocarpa* (Gray) Sherff, Field Mus. Nat. Hist. Bot. 16: 105, 1937], "Sandwich Islands on the mountains of Oahu, U.S. Exploring Expedition" (Holotype: US).

126. *Coreopsis Macraei* Gray [= *Bidens Campylotheca* Sch. Bip., Flora 39: 359, 1856], *See* Sherff (Field Mus. Nat. Hist. Bot. 16: 137, 1937), "Sandwich Islands, Macrae, Remy." Mt. Kaah [= *Mauna Kea*], June 1825, Macrae" (Holotype: G).

126. *Coreopsis cosmoides* Gray [= *Bidens cosmoides* (Gray) Sherff Bot. Gaz. 70: 98, 1920], "Hawaii, Sandwich Islands; also the coll. Remy 278." The expedition collection from Hawaii (US) is the holotype.

127. *Coreopsis Menziesii* Gray [= *Bidens Menziesii* (Gray) Sherff, Bot. Gaz. 70: 98, 1920], "Hawaii and Maui, Sandwich Islands." The Hawaii specimen was chosen by Sherff (Field Mus. Nat. Hist. Bot. 16: 15, 1937); (Lectotype: US).

127. *Coreopsis micrantha* (Gaud.) Gray [= *Bidens micrantha* Gaud., Bot. Voy. Uranie 464, 1829; Atlas pl. 85, 1826–30], (Holotype: P); "Sandwich Islands, especially Oahu." *See* Sherff, (Field Mus. Nat. Hist. Bot. 16: 145, 1937).

127. *Coreopsis Sandwicensis* (Less.) Gray [= *Bidens sandwicensis* Less., Linnaea 6: 508, 1831], "Sandwich Islands, Oahu." *See* Sherff (Field Mus. Nat. Hist. Bot. 16: 120, 1937).

128. *Bidens Hawaiensis* Gray, "Hawaii, Sandwich Islands, at various stations" (Holotype: US). *See* Sherff (Field Mus. Nat. Hist., Bot. 16: 94, 1937).

129. *Lipochaeta australis* Less. [= *L. lobata* (Gaud.) DC.], "Oahu, Sandwich Islands," *See* Sherff (Bishop Mus. Bull. 135: 48, 1935).

129. var. *connata* (Gaud.) Gray [= *Lipochaeta connata* (Gaud.) DC.], Iles Sandwich, Gaudichaud., (Holotype: P), "Maui." *See* Sherff (Bishop Mus. Bull. 135: 28, 1935).

129. var. *decurrens* Gray [= L. *succulenta* (H. & A.) DC., var. *decurrens* (Gray) Sherff], "Kauai" (Lectotype: US), chosen by Gardner, (Rhodora 83: 305, 1979).

129. var. *lobata* (Gaud.) Gray [= *Lipochaeta lobata* (Gaud.) DC., Prodr. 5: 611, 1836], in insulis Sandwicensibus, 1819, Gaudichaud (Isotype: G). "Sandwich Islands." *See* Sherff (Bishop Mus. Bull. 135: 49, 1935).

130. *Lipochaeta subcordata* Gray, "Hawaii, on the coast" (Holotype: US). *See* Sherff (Bishop Mus. Bull. 135: 34, 1935).

130. *Lipochaeta calycosa* Gray, "Oahu, Diamond Hill [= Diamond Head]," (Holotype: US), indicated by Sherff (Bishop Mus. Bull. 135: 51, 1935), though Gardner (Rhodora 81: 313, 1979) tried to choose it as in (GH).

130. *Lipochaeta lavarum* (Gaud.) DC., in insulis Sandwicensibus, (Holotype: P). Collected by the Wilkes Expedition, "Sandwich Islands, on West Maui, hills along sea coast." *See* Sherff (Bishop Mus. Bull. 135: 56, 1935).

130. *Lipochaeta integrifolia* (Nutt.) Gray, based on *Microchaeta integrifolia* Nutt., (Am. Philos. Soc., Trans. II, 7: 451, 1841), Oahu, Nuttall, (Holotype: BM), though Gardner (Rhodora 81: 333, 1979) considered the type to be Atooi [= Kauai], T. Nuttall (BM). "Oahu and Maui." Found on all the major islands.

130. *Lipochaeta succulenta* (H. & A.) DC., based on *Verbesina succulenta* H. & A., Bot. Beechey Voy. 87, 1832, Oneeheow [= Niihau], Lay & Collie (Holotype: K), "Oahu."

131. *Lipochaeta heterophylla* Gray, "Maui" 1840, (US), (Holotype: US). Known from Molokai, Maui, and Hawaii. *See* Gardner (Rhodora 81: 310, 1979).

131. *Lipochaeta tenuifolia* Gray, "Oahu" (Lectotype: US), effectively chosen by Sherff (Bishop Mus. Bull. 135: 80, 1935), though he did not use the word lectotype. Gardner chose the same specimen, and called it a lectotype (Rhodora 81: 318, 1979).

131. *Lipochaeta micrantha* (Nutt.) Gray "Kauai, in mountains, Koloa" 1840, (US). Based on *Schizophyllum micranthum* Nutt., (Am. Philos. Soc., Trans. II, 7: 453, 1841), "Atooi [= Kauai], in shady woods near Kolao [= Koloa]" (Holotype: BM).

131. *Lipochaeta Remyi* Gray, "Oahu, 1851–55, Remy 260," (Holotype: GH), indicated by Sherff (Bishop Mus. Bull. 135: 81, 1935).

132. *Raillardia latifolia* Gray, "Island of Kauai," (Holotype: US), indicated by Sherff (Bishop Mus., Bull. 135: 111, 1935). The generic name has been corrected to *Railliardia*.

132. *Raillardia scabra* DC. "Hawaii and Maui," (US).

132. var. *hispidula* Gray, "Hawaii and Maui," (Syntype: US). This was discussed by Sherff, and reduced to *R. scabra* (Bishop Mus. Bull. 135: 114, 1935).

132. var. *leiophylla* Gray, "Hawaii and Maui." The specimen was evidently from Maui, and is here chosen as lectotype (US).

133. *Raillardia laxiflora* DC., "Hawaii," [= R. ciliolata DC., var. *laxiflora* (DC.) Sherff, Am. Journ. Bot. 20: 619, 1933]. The holotype is Hawaii, Macrae (CGE).

133. *Raillardia ciliolata* DC., "Hawaii." The holotype is "Hawaii," on volcano, 1825, Macrae (CGE). *See* Sherff (Bish. Mus. Bull. 135: 115, 1935).

133. *Raillardia linearis* Gaud., "Oahu, Hawaii, and Maui." The holotype is "Iles Sandwich, Gaudichaud" (P).

133. *Raillardia Menziesii* Gray, "Hawaii and Maui." The specimen "on mountain of eastern Maui, 1840", (US) was chosen as lectotype by Sherff (Bishop Mus. Bull. 135: 131, 1935).

134. *Raillardia playtyphylla* Gray, "on banks of crater, eastern Maui," 1840 (Lectotype: US) chosen by Sherff (Bishop Mus., Bull. 135: 135, 1935).

134. *Raillardia arborea* Gray, "Hawaii, on Mouna Kea" (Holotype: US).

134. *Raillardia struthioloides* Gray, "Hawaii, on Mouna Kea" (Holotype: US).

134. *Dubautia plantaginea* Gaud., var. *plantaginea*, "Oahu and Hawaii." "Iles Sandwich, Gaudichaud" (Holotype: P). The species is widely distributed and common in the mountains of Oahu. Gaudichaud's illustration showed the leaves somewhat broader than usual, and with some alternate branches in the panicle. Since he noted only two such collections, from Lanai, Sherff (Bishop Mus. Bull. 135: 85, 1935), assumed that Gaudichaud's type must have come from

Lanai, and that the var. *plantaginea* was restricted to Lanai. However, Gaudichaud did not visit Lanai, and the characters of the branching of the inflorescence stressed by Sherff seem insignificant. Hence, *P. plantaginea* is again maintained for the Oahu species, and var. *Chamissonis* Sherff (Am. Journ. Bot. 20: 610, 1933) becomes a synonym of the species.

135. *Dubautia laevigata* Gray, "Kauai, Sandwich Islands" (Holotype: US). It was so indicated by Sherff (Bishop Mus. Bull. 135: 94, 1935).

135. *Dubautia laxa* H. & A., "Oahu, Capt. Beechey's Expedition", (Holotype: K). Also, "Oahu, U.S. Exploring Expedition."

135. *Dubautia paleata* Gray, "Kauai, mountains," (Holotype: US). It was so listed by Sherff (Bishop Mus. Bull. 135: 105, 1935).

136. *Wilkesia gymnoxiphium* Gray, "Kauai, Sandwich Islands, alt. 3,700 feet" (Holotype: US). Synonym is *Argyroxiphium gymnoxiphium* (Gray) Keck [Bishop Mus. Occas. Papers 11(19): 23, 1936]. *See* St. John [Bishop Mus. Occas. Papers 24(8): 128–137, 1971].

136. *Argyroxiphium sandwicense* DC., "Hawaii, 6,300–12,000 feet" (Holotype: US).

136. *Argyroxiphium macrocephalum* Gray [= *A. sandwicense* DC], "Maui, above 9,000 feet," (Holotype: US), listed by Keck [Bishop Mus. Occas. Papers 11(19): 17, 1936].

137. *Artemisia australis* Less., var. *Eschscholtziana* (Besser?) Gray, Oahu and Kauai. "Wahu [= Oahu], Eschscholtz," (Holotype: L).

137. var. *Mauiensis* Gray, "Crater of Maui," [= Haleakala] [= *A. mauiensis* (Gray) Skottsb. (Bishop Mus. Bull. 43: 15, 1927)] (Holotype: US). Skottsberg also published regarding the typification of this plant (Bishop Mus. Bull. 43: 15, 1927), but he indicated the type as in both (US, and GH). To clarify this point, it is here stated as (Holotype: US).

LOBELIACEAE

147. *Delissea coriacea* Gray [= *Cyanea coriacea* (Gray) Hbd., Fl. Haw. Is. 254, 1888], "Kauai, Remy" (= no. 302) (Holotype: GH). There is also an unnamed variety.

148. *Delissea obtusa* Gray [= *Cyanea obtusa* (Gray) Hbd., Fl. Haw. Is. 254, 1888], "mountains of Maui" (Holotype: US).

148. var. ? *mollis* Gray, "Mouna Kea, Hawaii" (Holotype: US). Rock reduced this variety to the synonymy of the species, based only upon its diagnosis, without having seen the holotype, [Bishop Mus. Mem. 7(2): 203, 1919].

148. *Delissea ? platyphylla* Gray [= *Cyanea platyphylla* (Gray) Hbd., Fl. Haw. Is. 264, 1888]. "district of Puna, Hawaii" (Holotype: US).

148. *Cyanea Grimesiana* Gaud., var. ? *citrullifolia* Gray, "Mouna Roa and Mouna Kea, Hawaii." Rock [Bishop Mus. Mem. 7(2): 251, 1919] considered this a juvenile form of *C. tritomantha* Gray.

148. *Cyanea aspera* Gray, "Oahu" (Holotype: US). Rock, [Bishop Mus. Mem. 7(2): 381, 1919] made this a synonym of *Rollandia calycina* (Cham.) G. Don.

149. *Cyanea pilosa* "Mouna Kea, Hawaii" (Holotype: GH). In Gray's manuscript (GH) he recorded the data, windward side of Mouna Kea at lower edge of forest.

149. *Cyanea ? Rollandia* Gray, "Oahu" (Holotype: US). According to Rock [Bishop Mus. Mem. 7(2): 377, 1919], this is a synonym of *Rollandia crispa* Gaud. (Voy. Uranie, Bot. 459, 1829).

149. *Cyanea tritomantha* Gray, "Mouna Kea, Hawaii" (Holotype: GH). In Gray's manuscript (GH) he stated "windward side of Mouna Kea, at 3,000 feet."

149. *Cyanea superba* (Cham.) Gray, "Oahu" based on *Lobelia superba* Cham. (Linnaea 8: 223, 1833). The holotype was in (B).

149. *Cyanea leptostegia* Gray, "Upper edge of the forest near the tabular summit of Kauai" (Holotype: US).

150. *Clermontia grandiflora* Gaud.,

150. var. *brevifolia* Gray [= *Clermontia grandiflora* Gaud.]. fide Rock, [Bishop Mus. Mem. 7(2): 327, 1919]. Sandwicenses, Gaudichaud (Holotype: P).

150. var. *oblongifolia* (Gaud.) Gray [= *Clermontia oblongifolia* Gaud.], fide Rock, [Bishop Mus. Mem. 7(2): 315, 1919]. Sandwicenses, Gaudichaud (Holotype: P.)

150. var. *longifolia* Gray [= *Clermontia Kakeana* Meyen], fide Rock, [Bishop Mus. Mem. 7(2): 308, 1919].

150. *Clermontia parviflora* Gaud., ex Gray "Hawaii (and Oahu?), first collected by Macrae." Hawaii, Gaudichaud (Holotype: P). 1825, Macrae (GH). The Oahu specimen is dubious.
150. *Lobelia macrostachys* H. & A. [= *Trematolobelia macrostachys* (H. & A.) Zahlbr.], "Oahu and Hawaii."
150. *Lobelia Gaudichaudii* A. P. DC., var. *Kauaensis* Gray, "Kauai" (Holotype: US). Maintained by St. John, [Bishop Mus. Occas. Papers 14(8): 120, 1938]. Synonyms are *Lobelia kauaensis* (Gray) Heller, and *Galeatella kauaensis* (Gray) Deg. & Deg.
150. *Lobelia neriifolia* Gray (*non* Morris, 1835), [= Lobelia *Grayana* E. Wimm., Naturhist. Staatsmus, Wien, Ann. 56: 317–374, 1948], "East Maui, U.S. Exploring Expedition" (Holotype: US), indicated by E. Wimm. [Engler, Pflanzenreich IV, 276b, (107): 687, 1953].

GOODENIACEAE

151. *Scaevola coriacea* Nutt. ex Gray, "Sandwich Islands"; it was collected on Kauai (Holotype: GH), and Maui on sand hills. There are also two unnamed varieties.
151. *Scaevola Gaudichaudi* H. & A., Hawaiian Islands.
152. *Scaevola Chamissoniana* Gaud.
152. *Scaevola mollis* H. & A.
152. *Scaevola glabra* H. & A.

Species published by Gray in Proc. Amer. Acad. Arts 5: 321–352, (1861) = 1862 (Gray, 1862c)

ERICACEAE

323. *Vaccinium reticulatum* Sm., "Hawaii, Mouna Loa, 1840" (GH).
323. var. *calycinum* (Sm.) Gray, [= *Vaccinium calycinum* Sm.], "Hawaiian Islands," (US). *See* Skottsberg (Bishop Mus. Bull. 43: 70, 1927).
323. var. *dentatum* (Sm.) Gray, "Sandwich Islands" (US). [= *Vaccinium dentatum* Sm.]. *See* Skottsberg (Bishop Mus. Bull. 43: 74, 1927).

323. var. ? *lanceolatum* Gray [= *Vaccinium dentatum* Sm., var. *lanceolatum* (Gray) Skottsb., Horti Gotoburg, Acta 2: 253, 1926.]. "Kauai, tabular summit" (Holotype: US).

323. *Vaccinium penduliflorum* Gaud. [= *Vaccinium dentatum* Sm., fide Skottsberg, Bishop Mus. Bull. 43: 74, 1927]. "Sandwich Islands."

323. var. *berberifolium* Gray, "East Maui, on Mouna Haleakala" (Holotype: US), "and apparently on the mountains of Oahu" [= *Vaccinium berberifolium* (Gray) Skottsb., (as *berberidifolium*), Bishop Mus. Bull. 43: 79, 1927].

EPACRIDACEAE

325. *Cyathodes Tameiameiae* Cham. [= *Styphelia Tameiameiae* (Cham.) F. Muell.], "Oahu &c."

325. var. *Chamissoi* Gray, = the above species.

325. var. *Brownii* Gray [= *Styphelia Tameiameiae* (Cham.) F. Muell., var. *Brownii* (Gray) St. John, Bishop Mus. Occas. Papers 17(7): 84, 1942], "Maui, Kauai, and especially Hawaii." Hawaii, Macrae (Lectotype: GH), here selected.

325. *Cyathodes Douglasii* Gray [= *Styphelia Douglasii* (Gray) F. Muell. ex Skottsb.] "Hawaii, on Mouna Loa, Mouna Kea; also Maui, on Mouna Haleakala." Mauna Kea, Douglas (GH) was made the lectotype by Sleumer, (Blumea 12: 157, 1963).

325. var. *struthioloides* Gray [= *Styphelia Douglasii* (Gray) F. Muell. ex Skottsb.] "Mouna Kea, Hawaii, high in the pastoral region" (Holotype: US). Gray also doubtfully included a plant from Kauai, and perhaps a form on the mountains of Kauai, without flowers or fruit.

EBENACEAE

327. *Maba Sandwicensis* A. DC, [= *Diospyros ferrea* (Willd.) Bakh., ssp. *sandwicensis* (A. DC.) Bakh., Buitenzorg Jard. Bot. Bull. III, 15: 58, 64, 1937]. "Oahu and Hawaii."

SAPOTACEAE

328. *Sapota Sandwicensis* Gray [= *Planchonella sandwicensis* (Gray) Pierre, Not. Bot. Sapot. 36, 1890]. "Oahu, where it

was also collected by Remy (no. 478) in fruit" (Holotype: GH), and so listed by Lam (Blumea 5: 24, 1942).

PRIMULACEAE

328. *Lysimachia Hillebrandi* Hook. f. ex Gray, "Oahu and Maui," "Oahu, Kalihi, Hillebrand 183" (Lectotype: K).

328. var. *daphnoides* Gray [= *Lysimachia daphnoides* (Gray) Hbd., Fl. Haw. Is. 285, 1888]. "Kauai" (Holotype: US).

328. var. *angustifolia* Gray, "Maui, Waiehu, Remy, 1851–55 (Holotype: GH).

328. *Lysimachia lineariloba* H. & A. [= *Lysimachia mauritiana* Lam.], "Sandwich Islands."

OLEACEAE

331. *Olea Sandwicensis* Gray [= *Osmanthus sandwicensis* (Gray) Knobl., Bot. Centralbl. 61: 82, 1895.], "Oahu" (Holotype: US), "also in Remy's collection from Kauai (no. 479), and a narrow-leaved form, with immature fruit similar to the common olive from Molokai, (no. 482)."

APOCYNACEAE

333. *Ochrosia Sandwicensis* sensu Gray non A. DC. [= *Ochrosia Holei* St. John, Adansonia II, 18: 208, 1978], "Oahu, Remy 366, 367" (Syntypes: GH). The Remy collections are *Rauvolfia Sandwicensis* A.DC. *See* St. John, Adansonia II, 18: 208, 1978.

HYDROPHYLLACEAE

338. *Nama Sandwicensis* Gray, "Oahu, Macrae, Nuttall, Remy no. 425, Kauai, Nuttall, sand hills of Maui, Dr. Pickering and Mr. Breckenridge [= Brackenridge]" Oahu, Mann and Brigham 97 (Lectotype: GH).

BORANGINACEAE

339. *Heliotropium anomalum* H. & A., "Coral Islands, and Sandwich Islands."

339. var. *argenteum* Gray, "Sandwich Islands" (Holotype: US).

LABIATAE

341. *Sphacele hastata* Gray [= *Lepechinia hastata* (Gray) Epling, Torrey Bot. Club Bull. 67: 511, 1940], "Mouna Haleakala, East Maui, 5,000–7,000 feet" (Holotype: US).

343. *Phyllostegia brevidens* Gray, "Hawaii, in the forest of Mouna Kea, 3,000 feet" (Holotype: US), so indicated by Sherff (Bishop Mus. Bull. 136: 23, 1935).

343. var. *ambigua* Gray, "West Maui," 1840 (Holotype: US), *See* Sherff (Bishop Mus. Bull. 136: 23, 1935).

344. *Phyllostegia parviflora* (Gaud.) Benth., var. *glabriuscula* Gray, "Hawaii, Mount Kaah [= Mauna Kea], Macrae (Holotype: GH), so listed by Sherff (Bishop Mus. Bull. 136: 37, 1935).

344. var. *Mollis* (Benth.) Gray [= *Phyllostegia mollis* Benth., Linnaea 6: 79, 1831], Oahu, Chamisso (Holotype: L), so listed by Sherff (Bishop Mus. Bull. 136: 40, 1935.)

344. *Phyllostegia stachyoides* Gray, "Hawaii, in the district of Waimea" 1840 (Holotype: US), and so listed by Sherff (Bishop Mus. Bull. 136: 29, 1935).

344. *Phyllostegia clavata* Benth., Owhyhee [= Hawaii], monte ignovomo, Macrae (Holotype: K), and so listed by Sherff (Bishop Mus. Bull. 136: 19, 1935).

344. *Phyllostegia racemosa* Benth., Hawaii, montem Kaah [= Mauna Kea], Macrae (Holotype: K), and so indicated by Sherff (Bishop Mus. Bull. 136: 49, 1935).

345. *Phyllostegia haplostachya* Gray [= *Haplostachys haplostachya* (Gray) St. John, Pacif. Trop. Bot. Gard. Mem. 1: 292, 1973], "Maui, on the sands of the low isthmus" (Holotype: US), and so listed by Sherff (Bishop Mus. Bull. 136: 6, 1935). "Also gathered by Remy on Hawaii." Another synonym is *Haplostachys Grayana* Hbd. (Fl. Haw. Is. 346, 1888).

345. var. *leptostachya* Gray [= *Haplostachys haplostachya* (Gray) St. John var. *leptostachya* (Gray) St. John, Pacif. Trop. Bot. Gard. Mem. 1: 292, 1973]. "On barren ridges of Kauai," 1840 (Holotype: US).

345. *Phyllostegia truncata* Gray [= *Haplostachys truncata* (Gray) Hbd., Fl. Haw. Is. 347, 1888], "Maui, Remy no. 395" (Holotype: GH). *See* Sherff (Bishop Mus. Bull. 136: 10, 1935).

345. *Phyllostegia florubunda* Benth., "Hawaii (as O-why-hee) D. Nelson" (Holotype: BM). *See* St. John (Pacif. Sci. 30: 33, 1973), "Hawaii, in the woods of the district of Puna."

347. *Stenogyne rotundifolia* Gray, "Mouna Haleakala, East Maui" 1840 (Holotype: US), and so listed by Sherff (Bishop Mus. Bull. 136: 93, 1935).

347. *Stenogyne calaminthoides* Gray, "Hawaii, in the forests of Mouna Kea" (Holotype: US), listed by Sherff (Bishop Mus. Bull. 136: 62, 1935).

348. *Stenogyne angustifolia* Gray, "Hawaii, in the district of Waimea" (Holotype: US), and so listed by Sherff (Bishop Mus. Bull. 136: 69, 1935).

348. *Stenogyne crenata* Gray, "Maui, on Mouna Haleakala" (Holotype: US), and so recorded by Sherff (Bishop Mus. Bull. 136: 99, 1935).

348. *Stenogyne diffusa* Gray, "Hawaii, in the forests of the district of Waimea" (Holotype: US), listed by Sherff, (Bishop Mus. Bull. 136: 98, 1935).

GESNERIACEAE

350. *Cyrtandra cordifolia* Gaud., "Oahu."

350. *Cyrtandra platyphylla* Gray, "Hawaii, in forests" (US, GH). In Gray's manuscript (GH), he recorded it as Hawaii, in wood between Puna and Pahuhali. Since Rock in his monograph (Amer. J. Bot. 5: 269, 271, 1918) twice listed the U.S. Exploring Expedition specimen as in the Gray Herbarium, we follow that choice, and make the same choice: (Holotype: GH).

350. *Cyrtandra Pickeringii* Gray, "Oahu, mountains" (Holotype: US). *See* St. John, (Bishop Mus. Bull. 229: 272–278, figs. 110, 11, 1966). It is known only from the type collection, and is now evidently extinct.

351. *Cyrtandra triflora* Gaud., in insulis Sandwicensibus, alt. 100–300 hex. (Holotype: P). *See* St. John, (Bishop Mus. Bull. 229: 86–92, figs. 26–28, 1966). It is known only from the type collection, and is considered extinct.

352. var. *Gaudichaudi* Gray, "Oahu, Hawaii." This equals the species.

352. var. *arguta* Gray, "Oahu, gathered by Macrae, Gaudichaud, voyage of La Bonite; U.S. Exploring Expedition, Brack-

enridge; at Woahoo [= Oahu], Maio, 1825, Macrae." *See* St. John (Bishop Mus. Bull. 229: 118–124, figs. 41–44, 1966). "Hawaii in mountain forest, U.S. Exploring Expedition" (Holotype: US).

Species Published by Gray in Proc. Amer. Acad. Arts 6: 37–55, (1866) = 1862 (Gray, 1862d).

GENTIANACEAE

41. *Erythraea sebaeoides* (Griseb.) Gray [= *Centaurium sebaeoides* (Griseb.) Druce, Bot. Exch. Club Brit. Is., Rept. 1916: 614, 1917.], (*Schenkia sebaeoides* Griseb.), "Oahu."

SOLANACEAE

42. *Solanum Nelsoni* Dunal in A. DC., "Hawaii; in the sands of the low isthmus of Maui. Collected by Nuttall on Kauai, and on Oahu by Remy no. 442."
43. *Solanum Sandwicense* H. & A., "Oahu."
43. var. *Kauaiense* Gray [= *Solanum Kauaiense* (Gray) Hbd., Fl. Haw. Is. 305, 1888.], "Kauai, leeward verge of the tabular summit" (Holotype: US).
43. *Solanum incompletum* Dunal, "Hawaii, D. Nelson" (Holotype: BM).
44. *Lycium Sandwicense* Gray, "on Diamond Hill, near Honolulu" (Holotype: US).
48. *Nothocestrum latifolium* Gray, "Oahu, on the ridge of the Kaala Mountains" (Holotype: US).
48. *Nothocestrum longifolium* Gray, "Oahu, mountains behind Honolulu, at the elevation of 1,500 feet" (Holotype: US).
49. *Nothocestrum breviflorum* Gray, "Hawaii, between the Great Crater and the upper base of Mouna Roa." (Holotype: US).

MYOPORACEAE

52. *Myoporum Sandwicense* Gray, "Sandwich Islands, leg. Menzies, Beechey, Gaudichaud, Douglas, Nuttall, (Remy nos. 461, 462, 463, &c. on almost all the islands." Oahu, Remy 462 (Lectotype: GH), chosen by Webster (Pacif. Sci. 5: 61, 1951). Sandwich Islands, U.S. Exploring Expedition (US).

PLANTAGINACEAE

54. *Plantago princeps* C. & S., Sandwich Islands.
    var. *laxifolia* Gray, "Hawaii, growing among stones by the sea-side, at the northern base of Mouna Kea" (Holotype: US).

54. var. *hirtella* Gray, "On the tabular summit of Kauai" (Holotype: US).

54. *Plantago pachyphylla* Gray, "Sandwich Islands" (Holotype: US). This species is native to East Maui.

54. var. *Maviensis* Gray, "Maui, Mouna Haleakala, at 7,500 feet altitude" (Holotype: GH).

54. var. *Hawaiensis* Gray [= *Plantago hawaiensis* (Gray) Pilger, Fedde Repert. 19: 116, 1923], "Hawaii, on Mouna Kea and Mouna Loa, to the elevation of 6,000 feet to 8,000 feet, and in the environs of the Great Crater," the latter (Lectotype: US).

54. subvar. *gracilis* Gray [= *Plantago hawaiensis* (Gray) Pilger], "Hawaii, Remy 429" (Holotype: GH).

54. var. *Kavaiensis* Gray [= *Plantago Grayana* Pilger, Fedde Repert. 19, 115, 1923], "Kauai, on the tabular summit" (Holotype: GH).

LITERATURE CITED

GRAY, ASA. 1852a. Account of *Argyroxiphium*, a remarkable genus of Compositae, belonging to the mountains of the Sandwich Islands. Proc. Amer. Acad. Arts 2: 159–160.

———. 1852b. Characters of two new genera of plants of the order Violaceae, discovered by the naturalists of the United States Exploring Expedition (*Agatea, Isodendron*). Proc. Amer. Acad. Arts 2: 323–325.

———. 1853 (as 1857). Characters of some new genera of plants, mostly from Polynesia, in the collection of the United States Exploring Expedition, under Captain Wilkes. Proc. Amer. Acad. Arts 3: 48–54, 127–129.

———. 1854–1857. United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N., 15: Botany, Phanerogamia 1: 1–777; Atlas 1–4, pl. 1–100, 1857.

———. 1858 (as 1860). Notes upon some Rubiaceae, collected by the United States South Sea Exploring Expedition under Captain Wilkes, with Characters of New Species. Proc. Amer. Acad. Arts 4: 33–50, 306–318.

———. 1859a (as 1860). Notes upon some Polynesian plants of the order Loganiaceae. Proc. Amer. Acad. Arts 4: 319–324.

———. 1859b (as 1860). Diagnoses of the species of Sandal-wood (*Santalum*) of the Sandwich Islands. Proc. Amer. Acad. Arts 4: 326–327.

———. 1862a. (as 1861). 1. Characters of some Compositae in the collection of the United States South Pacific Exploring Expedition under Captain Wilkes, with observations. Proc. Amer. Acad. Arts 5: 114–146.

———. 1862b (as 1861). Characters of some Compositae in the collection of the United States South Pacific Exploring Expedition under Captain Wilkes, with observations, &c. 2. Notes on Lobeliaceae, Goodeniaceae, &c. of the collection of the U.S. Exploring Expedition, Proc. Amer. Acad. Arts 5: 146–152.

———. 1862c (as 1861). Characters of new or obscure species of plants of Monopetalous Orders in the collection of the United States South Pacific Exploring Expedition under Captain Charles Wilkes, U.S.N. with occasional remarks, &c. Proc. Amer. Acad. Arts 5: 321–352.

———. 1862d. Characters of some new or obscure species of plants of Monopetalous Orders, in the collection of the United States South Pacific Exploring Expedition under Captain Charles Wilkes, U.S.N. with various notes and remarks. Proc. Amer. Acad. Arts 6: 37–55.

International Code of Botanical Nomenclature. 1978. Bohn, Scheltema & Holkema, Utrecht. 427 pp.

BISHOP MUSEUM
1525 BERNICE ST.
HONOLULU, HAWAII 96819

NEW ENGLAND NOTE

VAUCHERIA UNDULATA JAO AGAIN IN NEW ENGLAND

LEBARON C. COLT, JR.

A small population of *Vaucheria undulata* Jao was found in clay areas in the bed of a small intermittent stream feeding into Crawford Pond, in the township of Union, Knox County, Maine. The general area has been previously described (Colt, 1977).

Although the type locality of this unusual chrysophycean alga is in the Province of Szechwan, China (Jao 1936), *Vaucheria undulata* has been reported from a number of widely separated places in North America. W. J. V. Osterhout reported it (as *V. terrestris* Lyngbye, P. B. A. No. 78b, 1894) from Rhode Island; Prescott (1953) listed it (as *V. crenulata*) from Alaska; Habeeb (1954) described it as *V. terrestris* var. *crenulata* (Prescott) Habeeb from New Jersey; Blum (1953) found *V. undulata* Jao in Massachusetts, and has since (Blum, 1972) reported it in Michigan.

Blum (1972) placed *Vaucheria crenulata* Prescott and *V. terrestris* var. *crenulata* (Prescott) Habeeb in synonymy with Jao's *V. undulata.*

Jao (1936) described the diameter of the type material as being 25–29 μ, the tubular axes slender and constantly undulate. Prescott (1953) reported material collected in Alaska as being 36–39 μ in diameter symmetrically undulate throughout. Blum (1972) cited diameters as 28–75 μ with the axes in regular spirals, "at least in part." Only Jao (1936, Pl. III, figs. 12, 13, p. 747) and Blum (1972, figs. 46, 47 p. 35) illustrated *Vaucheria undulata.* Axes of the Maine material were 7–60 μ diameter. Most axes were either 7–30 μ or 48–60 μ. Few filaments showed intermediate diameters. Other than the more slender thalli, the Maine *V. undulata* does not appear to be otherwise different from the previously described material.

The Maine material offers a clue as to the disparity of axis diameters and descriptions in previous reports. Geometrically spiral and undulate axes might be confused if only one or the other were present or if the material were either juvenile or fully mature, but not both. In the present material the more slender axes (7–30 μ) were usually spiral, while those of the larger diameters (48–60 μ)

were mostly undulate to subundulate. In this latter group there were portions of the thalli which were straight or nearly so for lengths to 20 μ, with alternate sections of undulate or subundulate appearance. As some of the larger filaments had side branches of the 7–30 μ range, it is assumed that the larger filaments represented the older portions of the plants. Active growth was found in all axes.

Prescott (1938) suggested that *Vaucheria* grows vigorously under ice and in cool or cold water, and that they may actively reproduce under such conditions. Although attempts to collect specimens from the Maine site during winter and early spring were unsuccessful because of snow and ice, collections made after ice-out tend to support the suggestion. The most extensive populations were found soon after ice-out when the water depth of the stream was 3–5 cm, and populations appeared as small green "lawns" on clear areas of clay (hardpan) within the stream bed. The clay areas are usually separated by areas of stream-borne rocks. Both late spring turbulent waters and ice movement tend to rearrange the rocks on the bottom of the stream annually. As a result, *Vaucheria* appears in a different location each spring, but it has been found in the same 10 meters of stream bed each year.

The portion of the stream bed from which *Vaucheria* was collected is under constant shade from such sub-boreal trees as Eastern Hemlock (*Tsuga canadensis*), Red Spruce (*Picea rubens*), and Balsam Fir (*Albies balsamifera*). The stream bank supports a cover of herbaceous plants, particularly ferns of the family Osmundaceae.

Information about chemical characteristics of collecting sites in previous reports is limited to the Alaska collection by Prescott (1953). He reported CO_2 as 3.0 ppm, Ca as 18.4 ppm, alkalinity as 27.0 and pH 7.2.

Samples of the substrate from the stream bed in Maine were sent to the Soil and Plant Tissue Laboratory, University of Massachusetts, Waltham, Massachusetts; results are provided in Table 1.

This report is the first of this alga in Maine, and the third report for New England.

Table 1. Results of analysis of clay substrate (pH 6.2).

Soluble Mineral	ppm	Soluble Mineral	ppm
Phosphorus	2.0	Nitrate (NO_3)	15.0
Potassium	30.0	Boron	0.1
Calcium	351.0	Molybdenum	0.1
Magnesium	58.0	Zinc	0.1
Ammonium (NH_4)	3.0	Copper	0.1
Manganese	1.5	Iron	31.0
		Lead	20.0

LITERATURE CITED

Blum, J. L. 1953. The racemose Vaucheriae with inclined or pendant oogonia. Bull. Torr. Bot. Club 80: 478–497.

———. 1972. Vaucheriaceae. N. Amer. Fl. Ser. II, Pt. 8. N. Y. Bot. Gard.

Colt, L. C. Jr. 1977. A new station for Coleochaetaceae in maine, with an account of a new variety. Rhodora 79: 300–304.

Habeeb, H. 1954. Three interesting algae from New Jersey. Rhodora 56: 41–42.

Jao, C. C. 1936. Studies on the freshwater algae of China. II. Vaucheriaceae from Szechwan. Sinensia 7: 730–747.

Prescott, G. W. 1938. A new species and a new variety of *Vaucheria* de Candolle with notes on the genus. Trans. Amer. Microsc. Soc. 57: 1–10.

———. 1953. Preliminary notes on the ecology of freshwater algae in the Arctic slope, Alaska, with descriptions of some new species. Amer. Midl. Nat. 50: 463–470.

DEPARTMENT OF BIOLOGY
SOUTHEASTERN MASSACHUSETTS UNIVERSITY
NORTH DARTMOUTH, MA 02747

BOOK REVIEW

Zichmanis, Zile, and James Hodgins. 1982. *Flowers of the Wild: Ontario and the Great Lakes Region.* xiv + 272 pp. Oxford University Press, Toronto, Ontario ($35.00)

This handsome, large-format book is not just another decorative coffee-table volume. Detailed presentations are made of 127 wild flowers, carefully selected from the 2000 or so species that grow in the geographic area covered. Information on each plant includes a large color photograph usually showing the plant in its habitat, an excellent line drawing, and an accompanying text. This text, while succinct, includes many facts such as the number of species local and world-wide, etymology of the Latin name, habitat, range, flowering and fruiting characteristics, ecology, horticultural information, and economic uses. Often the sketch concludes with a reference to an article in the botanical literature. The book ends with a glossary of terms, a listing of Ojibway and French common names, and a selected bibliography.

The book should be appealing and useful to a wide audience: those interested in native plants, in wild-flower gardening, in the natural history and ecology of species; those who wish to pursue more botanical information about a given species; and those who love a beautiful botanical book for its art and design.

Mary M. Walker, Librarian
New England Wild Flower Society
Framingham, MA 01701

BOOK REVIEW

Zomlefer, Wendy B. c. 1983. *Common Florida Angiosperm Families. Part 1.* iii + 107 pp. W. B. Zomlefer, 603-D N.E., 4th Ave., Gainesville, FL 32601 ($8.15)

Illustrators of plant families in textbooks tend to emphasize eastern taxa. Wendy Zomlefer has designed this laboratory manual for introductory taxonomy courses as a southeastern equivalent to

Carroll Wood's *A Student's Atlas of Flowering Plants*. It is especially for use in Florida in an effort to promote a greater understanding and appreciation of southern plants.

To this end the author has selected 67 families, carefully chosen for size, and floristic and economic importance in Florida. Each family plate has detailed botanical drawings of typical species, habit, stem, leaf details, and various flower and fruit dissections. The accompanying text includes technical family characteristics, distributions, major world genera and Florida representatives, and economic plants and products. Other facts of interest about each family are included, and numerous references are cited for further reading.

The drawings are outstanding. A great deal of information is contained in the 107 pages of this book: Part 1 describes 34 families; Part 2 will detail 33 additional ones.

Mary M. Walker, Librarian
New England Wild Flower Society
Framingham, MA 01701

HESLER VISITING PROFESSORSHIPS OF FLORISTIC BOTANY

Under the terms of an endowment from Dr. and Mrs. L. R. Hesler, the Botany Department of the University of Tennessee is able to support a limited number of visiting professors of floristic botany. Stipends will be awarded based on research proposals, and may be used for salary and expenses of floristic, revisionary, or monographic systematic research. All applicants must hold faculty (or equivalent) status at a recognized botanical or educational institution. Stipend amounts and residence periods will vary, and concurrent support from the applicant's institution is strongly encouraged. Preliminary correspondence with specific departmental faculty is invited or general inquiries may be sent to:

Hesler Endowment Fund
Department of Botany
The University of Tennessee
Knoxville, TN 37996-1100 USA

THE 1985 JESSE M. GREENMAN AWARD

The 1985 Jesse M. Greenman Award has been won by George K. Rogers for his publication "*Gleasonia, Henriquezia,* and *Platycarpum* (Rubiaceae)" (Flora Neotropica Monograph No. 39). This monographic study is based on a Ph.D. dissertation from the University of Michigan Herbarium under the direction of William R. Anderson.

The Greenman Award, a cash prize of $250, is presented each year by the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation that was published during the *previous* year. Papers published during *1985* are now being considered for the 18th annual award, which will be presented in the summer of 1986. Reprints of such papers should be sent to:

Greenman Award Committee
Department of Botany
Missouri Botanical Garden
P.O. Box 299
St. Louis, MO 63166-0299, U.S.A

In order to be considered for the 1986 award, reprints must be received by 1 July 1986.

NEBC 1986 AWARD
FOR THE SUPPORT OF BOTANICAL RESEARCH IN NEW ENGLAND, U.S.A.

The New England Botanical Club will again offer an award of $1,000 in support of botanical research to be conducted in the New England region during 1986. This award is being made to stimulate and encourage botanical research on the New England flora and to make possible visits to the New England region by those who would not otherwise be able to do so. The award will be given to the graduate student submitting the best research proposal dealing with field studies in systematic botany and plant ecology, but proposals for research in other areas of botany will also be considered. This award is not limited to graduate students at New England institutions, nor to members of the New England Botanical Club. Papers based on this research must acknowledge the NEBC's support, and it is encouraged that they be submitted to *Rhodora,* the Club's journal, for possible publication—subject to standard review processes.

Applicants should submit a proposal of no more than three double spaced pages, a budget (the budget will not affect the amount of the award), and their curriculum vitae. Two letters, one from the student's major professor, in support of the proposed research are also required. Proposals and supporting letters should be sent before 28 February 1986 to:

Awards Committee
The New England Botanical Club
22 Divinity Avenue
Cambridge, MA 02138.

The recipient of the award will be notified by 30 April 1986.

LIST OF REVIEWERS OF MANUSCRIPTS
JULY 31, 1984–JULY 31, 1985

The editors of RHODORA are grateful to each of the following specialists for participation in the reviewing process.

Ralph M. Adams
Kelly W. Allred
David S. Barrington
John H. Beaman
C. John Burk
Eric A. Christenson
George L. Church
Antoni W. Damman
Thomas C. Dent
William H. Drury
C. Barre Hellquist
Walter M. Hewitson
Harold R. Hinds
Robert Kral
Michael W. Lefor
Walter H. Lewis
Leslie J. Mehrhoff
John K. Morton
William H. Murdy
Guy L. Nesom
Dan Nicolson
William Niering
Richard W. Pohl
Charles Reimer
Anton A. Reznicek
Ruben P. Sauleda
Alfred E. Schuyler
John C. Semple
Stanwyn G. Shetler
Tod F. Stuessy
B. L. Turner
Lowell E. Urbatsch
Gerald A. Wheeler

Rhodora

JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

VOLUME 87

1985

The New England Botanical Club, Inc.
Harvard University Herbaria, 22 Divinity Ave., Cambridge, Mass. 02138

INDEX TO VOLUME 87

New scientific names are in **bold face**.

Vol 87, No. 851, including pages 293–448, was issued July 24, 1985

INSTRUCTIONS TO CONTRIBUTORS TO RHODORA

Submission of a manuscript implies it is not being considered for publication simultaneously elsewhere, either in whole or in part.

Manuscripts should be submitted in **triplicate** (an original and two xerographic copies) and *must be double-spaced* (at least 3/8 inch) **throughout** including footnotes, figure legends, and references. Please do not use corrasable bond. The list of legends for figures and maps should be provided on a separate page. Footnotes should be used sparingly. Do not indicate the style of type through the use of capitals or underscoring, particularly in the citation of specimens. Names of genera and species may be underlined to indicate italics in discussions. Specimen citations should be selected critically, especially for common species of broad distribution. Systematic revisions and similar papers should be prepared in the format of "A Monograph of the Genus Malvastrum", S. R. Hill, Rhodora 84: 1–83, 159–264, 317–409, 1982, particularly with reference to indentation of keys and synonyms. Designation of a new taxon should carry a **Latin diagnosis** (rather than a full Latin description), which sets forth succinctly just how the new taxon is distinguished from its congeners. Papers of a floristic nature should follow, as far as possible, the format of "Annotated list of the ferns and fern allies of Arkansas", W. Carl Taylor and Delzie Demaree, Rhodora 81: 503–548, 1979. For bibliographic citations, refer to the Botanico-Periodicum-Huntianum (B-P-H, 1968), which provides standardized abbreviations for journals originating before 1966. All abbreviations in the text should be followed by a period, except those for standard units of measure and direction (compass points). For standard abbreviations and for guidance in other matters of biological writing style, consult the *CBE Style Manual,* 5th ed. (original title: *Style Manual for Biological Journals*). In preparing figures (maps, charts, drawings, photos, etc.) please remember that the printed plate will be 4 × 6 inches; be sure that your illustrations are proportioned to reduce correctly, and indicate by blue pencil the intended limits of the figures. (Some "turn-page" figures with brief legends will be 3 1/2 × 6 in.) Magnification/reduction values given in text or figure legends should be calculated to reflect the actual printed size. An Abstract and a list of Key Words should be supplied at the beginning of each paper submitted, except for a very short article or note.

U.S. Postal Service

STATEMENT OF OWNERSHIP, MANAGEMENT AND CIRCULATION

Required by 39 U.S.C. 3685)

SEP 18 1985

A. TITLE OF PUBLICATION: RHODORA

1B. PUBLICATION NO.: ISSN 0 0 3 5 4 9 0 2

2. DATE OF FILING: Sept 17, 1985

FREQUENCY OF ISSUE: Quarterly

3A. NO. OF ISSUES PUBLISHED ANNUALLY: Four

3B. ANNUAL SUBSCRIPTION PRICE: $20.00

COMPLETE MAILING ADDRESS OF KNOWN OFFICE OF PUBLICATION *(Street, City, County, State and ZIP+4 Code) (Not printers)*

New England Botanical Club,Inc. 22 Divinity Ave.,Cambridge, MA 02138

COMPLETE MAILING ADDRESS OF THE HEADQUARTERS OF GENERAL BUSINESS OFFICES OF THE PUBLISHER *(Not printer)*

New England Botanical Club,Inc., 22 Divinity Ave., Cambridge,MA 02138

FULL NAMES AND COMPLETE MAILING ADDRESS OF PUBLISHER, EDITOR, AND MANAGING EDITOR *(This item MUST NOT be blank)*

UBLISHER *(Name and Complete Mailing Address)*

New England Botanical Club,Inc., 22 Divinity Ave., Cambridge,MA 02138

DITOR *(Name and Complete Mailing Address)*

Prof. Norton H. Nickerson, Tufts University, Dept.Biology, Medford,MA 02155

ANAGING EDITOR *(Name and Complete Mailing Address)*

Mrs. Joan Y.Nickerson, 299 Pearl Street, Reading,MA 01867

OWNER *(If owned by a corporation, its name and address must be stated and also immediately thereunder the names and addresses of stockholders owning or holding 1 percent or more of total amount of stock. If not owned by a corporation, the names and addresses of the individual owners must be given. If owned by a partnership or other unincorporated firm, its name and address, as well as that of each individual must be given. If the publication is published by a nonprofit organization, its name and address must be stated.) (Item must be completed.)*

FULL NAME	COMPLETE MAILING ADDRESS
No stockholders	
New England Botanical Club,Inc., 22 Divinity	Ave.,Cambridge,MA 02138 (non-profit organizatio

KNOWN BONDHOLDERS, MORTGAGEES, AND OTHER SECURITY HOLDERS OWNING OR HOLDING 1 PERCENT OR MORE OF TOTAL AMOUNT OF BONDS, MORTGAGES OR OTHER SECURITIES *(If there are none, so state)*

FULL NAME	COMPLETE MAILING ADDRESS
NONE	

FOR COMPLETION BY NONPROFIT ORGANIZATIONS AUTHORIZED TO MAIL AT SPECIAL RATES *(Section 423.12 DMM only)*
The purpose, function, and nonprofit status of this organization and the exempt status for Federal income tax purposes *(Check one)*

☒ (1) HAS NOT CHANGED DURING PRECEDING 12 MONTHS XX

☐ (2) HAS CHANGED DURING PRECEDING 12 MONTHS

(If changed, publisher must submit explanation of change with this statement.)

EXTENT AND NATURE OF CIRCULATION *(See instructions on reverse side)*	AVERAGE NO. COPIES EACH ISSUE DURING PRECEDING 12 MONTHS	ACTUAL NO. COPIES OF SINGLE ISSUE PUBLISHED NEAREST TO FILING DATE
TOTAL NO. COPIES *(Net Press Run)*	900	900
PAID AND/OR REQUESTED CIRCULATION 1. Sales through dealers and carriers, street vendors and counter sales	825	825
2. Mail Subscription *(Paid and/or requested)*	15	15
TOTAL PAID AND/OR REQUESTED CIRCULATION *(Sum of 10B1 and 10B2)*	840	840
FREE DISTRIBUTION BY MAIL, CARRIER OR OTHER MEANS SAMPLES, COMPLIMENTARY, AND OTHER FREE COPIES	12	12
TOTAL DISTRIBUTION *(Sum of C and D)*	852	852
COPIES NOT DISTRIBUTED 1. Office use, left over, unaccounted, spoiled after printing	48	48
2. Return from News Agents	0	0
TOTAL *(Sum of E, F1 and 2—should equal net press run shown in A)*	900	900

I certify that the statements made by me above are correct and complete

SIGNATURE AND TITLE OF EDITOR, PUBLISHER, BUSINESS MANAGER, OR OWNER

[illegible], Business Manager, Treasurer

Form 3526, July 1984

(See instruction on reverse)

RHODORA **October 1985** **Vol. 87, No. 852**

CONTENTS